Traits underpinning the eco-physiological processes linking drought and flammability

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Fire is common in many terrestrial ecosystems, and shapes species composition and the distribution of biomes. Fire regimes have been altered in many parts of the world due to global climate change, with increases in drought resulting in more intense and extensive wildfires. Drought can impact fires in many ways, including by changing the flammability of plants. Recognition of this link has led to the development of the new field of pyro-ecophysiology, which, among other things, seeks to understand how plant water relations can drive changes in live fuel moisture and, therefore, plant flammability. However, few studies have investigated the relationships of drought response traits to plant flammability. The main goal of this thesis is to identify the traits which underpin the ecophysiological processes linking drought and plant flammability, and so help determine how drought affects the propensity of plants to burn.

Firstly, I examined relationships between shoot flammability and drought response measures for 38 species of woody plants from New Zealand. I found that minimum leaf water potential and turgor loss point were both negatively correlated with flammability, suggesting that species with high drought tolerance were high in flammability. This suggests that while these traits are useful for the new field of pyro-ecophysiology, species with high drought tolerance should not be recommended by fire managers as low flammability plantings, as has been the case overseas.

Secondly, I examined how species flammability changes throughout the year, and assessed which traits are associated with this. I measured shoot flammability and a range of physiological and morphological traits of 10 species at four different times throughout one year. For some species flammability fluctuated throughout the year, identifying species which fire managers need to be careful of when planning fire reduction measures such as green firebreaks. Three species (*Griselinia littoralis*, *Pseudopanax crassifolius*, *Pseudopanax colensoi*) remained low in flammability year round, suggesting that these species could be safely deployed in green firebreaks to help reduce fire spread. Changes in flammability were associated with traits such as stem water potential, moisture content, leaf relative water content, and leaf area.

Thirdly, I investigated the existence of thresholds in the relationship between moisture content and shoot flammability to determine if changes in moisture content might lead to species flipping from low to high flammability. Thresholds in moisture content were found in all species and flammability variables, though threshold values were species specific. Threshold moisture content was positively related to leaf area and negatively to leaf dry matter content.

As predicted by the emerging field of pyro-ecophysiology, water relations traits such as water potential and relative water content were associated with differences in shoot flammability. While both traits are useful in understanding how drought affects plant flammability, water potential is harder to measure. Leaf relative water content holds great potential as an integrative trait that can be measured rapidly, including via remote sensing, which would enable collection of real-time data on fire risk over wide areas, providing critical information for fire managers.

Keywords: Wildfire, Forest, Plant flammability, drought, pyro-ecophysiolgy, physiological traits, morphological traits, green fire break, live fuel moiture content, fire risk.

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Ψ_{leaf}	Leaf water potential
Ψ_{tlp}	Turgor loss point
Ψ_{min}	Minimum water potential
Ψ_{stem}	Midday water potential
g_s	Stomatal conductance
MC%	Fuel moisture content
LFMC	Life fuel moisture content
LDMC	Leaf dry matter content
LMC	Leaf moisture content
LRWC	Leaf relative water content
LA	Leaf area
SLA	Specific leaf area
LT	Leaf thickness
BD	Bulk density

Chapter 1
Introduction

1.1 Importance of studying wildfire and drought

Wildfire is a common phenomenon in many terrestrial ecosystems (Bowman et al., 2009), and shapes global biomes by being a strong selective force on species composition and vegetation structure (Pausas & Keeley, 2009; Scott, 2018). Wildfire also influences food chains and the habitat of animal populations (Smith, 2000), and changes soil properties and nutrients (Crutzen & Goldammer, 1993; van der Werf et al., 2006; Wittkuhn, 2017). In fire-prone ecosystems, many plant species have acquired adaptive traits that help them to survive and reproduce under repeated fires (Keely & Zedler, 1998; Pausas & Ribeiro, 2013). Global wildfire regimes vary across ecosystems, especially in relation to productivity and as a result of human activities (Balch et al., 2017; Keeley & Pausas, 2019; Syphard et al., 2017). Increased temperatures, decreased rainfall, increased atmospheric carbon dioxide (CO_2), and other global change drivers, such as human population growth, changed land use and management activities, and invasive species strongly influence global wildfire activity (Keeley & Pausas, 2019; Krawchuk & Moritz, 2011; Pausas et al., 2004), and fire regimes (the frequency, intensity and season of fire occurrence (Archibald et al., 2013; Bowman et al., 2020; Pausas & Keeley, 2021). Global warming due to human activity is an important driver of increasing wildfire activity (Williams et al., 2019), with more severe droughts leading to more intense and extensive wildfires (Richardson et al., 2022; Ruffault et al., 2018). Therefore, it is important to understand the complex role of warming and human-induced climate change on fire regimes, and provide a mechanistic understanding of how drought influences fire, so we can predict and be prepared for future changes.

The impacts of global climate change on droughts and fires are also expected to be felt in New Zealand. Under climate change, New Zealand will experience higher temperatures in almost every region, and while the western parts of the country will be wetter, Northland and many eastern parts will be drier and warmer (Mullan et al., 2018; Salinger & Porteous, 2014). This is likely to result in longer fire seasons and increased drought risk according to climate change projections for the 2080s (Pearce et al., 2011; Seneviratne et al., 2014). Longer fire seasons are highly likely to increase fire occurrence (Salinger & Porteous, 2014). While New

Zealand does not yet have fire weather akin to that of Australia or North America, the 6th IPCC report from Working Group II indicates with high confidence that climate change will bring fire weather similar to that of south-eastern Australia to parts of New Zealand (IPCC, 2022; Reisinger et al., 2014). Currently, New Zealand experiences an average number of 3033 wildland fires each year that burn around average 5865 ha annually, and an increasing numbers of fires each year was also observed in 10 of the 13 regions of the country (Pearce, 2008). Fire number has already increased mostly with grassland comparative to forestland (McGlone & Walker, 2011). This changing baseline in fire risk has meant that flammable ecosystems are more likely to support dangerous and destructive fires. For instance, in 2017, Christchurch experienced a large, destructive fire in the adjacent Port Hills, which burned more than 1660 hectares of vegetation, took the life of a pilot, injured three other people, and destroyed nine homes and damaged five others (Pearce, 2018). Recently, the Lake Ōhau fire in the Mackenzie Basin was fuelled by severe wind, and destroyed 48 homes and buildings, damaging 5043 hectares of land (Foley, 2020).

The occurrence of very large and destructive wildfires has caused substantial shifts in fire regimes, including increased area burnt and fire frequency (Boer et al., 2020; Collins et al., 2021; Lindenmayer & Taylor, 2020). In the case of New Zealand ecosystems, the invasion of several exotic plant species potentially worsens the problem further by increasing flammability and causing successional changes of vegetation from less flammable forest to more flammable shrubland or forest-shrub landscape mosaics (Perry et al., 2014; 2015). There are now extensive areas of shrublands in New Zealand successional from forest, often composed of novel mixtures of indigenous and exotic species, that have the potential of positive feedbacks favouring recurrent fires (Kitzberger et al., 2016). Drought can facilitate the expansion of some invasive species, changing fuel properties, which can in turn affect fire behaviour and, ultimately, altering fire regimes (Brooks et al., 2004). Parts of New Zealand experience regular late growing-season drought and experience severe droughts on supra-annual intervals (Bennet & Kingston). In general, many of New Zealand’s native plants possess low levels of drought resistance (Bannister, 1986; Wardle, 1991). Moreover, Wyse et al., (2013) found drought sensitivity contributes to community composition with seedlings of drought sensitive species less likely to survive under dominant drought resistant species. Water relations strategies influence the distributions of angiosperm species with resistance to xylem embolism explaining climatic limitations of flowering trees but not conifers (Laughlin et al., 2020).

Future climate changes may increase mean temperatures globally (about 2 – 4°C) with significant drying in some regions (Seager et al., 2007), as well as increasing the frequency and severity of extreme droughts, hot extremes, and heat waves (IPCC, 2022). Droughts can trigger plant mortality and research on drought impacts on the New Zealand flora is ongoing (e.g. (Cranston et al., 2020). Droughts can trigger plant mortality, especially in interaction with other factors. For example, introduced animals and diseases may increase the risk of mortality when forests are subjected to disturbance. In New Zealand, mortality of canopy trees of northern rātā (*Metrosideros robusta*) in forests near Wellington was attributed to a combination of drought and possum (Cowan et al., 2001; Monks & Kelly, 2006). Thus, drought changes dominant plant species at shorter time scales and can alter fire activity and feedback fire (Harris et al., 2016). Australia’s Black Summer fires in 2019 – 2020 burnt c. 4.5 million ha of mainly temperate forest (Nolan et al., 2020b). Clearly, drought and wildfire can interact in complex ways, but there is still much to learn about this (Nolan et al., 2020a).

In this thesis I will explore the effect of drought on plant flammability. For this, I will review the literature on plant flammability, drought, and how drought influences plant flammability and fire behaviour.

1.2 Plant flammability

Flammability is a complex plant functional trait that is defined and measured differently by different authors and disciplines. Here I define flammability as being composed of ignitability (i.e. how easily a fuel ignites), sustainability (i.e. how long it continues to burn), combustibility (i.e. how rapidly it burns) and consumability (i.e how much of it burns) (Hogenbirk & Sarrazin-Delay, 1995; Anderson, 1970; Martin et al., 1994). The applicability of each of these components in assessing flammability, as well as the way in which the components are measured, are highly variable depending on the objectives and the scale of the experiment (e.g. small or large plant fragments, individuals, vegetation) (Pausas et al., 2017; Gill & Zylstra, 2005). Flammability is measured by burning fuels in the laboratory, either in the form of separate elements (e.g. a leaf, a twig), or as a fuel bed. Jaureguiberry et al., (2011) designed a low-cost device to measure flammability at the shoot level, which can measure many samples relatively quickly (Fig. 1.1). This has facilitated a number of studies, investigating topics such as the evolution of plant flammability (Alam et al., 2020; Battersby, et al., 2017; Burger & Bond, 2015; Cui et al., 2020b), traits associated with flammability (Santacruz-García et al., 2019; Alam et al. 2020), comparative flammability of species and ecosystems (Calitz et al., 2015); Burger and Bond 2015; Wyse et al., 2016), and ranking of species flammability to guide fire managers (Wyse et al., 2016).

1.2.1 Using low flammability plants as green firebreaks to help suppress fires

One way that knowledge of plant flammability can aid fire management is via the planting of green firebreaks, which are strips of low flammability vegetation established at strategic locations across the landscape (Curran et al., 2018; Johnson, 1975; Keely et al., 2012; White & Zipperer, 2010). This approach has been widely used in many parts of the world, including the United States, Australia, New Zealand, Europe, Asia, and Africa (Cui et al., 2019a; Curran et al., 2018). Green firebreaks are especially widely implemented in China, with over 364,000 km planted by 2003 and another 167,000 km planned by 2025 (Cui et al. 2019a). Green firebreaks function by breaking up flammable fuel-beds, blocking the wind, absorbing radiant heat and extinguishing embers ahead of the fire front, and halting the flames themselves (Cui et al. 2019a). To establish green firebreaks we first need to understand the flammability of a wide range of species. While the best way to do this is to test how well each species burns, this knowledge is not yet available for large numbers of species (Alam et al. 2020), so other measures need to be used. One option for this is to predict plant flammability based on plant functional traits.

Figure 1.1 Device used to measure shoot flammability. A handheld infrared laser thermometer (left) is used to measure the flame temperature.

1.2.2 Functional traits related to plant flammability

Flammability is a property of a plant’s morphological, eco-physiological, architectural and chemical traits (White and Zipperer, 2010 Archibald et al., 2018). At a leaf level, the size and density of the leaf, as well as its nutrient content and presence of volatile oils and resins all affect its tendency to ignite (Cornwell et al., 2015, Pausas et al., 2016). The arrangement of these leaves on a canopy (plant architecture) can strongly affect flammability: highly branched canopies with high surface area and low bulk density (g cm^{-3}) are better aerated and easier to ignite, although sparse branching may also reduce flammability (Schwilk and Ackerly, 2001, Simpson et al. 2016). Similarly, plants that retain dead leaf material have higher fuel loads and drier canopies and are therefore both more ignitable and have higher heat release (Jaureguiberry et al 2011, Schwilk, 2003, Dent et al. 2019). Moreover, the amount of fuel and its dryness are controlled by plant growth rates, phenology (deciduous vs evergreen) and decomposition rates, which represent the outcome of a range of plant traits and interact with many other aspects of plant ecological strategy. Variations in these traits across species can alter ignition probability and fire spread rates by an order of magnitude (Fernandes & Cruz, 2012; Plucinski et al., 2010). Many environmental factors interact to select for different combinations of chemical, morphological, physiological, and architectural traits (Endara and Coley 2011, Wright et al 2004), in turn affecting plant flammability.

So far, there has been some research to determine the functional traits that influence shoot flammability, but these have mainly focussed on morphological and some chemical traits (Santacruz- Garcia et al., 2019; Cui et al., 2020b; Alam et al., 2020; Padullés et al., 2018; Wyse et al., 2016). However, functional traits include all morphological, physiological, structural, biochemical and phenological characteristics which influence ecological performance and fitness (Díaz & Cabido, 2001; Violle et al., 2007). There have been few investigations into the physiological traits associated with flammability (Peacock, 1980; Owens et al., 1987; Nolan et al., 2020), particularly those traits associated with drought response.

1.3. Drought

Over the 21st century, global climate models predict an increase in the frequency and severity of droughts due to higher temperatures and changes in precipitation (Dai, 2012; IPCC, 2013; Trenberth et al., 2014; Cook et al., 2015). Droughts are often categorised as press-droughts or pulse droughts. Press-droughts are chronic but slight decreases in water availability, whereas pulse-droughts are short in duration but extreme (IPCC, 2013). Press-droughts can be caused by long-term reductions in precipitation (e.g., 10% decrease in mean annual precipitation), and/or warmer temperatures, which increase potential evapotranspiration and reduce soil moisture (Dai, 2012). When combined, press- and pulse-droughts may generate ‘hot droughts’ (Overpeck, 2013), which increase water deficits (Diffenbaugh et al., 2015) and can stimulate large and unexpected ecological responses (Hoover et al., 2015). Indeed, observations of the 20th century show increased aridity associated with warming have intensified droughts globally (Dai, 2012; Trenberth et al., 2014; Cook et al., 2015). The most prominent effects of drought are manifested in regional scale mortality events, which can kill millions of trees within a short timescale (Hubau et al., 2020; Yu et al., 2019). Large-scale mortality has been documented in dry tropical forests (Yu et al., 2019), tropical rainforests (Esquivel-Muelbert et al., 2020), temperate rainforests (Suarez, Ghermandi, & Kitzberger, 2004; Werner, 1988), semi-arid woodland and savannahs (Kannenberg, Driscoll, Malesky, Anderegg, & Management, 2021; Swemmer, 2020), boreal forests (Kharuk, 2013) and temperate deciduous to evergreen forests (Schuldt et al., 2020). Such mortality is subtle in the case of the slowly but steadily increasing, related mortality or dramatic in the case of die-off events (McDowell et al., 2009).

1.3.1 How does drought affect plants?

Drought reduces the water supply to plants via declining soil moisture, and is often accompanied by higher temperatures and increased evaporative water loss (Slayter, 1967; Brodribb et al., 2020; Choat et al., 2018). One consequence of these changes is disruption to the column of water that extends from the soil through the plant to the atmosphere (Choat et al. 2018). This disruption comes in the form of xylem, air bubbles forming in the water column when the column is under increasing tension (due to water stress). These bubbles may coalesce, causing xylem embolism, stopping the flow of water through that xylem conduit (Debenedetti, 1964). If drought continues, these embolisms become more likely and more extensive, stopping water supply to whole branches and potentially the entire plant, leading to mortality (Choat et al. 2018). Even if a plant is not killed outright by the drought, the high levels of stress that it is under render it more susceptible to other impacts, such as biotic agents (McDowell et al., 2002). For example, widespread canopy of *Nothofagus* mortality during 1914–1915 in New Zealand was attributed to severe drought combined with browsing from deer (Grant, 1984).

1.3.2 Drought response traits: how do plants survive drought?

Plants use a range of strategies to resist drought (Chaves et al., 2002). Species that survive drought conditions are described as drought resistant and those that do not as drought susceptible. Most plant species have some degree of resistance to drought, and the response will depend on the severity of the drought, as all plants are killed by total lack of water, and hence are ultimately drought susceptible. Species can then be further placed on a continuum from those that are drought tolerant to those that are drought avoiding (Ludlow, 1989). Drought avoidance is the ability to maintain a high water potential when exposed to an external water stress by minimising water loss (Ozeki et al., 2022) and maximizing water uptake (Jackson et al., 2000), for example by decreasing canopy leaf area, reducing growth and/or shedding leaves. These traits cause variation in the vulnerability of plants within communities (Blackman et al., 2012), and vary in a coordinated way that allows the benefits of photosynthetic carbon gain to be balanced against the risks of a decrease in threshold water potential and the occurrence of hydraulic failure (Mencuccini et al., 2015). At the other end of spectrum is drought tolerance, in which plant are able to survive at low water potentials (Levitt, 1972; Tyree, 2003), allowing them to maintain a favourable condition even though the environment is drier without injury in plants (Kozlowski & Pallardy, 2002), but may have declining cell water content (Mantova et al., 2021). Therefore, traits related to plant survival during drought will inform our understanding of water status of whole plants.

The drought tolerance strategy is underpinned by physiological traits that allow continuous water transport and gas exchange and cell survival at low relative water content and low water potentials ($\Psi_{\min}$), and increased resistance of xylem to embolism (Slayter, 1967; Tyree, 2003). Traits that enable species to maintain stomatal and hydraulic conductance and photosynthetic gas exchange at low soil water potentials include leaf water potential at turgor loss point, which is related to maintenance of cell turgor in leaves (Tyree & Zimmermann, 2002), and 50% loss of conductivity, which relates to xylem resistance to embolism (Martin-StPaul et al., 2017). Although it is possible to characterize a general sequence of events that describe the response of plants to drought, the traits that define drought response vary across species and environments (Bartlett et al., 2016; Choat et al., 2012; Maherali et al., 2004). Intraspecific variation across precipitation gradients have shown that populations adjust to greater aridity through increasing sapwood-to-leaf ratios, and increase hydraulic capacity relative to leaf area utilized (Pritzkow et al., 2020; Rosas et al., 2019). When plants are responding to drought, key consequences can include 1) death of parts of or the whole plant (Choat et al. 2018); and 2) decrease in water potential and water content (Brodribb et al., 2020; Choat et al., 2018), both of which are likely to increase plant flammability (Dent et al., 2018; Bowman et al., 2014; Weise et al., 2003; Calitz et al., 2015). Given that tree mortality leads to substantial changes in the structure and function of ecosystems, an understanding of drought-related mortality is fundamental to species' basic biology, ecosystem management and climate-feedback predictions (Anderegg et al., 2013; Hartmann et al., 2018). Hence, it is important to understand how drought affects plant flammability and wildfires.

1.3.3 How does drought influence wildfire?

At the landscape or ecosystem level drought can greatly exacerbate the intensity, severity, and extent of wildfires. For example, the Black Summer fires in south-eastern Australian forest (Nolan et al., 2020), recent fires in the western USA (Higuera & Abatzoglou, 2021) and severe fires in the Amazon over the last 20 years (Feng, Chen, Zhang, Zhang, & He, 2021), have provided evidence that drought conditions, in some cases the worst in recorded history, result in more destructive fires. In the Australian Black Summer fires, the unprecedented drought resulted in widespread and severe impacts on ecosystems (Adams et al., 2020), the largest extent of high severity fire ever recorded in these landscapes (Collins et al. 2021), and also led to many largely fire-free ecosystems burning (Williams et al., 2019). At a landscape-scale, wildfire needs four conditions to be simultaneously met: (i) the presence of spatially contiguous fuel; (ii) dry fuel to burn; (iii) weather conditions favourable to the spread of fire; and (iv) an ignition source (Bradstock, 2010; Pausas & Keeley, 2021). Drought greatly enhances the likelihood of (ii) and (iii) occurring.

Drought also affects fires by increasing the flammability of individual plants. Drought influences moisture content (Ruffault et al., 2018), which is a major determinant of flammability. Recognition of the key role that moisture content plays in determining plant flammability and fire behaviour has led to the development of the new discipline of pyro-ecophysiology (Jolly and Johnson, 2018).

1.4 Pyro-ecophysiology: integrating fire ecology and ecophysiology

Fuel moisture content is a function of both the water weight and dry weight of live fuels, and changes diurnally (Woodruff et al., 2015), seasonally (Jolly, Hadlow, & Huguet, 2014), and inter-annually (Wever et al., 2002). Therefore, dead and live fuel both influence flammability as how well a plant burns is influenced by water and dry matter content. Water is important because it has a high specific heat and the energy needed to evaporate water before solid fuel can be raised to ignition temperature increases the energy required for ignition (Simms & Law, 1967). Plant moisture status is governed by water cycle processes such as soil water uptake, plant water storage, and water loss through transpiration. On the other hand, dry weight changes to plant material are most directly related to carbon cycle processes such as photosynthesis, respiration, carbon allocation, and canopy phenology, and dry weight changes alone have been shown to heavily influence live fuel ignitability (Jolly et al., 2016). Whole plant scale canopy architecture quantifies how a network of stems and foliage are arranged to efficiently collect and transform solar radiation through photosynthesis (carbon cycle) while minimizing water loss (water cycle) (Figure 1.2). Cohen et al., (1990) found plant vascular systems can supply additional water to foliage when heated, as long as the plants are well hydrated. As plants become more water stressed, they are more susceptible to xylem embolism and cavitation, which breaks the flow of water from the roots to the leaves and could thus make plants behave like detached branches during heating (Tyree & Sperry, 1989). Plants that have already experienced some degree of xylem embolism can directly influence fire-induced cambium necrosis (Vines, 1968), as well as influence stem xylem deformation and cavitation potential (Michaletz et al., 2012). Both the internal and external canopy characteristics can heavily impact on whole plant burning behavior and both processes may have potential to influence plant flammability traits at both the leaf and whole plant level scale. Therefore, plant physiological changes in response to environmental change may influence plant flammability, and understanding these responses will ultimately allow better management for fire under an uncertain future (Blackman, et al., 2020). Recognition of this link between ecophysiology and fire ecology has led to the recent development of the field of pyro-ecophysiology (Jolly and Johnson, 2018; Resco de Dios et al., 2020; Nolan et al., 2020).

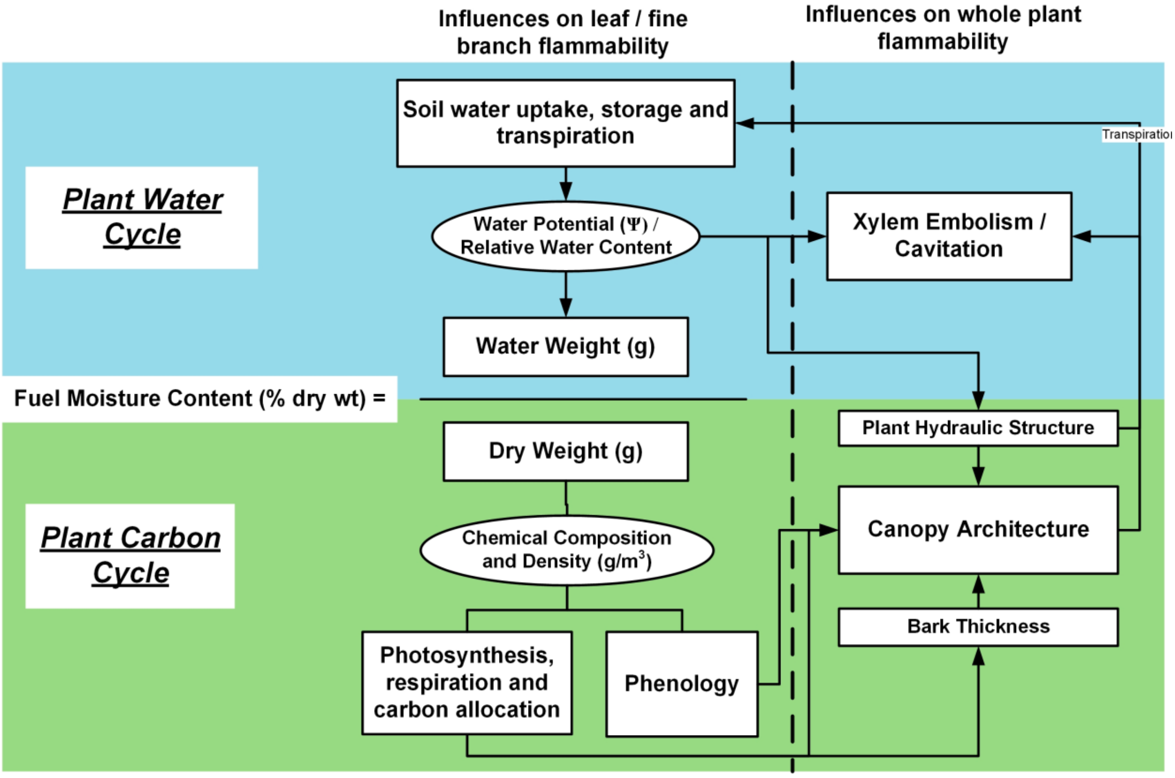

Figure 1.2 Conceptual model of the linkages between plant carbon and water cycles and how these two processes can individually impact fuel moisture content, and subsequently, leaf, branch, and whole plant flammability (Jolly and Johnson, 2018)

Pyro-ecophysiology is a new discipline that aims to bring together aspects of both ecophysiology and fire ecology to better understand live fuel flammability and fire-induced plant mortality (Jolly and Johnson, 2018). Ecophysiology contributes to an understanding of live fuel flammability by considering how plant water and carbon uptake, loss and storage might separately and collectively affect how well a plant burns (Jolly & Johnson, 2018; Nolan & de Dios, 2020). Ecophysiological traits are also useful when attempting to evaluate drought performance of plants, which in turn can be linked to patterns of plant mortality, and hence the production of dead fuels. Plant water status is regarded as a link between physiological traits and the flammability of live shoots (Bond & Midgley, 1995; Bowman et al., 2014a; Lavorel & Garnier, 2002; Weise et al., 2003). However, despite the importance of physiological traits, such as water potential, stomatal conductance and relative water content, and morphological traits, such as leaf moisture content, dry matter content, bulk density, to the flammability of a plant, relatively little research has been conducted on this topic.

1.5 Research objectives and thesis outline

In this thesis, my main goal is to identify the traits which underpin the eco-physiological processes linking drought and plant flammability, which will help answer the question of how drought affects the propensity of plants to burn. Key objectives of this thesis will be to assess recent ideas regarding the importance of key physiological traits (such as water potential, stomatal conductance, relative water content) in influencing plant flammability (i.e. the utility of different pyro-ecophysiological traits), and to provide further information to fire managers regarding the choice of low flammability species to be planted in green firebreaks to reduce fire spread.

To fulfil these objectives, the following questions were studied.
Q1) What is the relationship between indicators of drought response and shoot flammability, and are species that are drought tolerant also low in flammability? (Chapter 2)
Q2) Does shoot flammability change within species across different times of the year, and if so, which functional traits are associated with these changes? (Chapter 3)
Q3) Are there thresholds (i.e. inflection points) in the relationship between fuel moisture content (MC%) and shoot flammability, and if so, do these thresholds differ between species? Which morphological or physiological traits are associated with interspecific differences in % MC thresholds? (Chapter 4).

The thesis consists of a general introduction to outline the background of this study (Chapter 1), three data chapters dealing with the questions described above (Chapters 2-4), and a general discussion (Chapter 5) to synthesise the findings from these questions. The three data chapters are written as manuscripts for submission to international journals. 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 deals with different questions, requiring varied methodological approaches as briefly summarised below.

Chapter *2* investigates Q1 of the thesis. Testing key tenets of pyro-ecophysiology: Relationships between indicators of drought response and shoot flammability. To answer Q1, I tested the relationship between shoot flammability and six indicators of drought measures, to determine which indicators or pyro-ecophysiological traits are related to shoot flammability.

Chapter *3* investigates Q2 and examines the variation in shoot flammability throughout the year and its relationship to physiological and morphological traits. To address this, I measured shoot flammability, physiological and morphological traits over four sampling periods in one year.

Chapter *4* investigates Q3, and looked for threshold relationships between fuel moisture content and shoot flammability, before exploring relationships between interspecies difference and functional traits. To do this, I manipulated shoot moisture content of eight species by wetting up, air-drying and oven dry treatments.

Chapter 2

Testing key tenets of pyro-ecophysiology: Relationships between indicators of drought response and shoot flammability

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T.C., C.M-N., A.A., X.C, and N.S., conceived the idea; analyses were conducted by N.S., S.R. and A. A.; N.S. T.C. and C.M-N. wrote the first draft, which was then revised and approved by all co-authors. All authors contributed critically to the drafts and gave final approval for publication.

There are no conflicts of interest.

Abstract

1. Drought and fire are expected to become more frequent due to climate change; hence, it is important to examine how drought affects crucial aspects of fire ecology, such as plant flammability. The emerging sub-discipline of pyro-ecophysiology seeks to identify the ecophysiological traits that determine live fuel flammability, but empirical studies are rare. Pyro-ecophysiological traits may also have applications in fire management; for instance, it has been inferred that high drought tolerance implies low flammability in lists from the grey literature aimed at reducing fire hazard around homes. Trait studies suggest that this assumption is incorrect, and that drought tolerant species are instead highly flammable, but the relationship between drought tolerance and flammability has only been tested across a few species.

2. We examined the links between flammability and indicators of drought response for 39 woody plant species. We used existing data on shoot flammability and six drought-related variables: minimum leaf water potential (Ψ_{min}; N=15), leaf turgor loss point (π_{tlp}; N=20), root zone water deficits (N=19), days to plant death (N=14), xylem embolism resistance (P_{50}; N=20) and wood density (WD; N=20).

3. We found no support for the idea that drought-tolerant species had low shoot flammability for our indicators of drought response, except for ignition percentage and wood density, and then only for conifers. In direct contrast, there was a significant negative relationship between four of five shoot flammability variables and either or both of Ψ_{min} and π_{tlp}, showing that the most drought-tolerant species were also the most flammable.

4. The interplay between drought tolerance and flammability was complex. Ψ_{min} and π_{tlp} are closely tied to leaf water status, thus were more associated with shoot flammability than other indicators of drought response, though not in the direction that some fire managers have expected. These results provide the first direct support that pyro-ecophysiological traits such as Ψ_{min} and π_{tlp} are useful in explaining interspecific variation in live fuel flammability, reinforcing the promise of this new sub-discipline to understand the impacts to plants of a more drought- and fire-prone future.

Keywords: Pyro-ecophysiology, plant flammability, fire-wise plantings, drought tolerance

2.1 Introduction

Under anthropogenic climate change, changing rainfall patterns, increasing evaporative demand, increasing temperatures, and changing wind patterns are causing more frequent droughts and more severe fires (Higuera & Abatzoglou, 2021; Nolan et al., 2020a). Understanding the interplay between plant drought vulnerability and fire ecology is therefore a high priority (Varner et al., 2021; West et al., 2016). Drought can influence fire behaviour in a range of ways, with a primary driver being via changes in fuel moisture content (Abatzoglou et al., 2018), which can happen at a variety of scales, from the landscape to the individual plant or fuel particle. At the landscape scale, fuel moisture content will interact with other drivers, such as weather, fuel continuity and topography, to determine fire behaviour (Argañaraz et al., 2018), whereas for live fuels at the individual plant or plant part scale, fuel moisture content will also be affected by ecophysiological factors (Nolan, Foster et al., 2022).

Aspects of ecophysiology and fire ecology are integrated in the emerging discipline of pyro-ecophysiology, which seeks to better understand live fuel flammability and fire-induced plant mortality (Jolly & Johnson, 2018; Nolan, Foster et al., 2022; Nolan, Blackman et al., 2020b). Historically, research into live fuel flammability has mostly focused on environmental correlates rather than examining the core plant processes that dictate and limit plant functioning and cause variations in live fuel moisture that drive flammability in space and time (Jolly & Johnson, 2018). Pyro-ecophysiology examines links between physiological traits and plant flammability by explicitly addressing ecophysiological processes. Ecophysiology contributes to an understanding of live fuel flammability by considering how water and carbon uptake, loss and storage in plants separately and collectively influence plant combustion (Jolly & Johnson, 2018; Resco de Dios, 2020). A subfield of ecophysiology highly relevant to pyro-ecophysiology is plant water relations, due to the likely role of plant control of water content in determining live fuel moisture content, a key determinant of plant flammability (Karavani et al., 2018; Nolan, Foster et al., 2022; Nolan, Blackamn et al., 2020b; Resco de Dios, 2020; Scarff et al., 2021).

One key water relations trait is leaf water potential, Ψ_{leaf} (Jolly & Johnson, 2018; Nolan, Foster et al. 2022; Nolan, Blackman et al., 2020b), which describes the physical water stress a plant is experiencing and varies throughout the day and with a range of environmental drivers, especially soil moisture (Donovan et al., 2001). Within a given plant functional type, Ψ_{leaf} is predicted to be tightly linked with live fuel moisture content because plants with low water potentials have low leaf water status, and low fuel moisture content, and hence high flammability (Nolan, Foster et al., 2022; 2020b; 2018; Pivovaroff et al., 2019; Karavani et al., 2018). However, few studies have empirically tested the likely theoretical links between flammability and leaf water potential, or other water relations traits. Peacock (1980) reported no relationship between xylem water potential and flammability (represented by an ordinal scale that incorporated ease of ignition, percentage burnt biomass, and burn time) of branches of three shrub species in open woodland-grassland in Texas. Similarly, Owens et al. (1998) measured both water potential and flammability (maximum temperature reached and percentage mass lost) of needles and small twigs of *Juniperus ashei* (ashe juniper) throughout the year at two sites in Texas, but found that water potential was not an important predictor of flammability in a multivariate model. However, these empirical studies have included few species; more robust tests of relationships between pyro-ecophysiological traits and flammability are needed. Furthermore, how the less dynamic trait of minimum seasonal water potential (Ψ_{min}, lowest seasonal water potential, a key indicator of drought sensitivity; O'Brien et al. 2017) influences flammability remains unclear.

Other traits relevant to pyro-ecophysiology include turgor loss point (π_{tlp}) and xylem resistance to embolism/cavitation (P_{50}) (Pivovaroff et al., 2019; Nolan, Foster et al., 2020; Nolan, Hedo et al., 2018). Turgor loss point, also known as wilting point, is the Ψ_{leaf} at which the leaf becomes flaccid and loses function, and is widely recognised as an important indicator of plant water stress (Bartlett et al., 2012; Kramer & Boyer, 1995; McDowell, 2011). π_{tlp} is important to pyro-ecophysiology because of its effect on the relationship between Ψ_{leaf} and live fuel moisture content (Nolan, Blackamn et al., 2020b). Xylem embolism resistance (P_{50}, or conversely xylem cavitation vulnerability) is the branch water potential at which 50% of conduits have lost conductivity and is a useful predictor of species' drought mortality in woody plants (Choat et al., 2012). P_{50} likely influences plant flammability by causing death of branches or whole plants, thus increasing the amount of dead material in a fuel mix and increasing its flammability (Guillemot et al., 2022; Nolan, Gauthey et al., 2021; Johnson et al., 2021). There have been no previous empirical comparisons of these pyro-ecophysiological traits with plant flammability, nor have the relationships between flammability and other indicators of drought response been assessed.

