

Spatial and temporal heterogeneity of plant flammability

by

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Abstract

Heterogeneity in the natural environment has led to plants adapting traits to fit a niche. Within natural systems, fire has been a major driver of vegetation across the globe. Flammability has been suggested by many to be a trait adapted to reoccurring fire events. Much of the literature on flammability is theoretical and little has been done to cement it as a functional trait. In this thesis, I explore flammability across a wide range of plant species from both fire-free and -driven communities and compare observed results to other functional traits to identify if any link may exist between fire and being flammable. I further focus on the impact moisture availability may have on flammability as fire regimes are often correlated to rainfall season. Lastly, I investigate how different vegetation types respond to seasonal climate in terms of flammability. As a functional trait, flammability does correlate with traits associated with fire-driven system (e.g. small leaves in dense twig matrix). However, fire associated traits were also observed in fire-free species (Forest, Thicket, and Nama-Karoo), and in some cases traits not associated to fire proved flammable (e.g. large leaves on trees). I find that at a regional scale, plant moisture only correlates to flammability when rainfall amounts are well above or below average (e.g. drought). I also identify that species have different responses to moisture fluctuations and that inherent or accidental responses may influence observed flammability (e.g. trichomes). Lastly, I note that some biomes indicate strong association to season or climate (Fynbos and Thicket), while others indicate plasticity towards weather with species having different responses (Grassland). The study is the first to present estimates of flammability across a large number of species sampled at different times of the year. Future research will have to approach flammability as a meta-analysis by experimenting on different scales, particularly temporal and spatial scales.

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1. Introduction to flammability: plants to ecosystems.

1.1. Background

The topic of this thesis is the heterogeneity — both in time and space — of plant flammability. Fire plays a crucial role in increasing the diversity of vegetation (and species) and has driven fire adaptation over millions of years. Before focussing on fire as a driver of diversity, I first want to examine vegetation heterogeneity in general. Heterogeneity describes how distinct things are from each other within a setting. In landscape ecology, it is used to describe how dissimilar vegetation is among different areas (Chapin et al., 2011). The reason why broader landscapes are often more heterogeneous is due to the numerous environmental factors that impact upon them. Environmental heterogeneity is high in South Africa, which has nine distinct terrestrial biomes that often co-occur within a relatively small area. Chapin et al., (2011) suggest that landscape heterogeneity is a result of environmental variation, population and community processes, and disturbance. At a global scale, climate is primarily the controlling factor in determining vegetation (Bailey, 2004; Neilson, 1991). A text book example of this is the change from tropical vegetation near the equator to temperate vegetation near the arctic poles. Where climatic conditions are similar, still on global scale, we find similar vegetation, for example Mediterranean-type ecosystems. At a landscape scale we see that geology and soil, along with topography play an important role. The bontveld, found in the Eastern Cape is an example of this as Thicket clumps occur on calcareous soil within a matrix of Grassland found on shale-based soil. Geology strongly influences soil depth and thus, in many cases, the availability of moisture and nutrients (Chapin et al., 2011; Lévêque, 2003). Topography (hills and valleys) can further control vegetation pattern. Around the Eastern Cape, where climate is reasonably uniform, we tend to find afro-montane forest patches in valleys that act as fire refuge while grasslands appear on hills and mountain where they are more prone to burn. At an even finer scale we find other factors that influence vegetation and they themselves can be influenced by climate. These factors include nutrients, moisture availability, erosion, and wind (Lévêque, 2003; Richards et al., 2013; Schulze, 1997). At the local scale biotic factors play a role as well, specifically herbivory and competition (van As et al., 2016). Although fire is known as a driving factor for vegetation, the extent has mostly been researched and noticed in recent literature (past 50 years). Fire as a driving factor can be observed across the world and in vastly different vegetation types —

from the arctic tundra and boreal forests to the tropical grasslands and savannas (Bond and van Wilgen, 1996).