Plants respond to a drought in different ways, according to their water-saving strategies (Klein, 2014; Li et al., 2019). These can be typified as drought tolerance and drought avoidance strategies (Guillemot et al., 2022), and are characterised by different suites of traits including

Ψ_{min}, π_{tlp} and P_{50}, which are all indicative of drought response (Álvarez-Cansino et al., 2022; Choat, Brodribb et al., 2018; Martínez-Vilalta et al., 2021). High wood density (WD) can confer tolerance of drought, and species with dense wood can be associated with seasonally dry environments (Rossa et al., 2022; Serra-Maluquer et al., 2022; Martinez-Cabrera et al., 2009). Measures such as days to death under controlled drought are integrating traits that measure drought survival and could reflect either avoidance or tolerance. Another indicator of drought response also non-specific to drought response strategy is root zone water deficit, a niche-modelling based variable. This approach describes species optima/distribution in relation to environmental variables, and has been used to describe the water stress tolerances of tree species in New Zealand (Leathwick & Whitehead, 2001). This suite of indicators of drought response allows us to explore the relationships between drought vulnerability and flammability. Pyro-ecophysiological traits may also have applications in fire management; for instance, in identifying species that are low in flammability. Many jurisdictions around the world have proposed lists of species considered suitable for reducing fire hazard (i.e. altering fuels, *sensu* Hardy, 2005). However, such lists have been criticised as few of them explain the criteria by which species are included, and are rarely based on empirical measurements of flammability (White & Zipperer, 2010; Wyse et al., 2016). For example, some species have been recommended for planting near houses in fire-prone areas not because of their performance in flammability tests but based on other characteristics such as drought tolerance measures (Idaho Firewise, 2022; White & Zipperer, 2010; Dennis, 2012; Doran et al., 2004). The lack of a clear explanation for the inclusion of a species on a list has led to assumptions that species with low vulnerability to drought (equating to high drought avoidance, or high drought tolerance) have low flammability (White & Zipperer, 2010), and some plant flammability lists from the grey literature have explicitly used high drought tolerance as a surrogate for low flammability (Dennis, 2012; Idaho Firewise, 2022). However, the plant trait literature highlights the need for a more nuanced consideration of the relationship between flammability and drought vulnerability. For instance, some species that can readily survive drought are likely to be low in flammability, e.g., succulent species avoid drought stress by storing large amounts of water in their tissues to access during dry periods (Santos et al., 2021; Lamont & Lamont, 2000). This high tissue water content also makes such species unlikely to readily ignite or carry a fire (Rossa et al., 2016; Jolly et al., 2014; Alexander & Cruz, 2013). Conversely, several researchers have noted that certain drought tolerance traits (such as tolerance of low tissue water content and small leaves) actually make plants more flammable and elevate fire hazards (Bowman et al., 2014; Lavorel & Garnier, 2002; Weise et al., 2003; Bond & Midgley, 1995). These two contrasting examples highlight the conflicting results possible when inferring flammability from a species' drought response strategy, and show the potential danger in equating drought tolerance with low flammability. This issue is further clouded by the lack of research explicitly examining relationships between flammability and drought response measures.

To investigate the relationships between indicators of drought response and flammability, and also between key pyro-ecophysiological traits ($\Psi_{min,}$ π_{tlp}) and flammability, we compiled existing data for 39 species on shoot flammability and correlated them with six different indicators of drought response, including minimum leaf water potential ($\Psi_{min,}$ MPa; N=15 species), leaf turgor loss point (π_{tlp}, MPa; N=20), root zone water deficit (MPa days; N=19), days to plant death (days; N=14), xylem embolism resistance ($P_{50,}$ MPa; N=20) and wood density (WD, mg m^{-3}; N=20).

2.2 Methods

2.2.1 Measurements of drought response indicators

Indicators of drought response measure were collected from several previous studies (one study for each measure of drought response) across a range of species. Details of the species sampled for each drought response measurement are listed in Table S1. Two of these species are non-native (one shrub and one tree) and 37 species are native to New Zealand (36 tree species and one shrub species).

Data for mean minimum leaf water potential (Ψ_{min}) of each species (13 are native species; two are non-native species; Category a in Table S1) were collated from Bannister (1986). These data were collected in the field using a Scholander pressure bomb at two locations near Dunedin (mean annual precipitation (MAP): 812 mm, 1971–2000; NIWA, 2022) during a seasonal drought. Species were sampled from coastal and lowland forests, as well as planted sites (Dunedin Botanical Gardens and the Town Belt; Bannister 1986).

Data on the annual integral of the root zone water potentials being below field capacity (category b; Table S1) were collected for 19 common native tree species from indigenous forest throughout NZ (Leathwick & Whitehead, 2001). Root zone of water deficit (MPa days) of common tree species was derived from fitted values of a regression model (degree of correction, $\alpha = 0{\cdot}7$), which predicted maximum species distribution in different sites across NZ and then correlated these to relevant environmental variables. Species with a lower root zone water deficit spend fewer days per year with root zone water potentials below field capacity, are better suited to wetter conditions and are therefore not well-adapted to dry soils.

Data for days to death of plants (category c; Table S1) were taken from a controlled shade-house study on 14 native angiosperm tree species (Seward, 2016), following the approach of Wyse, Macinnis-Ng et al. (2013). Species were selected by Seward (2016) if they were commonly found in forests around Auckland, and included species often used in restoration projects in the region. These species are found in riparian, lowland or ridgetop forests. Two-year-old seedlings of each species were obtained from a nursery and potted with a mixture of compost, fine bark, pumice and organic fertilizers. The seedlings were grown in ambient temperatures in a shade house located at the University of Auckland's Tamaki campus in St Johns, Auckland (MAP: 1240 mm, 1971–2000; NIWA, 2022). The experiment was conducted from April 2014 to November 2014. Fourteen individuals of each species were subjected to drought treatment and nine seedlings were used as a control group. The control seedlings were watered twice a week to above 40% of soil moisture content. A pace-setting species (the species with the highest volumetric soil water content of all the plants in the drought treatment group (Sack, 2004); for most of this experiment, *Laurelia novae-zealandiae*) was used to determine the excess water to be added to the other seedlings under drought treatment. Mean volumetric soil moisture content at 4, 8 and 12 weeks was 33%, 26% and 20% respectively. Across the 12-week dry down experiment, seedlings were monitored weekly to assess signs of wilting. Days to death was recorded as the day plants had fully wilted. Death was confirmed by adding water to the dehydrated seedlings to show plants did not resprout.

Data on π_{tlp} (b; Table S1), stem P_{50} (e; Table S1) and WD (f; Table S1) were obtained from Laughlin et al. (2020) for 20 native tree species. These species were sampled from a range of temperate rainforests from multiple sites on both the North Island and the South Island of New Zealand. π_{tlp} was estimated from leaf osmotic potential using the equation, $\pi_{tlp} = 0.832\pi_{osm} - 0.631$ (Bartlett et al., 2012). Wood density (i.e. stem-specific density) was gathered from existing databases collected from forests and shrublands throughout NZ (Laughlin et al., 2020).

2.2.2 Measurement of shoot flammability of live fuels

Having identified native and exotic woody species in New Zealand for which there are drought response data from the various sources described above, we then collated existing shoot flammability scores from Wyse, Perry et al. (2016), Cui et al. (2020) and Alam et al. (2020), and from additional species sampled more recently using a similar device and methods.

Shoot flammability was measured for each species following the methods described by Jaureguiberry et al. (2011) and Wyse, Perry et al. (2016). Sun-exposed terminal branches were cut at 70 cm lengths from at least 6 healthy, mature plants of each species. Before burning, all shoot samples were air dried at room temperature for 24 h in ambient laboratory conditions to better match sample moisture content with the ignition source (for a discussion of this, see Wyse et al., 2016, Wyse, Perry et al., 2018)). Samples were preheated at approximately 150°C for 2 minutes on the burner prior to being ignited with a blowtorch. During burning, ignitibility was recorded as a binary variable (ignited or not) and used to calculate an ignition percentage for each species. The blowtorch was turned off after 10 s, and the remaining measurements taken. The maximum temperature of flames during burning was measured using an infrared laser thermometer (Fluke Corp., Everett, WA, USA) to represent combustibility. Samples that did not ignite were given a value of 150°C, representing mean grill temperature (Padullés Cubino et al., 2018; Wyse, Perry et al., 2018). Sustainability was measured as the period of time that a sample supported flaming combustion after the blow torch was turned off. Consumability was measured as the percentage of burnt biomass, assessed by visual observation by at least two observers. The four flammability components were converted to a single flammability index (known as the flammability score) via principal components analysis (PCA, using the *princom* function) with the first principal component scores representing this overall index (higher PC1 scores indicate higher flammability).

2.2.3 Statistical analysis

To examine the relationship between indicators of drought response measures and plant flammability, linear regressions were fitted. The data for π_{tlp} exhibited a non-linear relationship with flammability, however, linear regression was fitted despite the slightly poorer fit, because a linear relationship exists between turgor loss and relative water content (Abrams, 1988; Turner, 2018) so a linear relationship makes more sense biologically.

To examine the strength of the phylogenetic signal (Freckleton et al., 2002) in drought response measures and flammability traits, Pagel's lambda was estimated using the function *phylosig* in the R package 'phytools' (Revell 2012). The strength of the association between drought response measures and flammability components was assessed by applying phylogenetic generalised least squares (PGLS) to the given phylogenetic signal using function *pgls* in the R package 'caper' (Orme et al., 2018), with a hypothesised phylogenetic tree constructed using the function *phylo.maker* in the R package version 0.1.0 'V.PhyloMaker' (Jin & Qian 2019). All statistical analyses were performed in R statistical environment for windows (v.4.1.1) (R Core Team, 2022).

There was a significant phylogenetic signal for either the response or predictor variable in three of the 80 pairwise comparisons between flammability and drought traits (Table S2) and the results reported here are from the PGLS, to account for the phylogenetic signal (results of linear regressions are reported in Figures S1-5). No corrections were made to alpha for multiple tests.

2.3 Results

2.3.1 Plant flammability variables

A PCA on the four flammability variables found that all were positively correlated with the first axis (ignition percentage (0.47), maximum temperature (0.52), burning time (0.51) and burnt biomass (0.50); Figure 1). The first axis explained 83.9% of the variation in the flammability data and hence was used as a measure of overall flammability (flammability score – PC1, Table 1). Ignition percentage was positively loaded (0.80), while burnt biomass (0.48) and burning time (0.37) were negatively loaded with the second axis, which explained only 9.1% of the variation in flammability (Figure 1).

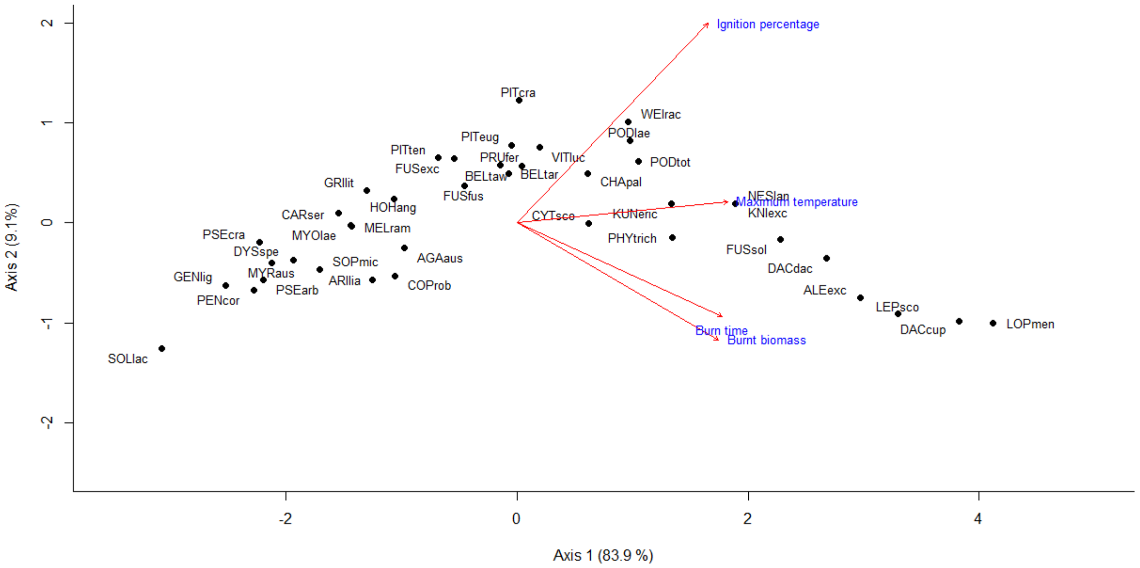

Figure 2.1 Principal component analysis of 39 species used in this study. PC1 scores were used to represent overall flammability, with higher PC1 scores representing higher flammability. Full names are listed in Table S1.

2.3.2 Drought response measures and plant flammability

Extensive phylogenetic analysis of relationships between drought response indicators and flammability scores produced very few significant results (Table A2.2). Results that were significant were: ignition percentage and wood density (for conifers) and burnt biomass and minimum water potential (for all species and angiosperms).

Flammability scores (PC1) were significantly negatively related to Ψ_{min} when all species were included ($P = 0.02$, $R^2 = 0.34$; Figure 2.2a), but this relationship was weaker (and not significant) among angiosperms (*P* = 0.07, R^2 = 0.25). Conifers were not analysed, due to low replication. Flammability scores (PC1) were also significantly negatively related to π_{tlp} for all species (*P* = 0.03, R^2 =0.24; Figure 2.2b), and again the relationship was weaker and not significant among angiosperms (*P* = 0.06, R^2 = 0.08). None of the remaining drought response measures (P_{50}, days to death, root zone water deficit, and WD) were related to the flammability scores (Figure 2.2). None of the PGLS results relating ignition percentage to the various drought response measures were significant (Figure 2.3), except for a significant negative relationship with WD for conifers (Figure 2.3f). In the linear regressions when phylogeny was not accounted for (Figs A2.1-2.5), there were negative relationships between almost all the flammability variables and Ψ_{min} and π_{tlp}.

Maximum temperature was not significantly related to Ψ_{min} when all species were included (*P* = 0.07, R^2 = 0.25; Figure 2.4a), while significantly negatively related to angiosperms (*P* = 0.04, R^2 = 0.30). Conifers were not analysed, due to low replication. Maximum temperature reached was also significantly negatively related to π_{tlp} across all species (*P* = 0.03, R^2 = 0.23; Figure 2.3b), and among angiosperms (*P* = 0.05, R^2 = 0.28), but not among conifers (*P* = 0.39; R^2 = 0.18). None of the remaining drought response measures (P_{50}, days to death, root zone water deficit, and WD) were related to the maximum temperature reached (Figure 2.4).

Burnt biomass was significantly negatively related to Ψ_{min} when all species were included (*P* = 0.02, R^2 = 0.34; Figure 2.5a), and this same relationship was found for angiosperms (*P* = 0.03, R^2 = 0.33). Conifers were not analysed, due to low replication. There was no significant relationship between burnt biomass and π_{tlp} for all species (*P* = 0.08, R^2 =0.16), but there was a significant negative relationship among angiosperms (*P* = 0.02, R^2 = 0.37; Figure 2.5b), though not for conifers (*P* = 0.53; R^2 = 0.10). None of the remaining drought response variables (P_{50}, days to death, root zone water deficit, and WD) were related to burnt biomass (Figure 2.5). The only significant relationship between burning time and drought response measures was a negative one for burning time and π_{tlp} for all species (*P* = 0.03, R^2 = 0.25; Figure 2.6b).

The negative relationship between many shoot flammability variables and Ψ_{min} and π_{tlp}, suggests a positive relationship between drought tolerance and shoot flammability, as more negative Ψ_{min} and π_{tlp} are indicative of greater drought tolerance. For instance, the overall flammability score (PC1) was negatively associated with Ψ_{min} (i.e., less drought tolerant species (with less negative Ψ_{min}) were less flammable (Figure 2.2)).

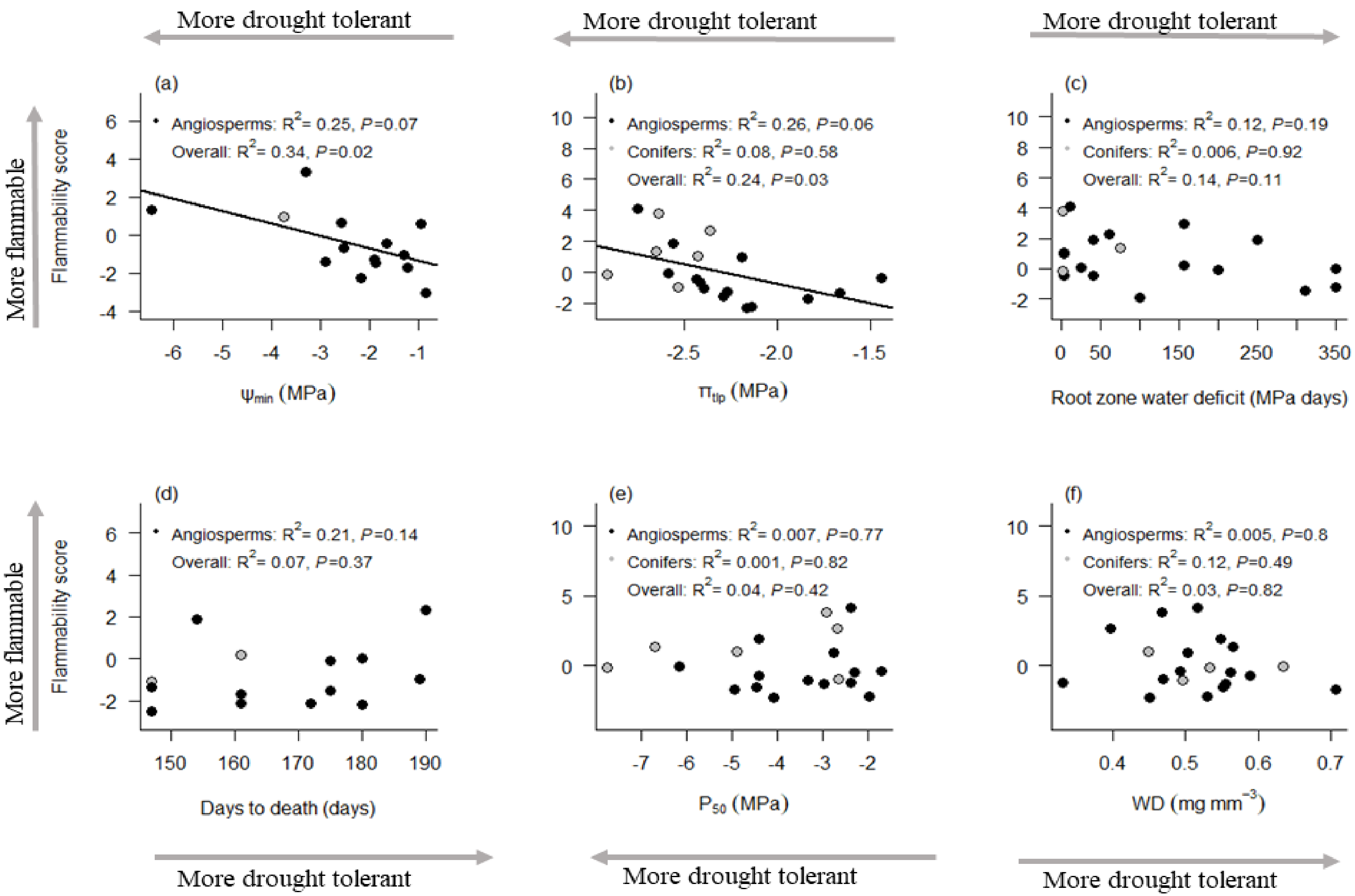

FIGURE 2.2 Relationships between mean flammability score (PC1) and means of (a) Ψ_{min}, (b) π_{tlp}, (c) Root zone water deficit, (d) Days to death, (e) P_{50}, (f) WD. Grey points = conifers; black points = angiosperms respectively. Fitted lines are from PGLS models; solid black line represents significant relationships for all (overall) species.

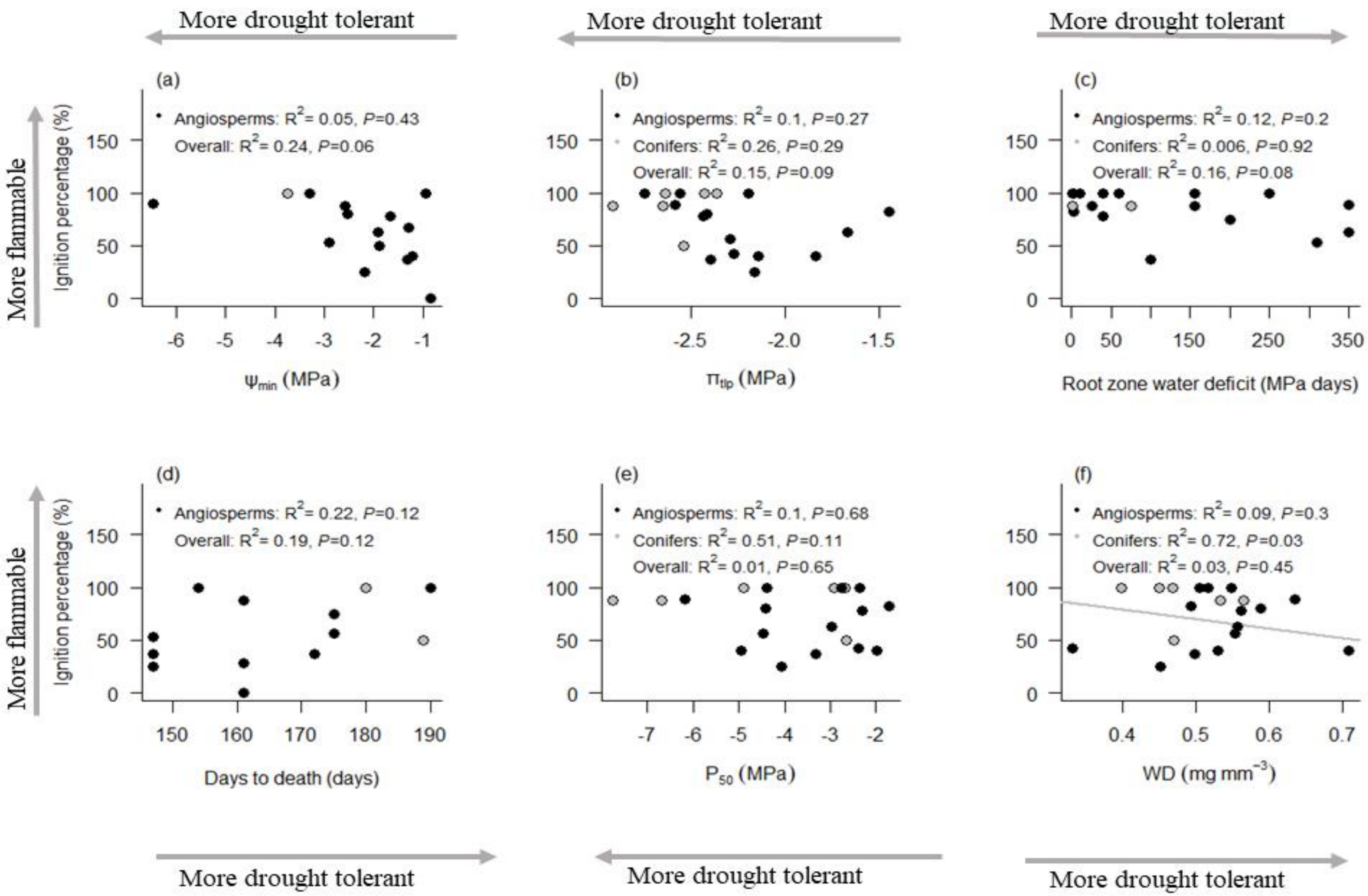

FIGURE 2.3 Relationships between mean ignition percentage (%) and mean of (a) Ψ_{min}, (b) π_{tlp}, (c) Root zone water deficit, (d) Days to death, (e) P_{50}, (f) WD. Grey and black points denote conifers and angiosperms, respectively. Grey line (f) is fitted from PGLS models represents significant relationships for conifers.

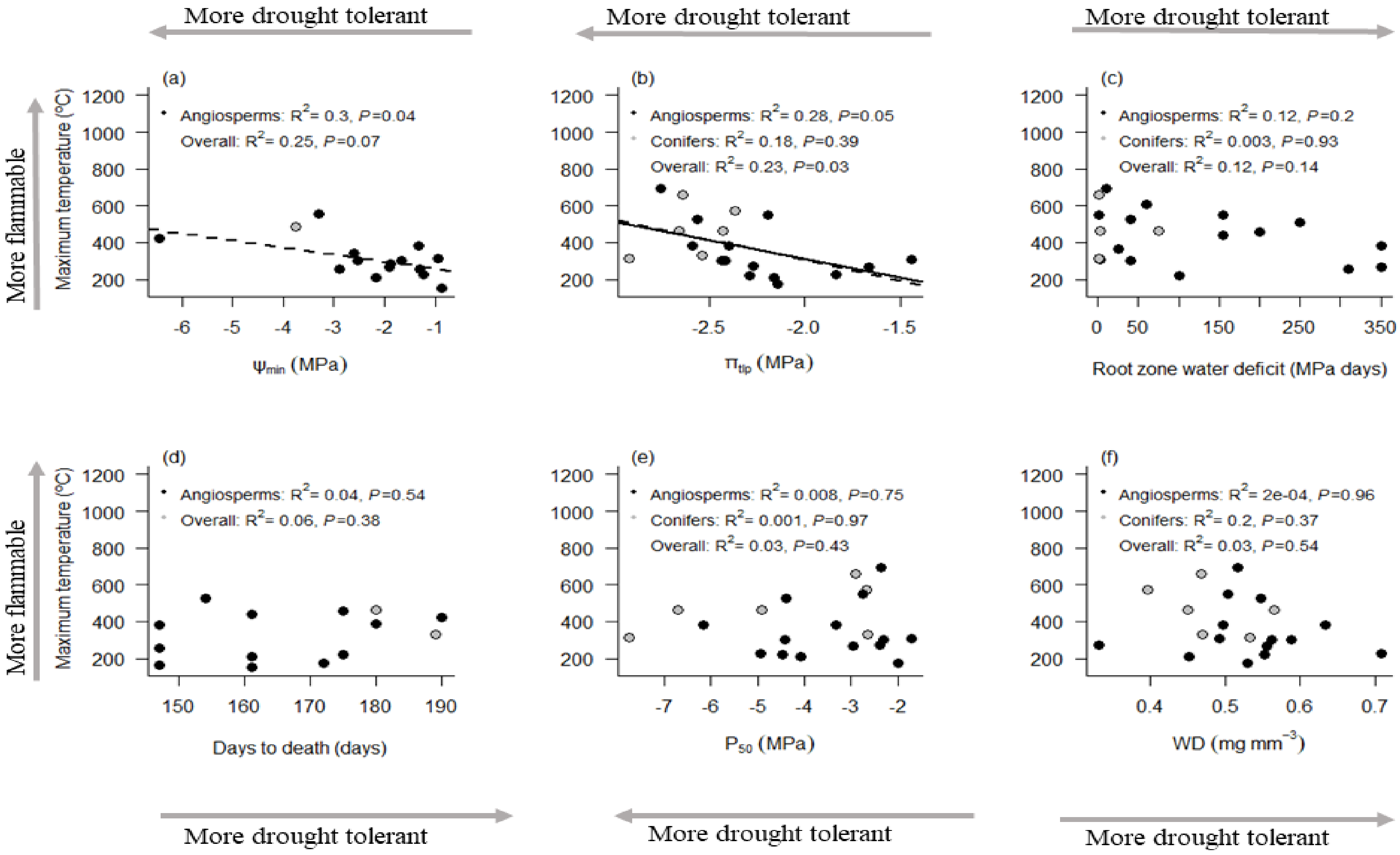

FIGURE 2.4 Relationships between mean maximum temperature (º C) and mean of (a) Ψ_{min}, (b) π_{tlp}, (c) Root zone water deficit, (d) Days to death, (e) P_{50}, (f) WD. Grey and black points denote conifers and angiosperm respectively. Solid (overall) and dashed (angiosperms only) black lines are fitted from PGLS models.

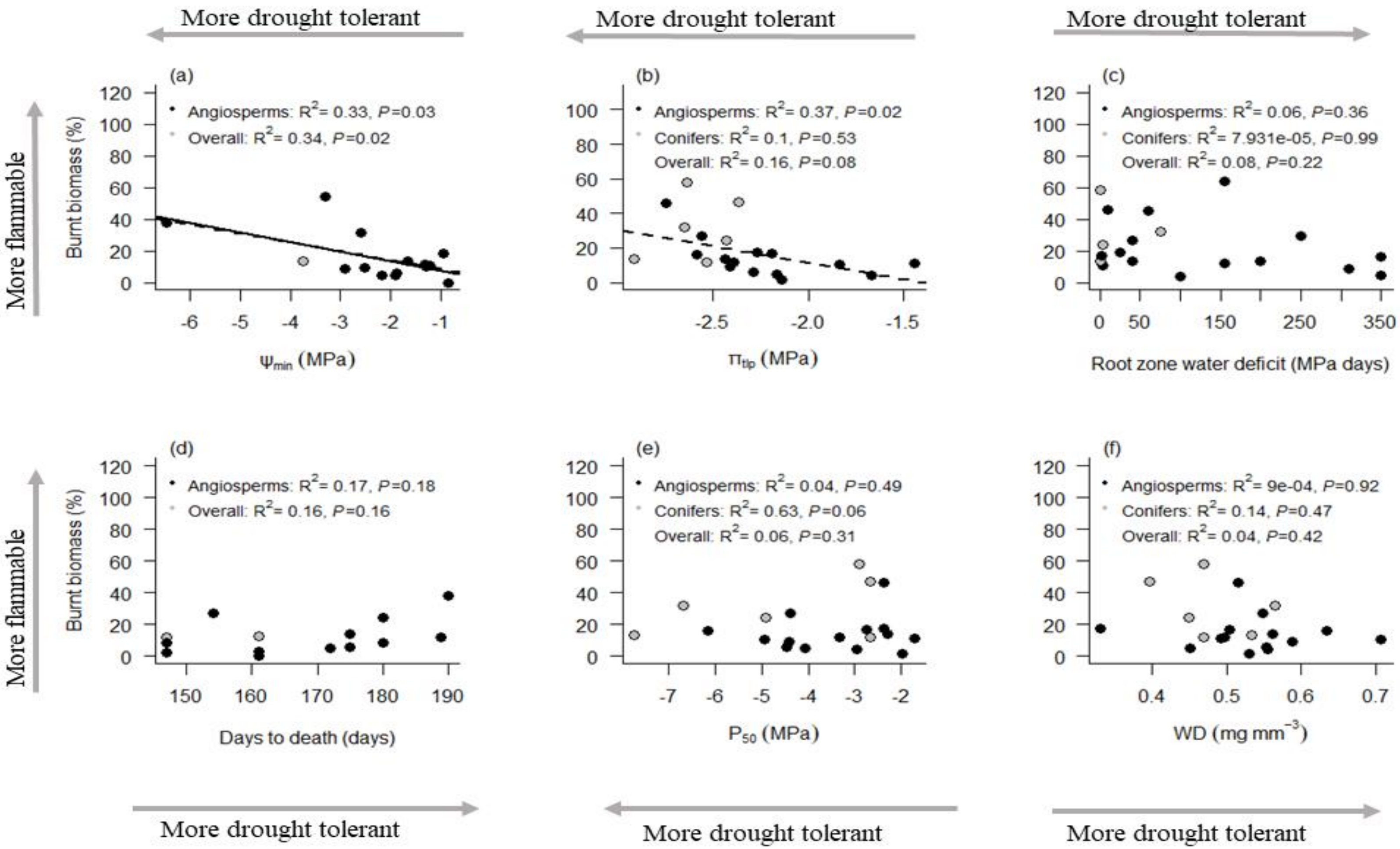

FIGURE 2.5 Relationships between mean burnt biomass (%) and mean (a) Ψ_{min}, (b) π_{tlp}, (c) Root zone water deficit, (d) Days to death, (e) P_{50}, (f) WD. Grey and black points denote conifers and angiosperm respectively. Solid (overall) and dashed (angiosperms only) black lines are fitted from PGLS models.

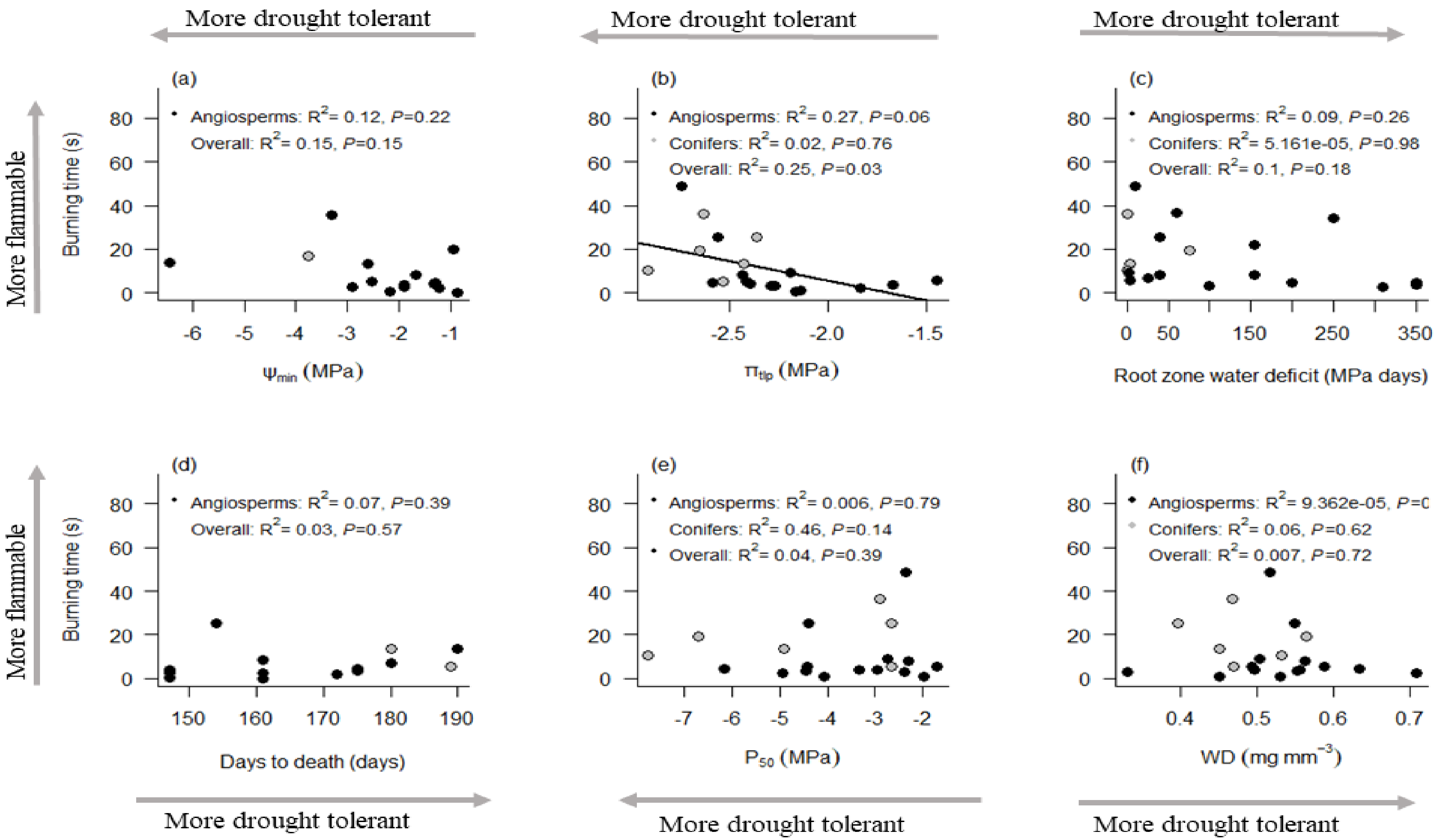

FIGURE 2.6 Relationships between mean burning time (s) and mean of (a) Ψ_{min} , (b) $\pi_{tlp,}$ (c) Root zone water deficit, (d) Days to death, (e) $P_{50,}$ (f) WD. Grey and black points denote conifers and angiosperm respectively. Fitted lines are from PGLS models; solid black line represents significant relationships for all (overall) species.

2.4. Discussion

Pyro-ecophysiology seeks to use ecophysiological processes to better understand inter- and intra-specific variation in live fuel flammability (Jolly & Johnson 2018), but empirical tests of relationships between ecophysiological traits and flammability based on large numbers of species are lacking. We have shown that some key pyro-ecophysiological traits (Ψ_{min} and π_{tlp}) are negatively associated with shoot flammability in woody species found in New Zealand, while another pyro-ecophysiological trait, P_{50}, was not linked to shoot flammability. These results provide the first direct support for the theoretical predictions of Jolly and Johnson (2018), Nolan, Blackman et al. (2020b) and Nolan, Hedo et al. (2018) that water relations traits can integrate ecophysiology with research on live fuel flammability.

Linking flammability and ecophysiological traits is appealing to fire managers because species' drought responses are often well-typified (albeit poorly defined), though species' flammability is not. While quantifying species flammability provides key information for fire hazard management, for example by identifying low-flammability species to plant in gardens, measuring the flammability of large numbers of species is costly and time-consuming. Consequently, traits such as high tissue moisture content, open and loose branching patterns and low amounts of dead material have been used to infer low flammability of some species (Chladil & Sheridan, 2006; Doran, et al., 2004), and surrogates, such as drought tolerance (Idaho Firewise 2022; Dennis, 2012), are frequently used to derive flammability lists (White & Zipperer, 2010). However, the assumption that plant species better able to survive drought also have low flammability has never been tested on a large number of species. We found that for a range of woody plant species, high drought tolerance was not associated with low shoot flammability. For three of our measures of drought response (root zone water deficit days, days to plant death, and P_{50}) there was no relationship with shoot flammability, and for another (WD) only one significant relationship (a negative one between WD and ignition percentage, and then only for conifers). Importantly, the other drought response measures (Ψ_{min} and π_{tlp}) showed species that are more tolerant to drought have a higher shoot flammability score. This result refutes the assumed negative relationship between drought tolerance and flammability (Dennis 2012; Idaho Firewise, 2022). Hence, we would recommend that drought tolerance is not used as a surrogate for flammability, and instead encourage direct measurement of plant flammability, such as those undertaken at the shoot-level (Jaureguiberry et al. 2011; Wyse, Perry et al. 2016; Cui et al., 2020).

2.4.1 Pyro-ecophysiological traits and their association with flammability

Leaf water potential is a trait likely to be associated with plant flammability (Nolan, Foster et al., 2022a; Nolan, Blackamn et al., 2020b; Nolan, Hedo et al., 2018; Pivovaroff et al., 2019), due to the tight relationship between relative moisture content and Ψ_{leaf} (Lemaire et al., 2021; Sapes & Sala, 2021). It is important to note that Ψ_{leaf} is not driving flammability, but that this link is indirect, due to the influence of leaf moisture content on these variables (Nolan, Blackman et al. 2020; Pivovaroff et al., 2019; Nolan, Hedo et al., 2018). We might expect that the dynamic measure of Ψ_{leaf} would be related to seasonal Ψ_{min}, because Ψ_{min} indicates the lower possible limit and therefore influences day-to-day fluctuations in Ψ_{leaf} (McClenahan et al., 2004; Ravi et al., 2021). Thus, a low mean Ψ_{min} reflects a species likely to have low leaf water status and therefore live fuel moisture content, and thus, when other traits are similar, higher shoot flammability, as was found in our analysis.

The mechanisms behind the relationship between π_{tlp} and flammability are likely similar to those associated with Ψ_{min} and flammability, because π_{tlp} also defines the lower limits of water status in which a plant can operate. π_{tlp} is negatively correlated with relative water content or live fuel moisture content (Jolly & Johnson, 2018, Pivovaroff et al., 2019; Nolan, Blackamn et al., 2020b). This relationship between π_{tlp} and moisture content suggests that the negative relationships with each of Ψ_{min} and π_{tlp} and shoot flammability is mediated by their links to leaf moisture content (Jolly & Johnson 2018, Pivovaroff et al., 2019; Nolan, Blackman et al., 2020b), helping explain why drought tolerant species also have high flammability. Nolan, Blackman et al. (2020b; see their Fig. 3) compared the relationship between Ψ_{leaf} and live fuel moisture content (LFMC; %) for saplings of eight *Eucalyptus* species. When we plotted values of π_{tlp} against LFMC at π_{tlp} derived from these curves (Nolan et al., 2020a; Nolan, Blackman 2020b) we found that more negative values of π_{tlp} were associated with lower LFMC (analyses not shown). Therefore, we would expect that plants with lower π_{tlp} values have higher flammability scores, consistent with our findings.

Stem P_{50} is the branch water potential at which there is 50% loss of stem hydraulic conductance, and hence is related to a plant's ability to avoid death from drought (Guillemot et al., 2022; Nolan, Gauthey et al., 2021; Johnson et al., 2021). However, these levels of loss of stem hydraulic conductance may not be sufficient to reduce tissue moisture levels of plants below the critical thresholds (~ 102% live fuel moisture content) associated with landscape-scale fires in eucalypt forests and woodlands, as reported in seven of eight eucalypt species (Nolan, Blackam et al., 2020). This suggests that while P_{50} is a good indicator of either branch or plant death from drought, it may not be a good indicator of tissue moisture content, potentially explaining the decoupling from shoot flammability. However, despite this lack of a relationship with shoot (or live fuel) flammability, P_{50} is likely to be an important indicator of ecosystem-level flammability, as it can help predict the mortality rates of plant species due to drought (Choat et al., 2012), and hence the addition of dead fuels to the fuel environment (Dent et al., 2019; Franzese et al., 2022).

None of the various drought response measures (including Ψ_{min} and π_{tlp}) were significantly related to ignition percentage (Figure 3), except WD for conifers only. This was surprising, as all other flammability variables, including the PC1 scores (an index of overall flammability) were significantly related to either or both of Ψ_{min} and π_{tlp}. Our interpretation is that Ψ_{min} and π_{tlp} do not influence the likelihood of ignition, but that once ignition does occur, these variables influence how well the plant burns. However, because a plant cannot burn if it does not ignite, it is important to further explore the role of pyro-ecophysiological traits in determining ignition, a crucial stage of the combustion process.

There were some differences in our results when phylogeny was not accounted for (Figures S1-5). For instance, there were significant negative relationships between ignition percentage and both Ψ_{min} and π_{tlp} when assessed across all species. This suggests that the relationship between these variables is quite strong among modern species, although it is weaker when phylogeny is considered, likely due to past divergences, such as those between conifers and angiosperms.

2.4.2 Indicators of drought response which were not related to shoot flammability

Root-zone water deficits were not related to shoot flammability in our dataset. One explanation lies with the nature of these drought response data. Root zone water deficit is not actually measuring the short-term water content of plant tissues (Bond & Kavanagh, 1999; Tyree & Sperry, 1988), rather it is measuring the hydrological optima of a plant species, as determined from estimates of root zone water deficit from the distribution of the species as represented in an extensive New Zealand- wide plot network (Leathwick & Whitehead, 2001). Accordingly, drought response as defined by a species' hydrological optima is likely to be a poor surrogate for shoot flammability.

Seedling death due to soil moisture reduction, which is another indirect measure of drought sensitivity, was not related to shoot flammability. The dry-down experiment (Seward

2016) provides an excellent measure of seedling performance under increasing moisture stress. However, plants can cope with moisture stress via a range of strategies, including drought avoidance (via leaf shedding), so some species that can survive longer during dry-down may also be species that generally have high tissue moisture content (Wyse, Macinnis-Ng et al. 2013).

Finally, wood density was not related to shoot flammability, except for ignition percentage for conifers only. Wood density is likely related with other physiological traits to predict growth response (Fu & Meinzer, 2018). In shoot-level tests, leaves and sometimes thinner twigs are the main fuel that burns (Alam et al., 2020); it is rare that thicker twigs burn. While WD has been recognized as a useful, easy-to-measure predictor of drought resistance in some ecosystems (O'Brien et al., 2017), it does not appear to influence flammability at the shoot-level, and therefore perhaps not at the whole plant scale (due to the association between shoot flammability and whole plant flammability (Alam et al., 2020). As with the other traits discussed here, it may still help predict the likelihood of plant death associated with drought; hence, it might influence the build-up of dead fuels in an ecosystem.

2.5 Broader implications of results

Most of our study species are native to New Zealand (37 of 39), a flora that is not well-adapted to fire with few traits allowing fire resistance or regeneration after fire (Perry et al., 2014). However, our suite of study species covers a range of flammability, from low to high. Similarly, our drought response measures included a range of species with low to high drought sensitivity. We encourage further study in the field of pyro-ecophysiology to determine whether these findings are consistent across different vegetation types, especially more fire-prone communities from Australia, North America, Africa and Europe. We also suggest expanding the work to include measures of dynamic traits to explore how plant water relations and flammability co-vary across seasons. Under a changing climate, the ecological consequences of how drought and fire impacts interact is a growing concern and pyro-ecophysiology offers new insights into vulnerability of different species to these combined stressors.

2.6 Conclusions

The relationships documented here between shoot flammability and water relations traits, such as Ψ_{min} and π_{tlp}, provide important empirical data on concepts of pyro-ecophysiology, particularly patterns of live fuel flammability across species (Resco de Dios et al., 2020; Nolan, Blackman et al., 2020a; Jolly & Johnson 2018), and demonstrate the promise of this new field of research. We have shown that drought-tolerant species are not necessarily low in flammability, and hence we question the assumption that drought tolerance is a surrogate for flammability. When pyro-ecophysiological studies are conducted in a wider range of biomes, functional groups, and species, we anticipate that universal patterns will be uncovered. Such findings will improve our understanding of how traits like plant water relations relate to flammability and provide insights into the ecological significance of relationships between these traits, and provide critical data for fire managers in an increasingly fire-prone world.

Chapter 3

Shoot flammability varies throughout the year in some species, and is related to plant water relations and leaf size

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Abstract

1. Evaluation of plant flammability is becoming increasingly important to help manage fires and understand fire behaviour in the wildland-urban interface. However, flammability can vary within individuals and species throughout the year, for instance due to biotic and environmental factors associated with changing seasons. Past research has found that while some species may vary seasonally in flammability, others may not. Documenting variability of flammability across the year will provide better information to improve fire behaviour models and better guide fire management decisions.
2. We measured shoot flammability and plant traits for ten species from mixed regenerating rainforest / shrubland four times across a year on the same individuals, to test for changes in flammability and to determine the relationship between flammability and several physiological and morphological traits.
3. We found that flammability changed throughout the year in several, but not all, of our species. For instance, three species (*Pseudopanax crassifolius*, *Pseudopanax colensoi* and *Griselinia littoralis*) had consistently low flammability across all sampling times and all flammability variables. Two highly flammable species, *Kunzea robusta* and *Ulex europeaus*, generally maintained high flammability throughout the year, although there were significant differences between sampling times for some flammability variables. One species, *Melicytus ramiflorus*, varied significantly throughout the year for all flammability variables, shifting from very low flammability in April and July, to high flammability in October and February.
4. Flammability variables were negatively correlated with three plant water relations traits (Stem water potential, leaf relative water content and leaf moisture content), and two leaf size traits (Leaf area and Leaf thickness) and positively correlated with leaf dry matter content, suggesting that highly flammable species had low leaf moisture content, leaf relative water content, *stem water potential*, and high leaf dry matter content with small leaves.
5. These findings suggest that some of these species, including those recommended for planting in green firebreaks (e.g. *M. ramiflorus*), may show seasonal variation in flammability, though additional multi-year sampling will be required to confirm this. The relationship between flammability and water relations traits shows the potential for changes in in real time via remote sensing, given recent advances in this field. These findings will help guide fire management in the wildland – urban interface throughout the year.

Keywords: Seasonal flammability, drought forest, physiological traits, morphological traits. Fire risk.

3.1 Introduction

Flammability is an important plant trait for fire management. Knowledge of plant flammability enhances our understanding of fire behaviour by allowing comparisons of how well different species burn (Jolly et al., 2016; Rasooli et al., 2021), can be used to estimate fire risk at wildland-urban interfaces (Ganteaume et al., 2018; Romero et al., 2019; Simeoni et al., 2012), and to guide planting choices to reduce fire spread across landscapes (Wyse et al., 2016). However, the flammability of a species or individual is not necessarily fixed (Bajocco et al., 2010; Ripley et al., 2010); it can change due to biotic and environmental factors, including across seasons (Bowman et al., 2014b; White & Zipperer, 2010); with plant age (Bragg, 1982; Franzese et al., 2022; Jolly et al., 2014); during changing environmental conditions, e.g. drought (Breton et al.; 2022; Nolan et al., 2016); due to pests or pathogen attack (Page et al., 2012; Sheehan & Klepzig, 2021); and with changing disturbance regimes, e.g. fire (Bond, 2022; Bowman et al., 2015; Pausas & Bond, 2020). Because of the importance of flammability for fire management, and its potential to change within species and individuals, it is important to document such plasticity and the reasons for it.

One of the main reasons why flammability changes in some species is due to seasonal fluctuations in response to environmental change. For instance, the flammability of small shoots of white spruce (*Picea glauca*) varied seasonally, particularly among new shoots, with flammability peaking in late summer and maintaining this through autumn (Melnik et al., 2022). Seasonal changes in shoot flammability were inferred based on correlations with plant functional traits for woody species in the Chaco region of Argentina (Santacruz-García et al., 2019). Flammability of 70 cm shoots was positively correlated with the primary axis of functional trait variation (for instance, low leaf dry matter content and fast twig drying time). These functional traits were then measured seasonally, with values indicative of higher flammability being recorded in late winter (August) and spring (October), coinciding with the dry season (and main fire season) (Santacruz-García et al., 2019). However, Gowda et al., (2022) studied eight woody species in temperate forests and shrublands along the Andean forests of Northwestern Patagonia and found that flammability varied in only one of these species for two of four flammability variables, when compared between four months of the austral summer. Essaghi et al., (2017) derived a flammability index (time to ignition, duration of combustion and flame height) in 13 species from

Moroccan forest across two seasons (winter and summer) and found that some but not all species increased flammability during summer (July-September). Together these findings show that while flammability can vary seasonally for some species, this is not necessarily consistent across seasons, species or different studies and is potentially highly site-specific.

Given there is seasonal variation in flammability, identifying plant traits associated with changing flammability will improve ability to generalize across different species. Dry matter content was found to be positively related with flammability traits during spring/summer; species that shifted to high dry matter content were highly flammable during those seasons (Alam et al., unpublished; Santacruz-García et al., 2019), while species in another study increased their combustibility (heat of combustion) with an associated increase in shoot dry matter content (Melnik et al., 2022). Digestibility of dry matter and nitrogen of foliage (fiber and protein) of Andean forest species were positively correlated with time to ignition, and negatively correlated with maximum temperature and flame duration during most of the growing season except late spring, showing that species with less digestible leaves had high dry matter content and were highly flammable, and that digestibility (and flammability) changed throughout the year (Gowda et al., 2022). In other studies, leaf moisture content was negatively related with high ignition score (low time to ignition), and high sustainability (duration of combustion) (Blackhall et al., 2012; Essaghi et al., 2017; Güney et al., 2022; Pellizzaro et al., 2007). In wildland-urban French Mediterranean, moisture content increased in cold months, but flammability remained high due to an increase in volatile organic compounds (VOCs) at the same time (Ganteaume & Romero, 2019), showing that the interplay between different traits and flammability can be complex, VOCs were positively correlated with seasonal flammability in *Rosmarinus officinalis* (Pausas et al., 2015). These findings suggest that traits such as dry matter content, leaf moisture content and leaf chemistry are associated with seasonal changes in flammability; however, leaf chemical traits can be difficult to measure due to high processing costs.

There are some other ecophysiological and morphological traits that change seasonally and which are linked with flammability, and thus could cause seasonal changes in flammability. Given that small leaves and specific leaf area are associated with a short time to ignition (high ignition score), but with sustainability (Blackhall et al., 2012; Bowman et al., 2014; Calitz et al., 2015), changes in leaf size could lead to seasonal changes in flammability. Furthermore, we also expect leaf water potential to influence flammability. Midday stem water potential is associated with live fuel moisture content, plants that tolerate dehydration may have hydraulic adjustments during water-limited periods (Jolly & Johnson, 2018; Nolan et al., et al., 2020b; Pivovaroff et al., 2019; Scarff et al., 2021). An alternative strategy is reduced stomatal conductance to save water but when stomata are closed, evaporative cooling declines, potentially exposing a plant to heat damage (Brodribb & Holbrook, 2003; Peñuelas et al., 2004). Leaf relative water content is an informative value as an integrative measure of plant water status and drought vulnerability at a given point in time (Brodersen et al., 2010; Sapes et al., 2019; Sevanto et al., 2014). Relationships between some of these traits and flammability measures have not been explored under changing environmental conditions. Hence, it would be useful to examine which physiological and morphological traits are related to seasonal changes in flammability across species.

There are limitations when comparing flammability fluctuation across seasons. To properly assess the effect of seasons on plant flammability it is necessary to conduct sampling across multiple years so that replicates are obtained for each season (Jaureguiberry et al., 2011). However, many studies of seasonal changes in plant flammability have only assessed changes during one year (Gowda et al., 2022; Santacruz-García et al., 2019; Essaghi et al., 2017), meaning that there is no replication across seasons. Research which measures flammability throughout only one year is better expressed as examining changes in flammability across different sampling times, rather than seasons since values from a single season may not be representative of that season in the long-term. Due to logistical issues (sampling several hard-to-measure physiological traits and a covid pandemic, this chapter examined changes in flammability in plants at four different sampling times throughout one year. Despite this limitation, the dataset did capture sufficient variation in both traits and flammability to allow robust examination of the research questions.

This chapter aims to:

1) To assess if shoot flammability changes within species across different times of the year;
2) To determine which physiological and morphological traits are correlated with shoot flammability across species and any changes throughout the year.

3.2 Materials and Methods

3.2.1 Study area and sample collection

The study was conducted in Hinewai Reserve (172° 08' 47.1" E ; 41° 25' 38.2" S) near Akaroa, in the south east of Bank Peninsula New Zealand. Hinewai Reserve is a mix of old-growth rainforest, regenerating rainforest and exotic shrubland situated on land formed by the Akaroa Volcano which erupted basaltic lavas between 9 and 8 million years ago (Wilson, 1994). The climate of Hinewai has cool, wet winters and warm, dry summers (Figure 3.1). The study was conducted on 10 species of common woody plants growing in this community. For each species, replicate samples were collected from eight different plants, on the following occasions: autumn (April, 2019), winter (July, 2019), spring (October, 2019) and summer (February, 2020). Individuals were tagged and samples collected from the same plant throughout the year. While this study aimed to look at seasonal differences in flammability, there was no replication across seasons (i.e. sampling took place for one year), so from here on ‘sampling time’ is used instead of ‘season’.

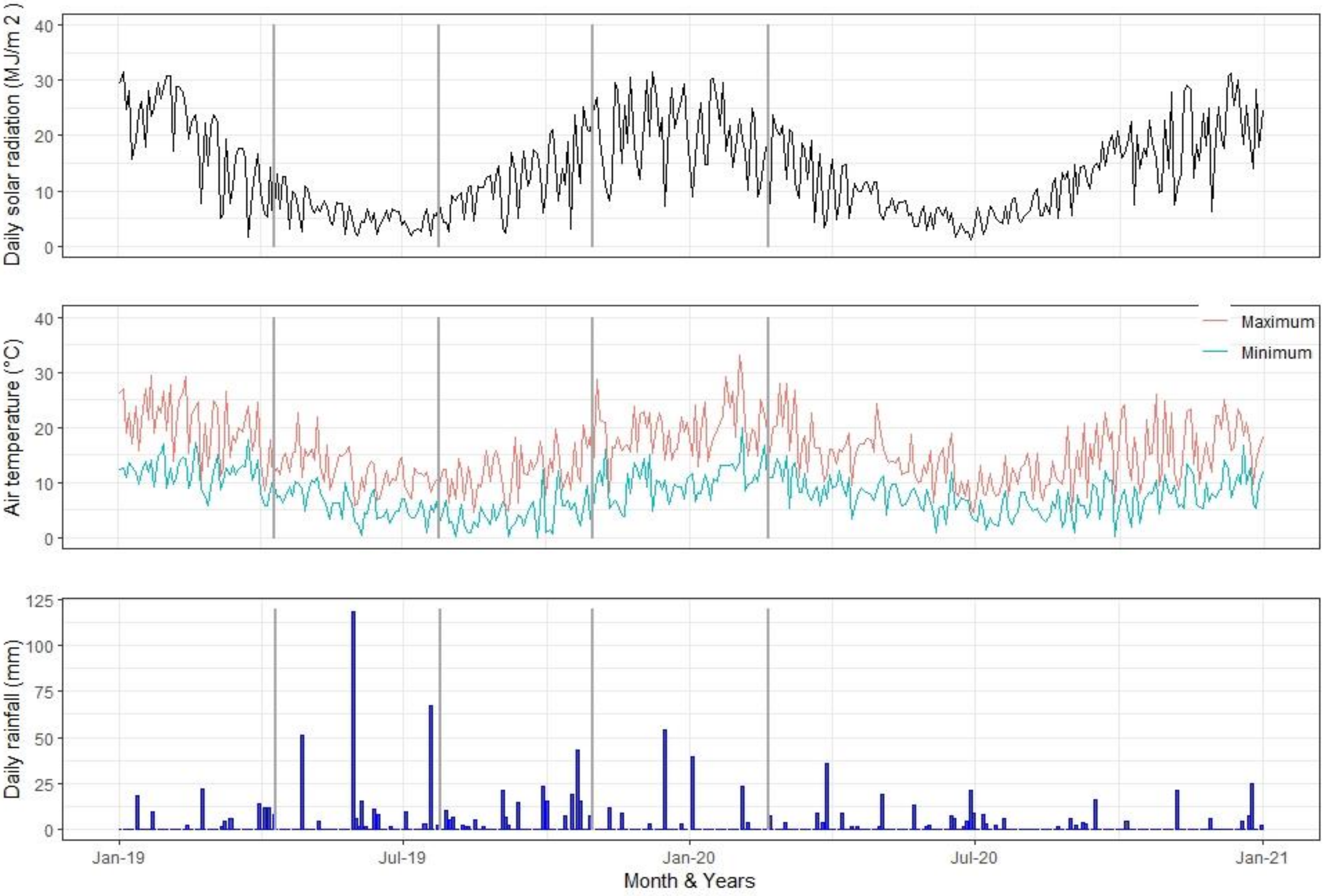

Figure 3.1 Daily rainfall, temperature, solar radiation during 2019/20 in Hinewai Reserve (NIWA, 2021). Black lines indicates sampling times (April, 2019 July, October and February,2020) respectively.

3.2.2 Sampling and measurements of traits

To measure physiological and morphological traits at the leaf scale, a terminal shoot was cut from the part of canopy exposed to direct sunlight at the time of sampling (between 8 am to 4 pm) from eight individual plants four times throughout the year (April, 2019 – Feb, 2020). Stomatal conductance (gs) was measured on three leaves of each shoot using a portable porometer (Decagon SC-1) at the site of each individual plant, immediately after the shoot was cut. For small leaves, two or more leaves of cutting shoots were placed together in the cuvette for the readings. Direct measurements of *gs* on shoots attached to live plants were not possible because of the different heights of each woody species (foliage of some trees was inaccessible from the ground). As an index of maximum water stress (Ackerly, 2004), midday water potentials were measured at each sampling time on three terminal shoots from each of three individual plants of each species. Water potential was measured with a scholander type pressure chamber (Scholander, et al.,1965 PMS, Corvallis, Oregon, USA). To avoid trait difference due to both shade and age, young fully expanded sun leaves were collected as per methods recommended by Reich et al., (1999) and Cornelissen et al., (2003). Precautions were taken to minimize water loss from excised shoots by immediately sealing samples in plastic bags prior to actual measurements of water potential in the field at a central location.

Additional samples were collected to measure other morphological and physiological traits in the laboratory. Shoots were immediately placed in opaque, double-plastic bags, kept cool and moist to avoid turgidity fluctuations (Read et al., 2005), then placed in a covered trailer which was cooled with ice to transport 1.30 h to the laboratory at Lincoln University. Samples were stored at 4-5°C to maintain hydration (Garnier et al., 2001). All trait measurements and flammability testing were performed within four days after the samples were collected.

We measured leaf thickness (LT), leaf moisture content (LMC) (Equation 3.1), leaf dry matter content (LDMC) (Equation 3.2), specific leaf area (SLA) and leaf relative water content (LRWC) (Equation 3.3) following by methods of Perez-Harguindeguy et al. (2013). Three leaves were immediately weighed to obtain fresh mass, and then leaf thickness (mm) was measured with callipers up to four decimal places, and leaf area (LA) values (cm^2) were obtained from digital images through image processing software ImageJ 1.50i (National Institute of Health, USA). For leaves with a needle shape, leaf area was calculated as $2 \times length \times width$ and thickness by $diameter \times \pi/4$ (Pérez-Harguindeguy et al. 2013).

Leaf moisture content, LMC =100 × [(M_f -- M_d)/M_d] ………………………..………………3.1
where, M_f is the fresh mass, and M_d is the dry mass after drying at 65° C until constant weight in the oven.

The leaves were then rehydrated for 24 hours in a cool dark place to obtain water-saturated mass in deionized water before being placed in a drying oven at 65°C until constant mass was reached. These parameters indicated water content of leaves under field conditions in relation to leaf dry mass.

The leaf dry matter content, LDMC (mg g^{-1}) = M_d/M_t ……………………………............. 3.2
where, M_d is the dry mass, M_t is the water-saturated mass after rehydrating of leaves in denoised water for 24 hours, thus LDMC is the proportion of the dry matter content without water related to the mass of the leaf with maximum water content.

Leaf relative water content, LRWC (%) = 100 × (M_f -- M_d)/(M_t -- M_d) ……………………… 3.3
It is the proportion of leaf water content related to maximum water content.

Bulk density, BD (Kg/ cm^3) = dry biomass/(length × width × height) ……………………….. 3.4
Dry biomass per sample was calculated from pre-burn weight of subsample moisture content as a calibration factor to convert fresh sample biomass to its approximate dry biomass (Ganteaume et al. 2011; Scarff and Westoby, 2006).

Table 3.1 Abbreviations of measured traits with units

Abbreviation	Trait	Units
Ignition score	ISC	
Maximum temperature	MT	°C
Burning biomass	BB	%
Burnt time	BT	s
Midday stem water potential	Ψ_{stem}	MPa
Leaf relative water content	LRWC	%
Stomatal conductance	gs	mmolm^{2}s^{-1}
Leaf area	LA	cm^2
Leaf thickness	LT	mm
Specific leaf area	SLA	mm^{2}gm^{-1}
Bulk density	BD	Kgcm^{-3}
Leaf dry matter content	LDMC	mg g^{-1}
Leaf moisture content	LMC	%

3.2.3 Flammability measurements

Shoot flammability was measured for each species following the methods described by Jaureguiberry et al. (2011) and Wyse et al. (2016), using the same device as Wyse et al. (2016; Figure 4.1). In this study, samples were air-dried at room temperature for 24 h on the bench prior to burning according to the protocol of Wyse et al. (2016; 2017) for measuring shoot flammability. As per Wyse et al. (2016) samples were preheated for 2 minutes on the burner at 150°C, before a blowtorch was turned on for 10 s. During burning, ignitibility was recorded as the time to ignition (between 0 and 10 s), which was then converted to an ignition score by subtracting the time to ignition from 10; for example, a sample which took 1 s (i.e rapid ignition) to ignite had an ignition score of 9 (Padullés Cubino et al., 2018). Samples that did not ignite were given a value of zero for ignition score. The total time (s) that a sample experienced flaming combustion was measured with a stop watch to represent sustainability, while the maximum temperature (°C) recorded during burning was measured by infrared laser thermometer (Fluke Corp., Everett, WA, USA) to represent combustibility. Samples that did not ignite were given a value of 150°C, representing grill temperature (Padullés Cubino et al., 2018; Wyse et al., 2017). Sustainability (s) was measured as the period of time that a sample exhibited flaming combustion after the blow torch was turned off. Consumability (%) was measured as the percentage of burnt biomass, assessed by visual observation by at least two observers.

3.2.4 Data analysis

3.2.4.1 Variations in shoot flammability among species and sampling times

Two-way repeated measures analysis of variance (ANOVA) of mixed models with Kenward-Rojer's approximated degrees of freedom (DF) were performed to test the effects of sampling time and species on flammability, morphological and physiological traits. The mixed effect models were constructed by putting an interaction term of species and sampling time as fixed effect. In this study, eight individual plants of each species were repeatedly measured over four different sampling times and those samples were considered as replicates. Replicates were included as a random term. The model for repeated measure ANOVAs were constructed through the ‘lmer’ function in the ‘lmerTest’ package (Kuznetsova et al., 2017). Variables were not transformed as they were found to meet the assumptions of ANOVA. To examine how flammability traits changed across sampling times, one-way analysis of variance (ANOVAs) of linear model were performed for each species. Post-hoc comparisons between the different sampling times were carried out using Tukey’s least significance difference (LSD). Post hoc tests were done by using the ‘emmeans’ and ‘cld’ functions from the ‘emmeans’ package (Lenth, 2021).

3.3.4.2 Relationships between physiological, morphological and flammability traits

We used principal component analysis PCA to examine relationships between all four flammability traits of each species, and to determine if flammability could be reduced to a single index in this dataset (e.g. PC1 or PC2, as per Wyse et al. 2016; Padulles Cubino et al., 2018). To explore associations among morphological, physiological and flammability traits at the species level, we performed a PCA with all flammability traits (ignition score, maximum temperature, burning biomass, and burning time), physiological traits (midday stem water potential, stomatal conductance, relative water content), morphological traits (leaf moisture content, dry matter content, leaf area, specific leaf area and bulk density) using the species means for each trait for each sampling period. PCAs were implemented using the “PCA” function from the “FactoMiner” $_{R}$ package (v 1.28**)** (Lê et al., 2008) on centered and standardized data. Furthermore, we calculated

Pearson correlation coefficients to evaluate whether (PC1 and PC2) from the species flammability index and measured flammability traits were associated with plant physiological and morphological traits at the species level; these correlations were performed using mean trait values for each species and sampling time for all physiological and morphological traits. Mean trait values of physiological and morphological traits were calculated per season for each species from three individual plants, mean flammability traits were obtained from eight individuals per species for each season.

All statistical analyses were performed in R statistical environment for windows (v.4.1.1) through RStudio integrated development environment (v.1.4.1714) (R CoreTeam, 2021).

3.3 Results

3.3.1 Variations in shoot flammability among species and sampling times

There were significant effects of species and sampling time for all four flammability variables (Table 3.2 and Figure 3.2–3.5). However, for all four flammability variables there were also significant interactions between species and sampling time (Table 3.2), indicating that species flammability was differentially affected by sampling time. For instance, three species (*Pseudopanax crassifolius*, *P. colensoi* and *Griselinia littoralis*) did not vary in their flammability across sampling times for any of the flammability variables (Figs 3.2-3.5); they retained low flammability scores throughout the year. All other species showed significant variation in flammability across sampling times, except for *Ulex europeaus* for ignition score and burning time, and *Cytisus scoparius, Kunzea robusta* and *Pittosporum eugenioides* for maximum temperature and burn time. *Podocarpus cunninghamii* and *Pseudowintera colorata* showed variation for ignition score, maximum temperature and burnt biomass. Only *Melicytus ramiflorus* had significant differences in flammability across sampling times for all four flammability variables. *Kunzea* and *Ulex* had consistently high (though sometimes significantly different) flammability across sampling times, while *G. littoralis, P. crassifolius, and P. colensoi* had consistently low flammability. Species such as *M. ramiflorus, C. scoparius, P. eugenioides, P. colorata* and *P. cunninghamii* varied significantly in flammability throughout the year.

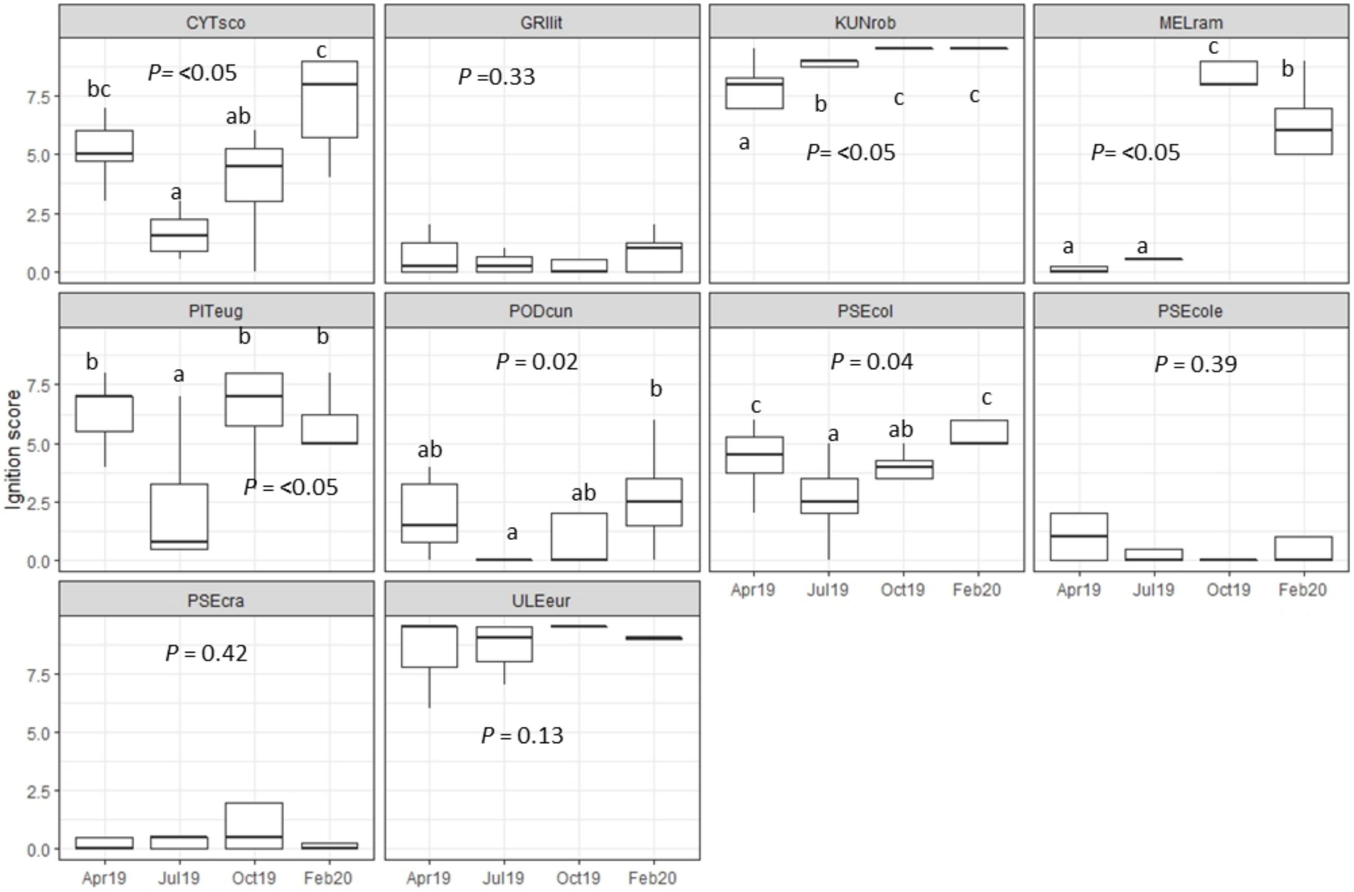

Figure 3.2 Mean ignition score of each species across sampling times (April 2019, July 2019, October 2019 and February 2020). Whisker denotes standard error. Different superscript letters indicate significant differences at $P < 0.05$ in post hoc Tukey test, (n=8 per species). Plant names abbreviations for selected species shown are as follows: CYTsco(*Cytisus scoparius*),GRIlit(*Griselina littoralis*), KUNrob(*Kunzea robusta*), MELram(*Melicytus ramiflorus*), PITeug(*Pittosporum eugenioides)*, PODcun(*Podocarpus cunninghamii*), PSEcol(*Pseudowintera colorata*),PSEcole(*Pseudopanax colensoi*), PSEcra(*Pseudopanax crassifolius)*,ULEeur(*Ulex europeaus*).