Fire has influenced ecosystems for millions of years (Bowman et al., 2009) and is capable of dictating the distribution of vegetation within the landscape. Fire is said to have been driving adaptation of vegetation and traits since the Miocene (Keeley et al., 2011), particularly grass dominated systems. Here in South Africa, it has been demonstrated that Fynbos species such as the *Ericas* and *Proteas* have been adapting to fire since the late Miocene in a low CO₂ environment (Bond et al., 2003; Lamont et al., 2013). Fire, as a frequently occurring variable in an ecosystem, is best characterised using fire regime categories (Whelan, 1995). The regimes are determined from a range of aspects such as fire frequency, fire season, and fire intensity (Bond & van Wilgen, 1996). Fire frequency is the interval between fire events, for example: ~4-14 years are common in Fynbos compared to ~2-5 years in Savanna systems (Van Wilgen and Scholes, 1997). Fire events may occur if there is sufficient biomass and suitable weather conditions — suitable conditions would include dry spells with chance of lightning and often coupled with wind (Bond, 1997). These conditions are usually seasonal, restricted to parts of the year, and this determines the fire season. Even though fire is prevalent across South Africa, the seasons of fire vary spatially. Fires commonly burn during the summer-drought prevalent in the south-western region of the country, whereas the eastern half of the country experiences fire during the winter-drought period (van Wilgen & Scholes, 1997). In both cases, rainfall seasons precede the fire season usually allowing for sufficient biomass build-up. Lastly, fire intensity forms part of the fire regime and is strongly influenced by the plant species present (their biomass accumulation and individual flammability), the time since the last fire, as well as the current and preceding weather conditions at time of fire (e.g. Berg winds and drought).

Returning to the topic of heterogeneity, we often see that a landscape, such as a mountain range, is rarely uniformly covered by a single vegetation type. Thus, one needs to look at the links amongst environmental factors between different scales. Despite a mountain ridge and adjacent valley receiving the same regional climatic conditions, the vegetation will rarely be similar across the range. An apt example is the area in which the research for this thesis was conducted: the Suurberg Mountain range in the Eastern Cape of South Africa. More specifically, my study site was an area within this range characterised by two parallel valleys

with near straight mountain ridges enclosing the valleys. The north-facing upper slopes of the mountains are covered in Grassland while the south-facing is covered in Fynbos. The valley sides are dominated by Thicket with Forest patches in the sheltered gorges. The valley bottoms are dominated by Nama-Karoo with few clumps of Xeric Thicket. Fire is able to control the boundary between the fire-prone biomes and the Thicket by negatively affecting the establishment of thicket species in the fire-prone systems. This boundary is strongly related to fire as Thicket would be able to occur in the same conditions as either Fynbos or Grassland, given time to establish (Hoare et al., 2006). Clearly fire is of great ecological importance but what do we know about the plant-fire interactions at the different scales?

At a global scale, we can — often using satellite-based technology — discern where fires have occurred and we are able to classify vegetation as being either fire-prone or not. Grasslands, Savannas and the Mediterranean-type shrublands are the most notable fire-prone vegetation while tropical forests are some of the strongly fire-excluding vegetation types. In their seminal paper on the extent to which fire may drive global vegetation patterns, Bond et al. (2005) explored the distribution and extent of ecosystems in a world without fire by simulation and demonstrate the global importance of fire in determining vegetation distribution — in a world without fire, present day humid grasslands and savannas would be forests. In many places, fire-prone and fire-suppressing vegetation co-occur without notable changes in the environment (Coetsee et al., 2015) — this has led to the term “alternative stable state” which refers to biomes that are capable of occupying a terrain under the same environmental conditions (Staver et al., 2011). An example of this is the research done in the Kruger National Park where fires were excluded from a large Savanna dominated area for more than 50 years and savanna has been replaced by forest (Biggs et al., 2003; Higgins et al., 2013). In this situation, the Forest would be called a climax community, a community that dominates when disturbances are removed. As grasslands began to spread 6-8 Mya, it had effectively split large parts of the world into fire tolerant and intolerant biomes. But, how exactly does fire interact with vegetation?