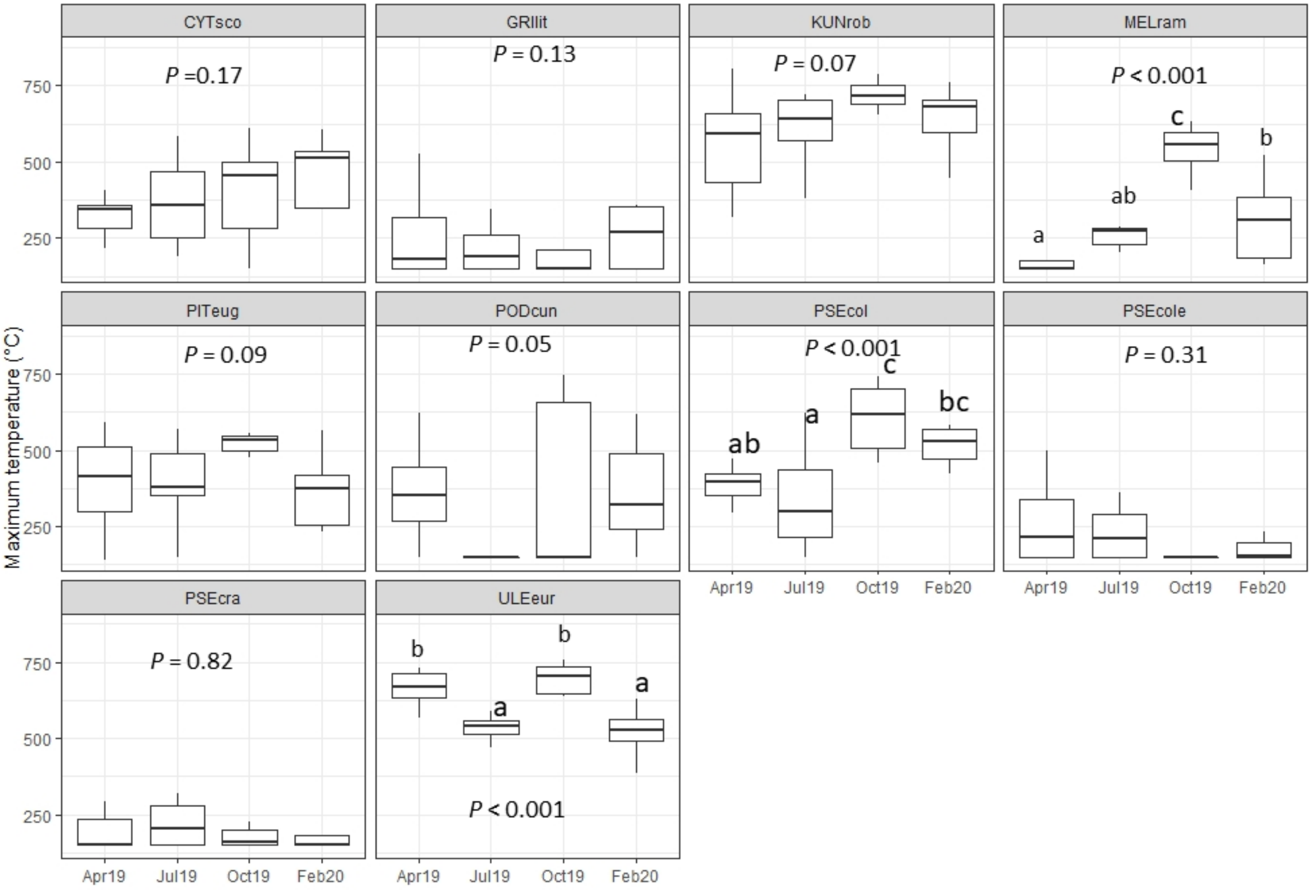

Figure 3.3 Mean maximum temperature (°C) of each species across sampling time (April 2019, July 2019, October 2019 and February 2020). Whisker denotes standard error. Different superscript letters indicate significant differences at $P < 0.05$ in post hoc Tukey test, (n=8 per species). Plant names abbreviations for selected species shown are as follows: CYTsco(*Cytisus scoparius*),GRIlit(*Griselina littoralis*), KUNrob(*Kunzea robusta*), MELram(*Melicytus ramiflorus*), PITeug(*Pittosporum eugenioides)*, PODcun(*Podocarpus cunninghamii*), PSEcol(*Pseudowintera colorata*),PSEcole(*Pseudopanax colensoi*), PSEcra(*Pseudopanax crassifolius)*,ULEeur(*Ulex europeaus*).

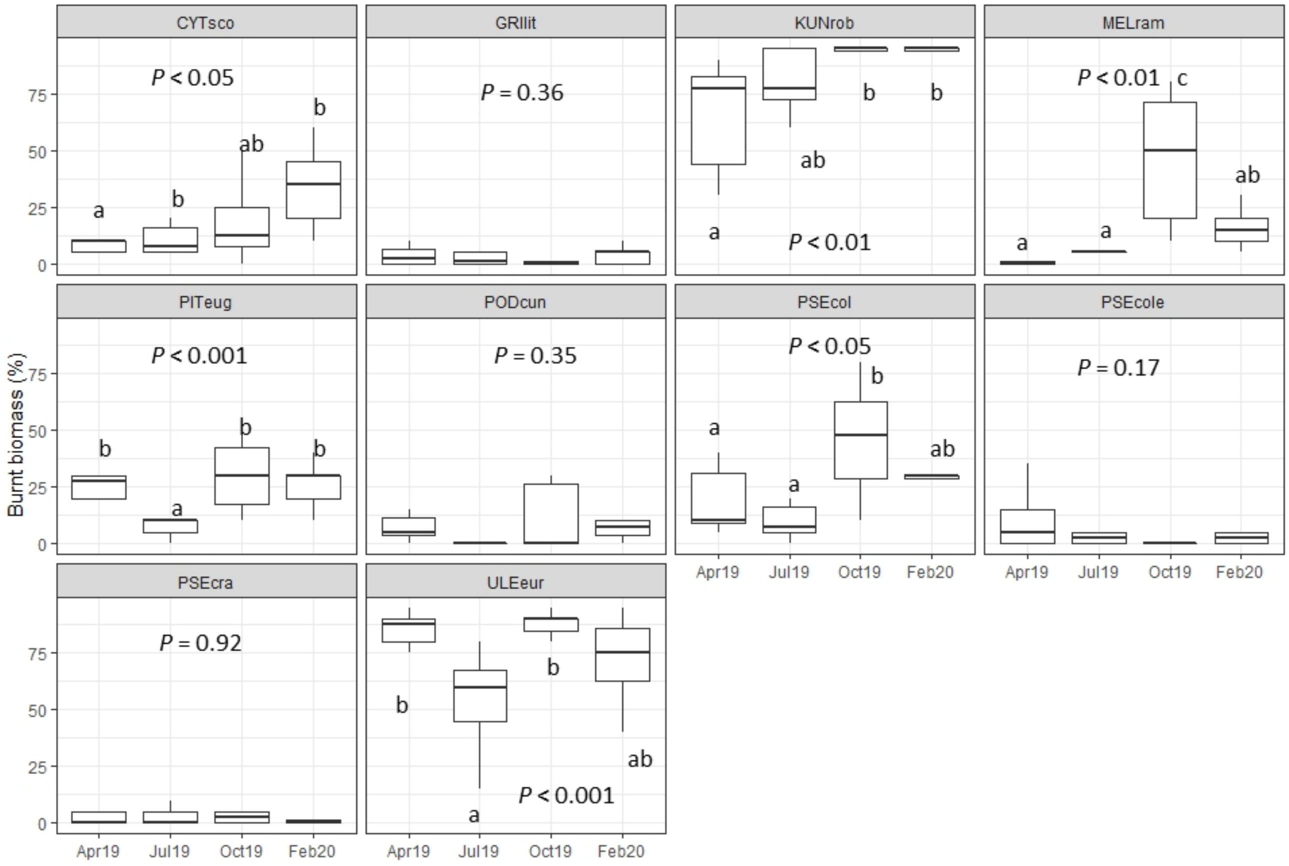

Figure 3.4 Mean burnt biomass (%) of each species across sampling times (April 2019, July 2019, October 2019 and February 2020) within community. Whisker denotes standard error. Different superscript letters indicate significant differences (P <0.05) in post hoc Tukey test, (n=8). Plant names abbreviations for selected species shown are as follows: CYTsco(*Cytisus scoparius*),GRIlit(*Griselina littoralis*), KUNrob(*Kunzea robusta*), MELram(*Melicytus ramiflorus*), PITeug(*Pittosporum eugenioides)*, PODcun(*Podocarpus cunninghamii*), PSEcol(*Pseudowintera colorata*),PSEcole(*Pseudopanax colensoi*), PSEcra(*Pseudopanax crassifolius)*,ULEeur(*Ulex europeaus*).

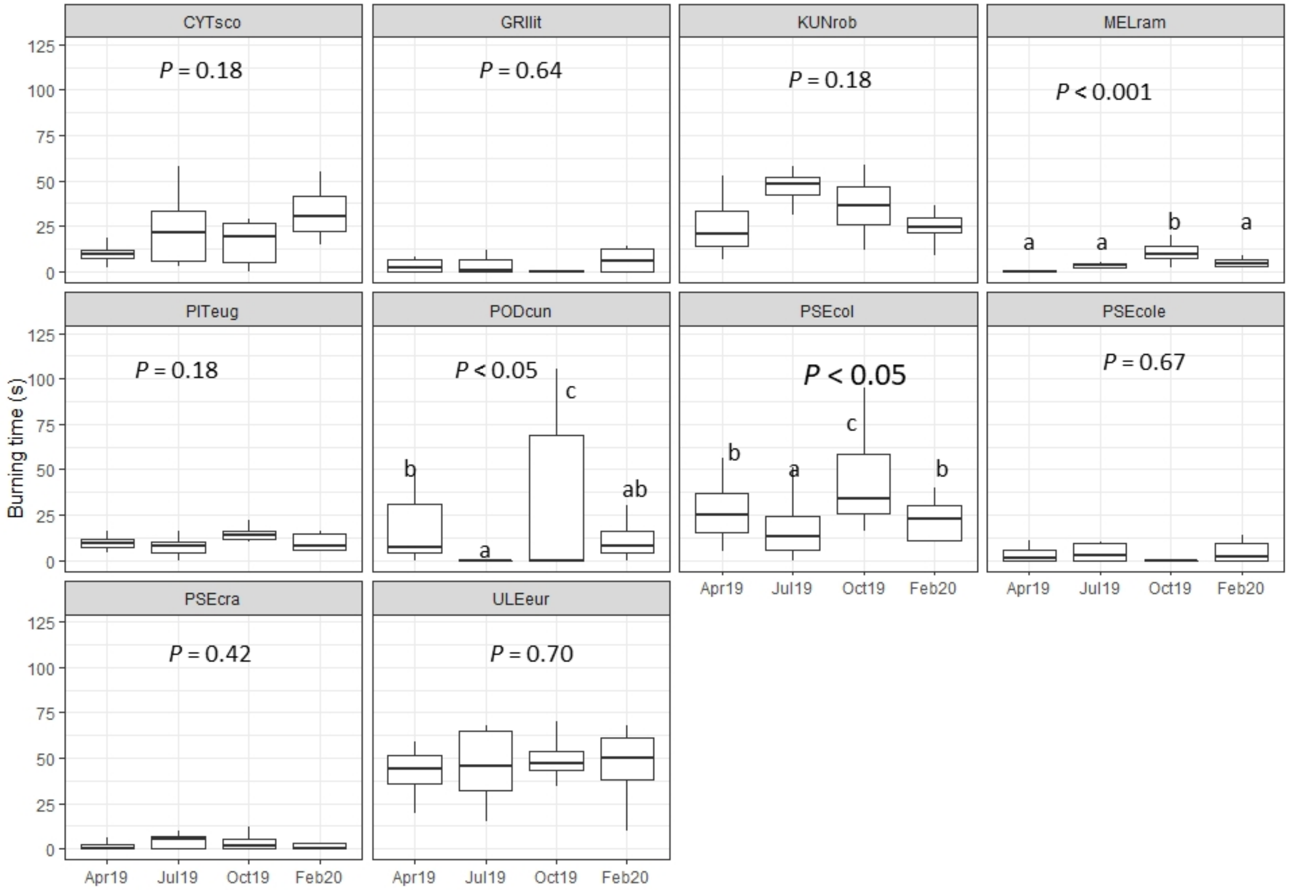

Figure 3.5 Mean burning time (s) of each species across sampling times (April 2019, July 2019, October 2019 and February 2020). Whisker denotes standard error. Different superscript letters indicate significant differences ($P < 0.05$) in post hoc Tukey test, (n=8). Plant names abbreviations for selected species shown are as follows: CYTsco(*Cytisus scoparius*),GRIlit(*Griselina littoralis*), KUNrob(*Kunzea robusta*), MELram(*Melicytus ramiflorus*), PITeug(*Pittosporum eugenioides)*,PODcun(*Podocarpus cunninghamii*), PSEcol(*Pseudowintera colorata*), PSEcole(*Pseudopanax colensoi*), PSEcra(*Pseudopanax crassifolius)*,ULEeur (*Ulex europeaus*).

3.3.2 Variations in functional traits across species and sampling times

There were significant effects of species and sampling time for most functional traits (Table 3.2). For most physiological and morphological variables (leaf moisture content, leaf area, specific leaf area, leaf thickness, bulk density, stem water potential and stomatal conductance) there were also significant interactions between species and sampling time (Table 3.2), indicating that the effects of sampling time on flammability vary among species. There was no significant interaction between species and sampling time for leaf relative water content (Table 3.2). There was no significant effect of sampling time on leaf dry matter content while there was significant interaction between species and sampling time. Range of traits across sampling times (mean ± standard error) is listed in table B3.3.

Table 3.2 Among species and sampling time variations in flammability, physiological and morphological traits for 10 species under this study, indicated by two-way repeated measures ANOVA (analysis of variance) of mixed model results with Kenward-Rojer approximation degrees of freedom (DF)

Variables	Species	Sampling time	Sampling time × Species
Ignition score	$F_{9, 68}$ =86.73, *P*<0.001	$F_{3, 205}$ =50.53 *P* <0.001	$F_{27, 205}$ =9.47, *P* <0.001
Maximum temperature (°C)	$F_{9, 67}$ =29.37, *P*<0.001	$F_{3, 204}$ =11.66, *P* <0.001	$F_{27, 205}$=5.39, *P* <0.001
Burnt biomass (%)	$F_{9, 68}$ =106.71, *P*<0.001	$F_{3, 205}$ =33.89, *P* <0.001	$F_{27, 21}$ =7.25, *P* <0.001
Burnt time (s)	$F_{9, 274}$ =18.82, *P*<0.001	$F_{3, 274}$ =6.82, *P* <0.01	$F_{3, 274}$ =2.61, *P* <0.001
Bulk density (kg/m^3)	$F_{9, 69}$ =9.1, *P* <0.001	$F_{3, 207}$=2.19, *P* =0.09	$F_{9, 207}$ =9.83, *P* <0.001
Leaf moisture content (%)	$F_{9, 23}$=21.96, *P* <0.001	$F_{3, 58}$ =4.14, *P* = 0.01	$F_{27, 52}$ =3.28, *P* < 0.001
Relative water content (%)	$F_{9, 20}$=1.5, *P* =0.23	$F_{3, 60}$ =1.42, *P*=0.24	$F_{27, 80}$ =0.44, *P* =0.92
Leaf thickness (mm)	$F_{9, 80}$=106.46, *P* <0.01	$F_{3, 80}$ =6.09, *P* <0.001	$F_{27, 28}$ =9.61, *P* <0.01
Leaf dry matter content (mg gm^{-1})	$F_{9, 28}$=14.1, *P* <0.001	$F_{3, 62}$ =1.99, *P* = 0.12	$F_{27, 61}$ =2.25, *P* =0.004
Specific leaf area (cm^{2}gm^{-1})	$F_{9, 80}$ =87.56, *P* <0.01	$F_{3, 57}$ =8.94, *P* <0.01	$F_{27, 80}$ =8.61, *P* <0.01
Leaf area (cm^2)	$F_{9, 80}$ =210.82, *P* <0.001	$F_{3, 80}$ =24.94, *P* <0.001	$F_{27, 80}$ =3.61, *P* <0.001
Stem water potential (MPa)	$F_{9, 80}$ =15.69, *P* <0.001	$F_{3, 80}$ =37.94, *P* <0.001	$F_{27, 80}$ =4.45, *P* < 0.001
Stomatal conductance (mmolm^{2}s^{-1})	$F_{9, 80}$=7.61, *P* <0.001	$F_{3, 80}$ =3.12, *P* =0.03	$F_{27, 80}$= 3.70, *P* <0.001

3.3.3 Relationships between flammability variables and deriving a flammability index

All flammability traits were strongly positively correlated with each other ($0.93 \geq r \geq 0.85$; $P < 0.001$). Among all flammability traits, three (ignition score, maximum temperature and % burnt biomass) were strongly positively correlated with species flammability score (PC1) ($0.93 \geq r \geq 0.87$; $P < 0.001$) but not with (PC2) (Figure 3.6). The first two axes together explained 95.94% of the variation, with the first axis contributing much of (89.2 %; Figure 3.7 (a); Table B3.2), suggesting that the four shoot flammability variables measured here can be represented as a single dimension or index (the PC1 scores). Higher PC1 scores reflect higher flammability (Figure 3.7a).

3.3.4 Relationships between flammability variables and physiological and morphological traits

Several morphological and physiological traits were significantly correlated with flammability variables (Figure 3.6). Ignition score, maximum temperature, burnt biomass and the overall flammability index (PC1) all had consistent relationships with functional traits. These flammability variables had a higher correlation coefficient with Ψ_{stem} (negative relationship), and LRWC (negative), followed by LA (negative), LT (negative, but not for PC1) and LDMC (positive) compared to other traits, suggesting that highly flammable species had small, thin leaves with low LRWC, low Ψ_{stem} and high LDMC. The correlation coefficient for burn time was highest for LA (negative), then Ψ_{stem} (negative), LRWC (negative), LMC (negative) and LDMC (positive), but not for LT.

These relationships between flammability variables and functional traits were confirmed by a PCA on all flammability, physiological and morphological traits, with LRWC and LA being negatively related, and LDMC positively related to the flammability variables (Figure 3.7b). The first and second axes of this PCA collectively accounted for 63.8 % of trait variance (Figure 3.7). All flammability traits (ISC (loading=0.87), MT (0.93), BB (0.90) and BT (0.86), gs (0.03) and LDMC (0.64) were positively loaded with PC1 of the PCA with all flammability, physiological and morphological traits, while LMC (-0.68), LA (-0.76), LRWC (-0.68), SLA (-0.23), LT (-0.34), BD (-0.06), Ψ_{stem} (-0.64) were also negatively loaded (Fig. 3.6b). All flammability variables (except BT) were positively loaded on PC2 (Figure 3.6b) (ISC=0.33, MT=0.19, BB=0.26), as were

LMC (0.49), Ψ_{stem} (-0.22), gs (0.15), LA (0.35), and SLA (0.80), LT (-0.56), BD (-0.69), and LRWC (-0.10), were all negatively loaded on PC2 (Figure 3.7b).

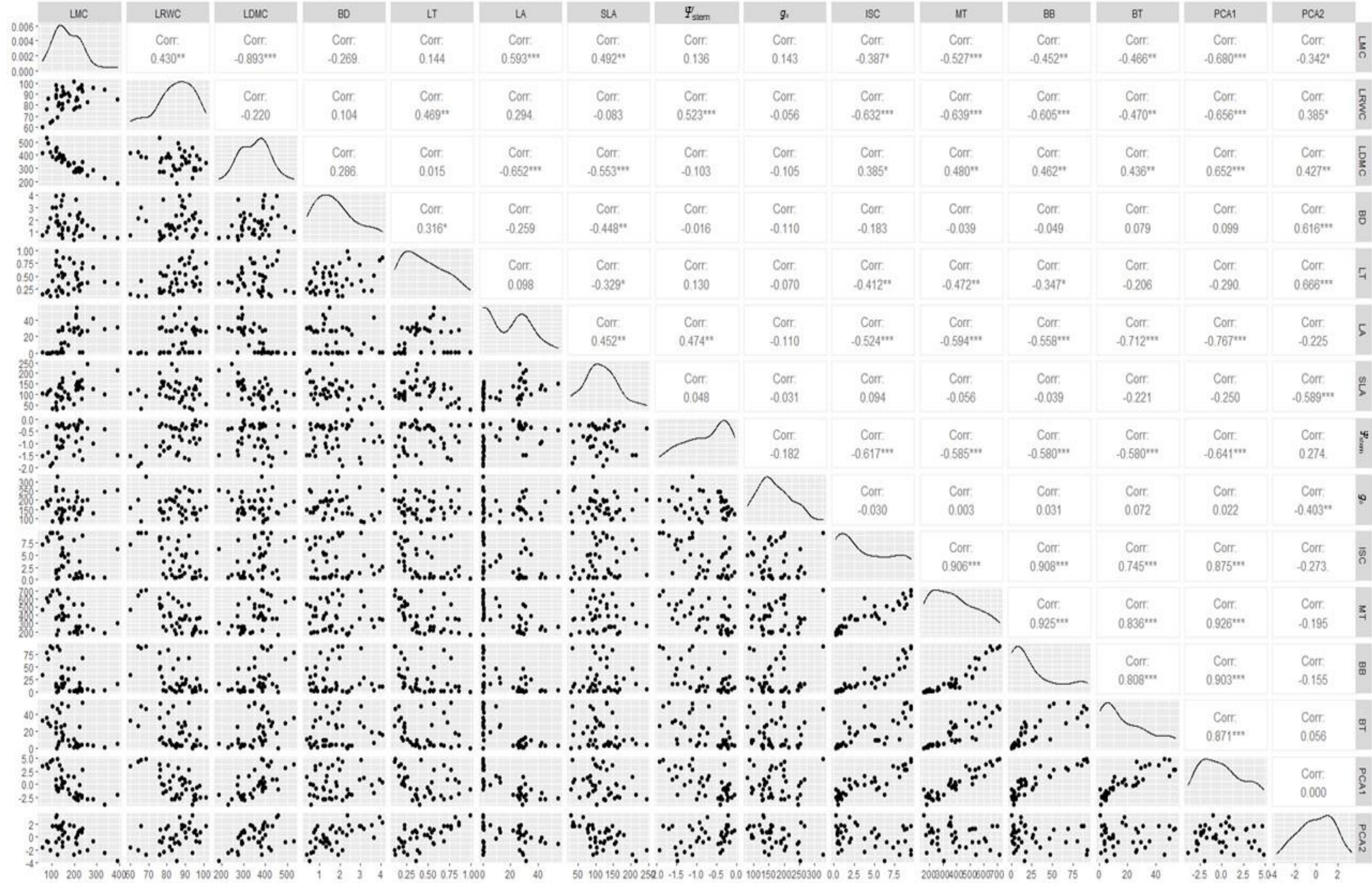

Figure 3.6 Pearson correlation coefficients (r) between physiological and morphological traits at shoot and leaf level and flammability traits. “***”,“**”,“*” denotes significant at *P* <0.001, *P* <0.01, and *P* <0.05 respectively. Trait abbreviations as in Table 3.1

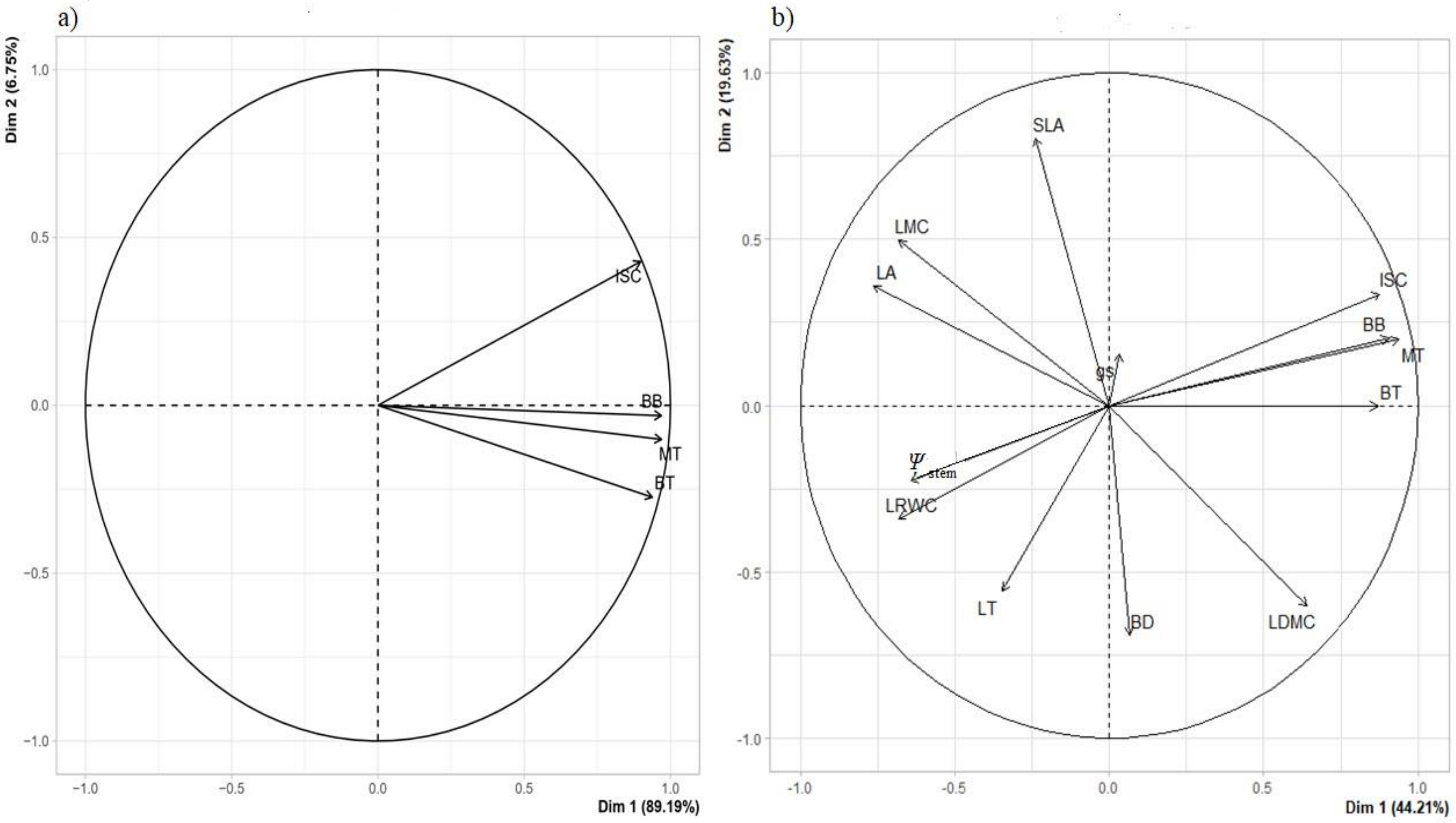

Figure 3.7 Principal components analysis (PCA) of the four measured flammability (Species Flammability Traits PCA) for the 10 tested species. Arrows indicate the individual scores for each species based on measurements of individuals (a), Principal component analysis (PCA) with the mean values of each species flammability traits and functional traits of 10 rain forest tree species (ten species sampled along four sampling times) (b). Species flammability scores were not included in the PCA analysis along the first two PCA axes with the percentage of explained variation given species flammability scores, the higher the score the more flammable species is. Trait abbreviations as in Table 3.1

3.4 Discussion

We sampled the flammability of 10 woody species four times throughout a year and found that some, but not all, species varied in their flammability. Three species with particularly low flammability did not differ in their flammability at all across sampling times, while for other species there were differences for certain sampling times and flammability variables. Inconsistent patterns in seasonal flammability across species have been reported in other ecosystems (Gowda et al., 2022; Santacruz-García et al., 2019; Essaghi et al., 2007). Flammability was correlated with several morphological traits, including LMC, LDMC, LA, and LT, suggesting that these traits are driving flammability variability throughout the year in this system, as has been noted in some studies in other ecosystems (Güney et al., 2022; Santacruz-García et al., 2019, Blackhall et al., 2012). However, we also found that water relation traits, such as Ψ_{stem} and LRWC, were associated with flammability in our temperate rainforest and shrubland species.

3.4.1 Variation of flammability traits and species flammability throughout the year

The response of flammability to different sampling times throughout the year was highly variable across the 10 species we measured. This ranged from three species that exhibited no change in any flammability variable across any sampling time, to *Melicytus ramiflorus*, which had significant variation across sampling times for each flammability trait. The other six species all showed some changes in flammability across sampling time for at least some flammability variables. Studies from other ecosystems, including Andean temperate forests and shrublands in Argentina Gowda et al., (2022), urban and forest areas of Mediterranean Turkey Güney et al., (2022), the wildland urban-interface of the French Mediterranean Ganteaume & Romero, (2019), and Moroccan forests Essaghi et al., (2017), have also found inconsistent responses across species, suggesting that such variability in seasonal response to flammability may be a widespread phenomenon.

The three species for which flammability remained constant throughout the year (*Pseudopanax crassifolius*, *P. colensoi* and *Griselinia littoralis*) were all species with large leaves, low LDMC, high LMC and very low flammability. The two most flammable species, *Ulex europeaus* and *Kunzea robusta*, generally had very high flammability across all sampling periods, although this did vary significantly within each species for some flammability traits. Many of the greatest changes in flammability throughout the year seemed to come from species with moderate flammability, or those like *Melicytus ramiflorus*, which went from very low at certain times of the year (such as autumn and winter) to high (especially in spring).

The time of the year with the highest or lowest flammability also varied according to species. The only species with a consistent pattern for all flammability traits was *Melicytus ramiflorus*, for which flammability was always highest in spring (Figs 3.2-3.5). *Cytisus scoparius* showed highest values in summer for all flammability traits except burning time. *Ulex europeaus* had the highest flammability in all variables except burning time in autumn, spring and summer. *Kunzea robusta* and *Podocarpus cunninghamii* did not change throughout the year for maximum temperature. Such variable results across species in peak flammability throughout the year has been reported in other studies (Melnik et al., 2022; Ganteaume & Romero, 2019; Essaghi et al., 2017).

3.4.2 Relationship between physiological, morphological and flammability traits

Two water relations traits, midday stem water potential and LRWC, were both found to be negatively correlated with seasonal changes of flammability in our study; as Ψ_{stem} and LRWC increased all flammability variables decreased (Chapter 2). Tissue RWC is a useful integrator of plant water status (Brodersen et al., 2010; Sapes et al., 2019; Sevanto et al., 2014), and low LRWC was identified a key driver of fuel moisture content, one of the four main 'switches' of fire: that of fuel being dry enough to burn (see Fig. 1 in Nolan et al. 2020b). However, despite the likely importance of LRWC as a determinant of fire behavior, to our knowledge, the empirical link between LRWC and plant flammability has rarely been tested, though Peacock (1980) found that LRWC was a useful predictor for seasonal flammability in three Texan shrub species. Ψ_{leaf} is likely to be correlated with live fuel moisture, and thus linked to plant flammability (Nolan et al., 2020b; Pivovaroff et al.,2019; Nolan et al., 2018; unpublihed), but there is also very limited empirical testing of this. Contrary to our findings, neither Owens et al. (1998) nor Peacock (1980) found a relationship between flammability and Ψ_{leaf}. However, the strong relationship between flammability and both LRWC and Ψ_{leaf} in our study supports calls by Jolly and Johnson (2018) and Nolan et al. (2020b) to consider the role of ecophysiological variables in driving plant flammability. As measures of tissue water availability across species and sampling periods, our results indicate these are informative indicators of both plant water status, morphological traits and flammability.

Leaf moisture content (LMC) was negatively related with flammability variables. Leaf moisture content was significantly negatively correlated with some or all flammability variables in other studies (Gowda et al., 2022; Güney et al., 2022; Pellizzaro et al., 2007). Furthermore, as shown by the few studies that have examined seasonal changes in LMC and flammability, this relationship can be complex, and dependent on other traits, such as VOCs (Ganteaume & Romero, 2019). LMC is a measure of water in leaves relative to tissue density while LRWC is a measure of leave water content relative to the maximum amount of water that leaf can hold. From a biological perspective, LRWC indicates how full a plant's foliar water 'bucket' is relative to the potential full capacity of that water storage compartment. A clear relationship between the amount of water in leaves and the flammability of those leaves is reasonably intuitive as described by Nolan et al. (2020b).

Leaf thickness (LT) was negatively related with flammability traits, as has been observed in several other studies (Alam et al. 2020; Blackhall et al. 2019; Calitz et al. 2015, Montgomery 1971; Mason et al. 2016). One potential reason for LT being marginally associated with seasonal changes in species flammability relates to the capacity of thickness (or succulence) to fluctuate according to water storage (Stratton, 2000; Lamont and Lamont, 2000). Indeed, intraspecific variation in leaf thickness is used in crop science to infer changes in plant water status (Afzal et al., 2017; Búrquez, 1987; Seelig et al., 2012), with thicker leaves being associated with higher moisture content since leaf tissues expand when cells are turgid. This suggests the mechanism by which LT could drive seasonal changes in flammability.

Previous studies linking changes in leaf size (reported here as leaf area, LA) to seasonal changes in flammability have suggested that this relationship was mediated by disturbance; either fire or grazing resulted in smaller leaves, thus increasing flammability (Blackhall et al., 2012; Cui et al., 2020a). However, there is no frequent fire nor grazing in our study system, so why is LA negatively correlated with flammability in our species? Some studies have found leaf size to be negatively correlated with flammability in certain taxonomic groups (e.g. *Dracophyllum*, Cui et al., 2020a), but this relationship does not appear to be universal (Alam et al., 2020). In our study LA was correlated with other traits (positively with LMC and negatively with LDMC) which may have a more direct effect on flammability. Therefore, in our study it seems likely that LA is associated with flammability via these other traits, rather than changes in leaf size due to disturbance.

Leaf dry matter content (LDMC) was positively related with flammability variables as has been observed in other studies reporting seasonal flammability (Melnik et al., 2022; Gowda et al., 2022; Santacruz-García et al., 2019). Because LDMC is related to tissue density and water content; leaves with higher LDMC tend to have high dry mass per volume of the tissue and lower water content (Perez-Harguindeguy et al., 2013; Wilson et al., 1999; Garnier et al., 2001). In this study LDMC is related with flammability variables because sampling time had no differences on LDMC and might be due to the high flammable species were high dry matter content.

There was no relationship between flammability traits and stomatal conductance, one of our measures of plant water relations. There are two potential reasons for this. The first is that stomatal conductance is a variable that is highly responsive to light fluctuations and dynamic within individuals, potentially at hourly (or finer) scales (Vialet-Chabrand et al., 2013). Consequently, stomatal conductance likely changes more readily than flammability does, potentially explaining the lack of a clear relationship. Second, our analyses have attempted to examine broad patterns in trait-flammability relationships across a range of species, when those species likely have different water use strategies, ranging across the isohydric to anisohydric continuum (Klein, 2014; Tardieu & Simonneau, 1998). Consequently, by lumping these species together we are missing important nuances in the way they use and conserve water, though that is beyond the scope of this study.

3.5 Applications to wildfire

These findings could help fire managers in several ways. First, it provides additional data about possible seasonal changes in flammability in species that have been recommended for planting in green firebreaks. Two of the species tested here (*G. littoralis*, *P. crassifolius*) have been widely recommended to be planted in New Zealand as green firebreaks to help stop fire spread (Evans, 1983; Fogarty, 2001; Wyse et al., 2016). A third, *P. colensoi*, is closely related to another species widely recommended for green firebreaks (*P. arboreus*). Our results further support previous findings that these three species are low in flammability, but importantly also show that their flammability does not vary throughout the year. This suggests that *G. littoralis*, *P. crassifolius*, and *P. colensoi* will all likely help suppress wildfires across different seasons, confirming their suitability for planting in green firebreaks. However, *M. ramiflorus* has also been recommended for planting in green firebreaks (Evans1983; Fogarty 2001; Wyse et al. 2016). Our results show that *M. ramiflorus* had high flammability during the October (spring) sampling. While further research over multiple years is required to confirm if this species often has higher flammability in spring, these results do suggest that caution may be needed in planting this species in green firebreaks.

High flammability species such as *Kunzea robusta* and *Ulex europaeous* remained flammable throughout the year in our study and so have the potential to spread fire in many seasons. While other factors, such as weather (e.g. cooler temperatures, higher humidity, lower VPD) will likely determine how well a fire will burn and spread, our results provide a warning for fire managers that vegetation dominated by these species has the capacity to burn well even outside of fire season. These species are often dominant species of extensive tracts of vegetation (McAlpine et al., 2009; Perry et al., 2014; Sullivan et al., 2007), further requiring caution when managing fire in such landscapes. Indeed, the largest fire at Hinewai Reserve, the site of this study, occurred in winter (July) 2011, when a lightning strike hit vegetation, causing a fire which burnt through hundreds of hectares of gorse shrubland and gorse-dominated regenerating forest, albeit during an exceptionally dry winter (Wilson, 2013). Regardless, our results suggest that fire mangers need to be careful during prescribed burning activities near *Kunzea robusta* and *Ulex europaeous* dominated communities, even outside of the Nov-April fire season. The year-round high flammability of these species warrants greater caution for fire managers and landowners in these landscapes.

The variability in the flammability of other species, such as *Cytisus scoparius, Pittosporum eugenioides, Podocarpus cunninghamii* and *Pseudowintera colorata*, throughout the year also suggests (pending further seasonal study), that these species can also be flammable in a range of seasons. Again, this points to the need for added caution by fire managers.

Our results, and particularly the link between LRWC and flammability, show the potential for changes in vegetation flammability being monitored in real time via remote sensing. Current advances in remote sensing allow for the capture of seasonal dynamics of volumetric water content (VWC) to different drought responses (e.g. disturbance dynamics, canopy dehydration) (Chuvieco & Dimitrakopoulos, 2004; Desbois & Vidal, 1996; Dimitrakopoulos & Papaioannou, 2001; Konings et al., 2021). VWC at ecosystem scale is equivalent to LRWC. Such real time measurements of relative water content may allow fire managers to make real-time assessments of comparative flammability, thus enhancing predictions of fire risk across the landscape.

3.6 Conclusion

Plant flammability is an important trait that can change within species and individuals, including seasonally. Here we have demonstrated that flammability changes in some, but not all, of ten woody species sampled in regenerating forest in New Zealand. Among all, three species (*Pseudopanax crassifolius, P. colensoi* and *Griselinia littoralis*) did not vary in their flammability across sampling times for any of the flammability variables. Species such as *Malicytus ramiflorus, Cytisus scoparius, Pittosporum eugenioides, Pseudowintera colorata* and *Podocarpus cunninghamii* varied significantly in flammability throughout the year. Flammability variables were most positively correlated with Ψ_{stem} and LRWC. These physiological traits will help fire managers to select species for planting in green firebreaks that are more likely to be low in flammability year round, hence better ensuring that green firebreaks function to help stop fire spread throughout the year. Morphological traits, such as leaf moisture content, may also help fire managers predict plant changes in flammability throughout the year.

Chapter 4

Moisture content exhibits threshold relationships with shoot flammability variables, and threshold values were related to species' leaf dry matter content and leaf area.

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Abstract

1. The search for threshold relationships is important in flammability research. A threshold is where a critical value of some variable must be reached for another phenomenon to occur, for instance, the moisture content of fuel at which ignition and thereafter combustion, can happen.

2. We manipulated shoot moisture content of eight species of trees by oven-drying, air-drying or wetting up to assess whether moisture content thresholds existed in relation to shoot flammability in these species, if thresholds varied across species, and to identify relationships between these thresholds and morphological and physiological traits.

3. All eight species and all four shoot flammability variables (time to ignition, maximum temperature reached, burnt biomass, and burning time) exhibited threshold moisture contents and only two species–flammability variable combinations (out of 32) did not. Threshold moisture contents were found to be species specific, ranging from 116 –108% in *Pseudowintera colorata* to 258 – 211% in *Melicytus ramiflorus*.

4. Leaf dry matter content and leaf area were correlated with threshold moisture content, but leaf thickness, relative water content and minimum seasonal Ψ_{stem} were not. Species with low leaf dry matter content and large leaves, such as *Melicytus ramiflorus, Pseudoponax colensoi, Greselinia littoralis* and *P. crassifolius* had higher moisture thresholds than species with high leaf dry matter content and small leaves such as *Podocarpus cunninghamii, Kunzea robusta* and *Pseudowintera colorata.* The percentage of moisture thresholds reported in our study are higher than those recorded elsewhere from dry, fire-prone environments, perhaps due to the regenerating rainforest habitat of our study site.

5. These findings could help fire managers by highlighting key moisture content thresholds at which green firebreak species may switch from low to high flammability, for instance during drought. Critical moisture thresholds will also be helpful when planning prescribed burning treatments.

Keywords: Threshold moisture content, Species flammability, Wildfire, Drought

4.1 Introduction

The search for threshold relationships is important in flammability research (Newberry et al., 2020) because thresholds are key to whether a fire establishes or not. A threshold is where a critical value of some variable must be reached for another phenomenon to occur. In flammability research, such a threshold might be the moisture content of fuel at which ignition and thereafter combustion, can occur (Davies & Legg, 2011; Santana & Marrs, 2014). Flammability thresholds can occur at a variety of scales. At the landscape level, thresholds in vegetation structure and species composition can greatly influence fire behavior around savanna-forest transitions (Dantas et al., 2013; Hoffmann et al., 2012; Murphy & Bowman, 2012), with higher levels of tree cover suppressing fires (Archibald et al., 2009; Hoffmann et al., 2012), for instance, by causing shifts to lower flammability species of grass (Cardoso et al., 2018). At the scale of the whole plant or plant organ level, flammability thresholds can occur in relation to the water content of fine fuels (leaves, twigs) (Gill and Moore, 1996; Alessio et al., 2008b; De Lillis et al., 2009; Murray et al., 2013), or the proportion of dead biomass retained on the plant or organ (Dent et al., 2019; Santana et al., 2011). Finding flammability thresholds is important for many applications, including estimating the fuel moisture content (MC%) threshold at which ignition can occur and fire can spread, and forest fire management (Resco de dios, 2022).

Potentially one of the most important threshold relationships for plant flammability is with the moisture content of fuels. Live fuel moisture content is the water content of live foliage relative to dry mass. Forest fuels are complex in nature, and are a mixture of leaves, trunks, and branches. Therefore, to simplify measurements of MC% in live fuels, many methods sample foliage (Johansen, 1985). Leaves generally have a higher moisture content than woody organs (Chuvieco & Dimitrakopoulos, 2004), however, the moisture content of leaves is the most critical for fire ignition and propagation as leaves are often the first fuels to ignite (Belcher, 2016). Leaf moisture content is often related to time to ignition in a nonlinear way (Beverly & Wotton, 2007), though this relationship can be linear as well with higher moisture contents (Dimitrakopoulos & Papaioannou, 2001) resulting in a longer time to ignition and less heat released. A higher moisture content renders fuel less ignitable because of the higher specific heat capacity (SHC) of water compared to many other compounds (Etlinger & Beall, 2004; Possell & Bell, 2013). This high

SHC of water means that it functions as a latent heat sink (through evaporation of water), meaning more heat is required by the fire to drive out the moisture, delaying the preheating phase of fuel (Richards 1940, Bradshaw et al.1983).

Moisture content has been found to have a threshold relationship with some flammability variables (Popović et al., 2021), particularly with ignitability (time to ignition) (Dimitrakopoulos and Papaioannou, 2001; Possell & Bell 2013). These threshold moisture values can vary across species. For instance, Dimitrakopoulos and Papaioannou (2001) found an ignition threshold range of 40–140% MC for leaf litter beds of 24 species in fire-prone Mediterranean Basin habitats, although Possell and Bell (2013) reported a MC threshold of 89–80% for 50% probability of ignition in three *Eucalyptus* species in fire-prone Australian forest, with no significant differences between these species. In a field-based experiment on gorse (*Ulex europaeous*), Anderson and Anderson (2010) found that a live fuel moisture content of 30% provided a 50% probability of ignition. For four species from British heathland, Santana and Marrs (2014) found moisture thresholds of 35–59% resulted in the ignition and sustainability of fuels from the upper canopy layer, while moisture thresholds of 19–55% allowed the ongoing combustion (sustainability) of litter bed (dead fuels). Beverly & Wotton (2007) found 86 – 90% MC at sustainability for different litter fuels in Canada. These results show that moisture content thresholds exist when considering the ignition score, maximum temperature and burning time of species, and that species can differ in these thresholds. However, to our knowledge no studies have looked for moisture content thresholds for consumability, nor have such studies been attempted using measurements of shoot flammability, or on species which are found in non-fire-prone environments.

If there are differences in moisture content thresholds across species, which plant traits might be associated with these? Thus far, there have been no attempts to link plant traits to moisture content thresholds for flammability, although certain easy-to-measure morphological traits could prove useful in this regard. Leaf size (e.g. leaf area or leaf length) (LA) has been found to be negatively correlated with shoot flammability, with large-leaved species being less flammable (Blackhall et al., 2012; Calitz et al., 2015; Cui et al., 2020); although these same large-leaved species have high flammability in the leaf litter layer as they pack less-densely than small leaves and hence are well-aerated (de Magalhães & Schwilk, 2012; Scarff & Westoby, 2006; Schwilk &

Caprio, 2011). Furthermore, leaf dry matter content (LDMC) has been identified as a key trait positively correlated with shoot-level flammability (Pompe and Vine, 1966; Perez-Harguindeguy et al., 2013; Alam et al., 2020;), so it may also be helpful in understanding species differences in moisture content thresholds. Leaf thickness was also strongly negatively associated with shoot flammability variables, suggesting that thick-leaved plants are less flammable, as thicker leaves are hard to ignite and release less heat during burning (Alam et al., 2020; Grootemaat et al., 2015; Mason et al., 2016; Montgomery & Cheo, 1971). One attribute of thicker leaves is a greater capacity to store moisture and maintain higher leaf moisture content (Afzal et al., 2017; Búrquez, 1987; Seelig et al., 2012), providing further evidence to suggest leaf thickness may influence moisture content thresholds. At the tissue scale, relative water content (LRWC) quantifies water content storage potential, which is strongly associated with dynamics of live fuel moisture content (Jolly et al., 2014; Peñuelas et al., 2004), and thus species with high LRWC are often less flammable (Jolly & Johnson, 2018; Nolan et al., 2020b). Some physiological traits could be useful too, such as water potential. Minimum midday leaf water potential is negatively correlated with tissue dehydration (Markesteijn et al., 2011; Nelson, 2001; Tyree et al., 1994; Zimmermann, 1978), and has been negatively correlated with shoot flammability (*Chapter 2*). Thus, species with lower seasonal minimum water potentials might be have lower moisture content thresholds (i.e. be more flammable) than those with higher seasonal minimum water potentials.

Here this chapter addresses three questions:

1) Are there thresholds (i.e. inflection points) in the relationship between fuel moisture content (MC%) and shoot flammability?
2) If there are thresholds, do these differ between species, or do many species have a similar moisture threshold?
3) If the thresholds do differ between species, which morphological (LA, LT, LDMC) or physiological ($\Psi_{\text{stem,}}$ LRWC) traits are associated with such differences?

4.2 Materials and Methods

4.2.1 Study area and sample collection

A total of 160 sun-exposed terminal shoots from eight species were collected from regenerating and old growth rainforest at Hinewai Reserve (172° 08' E; 41° 25' S), near Akaroa, in the south east of Banks Peninsula of the South Island, New Zealand. These eight species are common and widespread throughout New Zealand (Table B3.1). Hinewai Reserve is a mix of old-growth native rainforest, regenerating rainforest and exotic shrubland situated on land formed by the Akaroa Volcano which erupted basaltic lavas between 9 and 8 million years ago (Wilson, 1994). Soils are mostly moderate to high fertility, and are broadly classified as yellow, brown-earth, yellow-grey earth, and brown granular loams. All samples were collected on the same day (11 February 2020) to minimize climatic effects on plant flammability. Mean temperatures of the hottest month (December – February) are 10.12° C, while mean temperatures of the coldest month (June -August) are 6.66 ° C. The total precipitation of summer (December, 2019 – February, 2020) was 148 mm (NIWA, 2021), Mean annual precipitation for 30 years was 2406 mm (Pipipi, 2018).

A 70 cm terminal shoot was cut in air from each individual plant. The shoots were immediately placed in opaque, double-plastic bags, wrapped in a piece of wet tissue paper to minimize post-cutting dehydration, then placed in a covered trailer which was cooled with ice to transport 1.30 h to the laboratory at Lincoln University. Samples were refrigerated at 4-5°C until manipulation of shoot moisture, and flammability testing was performed within four days after the samples were collected (Figure 4.1).

4.2.2 Shoot moisture manipulation

To seek critical moisture thresholds in species' shoot flammability, 20 plants per species were each exposed to different treatments to create a gradient in tissue moisture content, based on wetting up, air-drying and oven drying for different periods, along with one sample being burnt fresh, without moisture manipulation (Figure 4.1a-c, C4.2). To measure the moisture content of each sample (which were later burnt), one 10 cm subsample (including leaves and twigs) was cut and tied to the main shoot and subjected to the same moisture treatment. In wet up treatments, shoots with subsamples were placed with their cut stems in water inside buckets covered with black plastic bags stored at room temperature for different lengths of time (5 min, 10 min, 30 min, 2 h, 18 h and 24 h) (Figure 4.1). In air-dried treatments, shoots were dried on a bench for different times (1 h, 2 h, 6 h, 18 h and 24 h), while in oven-dried treatments, shoots were put in oven at 50°C for 30 min, 60 min, 90 min, 2 h, 4 h, 5 h, 6 h or 24 h (Figure 4.1). Thus, each of the 20 samples for each species had a different tissue moisture manipulation. One treatment is given to each sample. That means, fresh sample was one among 20 treatments, other 6 shoots were treated by wet up treatments, 5 shoots were treated by air drying and 8 shoots were treated with oven drying. So, there could be different amount of MC% of each shoot. To estimate the moisture content of samples at the time of burning, subsamples were dried in an oven at 65° C to constant dry weight, and the fuel moisture content calculated on a dry weight basis (Equation 4.1) (Van Wilgen et al., 1990).

$$\text{Fuel moisture content } \% = \frac{\text{fresh weight} - \text{oven dry weight}}{\text{Oven dry weight}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \ \ldots\ldots\ldots \qquad 4.1$$

Figure 4.1. Wetting and drying treatments for samples and plant flammability device. (a) wet up treatments (plants with cut stems in water in darkness at room temperature), (b) air dry treatments, (c) oven dry treatment, and (d) apparatus for measuring shoot flammability.

4.2.3 Flammability measurements

Shoot flammability was measured for each species following the methods described by Jaureguiberry et al. (2011) and Wyse et al. (2016), using the same device as Wyse et al. (2016; Figure 4.1 d). To measure shoot flammability, in this study, unlike the protocol of Wyse et al. (2016; 2017), samples were not air-dried at room temperature for 24 h on the bench prior to burning, rather they were burned after the relevant moisture manipulation treatment had been applied. As per Wyse et al. (2016) samples were preheated for 2 minutes on the burner at 150°C, before a blowtorch was turned on for 10 s. During burning, ignitibility was recorded as the time to ignition (between 0 and 10 s), which was then converted to an ignition score by subtracting the time to ignition from 10; for example a sample which took 1 s (i.e rapid ignition) to ignite had an ignition score 9 (Padullés et al., 2018). Samples that did not ignite were given a value of zero for ignition score. The total time (s) that a sample experienced flaming combustion was measured with a stop watch to represent sustainability, while the maximum temperature (°C) recorded during burning was measured by infrared laser thermometer (Fluke Corp., Everett, WA,USA) to represent combustibility. Consumability was measured as the percentage of burnt biomass, assessed by visual observation by at least two observers. After finishing each treatment, shoots were selected for flammability testing in random order. Climate variables during flammability testing consisted of averaged 22.6 °C (±3.2), wind speed of 4.5 (km/h) (±3.8) and humidity of 48.7% (±5.5) and measured by thermocouple temperature.

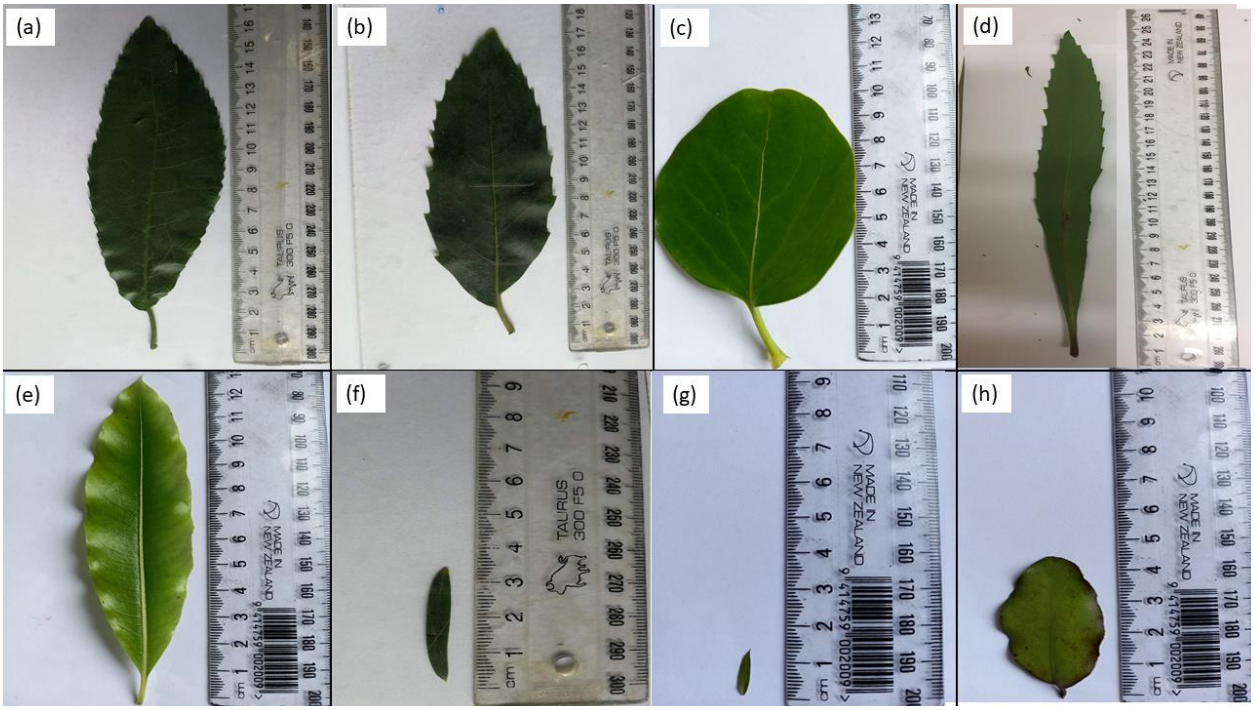

Figure 4.2 Leaf size variation of eight studied species. (a) *Melicytus ramiflorus*, (b) *Pseudopanax colensoi*, (c) *Griselina littoralis*, (d) *Pseudoponax crasifolious*, (e) *Pittosporum eugenioides*, (f) *Podocarpus cunninghamii* (g) *Kunzea robusta* and (h) *Psedowintera colorata*

4.2.4 Data analysis

4.2.4.1 Threshold identification

We used piecewise regression models (Toms & Lesperance, 2003) to test for the existence of abrupt changes in the relationship between species flammability and fuel moisture content. Abrupt changes occur at critical thresholds when the response of species or an ecological process is not linear. Piecewise regression models are "broken-stick" models, where two lines are joined by unknown points, called "breakpoints" (Toms & Lesperance, 2003), which can be used as estimates of thresholds. Linear regressions were also fitted to all flammability-moisture content relationships. Piecewise regressions were fitted with arbitrary initial moisture thresholds for different species following the steps of Muggeo, (2021). Threshold points were detected using the *segmented* package in R (Muggeo, 2021). Once the threshold point (if any) was detected, we used AIC (Akaike Information Criteria) to compare with the linear regression models to find the most plausible model of these two for each relationship.

4.2.4.2 Functional traits associated with moisture content thresholds

Morphological (LDMC, LA and LT) and physiological (Ψ_{stem} and LRWC) traits of the eight species were obtained from field-based sampling (C*hapter 3*), and averaged (except midday Ψ_{stem}, Table S4.2) across four seasons to examine the associations between threshold moisture content and traits across species. The lowest midday Ψ_{stem} of each species from any seasons was used for this variable. Pearson correlation analyses were used to examine these relationships.

All analyses were done in R statistical environment (version 4.1.0) through R studio (IDE) (R core team, 2018). All graphical operations were carried through “ggplot2” package (Wickham, 2016).

4.3 Results

4.3.1 Relationship between moisture content and flammability traits

As moisture content of shoots decreased, flammability components mostly increased (Table 4.1; Figs. 4.3-4.6). Piecewise regression was the best fit model for all species for ignition score (Fig. 4.3), maximum temperature (Fig. 4.4), and burnt biomass (Fig. 4.5), except for *P. crassifolius* (which had no threshold found for burnt biomass), and also for two species with burning time (Table 4.1; Fig 4.6). For burning time, there was no threshold found (i.e. the piecewise regression could not be fitted) for *P. cunninghami*, while linear regression was a better fit than piecewise regression for *G. littoralis* (Table 4.1). For some species and flammability traits, while the piecewise regression model was the best model, the linear model had a ΔAIC< 2, suggesting that the linear model was also a plausible model in these instances (Table 4.1). However, collectively these results demonstrate that thresholds in moisture content occur for most species and flammability traits.

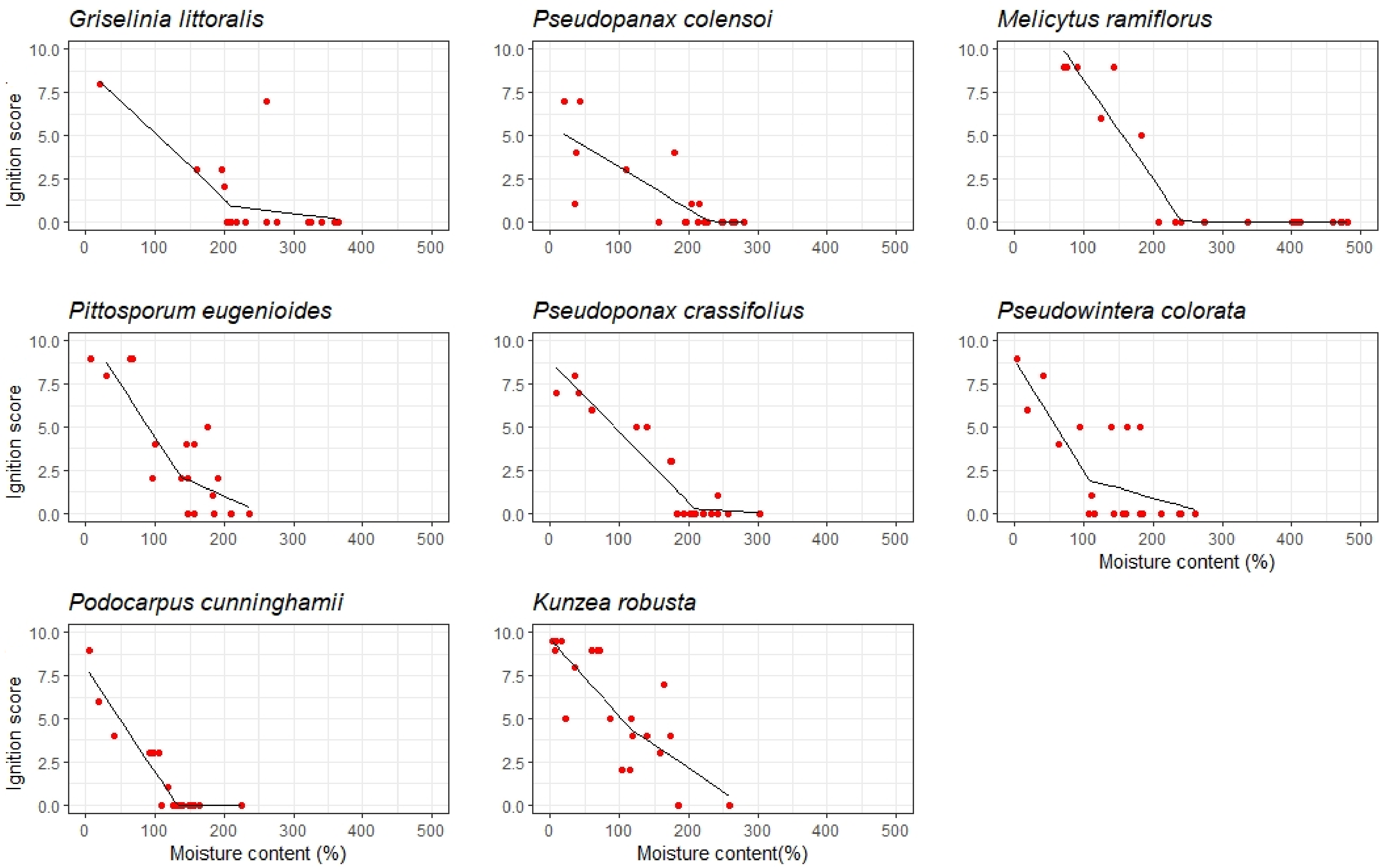

Figure 4.3 Relationship between moisture content (%, as manipulated in the laboratory) and ignitability (ignition score) for eight species of native tree species. Threshold starting points for each species are given in Table 4.2. Ignition score is out of 10, with the higher the score the quicker the ignition; samples which did not ignite within 10 s of a blowtorch have an ignition score of 0, an ignition in 1 s would have an ignition score of 9.

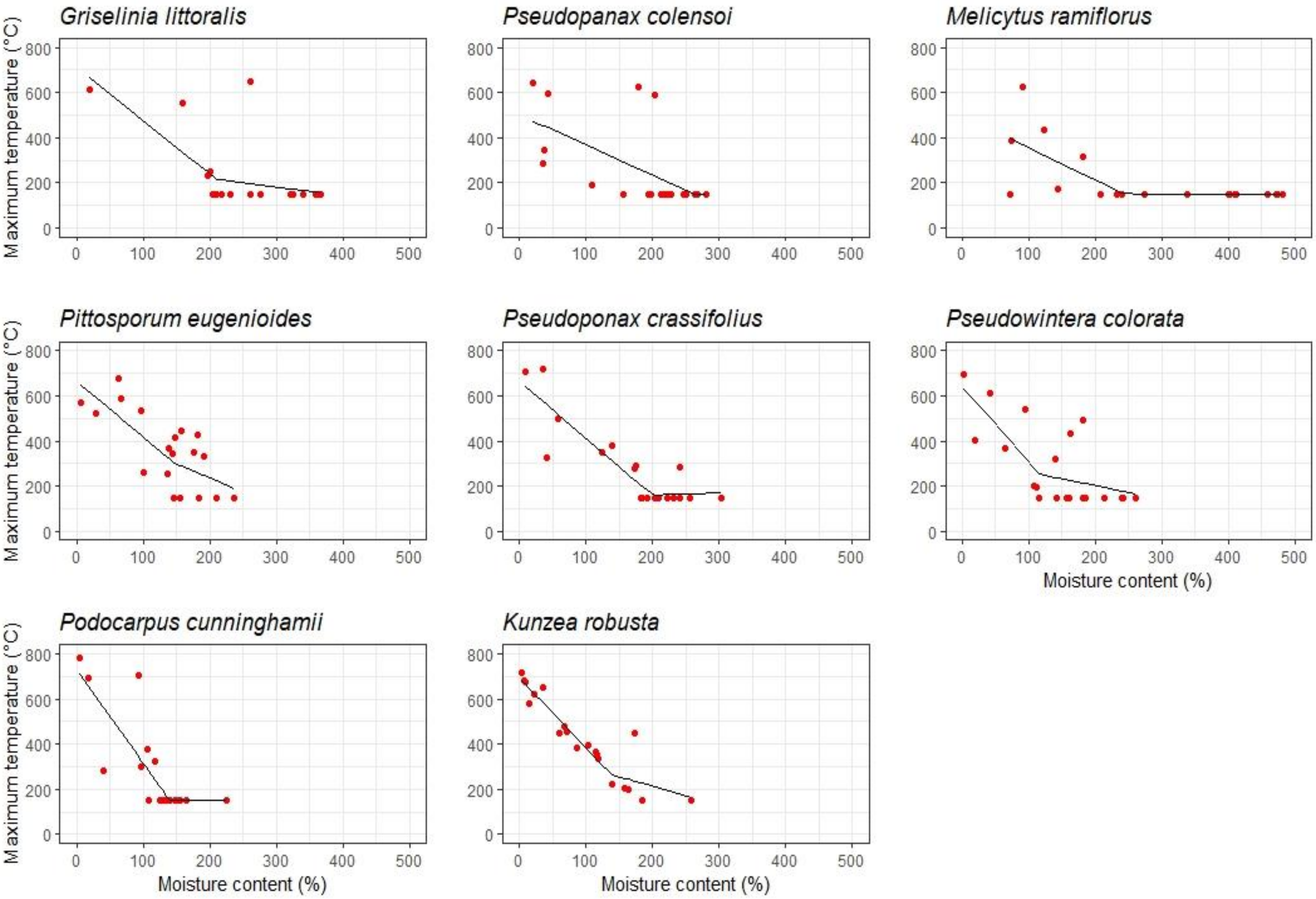

Figure 4.4 Relationship between moisture content (%, as manipulated in the laboratory) and maximum temperature (°C) for eight species of native tree species. Solid lines represent fitted lines found using piecewise regression. Threshold starting points for each species are given in Table 4.2.

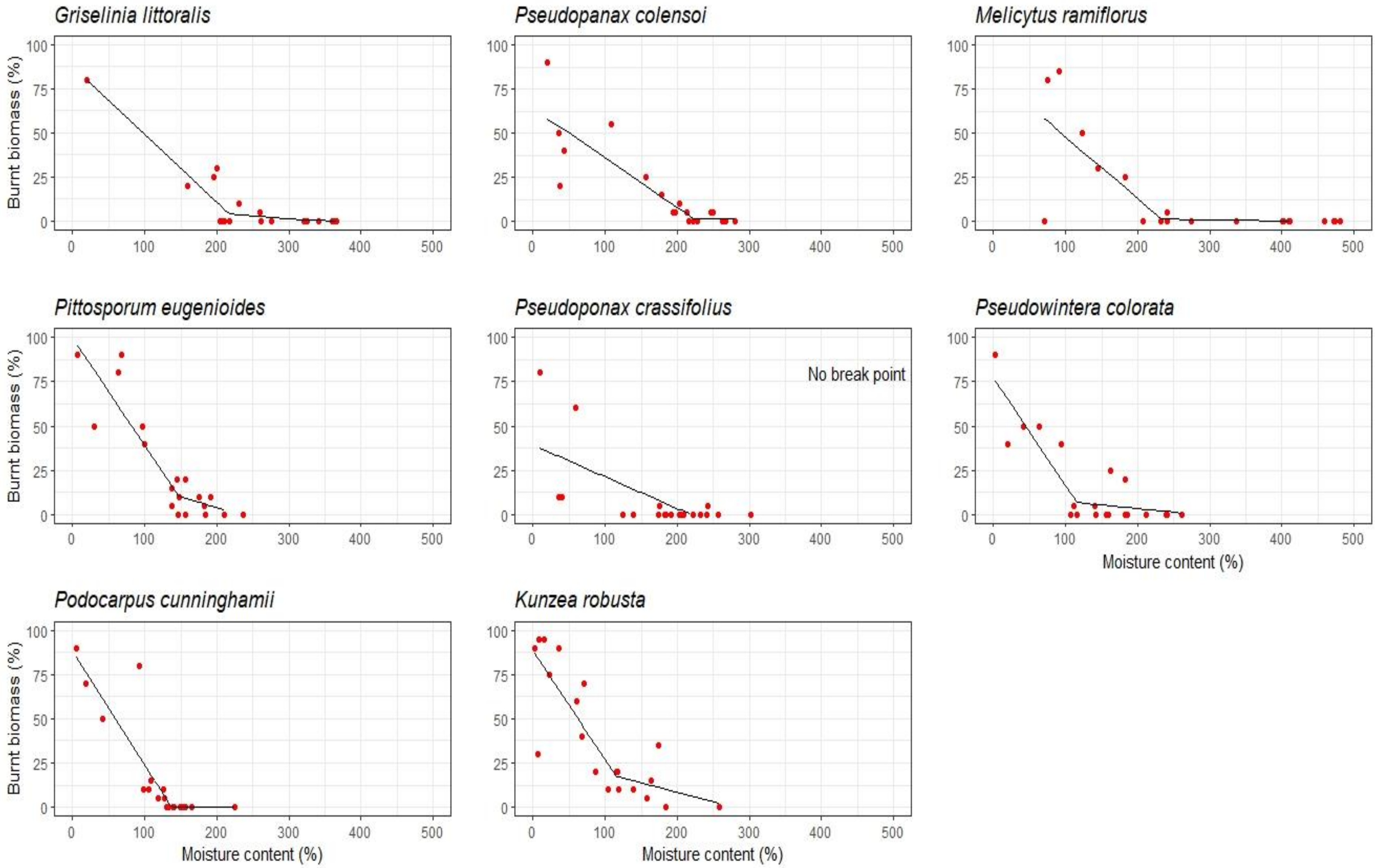

Figure 4.5 Relationship between moisture content (%, as manipulated in the laboratory) and burnt biomass (%) for eight species of native tree species. Solid lines represent fitted lines found using piecewise regression, while dotted lines represent fitted lines using linear regression. Threshold starting points for each species are given in Table 4.2.

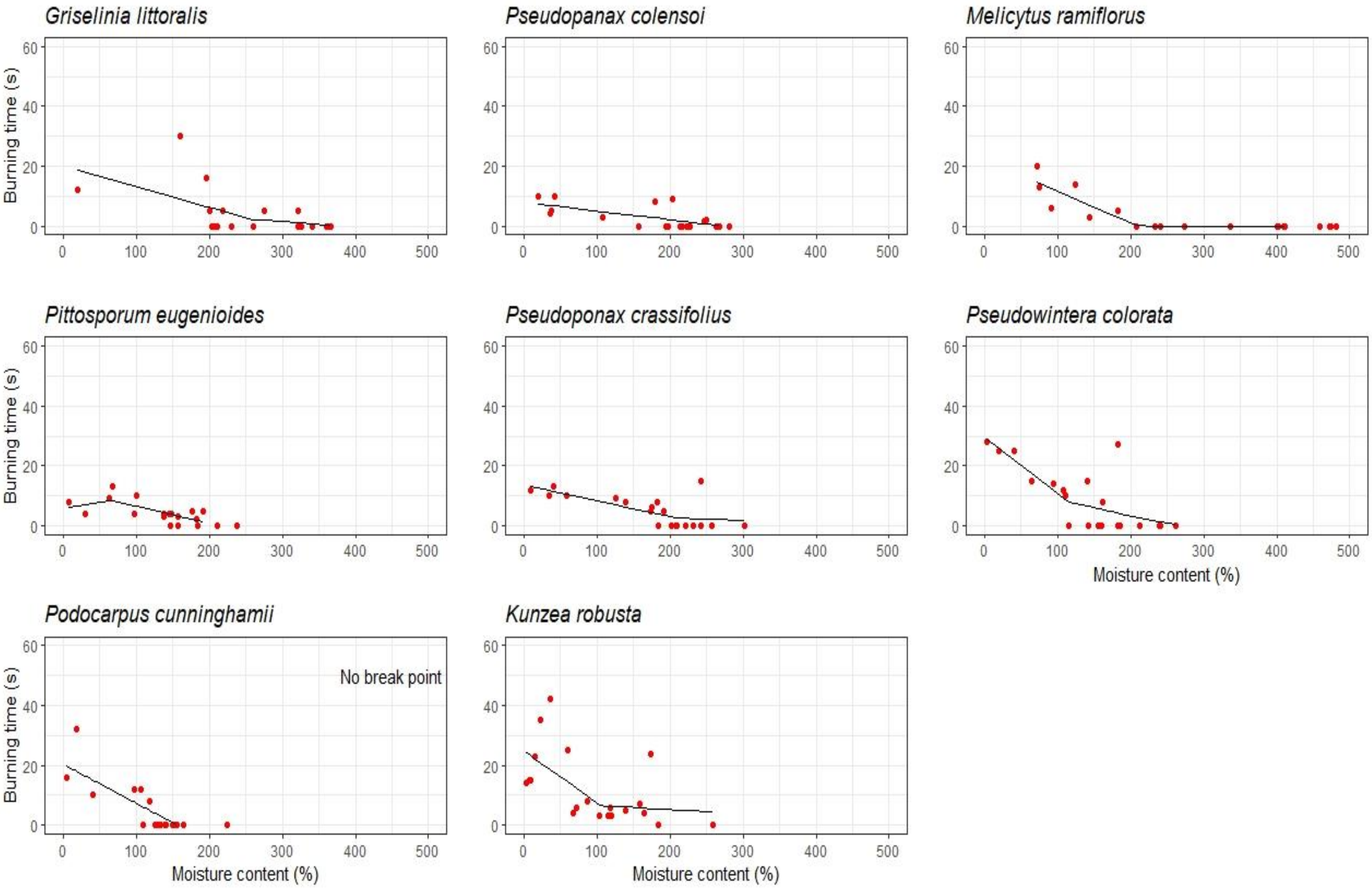

Figure 4.6 Relationship between moisture content (%, as manipulated in the laboratory) and burning time (s) for eight species of native tree species. Solid lines represent fitted lines found using piecewise regression, while dotted lines represent fitted lines using linear regression. Threshold starting points for each species are given in Table 4.2.

Table 4.1 Results of linear regression and piecewise regression for each species and flammability component. The comparison between linear and piecewise regression was performed by Akaike information criteria (AIC). Bolded values are those with better relationships with flammability components (linear or piecewise regression for each flammability trait for each species). Where both the linear and piecewise regression models had ΔAIC< 2, both models were bolded.

ISC= ignition score, MT=maximum temperature, BB= burning biomass and BT=burning time.

Species	**Flammability traits**	**Linear regression**				**Piecewise regression**			
		R^2	*P*	AIC	*SE*	R^2	*P*	AIC	SE
Melicitus ramiflorus	ISC	0.45	0.001	99.78	2.66	**0.59**	**<0.001**	**97.70**	**2.42**
	MT	**0.34**	**0.006**	**248.11**	**108.5**	**0.49**	**<0.001**	**247.10**	**101.5**
	BB	0.43	0.001	182.33	20.95	0.62	<0.001	178.42	18.23
	BT	0.51	<0.001	118.14	4.20	**0.82**	**<0.001**	**102.18**	**2.71**
Pseudopanax colensoi	ISC	0.28	0.016	88.83	2.02	**0.64**	**<0.001**	**79.02**	**1.52**
	MT	**0.18**	**0.061**	**267.25**	**175**	**0.36**	**<0.001**	**266.44**	**165**
	BB	0.33	0.007	181.28	20.4	**0.75**	**<0.001**	**166.02**	**13.37**
	BT	0.24	0.028	108.87	3.34	**0.46**	**<0.001**	**106.09**	**2.98**
Griselinia littoralis	ISC	0.37	0.004	87.19	1.94	**0.55**	**<0.001**	**85.05**	**1.70**
	MT	**0.32**	**0.009**	**258.40**	**140.3**	**0.45**	**<0.001**	**258.20**	**134**
	BB	0.58	<0.001	162.46	12.75	**0.88**	**<0.001**	**142.19**	**7.37**
	BT	**0.29**	**0.012**	**135.49**	**6.50**	0.33	<0.001	138.70	6.25
Pseudopanax crassifolius	ISC	0.84	<0.001	68.75	1.22	**0.90**	**<0.001**	**63.39**	**1.02**
	MT	0.73	<0.001	243.42	96.5	0.82	<0.001	239.83	84.65
	BB	0.45	0.001	173.58	16.42				
	BT	**0.47**	**<0.001**	**116.04**	**3.90**	**0.50**	**<0.001**	**115.09**	**4.02**
Pittosporum eugenioides	ISC	**0.66**	**<0.001**	**83.29**	**1.95**	**0.71**	**<0.001**	**82.23**	**1.89**
	MT	0.52	<0.001	255.64	121.5	0.54	<0.001	252.24	120.7
	BB	0.75	<0.001	171.31	15.91	**0.83**	**<0.001**	**168.03**	**14.06**
	BT	**0.44**	**0.001**	**103.42**	**2.84**	**0.53**	**<0.001**	**102.00**	**2.76**
Podocarpus cunninghamii	ISC	0.77	<0.001	69.29	1.24	**0.91**	**<0.001**	**53.20**	**0.79**
	MT	**0.60**	**<0.001**	**256.93**	**135.2**	**0.70**	**<0.001**	**255.69**	**125.8**
	BB	0.69	<0.001	173.89	16.96	**0.80**	**<0.001**	**168.74**	**14.31**
	BT	0.28	0.016	164.07	13.27				
Kunzea	ISC	0.62	<0.001	91.63	1.99	**0.67**	**<0.001**	**88.33**	**2.08**

robusta	MT	0.83	<0.001	234.76	77.69	**0.88**	**<0.001**	**231.51**	**69.74**
	BB	0.65	<0.001	182.60	21.09	**0.74**	**<0.001**	**180.56**	**19.23**
	BT	0.31	0.01	155.23	10.15	**0.38**	**<0.001**	**153.23**	**10.21**
Pseudowintera colorata	ISC	0.50	<0.001	93.00	2.25	**0.62**	**<0.001**	**91.01**	**2.08**
	MT	**0.46**	**<0.001**	**257.29**	**136.5**	**0.56**	**<0.001**	**256.40**	**131.5**
	BB	0.59	<0.001	172.85	**16.53**	**0.80**	**<0.001**	**162.61**	**12.28**
	BT	**0.54**	**<0.001**	**141.65**	**7.39**	**0.60**	**<0.001**	**140.41**	**7.23**

4.3.2 Threshold moisture content values where flammability changes

For most species, the threshold moisture content value identified using piecewise regression was similar within each species when compared across the different flammability components (Table 4.2). *Melicytus ramiflorus* had the highest threshold moisture values (257.5 – 210.9%), and *Griselinia littoralis* (260.4 – 210.6%), *Pseudopanax colensoi* (229.2 – 270.2%) and *Pseudoponax crassifolius* (209.2 – 199.9%) also had high moisture values, while *Psuedowintera colorata* (139.2 – 105.3%) and *Kunzea robusta* had the lowest (115.3 – 107.7%). One species, *Pittosporum eugenioides*, had a wide range (67.6 – 136.9%) moisture of threshold values, with the burning time threshold being half that of other flammability components (Table 4.2). Two species had flammability components for which no threshold value was found (*P. cunninghamii* for burning time and *P. crassifolius* for burnt biomass). These results confirm that species have different thresholds of moisture content.

Table 4.2 Threshold Moisture Content (± standard error) identified using piecewise regression for each of eight species and each of four flammability components. IT=Initial threshold (i.e. threshold value provided *a priori* as part of the analysis procedure). N/T=no threshold identified in analysis (i.e. relationship did not include a breakpoint). Initial threshold of all flammability traits of each species was same except *Pseudowintera colorata.* for maximum temperature, MT.

Species	Ignition score	Maximum temperature (°C)	Burnt Biomass (%)	Burning time(s)
Melicytus ramiflorus IT=150	257.52 ± 62.59	243.57 ± 73.76	232.91 ± 47.39	210.97 ±2 4.09
Pseudopanax colensoi IT= 150	229.17 ± 38.76	264.20 ± 101.41	222.67 ± 29.07	270.20 ± 110.26
Griselina littoralis IT=201	210.66 ±37.07	210.66 ± 45.44	217.78 ± 14.13	260.43 ± 103.46
Pseudopanax crassifolious IT=100	209.24 ± 22.10	199.86 ± 22.46	N/T	209.06 ± 63.56
Pittosporum eugenioides IT=100	136.9 4 ± 46.25	146.38 ± 72.35	146.66 ± 20.45	67.62 ± 33.51
Podocarpus cunninghamii IT=100	131.92 ± 8.33	140.16 ± 19.21	136.61 ± 13.96	N/T
Pseudowintera colorata IT=170 (MT= 201)	107.54 ± 33.40	115.77 ± 39.31	115.77 ± 17.76	115.67 ± 42.91
Kunzea robusta IT=150	115.31 ± 99.26	139.23 ± 25.27	114.17 ± 31.43	105.33 ± 52.53

4.3.3 What might explain the patterns in threshold values across different species?

There were significant relationships between flammability thresholds and two morphological traits, leaf dry matter content (LDMC) and leaf area (LA) (Figures 4.7 – 4.10; Table 4.3). LDMC was negatively correlated with threshold flammability values for all flammability traits, indicating that species with high LDMC had low threshold values. LA was positively correlated with threshold flammability values for all flammability traits except burning time; larger-leaved species had higher threshold values (Figs 4.7 – 4.10). There were no relationships between flammability thresholds and relative water content, minimum seasonal water potential, or leaf thickness (Figs 4.7– 4.10).

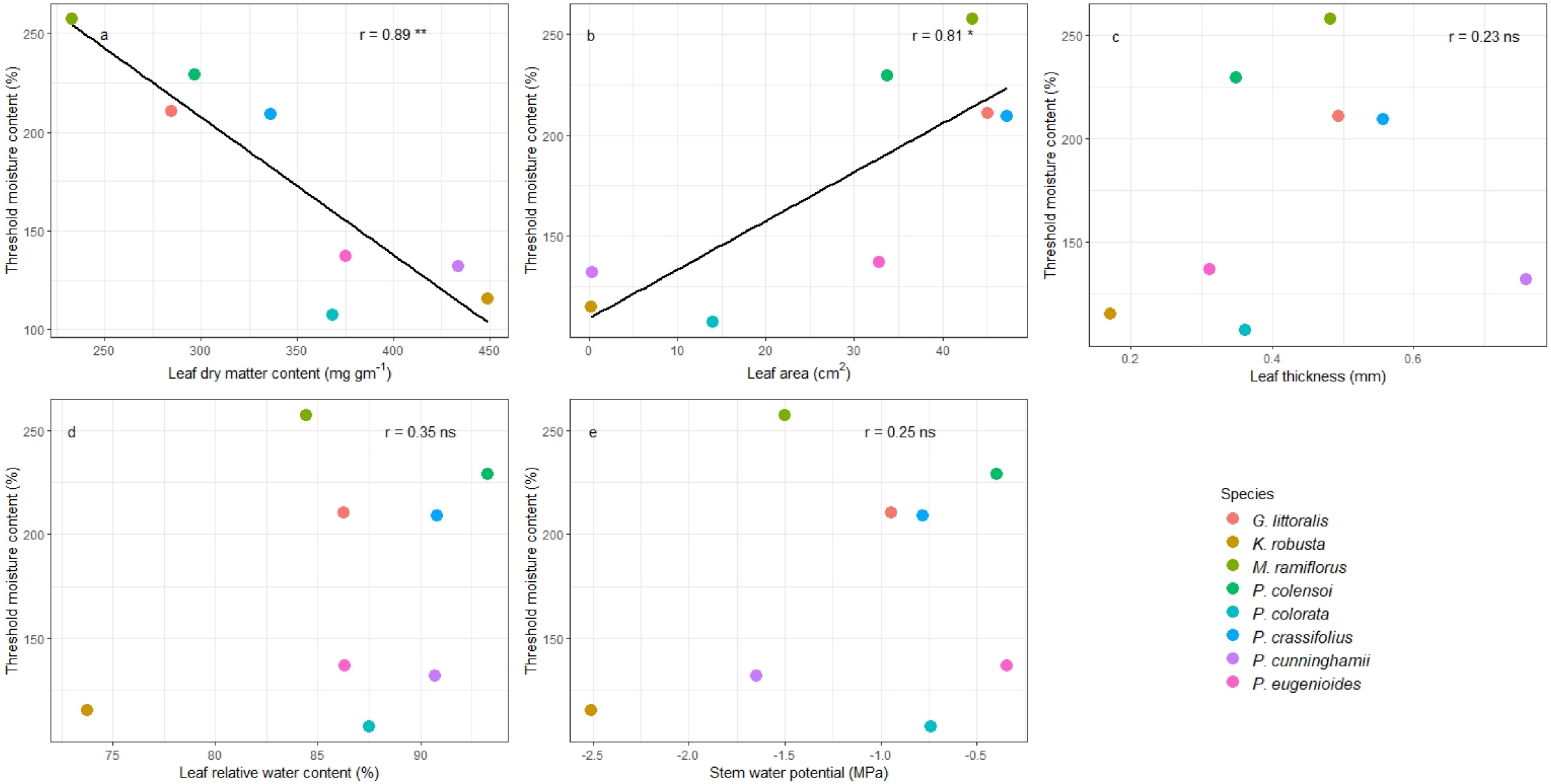

Figure 4.7 Associations between leaf dry matter content (a), leaf area (b), leaf thickness (c), leaf relative water content (d), stem water potential (e) and threshold moisture content of eight species for ignition score. Pearson correlation coefficients (r) and their level of significance are given. ^{ns}, non-significant; $^{*}P > 0.05$, $^{**}P > 0.01$.

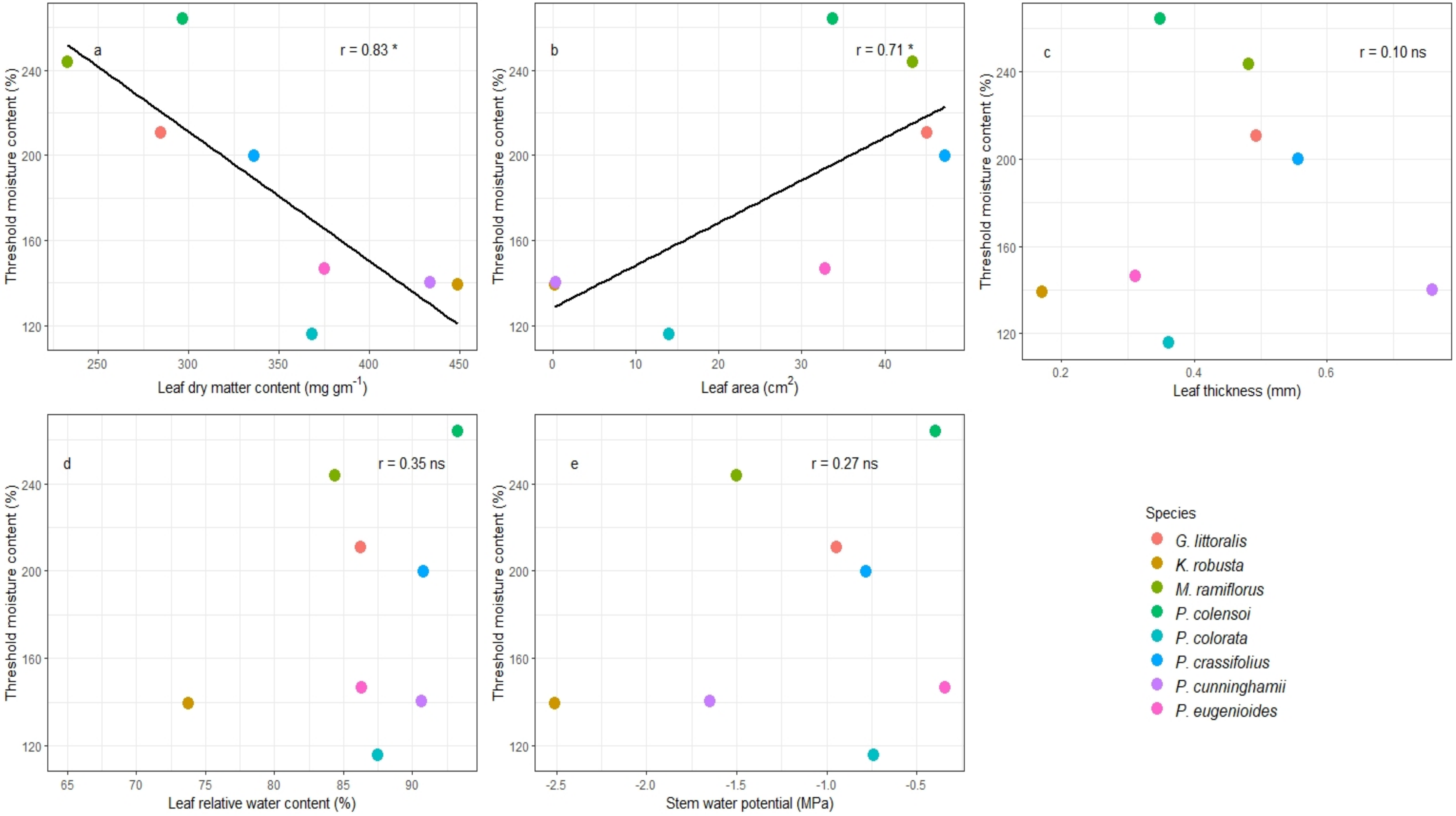

Figure 4.8 Associations between leaf dry matter content (a), leaf area (b), leaf thickness (c), leaf relative water content (d), stem water potential (e) and threshold moisture content of eight species for maximum temperature (°C). Pearson correlation coefficients (r) and their level of significance are given. ns, non-significant; *$P > 0.05$.

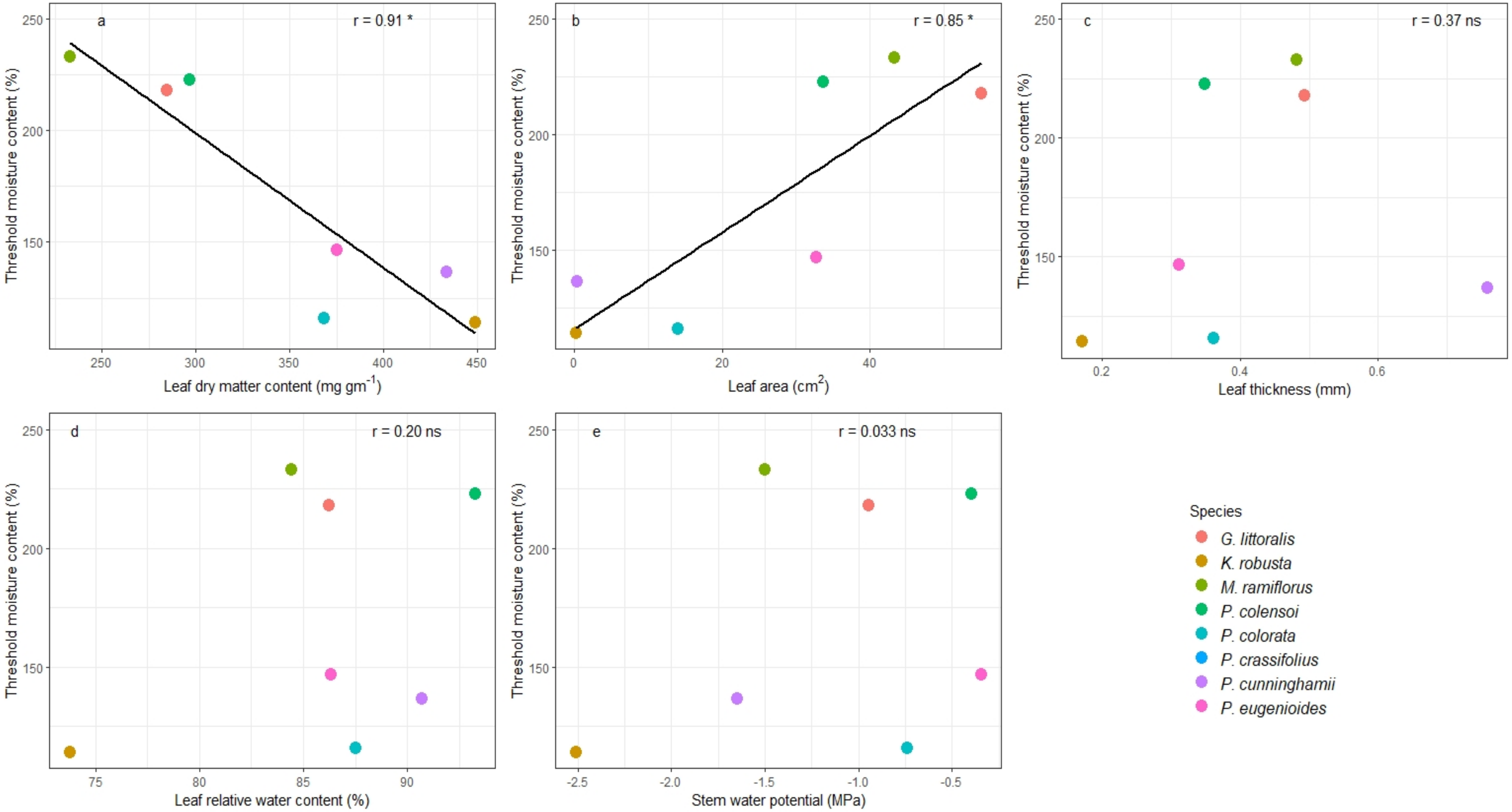

Figure 4.9 Associations between leaf dry matter content (a), leaf area (b), leaf thickness (c), leaf relative water content (d), stem water potential (e) and threshold moisture content of eight species at burnt biomass (%). Pearson correlation coefficients (r) and their level of significance are given. ns, *, indicates non-significant and $P > 0.05$.

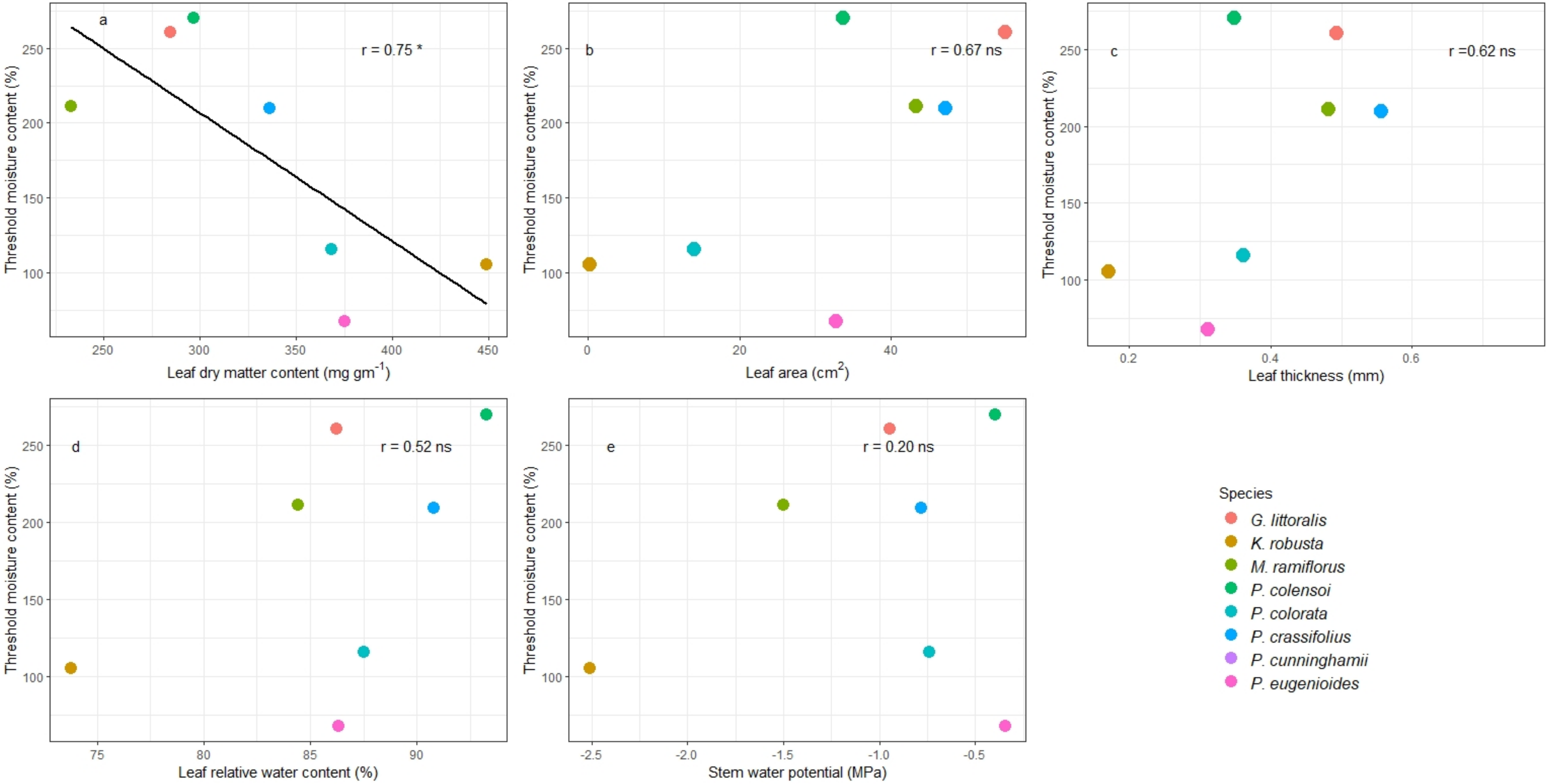

Figure 4.10 Associations between leaf dry matter content (a), leaf area (b), leaf thickness (c), leaf relative water content (d), stem water potential (e) and threshold moisture content of eight species at burning time (s). Pearson correlation coefficients (r) and their level of significance are given. ns, non-significant; $^{*}P > 0.05$.

4.4 Discussion

Our study documented the existence of threshold values in the relationship between % MC and shoot flammability traits in all eight tree species exposed to manipulations of moisture content. Finding such thresholds is important as they identify the critical moisture content necessary for plant fuels to ignite and propagate a fire (Davies and Legg, 2011). Below the moisture threshold species have potential to ignite and sustain fire. We also found differences in the moisture thresholds of our species, with these values ranging from 67 – 270%. Furthermore, we have identified functional traits that are associated with moisture content thresholds across species, with LDMC and LA being negatively and positively related to thresholds moisture content, respectively.

4.4.1 Thresholds relationships between flammability and moisture content

In our study, there were critical moisture thresholds in the relationship between moisture content and flammability traits, and these moisture thresholds were species specific. The existence of thresholds was consistent with other findings elsewhere (Masinda et al., 2021; Possell & Bell, 2013; Santana & Marrs, 2014), although not all studies found differences across species. For instance, Possell and Bell (2013), found no significant differences between the threshold values of three *Eucalyptus* spp. This suggests that closely related species may well have similar thresholds, though the two *Pseudopanax* species in our study did differ in their moisture thresholds (*P. colensoi*: 222.67– 270.20% and *P. crassifolius*: 199.86 – 209.24%). Future work on moisture content thresholds should examine the role of phylogeny in determining interspecific differences.

The range of moisture content thresholds in our study (64.2– 270.2%), was much wider than other studies (Table 4.3), with half our study species having particularly high thresholds (>200%). This difference with other studies could be explained by contrasting environments. Our study was conducted in regenerating temperate rainforest, in an area where mean annual precipitation is 1320 mm. While fires do occasionally occur in this area (Wilson, 1993), particularly in more flammable early-successional communities dominated by *K. robusta* or gorse (*Ulex europeans*), fire would be rare in the late-successional rainforest. Other studies were conducted on species that occur in fire-prone environments, and often in habitats that are much drier than our study area (Table 4.3), suggesting that species in wetter habitats may have higher moisture content thresholds than those of drier habitats. The frequency of fire in a habitat may also be important, but both these hypotheses should be tested on larger datasets encompassing a wider range of habitats. Understanding these traits will be important not only for understanding fire-induced mortality and to inform management on fuel reduction treatments, but also to understand the potential for evolutionary trade-offs between wet and dry habitats.

Podocarpus cunninghamii and *Pseudopanax crassifolius* showed linear relationships between moisture content and burn time and maximum temperature reached, respectively (Trollope, 1978; Sylvester and Wein, 1981; Guijarro et al., 2002; Msweli et al., 2020). This result for burn time could suggest that sustainability was more influenced by fuel biomass or bulk density than fuel moisture. Further exploration of the role of fuel bulk density and biomass is needed for a complete picture of differences in threshold flammability. Another issue that deserves future research attention is the influence of reproductive phenology on fuel moisture content. For instance, Emery et al., (2020) found that in *Adenostoma fasciculatum* moisture content was highest when plants were flowering. The influence of such changes in plant biology should be explored for future studies of critical moisture thresholds.

Table 4.3 Moisture threshold of species in different habitat types. P = precipitation; T = Temperature

Flammability traits and threshold MC%	Fire prone	Climate in study location	Location and vegetation type
Probability (1%) of ignition time 35–55%	Yes	T=15.8 °C, P = 447.8 mm per annum	Mediterranean-type climate in Greece (Dimitrakopoulos et al, 2010)
Ignition time (80 – 140%)		Not given	Mediterranean basin, (Dimitrakopoulos and Papaioannou, 2001)
Ignition time (10.5–40.4%) Sustainability (9.7–38.9%)	Yes	Mean T = – 0.3 °C/annum and 676 mm/annum	Temperate ecosystem in China (Masinda et al., 2020)
Ignition time (12 – 200%)	Yes	Not given	Mediterranean basin (Chuvieco et al., 2004).
Ignition time (23-30%) and sustainability (10 – 40%)	Yes	Not given	Heathlands and shrublands in Australia, (Plucinski & Anderson, 2008).
Ignition time (81–89%)	Yes	Not given	Australian eucalypt forest (Possel and Bell, 2013)
Probability of ignition time 70%	Yes	Not given	Heathland, Edinburgh, Scotland (Davies and Legg, 2011)
Ignition time (35 – 59%), Sustained ignition (19 – 55%)	Yes	Not given	Heath and moorland ecosystems in Britain (Santana and Moore, 2014).

4.4.2 Which traits explain the patterns in threshold values across different species?

In our study, species with low LDMC and large leaves (*M. ramiflorius, G. littoralis, P. crassifolious,* and *P. colensoi,*) had higher moisture content thresholds than species with small leaves and high LDMC (*P. colorata, P. cunninghamii, K. robusta*) (Fig: 4.2). It is not clear why large-leaved species with low LDMC have higher MC thresholds. There is evidence that larger-leaved material is lower in flammability when held in the canopy (Blackhall et al., 2012; Calitz et al., 2015; Cui et al., 2020a), and it is widely recognized that species with low LDMC are low in flammability (Alam et al., 2020; Perez-Harguindeguy et al., 2013; Pompe & Vines, 1966). Low LDMC likely results in low flammability because LDMC is related to tissue density and water content; leaves with higher LDMC tend to have high dry mass per volume of the tissue and lower water content (Garnier & Laurent 1994; Wilson et al. 1999; Shipley & Vu 2002; Perez-Harguindeguy et al. 2013).

A MC of 100% (on dry mass basis) indicates that there is as much as water in shoot as much as dry matter content. The higher moisture threshold of large-leaved, low LDMC species could also be due to their capacity to store high amounts of moisture (high capacitance) in their leaves (Tyree & Ewers, 1991; Zhang et al., 2021), although the lack of a relationship between relative water content and moisture content threshold does counter the idea that storage capacity plays a large role. Another potential reason why large-leaved species have higher moisture content thresholds is related to leaf vein density. Large-leaved species generally have wider leaf veins, which would better facilitate the water supply (Nobel et al., 2008; Boyce et al., 2009; Brodribb & Jordan, 2011; Schneider et al., 2017). The very high moisture content of species such as *M. ramiflorus* and *G. littoralis* when fresh or when wetted up (Figure C4.2) shows that such species are able to rapidly increase their moisture content when water is available.

4.5 Applications to wildland fire

These findings could help fire managers in several ways, particularly by highlighting key moisture content thresholds at which low flammability species may rapidly increase in flammability. Several of the species studied here (*G. littoralis, P. colensoi, M. ramiflorus, P. crassifolius*) have been widely recommended to be planted in New Zealand as green firebreaks to help stop fire spread (Evans, 1983; Fogarty, 2001; Wyse et al., 2016). Our results can be used to determine when these green firebreak species may switch from low to high flammability; i.e. when species cross their threshold %MC, for instance during drought. This is the point, given an ignition source, which could initiate positive feedback processes which enhance fire conditions and species flammability (Paritsis et al., 2015; Pausas, 2015), causing regenerating rainforests or planted green firebreaks to burn. Real-time assessment of when plant species reach their threshold moisture would allow for much better identification of fire hazard. An efficient way of doing this is via remote sensing (Yebra et al., 2013).

There have been rapid advances in the use of remote sensing data to assess fuel moisture content. At broader scales, remote sensing can be used for estimation of live fuel moisture content from a large number of species within vegetation and over different vegetation types such as forest, shrubland and grassland to predict fuel moisture content (Yebra et al., 2019) , which is relevant to asses fire danger (Chuvieco et al., 2004; Quan et al., 2021). At finer scales, unmanned aerial vehicles (UAV) can be used to assess the water status of individual plants. For instance, UAV-based camera systems has been used for collecting phenotype information and for detecting drought stress in cropping areas (Feng et al., 2021). Our results could be used in conjunction with fine-scale data collected from UAVs to identify when green firebreaks or other low-flammability vegetation have flipped beyond key moisture thresholds, and hence may cease to help stop a fire, and instead fuel it.

Our study also showed that easy-to-measure traits, such as LDMC and LA, are correlated with moisture thresholds. These traits are widely measured and so, if their relationship with species moisture thresholds are also found to hold for a wider range of species, LDMC and LA could be used to predict % MC across large numbers of species. Indeed, LDMC was one of predictors that has been used to map flammability weekly across the Australian continent (Casas et al., 2014; Trombetti et al., 2008; Yebra et al., 2018) and daily on a global scale (Riano et al., 2005), demonstrating the importance of this trait for flammability prediction.

Our results could also be vital to forest fire managers when carrying out prescribed burns. Threshold moisture will provide fire managers with a greater understanding of the requirements of prescribed burning and the level of good practice guidelines, allowing them to adjust management for forest recovery and sustainability (Hiers et al., 2020; Ryan et al., 2013). For instance, *G. littoralis, P. colensoi, M. ramiflorus, P. crassifolius* should readily burn when their MC% is below the their critical threshold.

4.6 Conclusions

We found the existence of threshold moisture in the relationship between moisture content and shoot flammability traits in all eight tree species exposed to manipulations of moisture content. Species with low leaf dry matter content and large leaves had higher moisture content thresholds than species with small leaves and high leaf dry matter content. These moisture content thresholds could warn fire managers of potential tipping points when species may have changed from low to high flammability. This could be especially important to identify when species planted as green fire breaks might flip from being fire retardant to fire promoting, such as during drought. Therefore, threshold moisture content are potentially of great value for fire managers.

Chapter 5

General discussions and conclusion

The main goal of this thesis was to assess the relationships between species flammability and functional traits associated with plant drought response, plant water relations, and seasonal changes. To achieve this goal, I investigated the following questions in *Chapters 2-4*:

Q1) What is the relationship between drought response traits and shoot flammability, and are species that are drought tolerant also low in flammability? (*Chapter 2*)

Q2) Does shoot flammability change within species across different times of the year, and if so, which functional traits are associated with these changes? (*Chapter 3*)

Q3) Are there thresholds (i.e. inflection points) in the relationship between fuel moisture content (MC%) and flammability, and if so, do these thresholds differ between species, and which morphological or physiological traits are associated with interspecific differences in threshold moisture content? (*Chapter 4*)

In this chapter, I will clarify how my study advances our understanding of the new field of pyro-ecophysiology (Section 5.1), and explain how this research can be applied by fire managers to help predict and control fires (Section 5.2). I will also discuss some limitations of this study and propose future research directions (Section 5.3).

5.1 Contributions to the field of pyro-ecophysiology

'Consideration of plant ecophysiology within the context of live fuel flammability work has the potential to vastly expand our understanding of inter- and intra-species variations in flammability and how those characteristics may change over space and time.' Jolly and Johnson, 2018, p. 4.

The new discipline of pyro-ecophysiology aims to bring together aspects of both ecophysiology and fire ecology to better understand live fuel flammability and fire-induced plant mortality (Jolly & Johnson, 2018). Ecophysiology contributes to an understanding of live fuel flammability by considering how plant water and carbon uptake, loss and storage might separately and collectively affect how well a plant burns (Jolly & Johnson, 2018; Resco de Dios, 2020). Plant water relations is a highly relevant subfield of ecophysiology in this regard, due to the likely role of water relations in determining live fuel moisture content, a key determinant of plant flammability (Resco de Dios, 2020; Nolan et al. 2020b; Karavani et al., 2018). My thesis has examined the relationship between flammability and many key ecophysiological and associated morphological traits and therefore, my findings have contributed to the new field of pyro-ecophysiology.

One plant water relations trait of great relevance to pyro-ecophysiology is water potential (Jolly and Johnson, 2018; Nolan et al., 2020b). Water potential is a dynamic trait that varies throughout the day and with a range of environmental drivers, especially soil moisture (Donovan et al., 2001). It describes the physical water stress that a plant is under and minimum water potential is positively correlated with 50 or 80% loss hydraulic conductance (P_{50}, P_{80}), and hence vulnerability to xylem embolism in many species and ecosystems (Bartlett et al., 2012; Markesteijn et al., 2011; Zimmermann, 1978). Within a given plant functional type, water potential is expected to be tightly linked with live fuel moisture content because plants with low water potentials will have low leaf water status, and low fuel moisture content, and hence high flammability (Karavani et al., 2018; Nolan et al., 2020b; Nolan et al., 2018; Pivovaroff et al., 2019). However, despite this likely link between plant water potential and flammability, this relationship has rarely been directly tested. Owens et al., (1998) measured both water potential and flammability of needles and small twigs of ashe juniper throughout the year at two sites in Texas, but found that water potential was not an important predictor of flammability in a multivariate model. Peacock (1980) also found no relationship between xylem water potential and flammability of branches of three shrub species in open woodland-grassland in Texas.

My thesis examined the relationship between shoot flammability and water potential expressed in two different ways: mean water potential per species per sampling time during a year-long field-based study of plant flammability during above-average rainfall (*Chapter 3*), and minimum seasonal water potential of species during a severe drought in Otago in 1985 (Bannister 1986; *Chapter 2*). The findings of each of these chapters were consistent, with shoot flammability being negatively correlated with minimum seasonal water potential during drought (species with low seasonal plant water potential had high flammability; *Chapter 2*), and with the water potential of trees and shrubs in regenerating forest when measured over the course of a year (*Chapter 3*). Hence, my results provide the first direct support for the theoretical predictions of Jolly and Johnson (2018) and Nolan et al. (2020) that water potential is a key trait integrating ecophysiology with research on live fuel moisture.

When measuring shoot flammability of trees and shrubs throughout the year (*Chapter 3*), there were three water relations traits that were each negatively correlated with flammability;

midday stem water potential (Ψ_{stem}), leaf relative water content (LRWC), and leaf moisture content (LMC). Of these three traits, Ψ_{stem} is the most time-consuming and expensive to measure, requiring specialized equipment and measurements taken either pre-dawn or at midday. However, water potential provides a detailed understanding of the water status of a plant at the time of sampling, and helps provide the theoretical links between water relations and flammability (Jolly and Johnson 2018; Nolan et al. 2020; de Dios 2020b). Hence, for studies seeking a deeper understanding of the ecophysiological basis for changes in live fuel moisture, and hence flammability, water potential is a worthwhile trait to measure. However, the cost and time required in measuring the water potential of plants makes it unrealistic to use this variable to monitor live moisture contents and track changes in flammability in real time, or indeed to measure water potentials of a wide range of plant species to assess comparative live fuel moisture content. A better candidate variable for this is LRWC.

The RWC of tissues, such as leaves, is another trait considered useful to the field of pyro-ecophysiology (Nolan et al., 2020). The relationship between Ψ_{leaf} and LRWC is usually a positive curvilinear one (Nolan et al., et al., 2020b; Scholander et al., 1965; Turner, 1981), with plants with high Ψ_{leaf} also having high LRWC. The non-linear relationship between relative water content and Ψ_{leaf} because of the changing contribution of osmotic adjustment at different water potentials, highlighting that osmotic adjustment can also contribute to determining live fuel moisture content and thus influences species flammability (Alessio et al., 2008; De Lillis et al., 2009). However, despite the likely link between LRWC and flammability (Nolan et al., 2020), this relationship has rarely been directly tested. Peacock (1980) found LRWC was a strong predictor of seasonal flammability in three Texan shrub species. LRWC was also correlated with shoot flammability for 10 trees and shrubs in regenerating rainforest (*Chapter 3*), suggesting that LRWC is a useful instantaneous measure of flammability. Furthermore, LRWC can be measured accurately and relatively cheaply in the field using remote sensing (*see section 5.2.2*), suggesting that there is great potential for this to be a widely measured pyro-ecophysiological trait. However, LRWC did not explain differences in thresholds moisture content for species when their moisture content was manipulated in the laboratory (*Chapter 4*), implying that other traits (for example leaf chemical composition) are also relevant for pyro-ecophysiological relationships (Ciccioli et al., 2014).

Further evidence for the utility of ecophysiological traits in understanding live fuel flammability comes from *Chapter 2*. Minimum seasonal water potential (Ψ_{stem}) during a severe drought and turgor loss point (Ψ_{TLP}) were both correlated with shoot flammability, suggesting that traits that describe the drought response of species can help differentiate interspecific variation in flammability. However, the generality of these relationships should be tested in a wider range of ecosystems, including those more fire-prone than the species studied in this thesis, which are mostly found in temperate rainforests.

The identification of moisture content thresholds could also be useful to the field of pyro-ecophysiology. Thresholds in fuel moisture content have been reported to vary substantially among species, suggesting mechanisms for different thresholds in wildfire risk across biomes (Nolan et al., 2020b). However, the potential linkages between thresholds in moisture content and flammability have rarely been examined. My thesis determined the threshold moisture content among eight species and found that these were related to LDMC and leaf area, with large-leaved species with low LDMC having higher moisture content thresholds. However, ecophysiological traits, such as LRWC and minimum seasonal midday Ψ_{stem}, were not associated with these threshold moisture content. Future research on this topic could include exploration of relationships with other ecophysiological variables associated with critical thresholds in live fuel moisture content, such as Ψ_{TLP} (Nolan et al., 2020b) and pyro-hydraulic traits, such as vulnerability to fire-induced cavitation (West et al., 2016).

The chapters in this thesis have provided important empirical data on concepts of pyro-ecophysiology, particularly patterns across species and over time (de dios et al., 2020; Nolan et al., 2020b; Jolly and Johnson 2018), and have demonstrated the promise of this new field of research. As pyro-ecophysiological studies are conducted in a wider range of biomes, functional groups and species, it is anticipated that more universal patterns will be uncovered. This will improve our understanding of how traits like plant water relations relate to flammability and provide insights into the ecological significance of relationships between these traits, as well as providing further useful insights for fire managers.

5.2 Applications of this research for fire managers

5.2.1 Identifying species to be used in green firebreaks

Green firebreaks are strips of low flammability vegetation established across the landscape to help reduce fire spread, and have been deployed in many countries around the world (Curran et al. 2018; Cui et al. 2019; Cheng et al., 2004). All three data chapters in this thesis contribute potentially useful information to fire managers regarding the choice of species used in green firebreaks.

As discussed in *Chapter 2*, the need to identify plant species which are low in flammability for planting in green firebreaks or around houses in fire-prone areas, has been the subject of considerable debate over recent decades, and has led to authorities in many jurisdictions providing lists of recommended species (Krix 2022a b; Murray et al., 2018; White & Zipperer, 2010). However, the validity of such lists is often unknown, and they are rarely based on empirical testing of flammability, and instead, in some cases, inferred from surrogates such as drought resistance (White and Zipperer, 2010). In *Chapter 2*, I provided the first empirical test of the relationship between plant flammability and different measures of plant drought response. Contrary to some previous suggestions, I found no support for the idea that species with traits indicative of drought tolerance were also inherently low in flammability. In fact, two measures of drought tolerance (leaf Ψ_{min} during drought and Ψ_{TLP}) were negatively related with flammability; species with low leaf Ψ_{min} and low Ψ_{TLP} (i.e. more drought tolerant) had higher flammability. This suggests that fire managers need to be very cautious in assuming that species that are drought tolerant are also low in flammability, but also that drought response traits associated with plant water relations (leaf Ψ_{min} and Ψ_{TLP}) may have some value in predicting the flammability of species. However, though this should be assessed across a wider range of species and habitats, especially fire-prone landscapes.

A desirable feature of species planted in a green firebreak is that they are low in flammability throughout the year. However, some species vary in their flammability seasonally (Gowda et al., 2022; Santacruz-García et al., 2019; Essaghi et al., 2017). In *Chapter 3*, I measured the flammability of 10 species at four times throughout the year to determine if they varied, and if so, examined the functional traits that were associated with such variation. Three species that are good candidates for planting in green firebreaks in New Zealand (*Griselinia littoralis, Pseudopanax crassifolius, Pseudopanax colensoi*) were found to be consistently low in flammability throughout the year, suggesting that these species could be safely deployed in green firebreaks. However, another species, *Melicytus ramiflorus*, which has also been recommended for planting in green firebreaks (Evan, 1983; Wyse et al., 2016), switched from very low flammability in autumn and winter to high flammability in spring and summer sampling times. If this pattern is replicated when studied in other populations and across other years, then fire managers should reconsider using this species, or only plant it sparingly, in green firebreaks. *Melicytus ramiflorus* does have the advantage of resprouting strongly following fire, a characteristic not shared by many other New Zealand forest tree species (Teixeira et al., 2020). Thus, *M. ramiflorus* could perhaps be planted on the outer edge of a green firebreak, as a sacrificial species which can regrow after fire, but providing some protection to other, less flammable species that comprise the bulk of the green firebreak.

Chapter 3 also identified a suite of ecophysiological and morphological traits associated with changes in flammability throughout the year. These included water relations traits, such as Ψ_{stem} and LRWC, other traits associated with moisture status, such as LMC and LDMC, and morphological traits, such as leaf area. Such traits could be used by fire managers to identify species that are more likely to have low flammability year round, such as those with large leaves, high Ψ_{stem}, LRWC and LMC, and low LDMC, and these species could be screened for their use in green firebreaks.

Identification of threshold relationships, such as between fuel moisture content and flammability (Nolan et al., 2016; Rao et al., 2022), is important in flammability research. In *Chapter 4,* I found that there were threshold relationships between moisture content and shoot flammability in most study species and for most flammability traits. I concluded that these results could help fire managers in two main ways. First, the moisture thresholds could be used to identify when species planted in green firebreaks would be become flammable, and second, the thresholds could be used when planning prescribed burns, with such fires avoided during conditions when moisture thresholds were low enough to support fire in low flammability species, meaning such fires could more readily escape containment. Both of these conclusions hinge on the moisture thresholds actually being a determinant of ignition in these species, a hypothesis which can be examined using field based LMC% data, such as that collected in *Chapter 3*. If the moisture thresholds in *Chapter 4* actually apply to plants in the field it would be expected that species with low flammability throughout the year are operating at moisture at or above their thresholds for changes in flammability, while those high in flammability should have moisture below their threshold year round. However, this was not consistently the case (*Figure 5.1*). For example, *Kunzea robusta* had its lowest flammability during the autumn and winter sampling times (*Figure 3.2*), but these were also times when its moisture was lowest (*Figure 5.1*). *Pittosporum eugenioidies* had LMC% at or near its threshold throughout the year (*Figure 5.1*), suggesting unchanged flammability year round, but it had lower flammability in winter, and increased in flammability in autumn, spring and summer (*Figure 3.2*). Contrastingly, in support of the expected link between threshold moisture content and seasonal flammability, species which were low in flammability throughout the year, such as *Pseudopanax colensoi, P. crassifolius* and *Griselina littoralis* had moisture values which were above or near to their threshold values during all sampling times. This suggests that traits other than moisture are influencing whether a plant burns, and that the moisture threshold may in fact not be a useful singular measure to predict flammability.

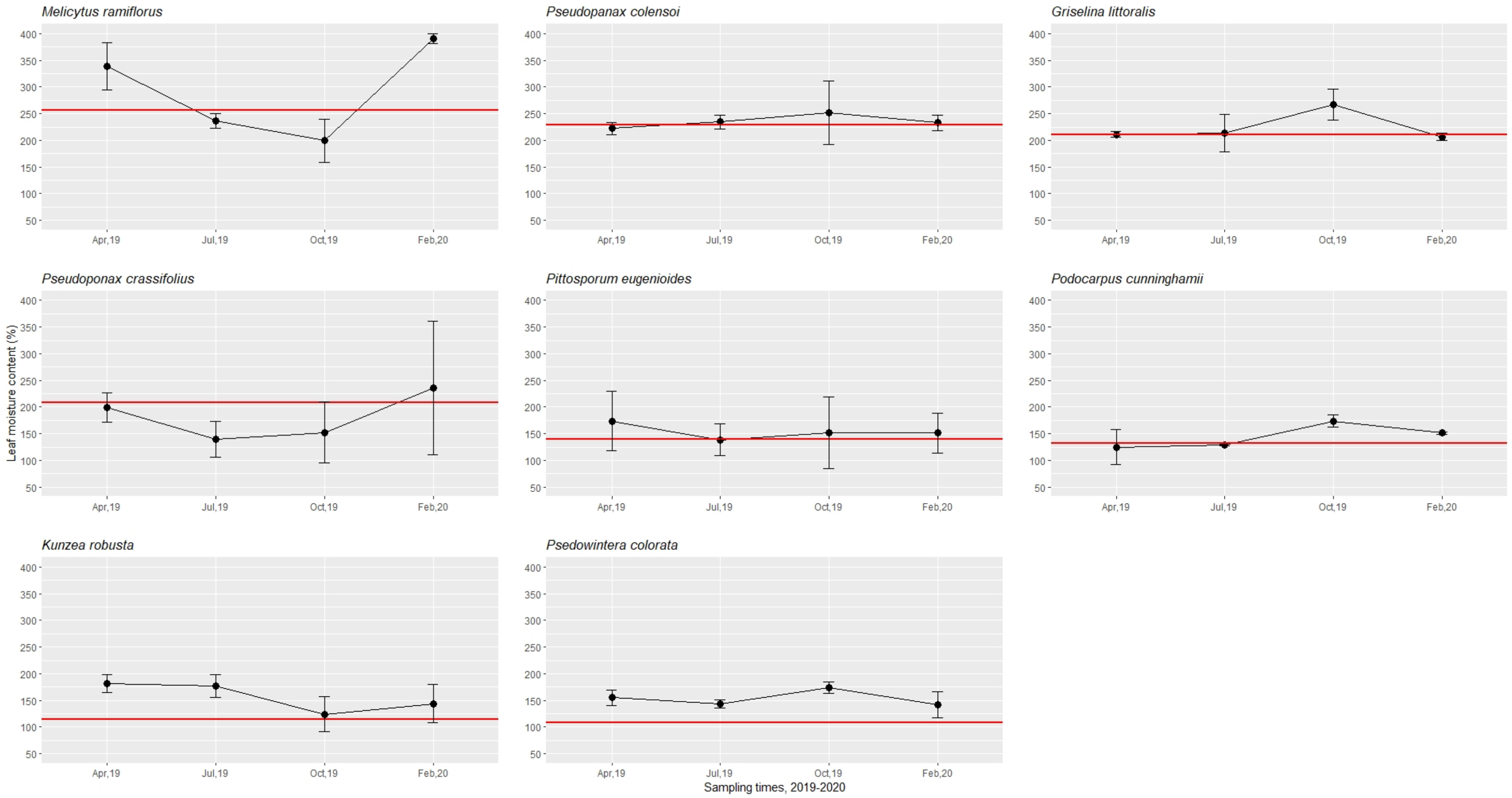

Figure 5.1 Percentage leaf moisture content for each species during each sampling time (black lines and dots, ± one standard error) derived from field measurements in *Chapter 3*, along with critical moisture threshold for each species (red line), derived from laboratory experiments in *Chapter 4*. Black dot points below the threshold lines (red) denotes that moisture content during the field experiment (2019-2020, *Chapter 3*) was lower than the threshold moisture identified from laboratory work (*Chapter 4*), while black dot points above the red line indicate field moisture content was higher than the threshold value for that species.

5.2.2 Predicting changes in flammability to assess fire risk using remote sensing of fuel moisture content

Live fuel moisture can be measured through field and laboratory techniques (*Chapters 3* and *4*), or remotely assessed (Fare et al., 2017). LFMC is a metric responsive to long-term climate and is used in a number of fire modelling systems as a key predictor for the ignition and propagation of fire (Resco de Dios et al., 2021).

Given recent advances in remote sensing, such as microwave frequencies, there is the potential to identify daily, weekly or seasonal dynamics of vegetation water content, capture variations of different processes relating to tree response to water stress and soil moisture. It is now possible to incorporate real-time measurements of tissue water content, and so detect increasing species flammability and fire hazard at ecosystem scales (Desbois & Vidal, 1996; Konings et al., 2021). There is a tissue water content threshold beyond which flammability increases (Scholander, 1964). My thesis determined that easier-to-measure traits, such as RWC, are related to LMC and negatively correlated with shoot flammability (*Chapter 3*). This opens up the possibility of relative flammability of different species being estimated in real time, if LRWC and LMC can be measured accurately using remote sensing. This refinement of remote sensing technology suggests that fire mangers would greatly benefit from using such morphological and physiological traits in fire modelling systems, though there is likely to be a need for ground-truthing of remote sensing data in the early stages of its use for this purpose.

Remote sensing includes using airborne or spaceborne platforms to predict LFMC for dynamic global vegetation models based on physiological drivers of spatiotemporal variation of LFMC at local, regional and global scales (Yebra; 2013; Yebra et al., 2019). Ψ_{min} and Ψ_{TLP} are eco-physiological traits related to LFMC (Scholander, 1964; Turner, 1981; Nolan et al., 2020), and so could be useful inclusions in such models. Remote sensing provides an alternative strategy to determine accurate LFMC in forest ecosystems. (Riano et al., 2005; Romero et al., 2012; Wang et al., 2011)). Furthermore, in lab based experiment I found that threshold moisturewas correlated with species LDMC (*Chapter 4*). If moisture thresholds do later prove to be useful in understanding switches in flammability within species (but see *section 5.2.1*), then the remote sensing advances that enable the rapid measurement of LDMC could alert fire scientists when such thresholds are reached and shifts to higher flammability are likely.

5.3 Limitations and recommendations for future research

The main limitation of this thesis was in *Chapter 3*, where sampling only occurred throughout one year, so differences in flammability across sampling times could not be attributed to seasonal differences. This sampling across only one year was due the time-consuming nature of measurements of plant water relations and unforeseen circumstances associated with the covid-19 pandemic. Future studies on this topic should undertake measurements of flammability across several years to provide a more robust examination of seasonal patterns and incorporate a wider range of environmental conditions (including soil moisture, temperature and relative humidity).

Several of the traits that I found to be associated with high flammability, high LDMC, small leaves and low LMC, are traits indicative of greater resistance to herbivory (Gowda et al., 2022). This suggests that trade-offs are occurring in these species, which while being less palatable are actually more likely to burn. Examination of plant traits associated with either flammability or herbivory resistance could make useful contributions to understanding the fate of plant communities under future disturbance regimes.

Finally, the work here should be repeated in other locations to examine the generality of these findings. These traits should be tested in different populations and so should be tested elsewhere, such as in different ecosystems in New Zealand, especially in drier climates. In particular, the experiments and studies conducted in this thesis should be repeated in more fire-prone ecosystems than the shrubland/regenerating rainforest ecosystems studied here. It is likely that species in fire-prone ecosystems will have different suites of traits to many of the species investigated here (except *Ulex* and *Kunzea*, both of which occur in fire-prone environments in New Zealand and elsewhere), potentially producing different outcomes. Ideally, these studies should be repeated over a larger scale across landscapes that experience different fire regimes, such as the dry sclerophyll forest / wet sclerophyll forest / rainforest gradients present in eastern Australia.

5.4 Conclusion

This thesis has examined the relationship between flammability and many key ecophysiological and associated morphological traits, demonstrating empirically the value of traits such as Ψ_{stem} and LRWC to the new field of pyro-ecophysiology. The findings of this thesis also contribute useful information to fire managers; for example, regarding the choice of species used in green firebreaks. Some of the key traits identified as being related to flammability dynamics (e.g. LRWC, LMC, and LDMC) can also be measured by remote sensing, presenting the possibility that changes on flammability could be assessed in real-time, or at least on short temporal and large spatial scales useful to fire managers. Such linking of pyro-ecophysiological traits with the real-time and large scale data of remote sensing will be crucial to fire managers in an increasingly fire-prone future.

Appendix A

Supplementary information of Chapter 2

A 2.1 Supplementary information

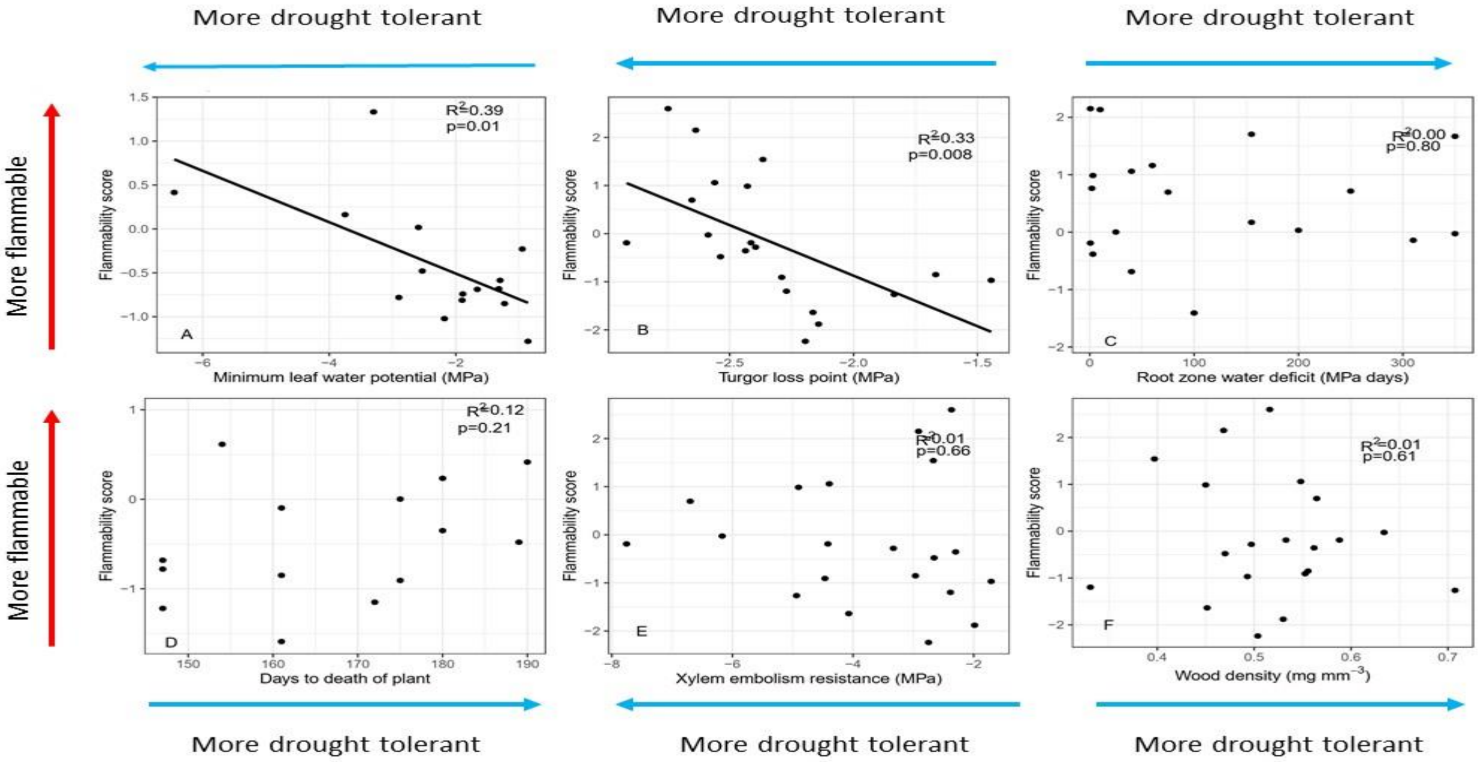

Figure A2.1 The relationship between a plant's shoot flammability score (a combined measure of overall flammability) and drought response measures, minimum leaf water potentials (A), leaf turgor loss point (B), root zone water deficit (C), days to death of plants (D), xylem embolism resistance (E) and wood density (F).

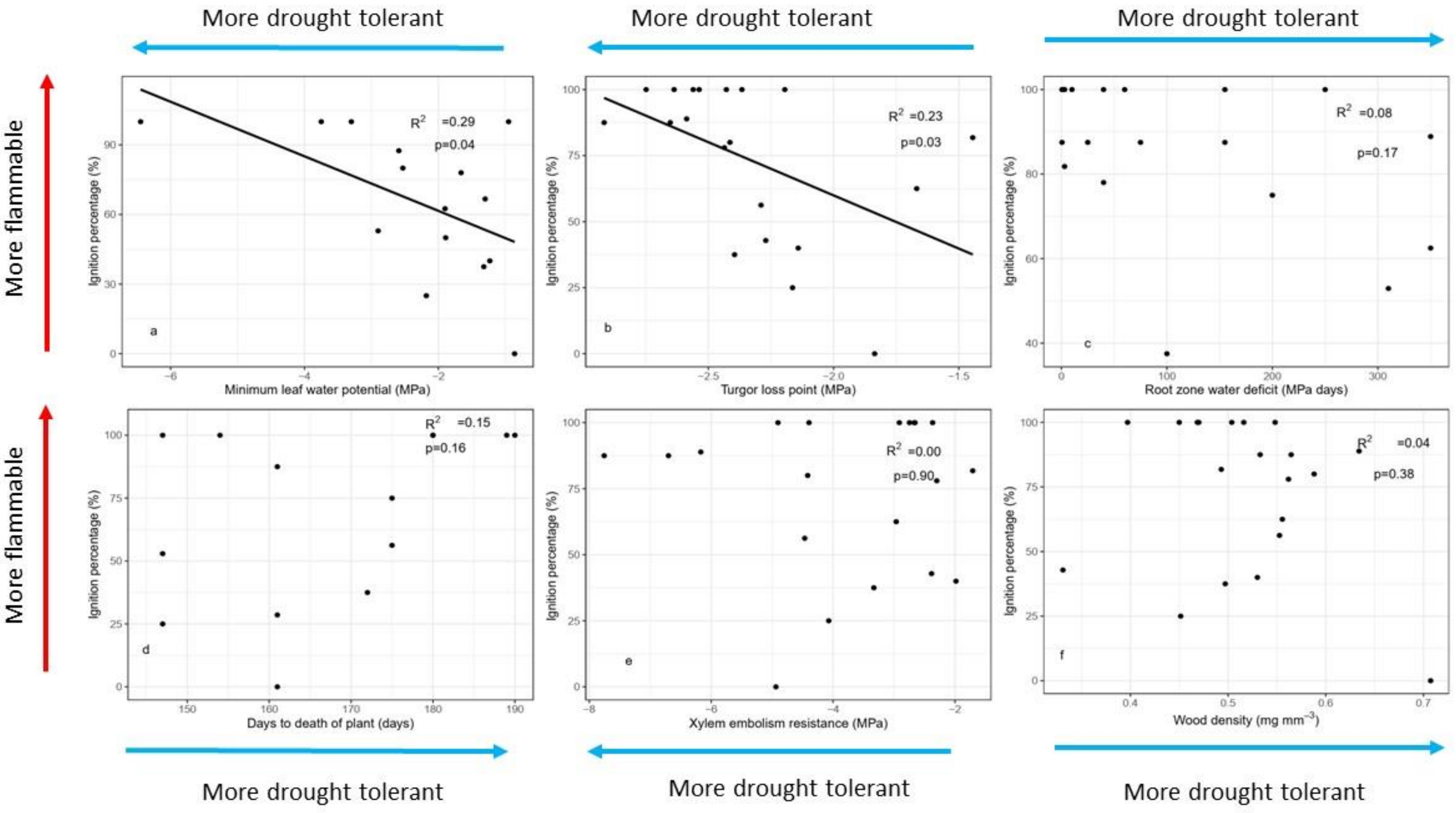

Figure A2.2 The relationship between ignition percentage (%) and drought tolerance traits minimum leaf water potentials (a), leaf turgor loss point (b), root zone water deficit days (c), days to death of plants (d), xylem embolism resistance (e), wood density (f).

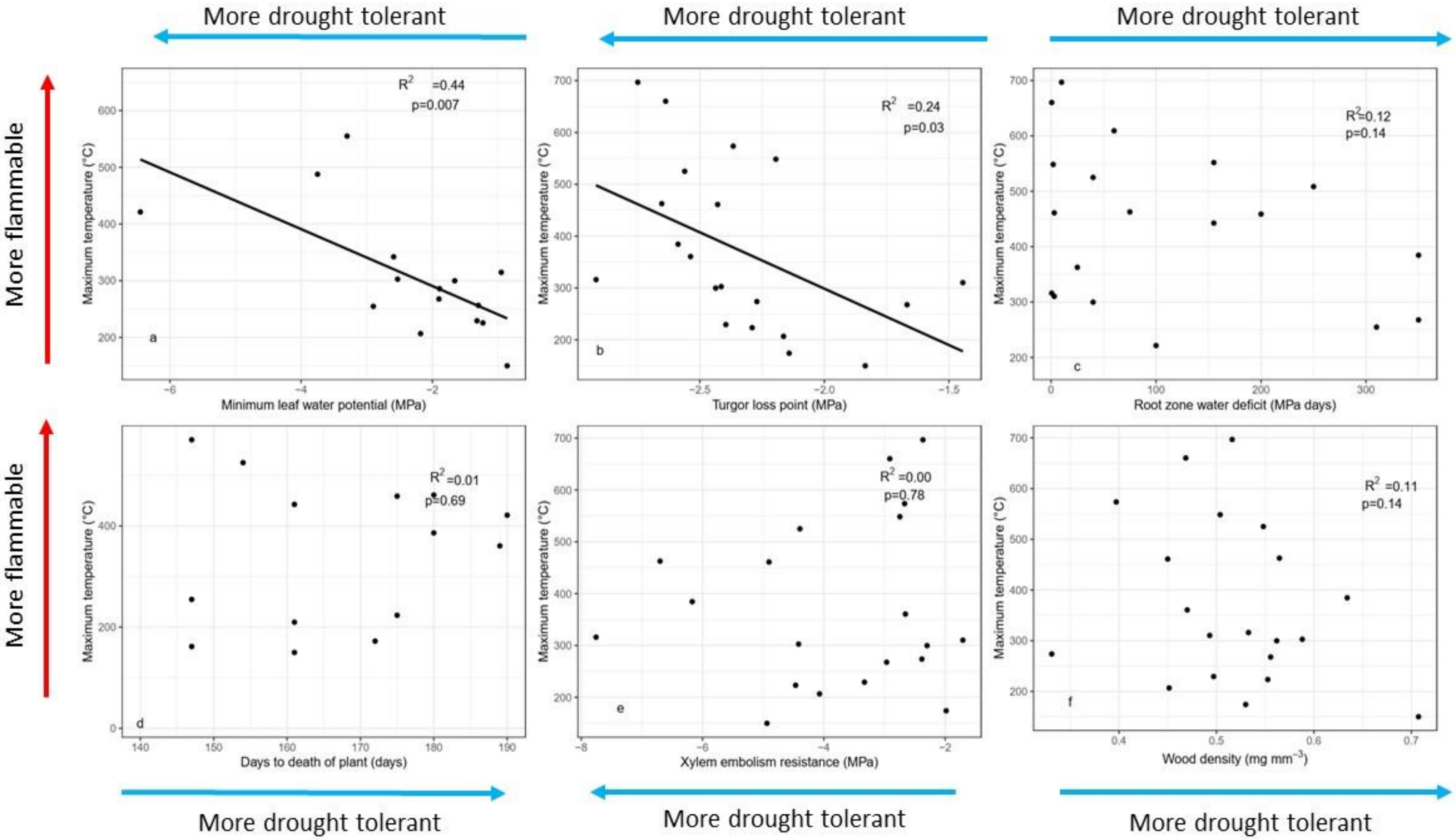

Figure A2.3 The relationship between maximum temperature (°C) and drought tolerance traits minimum leaf water potentials (a), leaf turgor loss point (b), root zone water deficit days (c), days to death of plants (d), xylem embolism resistance (e), wood density (f).

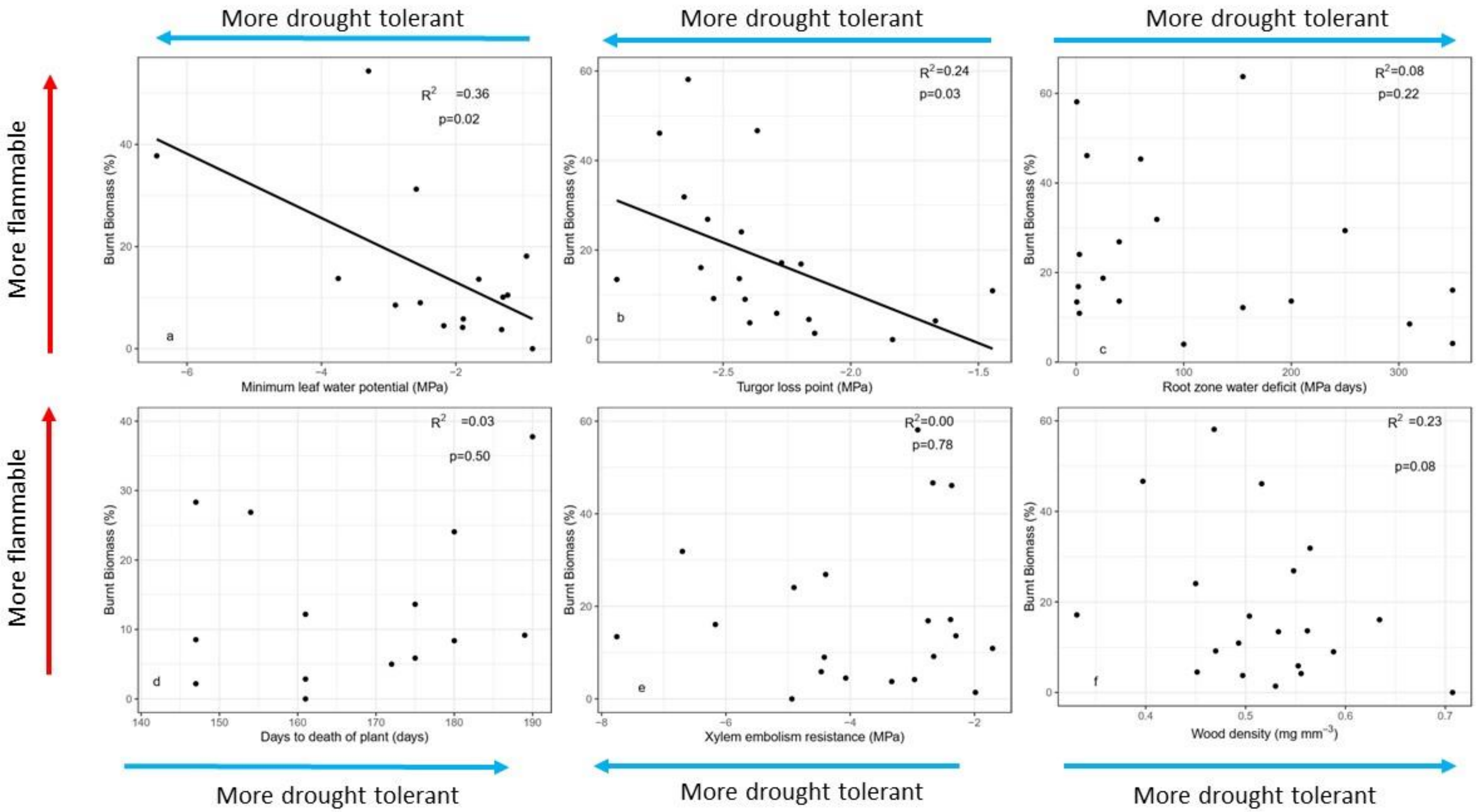

Figure A2.4 The relationship between burnt biomass (%) and drought tolerance traits, minimum leaf water potentials (a), leaf turgor loss point (b), root zone water deficit days (c), days to death of plants (d), xylem embolism resistance (e), wood density (f) .

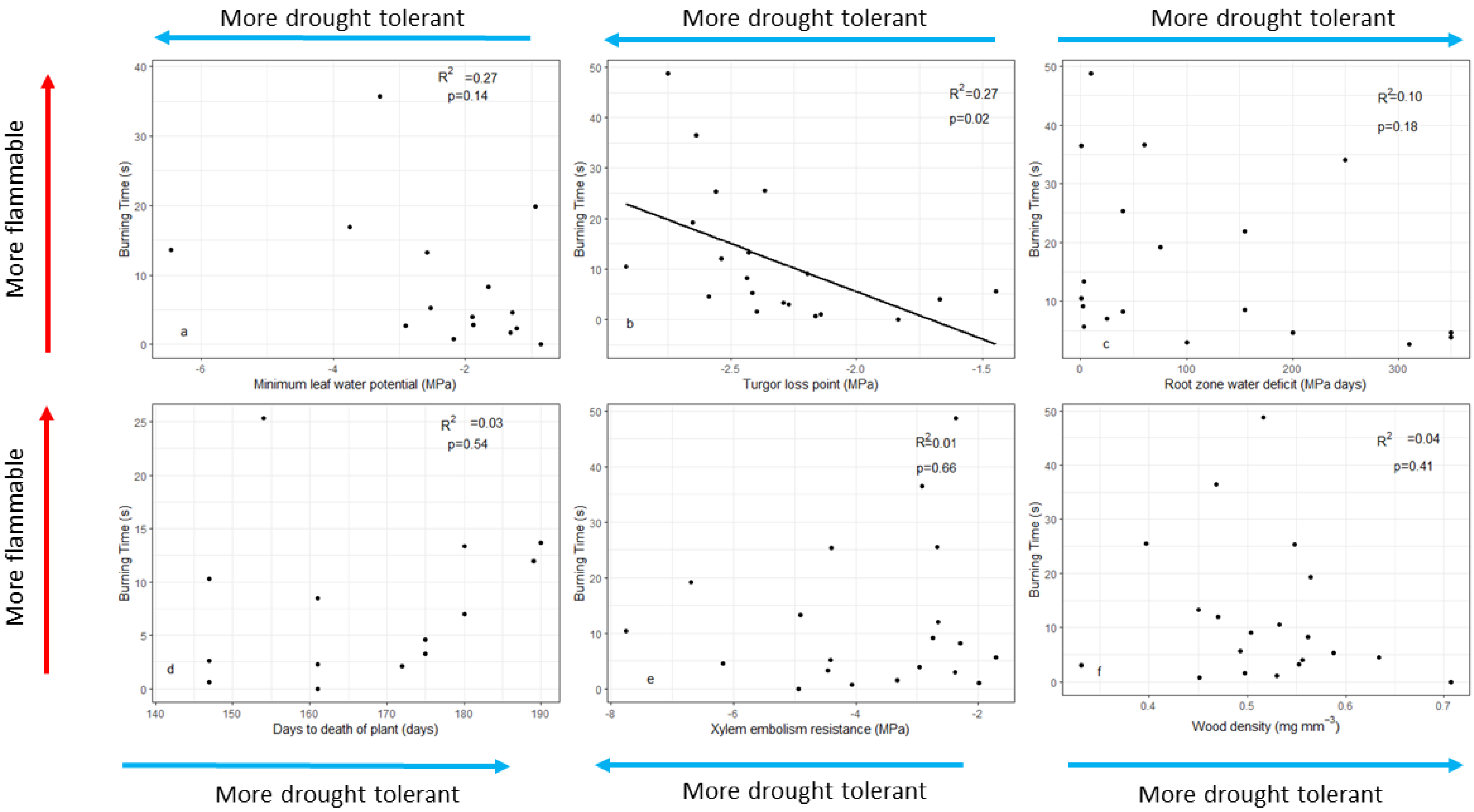

Figure A2.5. The relationship between burning time (s) and drought tolerance traits, minimum leaf water potentials (a), leaf turgor loss point (b), root zone water deficit days (c), days to death of plants (d), xylem embolism resistance (e), wood density (f).

Table A2.1 Species, authority, family, life form, origin, and the approach used to estimate drought response measures (drought study). Drought study categories were drought tolerance of plants measured from a = minimum leaf water potential of unwilted leaf; b = turgor loss point; c = hydrological optima of plants measured from root zone water deficits; d= drought tolerance of plants measured from shade-house dry-down method; e= stem xylem embolism resistance; f= Wood density. Taxonomy follows the New Zealand Plant Conservation Network (see: http://www.nzpcn.org.nz)

Species	**Codes**	**Family**	**Origin**	**Life form**	**Drought study**
Kauri (*Agathis australis* (D.Don) Lindl. ex Loudon)	AGAaus	Araucariaceae	Indigenous	Gymnosperm tree	b, c, d, e, f
Tītoki (*Alectryon excelsus* Gaertn.)	ALEexc	Sapindaceae	Indigenous	Dicotyledenous tree	c
Mākomako (*Aristotelia serrata*) (J.R.Forst. & G.Forst.) W.R.B.Oliv.	ARIser	Elaeocarpaceae	Indigenous	Dicotyledenous tree	b, e, f
Taraire (*Beilschmiedia tarairi* (A.Cunn.) Benth. And Hook.f. ex Kirk)	BEItar	Lauraceae	Indigenous	Dicotyledenous tree	c, d
Tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. and Hook.f. ex Kirk)	BEItaw	Lauraceae	Indigenous	Dicotyledenous tree	c
Marble Leaf (*Carpodetus serratus* J.R.Forst & G.Forst.)	CARser	Grossulariaceae	Indigenous	Dicotyledenous tree	b, d, e, f
Tree lucerne (*Chamaecytisus palmensis* (Christ) Bisby et K. Nicholls)	CHApal	Fabaceae	Exotic	Dicotyledenous tree	a
Karamū (*Coprosma robusta* Raoul)	COProb	Rubiaceae	Indigenous	Dicotyledenous tree	a, b, d, e, f
Scotch Broom (*Cytisus scoparius* (L.) Link)	CYTsco	Fabaceae	Exotic	Dicotyledenous shrub	a
Rimu (*Dacrydium cupressinum* Lamb.)	DACcup	Podocarpaceae	Indigenous	Gymnosperm tree	b, c, e, f
Kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.	DACdac	Podocarpaceae	Indigenous	Gymnosperms tree	b, e, f
Kohekohe (*Dysoxylum spectabile* (G.Forst) Hook.f.)	DYSspe	Meliaceae	Indigenous	Dicotyledenous tree	c
Kōtukutuku (*Fuchsia excorticata* (J.R.Forst. and G.Forst.) L.f.)	FUSexc	Onagraceae	Indigenous	Dicotyledenous tree	b, c, e, f
Red Beech (*Fuscospora fusca* (Hook.f.) Heenan et Smissen)	FUSfus	Nothofagaceae	Indigenous	Dicotyledenous tree	a, b, c, e, f

Hangehange (*Geniostoma ligustrifolium* A.Cunn.)	GENlig	Loganiaceae	Indigenous	Dicotyledenous shrub	d
Broadleaf (*Griselinia littoralis* Raoul)	GRIlit	Cornaceae	Indigenous	Dicotyledenous tree	a, b, c, e, f
Narrow-leaved lacebark (*Hoheria angustifolia* (Raoul) Hook.f.)	HOHang	Malvaceae	Indigenous	Dicotyledenous tree	a
Rewarewa (*Knightia excelsa* R.Br.)	KNIexc	Proteaceae	Indigenous	Dicotyledenous tree	b, c, d, e, f
Kānuka (*Kunzea ericoides* (A.Rich) Joy Thomps. sensu lato.A)	KUNeri	Myrtaceae	Indigenous	Dicotyledenous tree	a, d
Manuka (*Leptospermum scoparium* J.R.Forst. and G.Forst.)	LEPsco	Myrtaceae	Indigenous	Dicotyledenous tree	a
Silver Beech (*Lophozonia menziesii* (Hook.f.) Heenan and Smissen)	LOPmen	Nothofagaceae	Indigenous	Dicotyledenous tree	b, c, e, f
Māhoe (*Melicytus ramiflorus* J.R.Forst. and G.Forst.)	MELram	Violaceae	Indigenous	Dicotyledenous tree	a, c, d
Ngaio (*Myoporum laetum* G.Forst.)	MYPlae	Scrophulariaceae	Indigenous	Dicotyledenous tree	a
Mapau (*Myrsine australis* (A.Rich.) Allan)	MYRaus	Myrsinaceae	Indigenous	Dicotyledenous tree	d
Maire (*Nestegis lanceolata* (Hook.f.) L.A.S.Johnson)	NESlan	Oleaceae	Indigenous	Dicotyledenous tree	c
Kaikomako (*Pennantia corymbosa* J.R.Forst. et G.Forst.)	PENcor	Pennantiaceae	Indigenous	Dicotyledenous tree	a, b, e, f
Tanekaha (*Phyllocladus trichomanoides* D.Don)	PHYtri	Phyllocladaceae	Indigenous	Gymnosperm tree	b, c, e, f
Karo (*Pittosporum crassifolium* Banks and Sol. ex A.Cunn.)	PITcra	Pittosporaceae	Indigenous	Dicotyledenous tree	d
Tarata (*Pittosporum eugenioides* A.Cunn)	PITeug	Pittosporaceae	Indigenous	Dicotyledenous tree	b, c, e, f
Kohuhu (*Pittosporum tenuifoluum* Sol. ex Gaertn.)	PITten	Pittosporaceae	Indigenous	Dicotyledenous tree	a, b, e, f
Mountain totara *(Podocarpus laetus* (Hooibr. ex Endl.)	PODlae	Podocarpaceae	Indigenous	Gymnosperm tree	a
Tōtara (*Podocarpus totara* G.Benn. ex D.Don)	PODtot	Podocarpaceae	Indigenous	Gymnosperm tree	b, c, d, e, f
Miro (*Prumnopitys ferruginea* (D.Don) de Laub.)	PRUfer	Podocarpaceae	Indigenous	Gymnosperm tree	b, d, e, f
Five-finger (*Pseudopanax arboreus* (Murray) Philipson)	PSEarb	Araliaceae	Indigenous	Dicotyledenous tree	d
Lancewood (*Pseudopanax crassifolius*) (Sol. ex A.Cunn.) C.Koch	PSEcra	Araliaceae	Indigenous	Dicotyledenous tree	b, e, f

Poroporo (*Solanum laciniatum* (f. novozelandicum) Herasim)	SOLlac	Solanaceae	Indigenous	Dicotyledenous tree	a
Kōwhai (*Sophora microphylla* (Aiton) Salisb.)	SOPmic	Fabaceae	Indigenous	Dicotyledenous tree	a, b, d, e, f
Priūri (*Vitex lucens* Kirk)	VITluc	Lamiaceae	Indigenous	Dicotyledenous tree	c, d
Kāmahi (*Weinmannia racemosa* L.f.)	WEIrac	Cunoniaceae	Indigenous	Dicotyledenous tree	b, c, e, f

TABLE A2.2 Phylogenetic signal of flammability variables (flammability (PC1) score, ignition percentage, maximum temperature reached, burnt biomass, burn time) and drought response traits. Bold denotes statistically significant (*P* < 0.05) phylogenetic signal. Conifer analysis was only included when there were four or six replicates (numbers of conifer species). No correction of alpha was made for multiple tests.

Data source	**N= number of species**	**Response traits**	**Predictor trait**	**Response trait Pagel's λ**	**Predictor trait Pagel's λ**	**PGLS coefficient (1 SE)**
Bannister (1986)	15	Flammability score	Minimum leaf water potential	0.90 (*P* = 0.31)	<0.06 (*P* = 1)	-0.65 (0.26)
			Angiosperm	0.35 (*P* = 0.38)	0.85 (*P* =0.06)	0.54 (0.26)
Laughlin et al. (2020)	20	Flammability score	Turgor loss point	0.28 (*P* = 0.32)	0.30 (P =0.28)	-2.44 (1.18)
			Angiosperm	1.09 (*P* = 0.31)	1.01 (*P* =0.72)	2.44 (1.18)
			Conifer	0.56 (*P*=1)	1.1 (*P* =0.67)	2.60 (4.32)
Leathwick & Whitehead (2001)	19	Flammability score	Root zone water deficit	<0.01 (*P* = 1.0)	0.80 (*P* = 0.19)	-0.005 (0.003)
			Angiosperm	<0.01 (*P* = 1.0)	<0.05 (*P* = 1.0)	-0.004 (0.003)
			Conifer	<0.01 (*P* = 1.0)	0.99 (*P* = 0.67)	-0.003 (0.03)
Seward (2016)	14	Flammability score	Days to death	<0.01 (*P* = 1.0)	0.33 (*P* = 0.84)	0.056 (0.02)
			Angiosperm	<0.01 (*P* = 1.0)	<0.01 (*P* = 1.0)	0.06 (0.023)
Laughlin et al. (2020)	20	Flammability score	Stem embolism resistance	0.32 (*P*=0.38)	<0.06 (*P* =1.0)	0.09 (0.23)
			Angiosperm	1.09 (*P*=0.50)	0.10 (*P* = 0.88)	-0.101 (0.354)
			Conifer	0.56 (*P* = 1.0)	1.37 (*P* = 1.82)	-15.37 (16.82)
Laughlin et al. (2020)	20	Flammability score	Wood density	0.30 (*P* =0.30)	<0.01 (*P* =1.0)	-1.21 (5.18)
			Angiosperm	1.09 (*P* = 30)	0.97 (*P* = 0.53)	1.50 (5.84)
			Conifer	0.56 (*P* = 0.1)	<0.01 (*P* = 1.0)	-10.37 (13.82)
Banister (1986)	15	Ignition percentage	Minimum leaf water potential	0.98 (*P* = 0.35)	<0.06 (*P* = 0.1.0)	-7.133 (5.14)
			Angiosperm	1.09 (*P* = 30)	0.97 (*P* = 0.53)	-4.07 (5.01)
Laughlin et al. (2020)	20	Ignition percentage	Turgor loss point	0.19 (*P* =0.56)	0.30 (P=0.28)	-28.0 (15.6)

			Angiosperm	1.01 (*P* = 0.72)	1.07 (*P* = 0.56)	-23.0 (19.9)
			Conifer	1.37 (*P* = 0.1)	<0.01 (*P* = 1.0)	14.4 (11.90)
Leathwick& Whitehead (2001)	19	Ignition percentage	Root zone water deficit	<0.01 (P=1.0)	0.80 (*P* = 0.19)	-0.06 (0.03)
			Angiosperm	1.01 (*P* = 0.72)	0.59 (*P* = 0.27)	-0.05 (0.03)
			Conifer	0.99 (*P* = 0.30)	0.99 (*P* = 0.30)	0.14 (0.51)
Seward (2016)	14	Ignition percentage	Days to death	<0.01 (*P* = 1.0)	0.32 (P=0.84)	0.54 (0.03)
			Angiosperm	<0.09 (*P* = 1)	<0.05 (*P* = 0.1)	0.64(0.75)
Laughlin et al. (2020)	20	Ignition percentage	Stem embolism resistance	1.02 (*P* = 0.56)	0.10 (*P* = 0.88)	-1.34 (2.96)
			Angiosperm	1.09 (*P* = 30)	0.97 (*P* = 0.53)	-2.19(5.27)
			Conifer	1.37 (*P* = 0.18)	1.37 (*P* = <0.08)	21.1 (0.23)
Laughlin et al. (2020)	20	Ignition percentage	Wood density	<0.05 (*P*=1.0)	0.15 (*P* = 0.56)	51.8 (67.17)
			Angiosperm	1.07 (*P* = 56)	0.97 (*P* = 0.53)	2.05(1.00)
			Conifer	**1.38 (*P* = <0.008)**	<0.05 (*P* = 1.0)	-90.2 (28.1)
Bannister (1986)	15	Maximum temperature	Minimum leaf water potential	0.83 (*P* =0.41)	<0.06 (*P* =1.0)	-30.86 (16.19)
			Angiosperm	0.18 (*P* = 0.71)	0.35 (*P* = 0.38)	-30.90 (16.19)
Laughlin et al. (2020)	20	Maximum temperature	Turgor loss point	0.13 (*P* =0.57)	0.30 (*P* =0.28)	-203.01 (88.45)
			Angiosperm	0.13 (*P* = 0.86)	1.01 (*P* 0.72)	-224.67 (102.9)
			Conifer	<0.05 (*P* = 1)	<0.05 (*P* = 1)	293.01 (308.5)
Leathwick & Whitehead (2001)	19	Maximum temperature	Root zone water deficit	<0.01 (*P*=1.0)	0.81 (*P*=0.19)	-0.39 (0.24)
			Angiosperm	<0.06 (*P* = 1)	0.59 (*P* = 0.27)	-0.39 (0.29)
			Conifer	<0.05 (*P* = 1)	1.0 (*P* =0.67)	293.01(308.5)
Seward (2001)	14	Maximum temperature	Days to death	<0.01 (P=1.0)	0.32 (P=0.84)	0.88 (2.72)
			Angiosperm	<0.05 (*P* = 1)	<0.06 (*P* = 1)	-0.39 (0.29)
Laughlin et al. (2020)	20	Maximum temperature	Stem embolism resistance	0.13 (*P* = 0.57)	<0.01 (*P* = 1.0)	16.095 (20.23)
			Angiosperm	0.12 (*P* = 0.86)	0.10 (*P* = 0.88)	-0.10.02 (31.36)
			Conifers	<0.05 (*P* = 1)	<0.06 (*P* = 1)	11.95 (20.81)

Laughlin et al. (2020)	20	Maximum temperature	Wood density	0.19 (P=0.45)	<0.01 (*P* = 1.0)	-266.77 (423.04)
			Angiosperm	0.97 (*P* = 0.53)	0.12 (*P* = 0.86)	96.81 (524.05)
			Conifers	<0.05 (*P* = 1)	<0.06 (*P* = 1)	-996.4(999.4)
Bannister (1986)	15	Burnt biomass	Minimum leaf water potential	**0.74 (*P*=0.04)**	0.35 (*P* =0.38)	-6.01 (2.23)
			Angiosperm	**0.74 (*P*=0.03)**	0.35 (*P* =0.38)	-5.66 (2.23)
Laughlin et al. (2020)	20	Burnt biomass	Turgor loss point	0.33 (*P* =0.14)	0.29 (*P* = 0.28)	-19.54 (7.11)
			Angiosperm	0.57 (*P* = 0.38)	1.01 (*P* = 0.72)	-16.18 (9.35)
			Conifers	<0.05 (*P* = 1)	<0.06 (*P* = 1)	30.13 (44.6)
Leathwick & Whitehead (2001)	19	Burnt biomass	Root zone water deficit	<0.01 (*P* =1.0)	0.80 (*P* =0.19)	-0.041 (0.033)
			Angiosperm	<0.06 (*P* = 1.0)	0.59 (*P* = 0.27)	-0.034 (0.036)
			Conifers	0.99 (*P* = 0.67)	<0.06 (*P* = 1)	-0.004(0.366)
Seward (2016)	14	Burnt biomass	Days to death	<0.01 (*P* = 1.0)	0.32 (*P* = 0.84)	0.147 (0.215)
			Angiosperm	<0.06 (*P* = 1.0)	<0.07 (*P* = 1.0)	0.16 (0.261)
Laughlin et al. (2020)	20	Burnt biomass	Stem embolism resistance	0.63 (*P* = 0.35)	0.10 (*P* = 0.88)	2.02 (1.96)
			Angiosperm	<0.06 (*P* = 1.0)	<0.07 (*P* = 1.0)	0.16 (0.261)
			Conifers	<0.05 (*P* = 1)	1.37 (*P* = 0.18)	-0.33 (0.19)
Laughlin et al. (2020)	20	Burnt biomass	Wood density	0.35 (P=0.13)	<0.01 (P=1.0)	-31.70 (42.26)
			Angiosperm	0.63 (*P* = 0.35)	0.97 (*P* = 0.53)	-0.83 (38.84)
			Conifers	0.99 (*P* = 0.67)	<0.06 (*P* = 1)	-0.004 (0.37)
Bannister (1986)	15	Burning time	Minimum water potential	<0.06 (*P*=1.0)	<0.06 (*P*=1.0)	-2.53 (1.76)
			Angiosperm	0.35 (*P* = 0.38)	0.39 (*P* = 0.31)	-2.46 (1.861)
Laughlin et al. (2020)	20	Burning time	Turgor loss point	0.08 (P=0.73)	0.30 (P=0.28)	-17.91 (7.31)
			Angiosperm	1.12 (*P* = 0.06)	1.01 (*P* = 0.72)	-18.46 (8.92)
			Conifers	<0.05 (*P* = 1)	<0.05 (*P* = 1)	-9.16 (28.51)
Leathwick &Whitehead (2001)	19	Burning time	Root zone water deficit	<0.06 (P=1.0)	0.80 (*P*=0.19)	76.5 (0.025)
			Angiosperm	<0.06 (*P*=1.0)	0.59 (*P* =0.27)	-0.03 (0.023)

			Conifers	<0.06 (*P* =1.0)	0.99 (*P* =0.67)	-0.03 (0.023)
Seward (2016)	14	Burning time	Days to death	<0.01 (*P* = 1.0)	0.33 (*P* =0.84)	0.0813 (0.130)
			Angiosperm	<0.06 (*P*=1.0)	0.59 (*P* =0.27)	-0.03 (0.023)
Laughlin et al. (2020)	20	Burning time	Stem embolism resistance	0.18 (*P*=0.50)	<0.01 (*P* = 1.0)	1.51 (1.69)
			Angiosperm	1.1 (*P*=0.06)	10.06 (*P* =0.88)	69.03 (2.64)
			Conifers	<0.504 (*P* =1)	1.37 (*P*=0.18)	104.04 (5.74)
Laughlin et al. (2020)	20	Burning time	Wood density	0.69 (*P*=0.07)	<0.01 (*P* = 1.0)	-13.51 (36.12)
			Angiosperm	54 (*P* =0.58)	0.97 (*P*=0.53)	-0.74 (43.58)
			Conifers	<0.06 (P=1.0)	0.99 (*P* =0.67)	-0.47 (91.23)

Appendix B

Supplementary information of Chapter 3

B 3.1 Supplementary information

Table B3.1 Details of plant species included in this study. Taxonomic follows the New Zealand plant conservation network (see: https://www.nzpcn.org.nz/)

Species	Code	Family	Origin	Life form
Scotch Broom (Cytisus scoparius L.)	CYTsco	Fabaceae	Western and central Europe	Angiosperm trees
Broadleaf (*Griselinia littoralis* Raoul)	GRIlit	Cornaceae	New Zealand	Angiosperm trees
Kanuka (*Kunzea robusta* de Lange et Toelken)	KUNrob	Myrtaceae	New Zealand	Angiosperm trees
Mahoe (*Melicytus ramiflorus* J.R.Forst. and G.Forst.)	MELram	Violaceae	New Zealand	Angiosperm trees
Lemonwood (*Pittosporum eugenioides* A.Cunn)	PITeug	Pittosporaceae	New Zealand	Angiosperm trees
Mountain totara (*Podocarpus cunninghamii* Colenso)	PODcun	Podocarpaceae	New Zealand	Gymnosperm Trees
Lancewood (*Pseudopanax crassifolius* (Sol.exA.Cunn.) C.Koch)	PSEcra	Araliaceae	New Zealand	Angiosperm trees
Horopito (*Pseudowintera colorata* (Raoul) Dandy)	PSEcol	Winteraceae	New Zealand	Angiosperm trees

Mountain five-finger (*Pseudopanax colensoi* (Hook.f.) Philipson var. colensoi)	PSEcole	Araliaceae	New Zealand	Angiosperm trees

Table B3.2 Factors loadings from the principal component analysis of all flammability traits of 10 species.

Flammability Traits	PCA1	PCA2
Ignition score	0.899	-0.274
Maximum temperature (°C)	0.969	-0.101
Burnt biomass (%)	0.970	-0.031
Burning time (s)	0.938	-0.274
Variation (%)	89.19	6.75

Table B3.3 Mean and (±1 standard error) of functional traits of 10 species under this study across sampling time. In the table, *Cytisus scoparious* and *Ulex europaeous* were not used for Chapter 4.

Functional traits	Species	Mean ± standard error			
		April, 19	July, 19	October, 19	February, 20
LMC (%)	*Cytisus scoparious*	57.12±9.8	119.99±12.66	224.53±19.58	57.12±62.3
	Melicytus ramiflorus	368.33±79.9	248.94±53.08	198.73±89.9	391.94± 42
	Pseudopanax colensoi	222.54±7.3	246.36±6.94	253.67±111	231.73± 20
	Griselinia littoralis	241.20±26.9	255.41±50.80	213.67±13.2	239.85± 30
	Pseudopanax crassifolius	291.47±97.4	226.95±14.67	158.14±90	232.89 ±105
	Pittosporum eugenioides	172.10±11.8	147.06±59.27	159.79±101	150.07± 25
	Podocarpus cunninghamii	147.37±9.1	145.35±16.16	152.33±50.1	151.30 ±10
	Kunzea robusta	163.98±9.4	176.56±12.24	123.63±60.1	143.98± 105
	Pseudowintera colorata	155.06±32.7	143.37±4.19	173.91±20.5	141.31± 60
	Ulex europaeous	235.65±18.6	142.78±15.80	103.34±69.3	235.92± 40

Ψ_{stem} (MPa)	*Cytisus scoparious*	-1.12±0.03	-0.83±0.02	-1.31±0.05	-1.52±0.04
	Melicytus ramiflorus	-0.42±0.05	-0.41±0.03	-1.47±0.07	-1.5±0.05
	Pseudopanax colensoi	-0.5±0	-0.24±0	-0.39±0	-0.12±0
	Griselinia littoralis	-0.46±0.02	-0.4±.02	-0.99±0.03	-0.95±0.06
	Pseudopanax crassifolius	-0.21±0.01	-0.27±0.02	-0.27±0.02	-0.78±0.09
	Pittosporum eugenioides	-0.29±0.06	-0.34±0.05	-0.18±0.07	-0.28±0.08
	Podocarpus cunninghamii	-0.72±0.09	-0.21±0.06	-1.64±0.03	-0.94±0.05
	Kunzea robusta	-1.39±0.08	-0.15±0.06	-0.21±0.09	-1.92±0.08
	Pseudowintera colorata	-0.38±0.03	-0.20±0.03	-0.74±0.05	-0.8±0.09
	Ulex europaeous	-1.17±0.06	-1.83±0.09	-1.24±0.05	-1.17±0.02
g_s (mmolm^{-2}s-^{1})	*Cytisus scoparious*	206.12±24.34	248.27±105.2	157.67±50.9	188.71±95.0
	Melicytus ramiflorus	246.54±30.3	201.23±78.5	148.83±19.9	253.97±48.2
	Pseudopanax colensoi	122.92±60.4	127.43±49.7	214.23±65.9	148.56±29.8
	Griselinia littoralis	248.42±21.5	189.57±45.6	130.04±78.2	87.54±13.6
	Pseudopanax crassifolius	175.1±15.1	218.5±98.1	156.59±12.3	156.70±29.8
	Pittosporum eugenioides	108.9±20.7	151.9±14.9	134.27±58.1	87.25±11.8
	Podocarpus cunninghamii	134.48±13.2	130.32±98.6	134.71±78.6	268.03±16.5
	Kunzea robusta	167.52±16.8	297.74±21.1	148.83±98.6	200.49±24.0
	Pseudowintera colorata	125.95±20.5	119.26±87.9	198.02±45.6	81.4±17.2
	Ulex europaeous	98.55±22.8	161.73±56.3	185.3±19.6	154.7±19.4
LRWC (%)	*Cytisus scoparious*	79.08±10.3	97.63±9.56	78.43±5.6	60.08±7.4
	Melicytus ramiflorus	93.87±10.8	82.40±9.8	76.13 ±12.1	85.22 ±3.8
	Pseudopanax colensoi	86.78±10.3	84.27±8.2	95.92±5.1	77.99 ±0.5
	Griselinia littoralis	95.49±6.9	94.52±12.3	85.06±7.6	97.97 ±3.8
	Pseudopanax crassifolius	101.10±9.6	79.66±6.5	88.06±52	79.66 ±1.7
	Pittosporum eugenioides	90.42±5.1	81.69±2.9	77.07±2.34	96.09±0.7
	Podocarpus cunninghamii	86.03±9.2	76.13±10.2	68.67±52	64.21 ±1.3
	Kunzea robusta	86.99±9.3	93.81±12.1	89.45±5.2	92.49 ±6.5

	Pseudowintera colorata	90.04±9.6	88.43±6.6	83.36±5.6	88.20 ±2.3
	Ulex europaeous	69.51±13.2	76.19±14	65.81±2.1	91.99 ±3.8
LDMC (mg gm^{-1})	*Cytisus scoparious*	380.76±52.1	366.98±10.61	270.76±23.43	414.57±17.15
	Melicytus ramiflorus	228.13±17.4	243.72±20.08	274.32±18.06	184.82±13.61
	Pseudopanax colensoi	301.25±5.1	304.47±10.56	284.11±7.35	273.36±16.56
	Griselinia littoralis	291.83±4.8	293.13±6.68	289.43±16.54	293.86±17.16
	Pseudopanax crassifolius	289.42±4.9	330.10±17.28	340.63±27.37	385.32±43.11
	Pittosporum eugenioides	397.45±21.7	343.15±25.62	345.05±17.73	397.14±17.3
	Podocarpus cunninghamii	495.49±15.6	430.32±21.58	451.82±38.2	451.91±36.2
	Kunzea robusta	424.25±55.2	382.12±46.28	492.03±6.28	530.51±46.87
	Pseudowintera colorata	388.71±11.4	324.10±15.32	371.28±34.21	388.74±8.8
	Ulex europaeous	349.38±62.6	389.35±24.36	407.88±6.48	349.38±26.4
LT (mm)	*Cytisus scoparious*	0.2041±0.0030	0.2152±.0.0046	0.2063±0.0039	0.5417±0.0017
	Melicytus ramiflorus	0.3573±0.0081	0.3948±0.017	0.2057±0.091	0.3744±0.0008
	Pseudopanax colensoi	0.3652±0.0025	0.4543±0.0019	0.3496±0.001	0.3103±0.0055
	Griselinia littoralis	0.5229±0.0005	0.5786±0.0011	0.5638±0.0081	0.5590±0.0078
	Pseudopanax crassifolius	0.6505±0.0021	0.5509±0.0098	0.7600±0.0087	0.5154±0.0098
	Pittosporum eugenioides	0.3854±0.0087	0.2877±0.0098	0.3637±0.0032	0.2922±0.0052
	Podocarpus cunninghamii	0.8534±0.0010	0.8253±0.0009	0.8152±0.0120	0.9872±0.0630
	Kunzea robusta	0.1292±0.0058	0.1812±0.0095	0.1145±0.085	0.1752±0.0093
	Pseudowintera colorata	0.2245±0.023	0.3055±0.045	0.2361±0.0561	0.2255±0.085
	Ulex europaeous	0.3847±0.0256	0.3885±0.058	0.3847±0.0098	0.4826±0.0078
LA (cm^2)	*Cytisus scoparious*	0.5551±0.0116	0.2152±0.0251	0.6225±0.0631	0.5001±0.0964
	Melicytus ramiflorus	45.20±4.5213	25.5±3.52	57.73±2.1365	44.80±2.1234
	Pseudopanax colensoi	30.36±1.36	24.41±2.85	36.61±2.36	43.53±7.12
	Griselinia littoralis	48.87±2.6	52.87±5.6	39.85±1.8	38.68±4.8
	Pseudopanax crassifolius	53.92±8.3	42.37±1.9	45.62±6.3	46.99±2.3
	Pittosporum eugenioides	35.92±5.6	22.86±6.9	36.59±1.8	35.92±5.2
	Podocarpus cunninghamii	0.33±0.0791	0.37±0.0254	0.4375±0.0154	0.4359±0.0083
	Kunzea robusta	0.20±0.071	0.20±0.009	0.27±0.0069	0.21±0.0041

	Pseudowintera colorata	9.80±0.742	12.69±0.456	19.49±0.406	14.18±0.362
	Ulex europaeous	0.4183±0.0025	0.3245±.001	0.3751±.0003	0.4546±0.000
SLA (gmcm-^{2})	*Cytisus scoparious*	102.93±30.5	159.03±25.4	83.47±12.2	98.56±10.4
	Melicytus ramiflorus	214.17±14.2	203.88±21.1	101.42±14.2	244.34±41.5
	Pseudopanax colensoi	167.42±80.1	160.33±14.2	137.51±17.8	127.23±19.2
	Griselinia littoralis	142.15±13.5	125.15±10.1	152.12±11.2	122.36±13.8
	Pseudopanax crassifolius	77.33±3.6	125.15±9.5	53.56±5.9	91.09±5.9
	Pittosporum eugenioides	178.60±8.5	157.72±12.1	98.90±9.6	135.04±8.9
	Podocarpus cunninghamii	35.44±3.6	39.30±4.5	63.91±9.8	29.33±8.7
	Kunzea robusta	120.03±7.8	91.2±5.2	112.2±12.1	99.19±7.9
	Pseudowintera colorata	76.34±6.1	84.29±6.3	111.08±10.5	89.77±2.9
	Ulex europaeous	130.77±9.8	33.40±4.9	129.98±11.9	129.98±14.9
BD (kgm-^{3})	*Cytisus scoparious*	1.29±0.32	1.82±0.14	0.67±0.08	0.76±0.13
	Melicytus ramiflorus	0.57±0.15	1.78±0.33	0.32±0.10	0.57±0.05
	Pseudopanax colensoi	2.58±0.33	2.12±0.11	2.31±0.40	1.8±0.30
	Griselinia littoralis	1.48±0.36	1.15±0.06	1.2±0.35	11.14±0.94
	Pseudopanax crassifolius	0.87±0.17	1.52±0.18	2.43±1.58	0.71±0.12
	Pittosporum eugenioides	1.21±0.15	2.09±0.38	0.82±0.38	1.17±0.17
	Podocarpus cunninghamii	3.91±1.1	2.35±0.28	2.96±0.4	4.05±0.64
	Kunzea robusta	1.41±0.8	0.15±0.45	1.90±0.21	2.12±0.09
	Pseudowintera colorata	1.78±0.5	3.17±0.19	1.33±0.25	3.12±0.29
	Ulex europaeous	1.62±0.09	0.78±0.08	1.47±0.21	1.95±0.09

Appendix C

Supplementary information of Chapter 4

C 4.1 Supplementary information

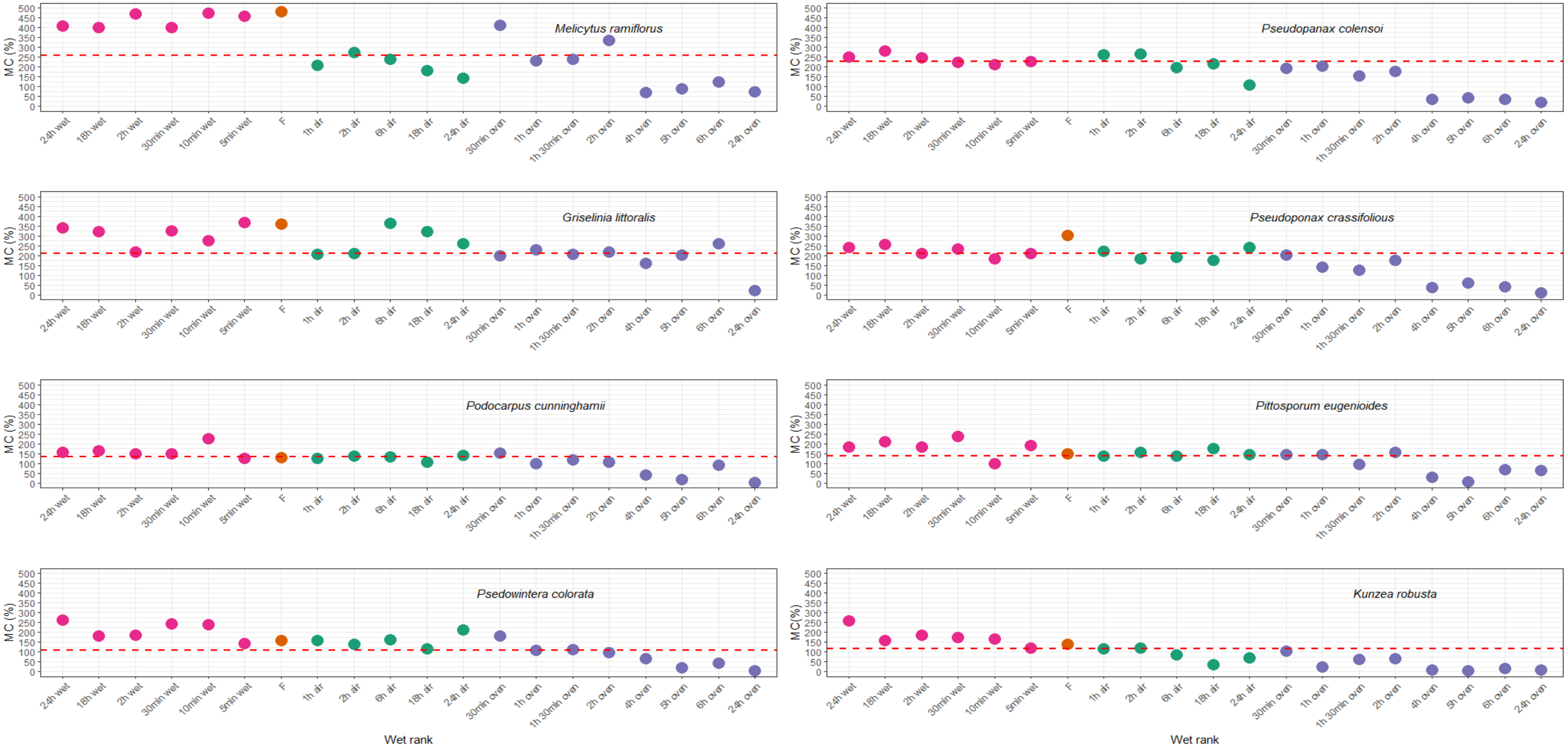

Figure C 4.1 Plot of shoot moisture content (MC%) of eight species according to different moisture manipulation treatments. Dotted red line shows breakpoint in MC% for each species at ignition score derived from piecewise regression (see section 4.3.2). F = fresh (samples were burnt fresh without additional moisture manipulation). Wet = wetting up for the specified time, air = air-dried for the specified time, oven = oven-dried for the specified time. Fresh MC% (700) taken out from *Pseudopanax colensoi*, because of outlier.

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