Fire is a non-selective herbivore that can devour any biomass if there is sufficient energy available and correct (i.e. dry) environmental conditions (Bond and Keeley, 2005). Thus, fire intolerant species should occur where the fire spread is retarded, as in fire refugia. In the setting of Kaboega, the Forests are found in the gorges where fire can't reach and the Thicket

is prolific along the steeper shale slopes where flammable grasses struggle to grow due to low soil moisture and sunlight. Along with prevailing weather conditions (e.g. drought) fire can also promote the change of nearly any vegetation type to Grassland or Fynbos. Several cases are known where the introduction of alien grass has led to fires that are then able to reduce the natural fire intolerant biomes and spread the invasive fire-promoting vegetation (Balch et al., 2013; Brooks et al., 2004). This process of invasion occurs as the grasses increase flammable fuel load, promoting fires and the natural vegetation (non-fire adapted) struggle to recover and compete in the post-fire environment. Thus, the type of vegetation can spread, or suppress, fire. In contrast, there are also the biomes that can lead to fire suppression. A familiar example in the southern Cape of South Africa is the Thicket biome. This biome accumulates above-ground biomass which is often coupled with high moisture content, which can limit the spread of fire in the landscape (Hoare et al., 2006). At best, the fire is able to burn the thicket edge shared with a fire-prone biome. Fire rarely infiltrates beyond the biome boundary, but can cause a few scattered patches or individuals to be burned (e.g. wind dispersed flames into drier patches). The question arises as to how fire is able to infiltrate and burn certain plants found in the non fire-driven biomes and similarly how some plants survive fire in a fire-prone setting.

To answer these questions, one needs to examine the fire-plant interactions. Most plant communities are made up of a wide range of species, or with widespread dominance of a single species being somewhat scarce. A succulent plant will take some time to wilt and dry out before it can carry a flame while a grass species may ignite instantly when exposed to fire. Considering this, it is important to note that a functional community is made up of multiple taxa that may be interacting with one another. If we look at any fire-prone biome, we have to consider the frequency of fire that this biome experiences in its fire regime. It is also important to note that there is an important feedback loop between vegetation and fire regimes. Although a 'random' fire event can be seen as being dependent on vegetation condition and fire regime, both of these exist in a balance with one another. If vegetation changes such as Fynbos to Grassland, the fire regime will shift to being more frequent and less intense. Fynbos has fires at intervals from 4-20 years (van Wilgen & Scholes, 1997). In the case of the Fynbos, if fires occurred every 2-3 years, the natural community would not be able to survive as its constituent species will eventually be unable to germinate or resprout enough for survival purposes, thus leading to the establishment of Grassland (Bond, 1984).

Similarly, if the frequency of fire events decreased beyond 40 years, then the Fynbos will gradually be replaced by Forest species, a process that can take a century (Bond and van Wilgen, 1996; Van Wilgen et al., 2010). As mentioned, it has been observed that certain individuals within a fire-intolerant community may burn and also that individual within fire-prone communities may stand to survive a fire event. As the environmental factors are mostly uniform within a community, it is suggested that a plant's ability to ignite relies on more than external factors. A subset of ecology is the focus on functional traits which, in evolutionary terms, are the components a species adapted to cope with the natural environment, such as succulent leaves are adaptations to xeric conditions. Although these traits help to understand a plant's survival ability, a different trait or measure was suggested for specifically focussing on a plant's flammability. Research on the flammability of plants is fairly recent (post 1950), but the scientific interest to understand this trait has been increasing. Community-based fire research has been limited to fire-prone vegetation, largely excluding fire intolerant biomes, with particular emphasis on fire survival and succession (Lawes and Clarke, 2011; Van Wilgen and Richardson, 2012). This limits understanding of traits as many traits may span both fire-prone and fire-resistant communities as well as different environments. Plant traits have been shown to greatly influence flammability. For example, the sclerophyllous shrublands of the Mediterranean are susceptible to fire due to higher dead-to-live material and fine fuel compared to the mesophytic forests in the tropics (Saura-Mas et al., 2010). It is important to note, however, that we cannot explore this topic without the consideration of the other factors in the environment. Moisture is of key importance when considering flammability as well as the production and retention of dead material (Pellizzaro et al., 2007). The retention of dead material, including the production of leaf litter, can greatly increase the susceptibility of burning (He et al., 2011; Keeley et al., 2011). Moving beyond the focus of community flammability to species or individual scales has been challenging as it posts an evolutionary conundrum. How can a species derive traits that increase flammability (thus self-immolate) and survive fire events?

1.2. Literature review

In 1970, Robert Mutch suggested that a species from a fire-prone environment would have “inherent flammable properties that contribute to the perpetuation of fire-dependent plant communities”. However, this was criticised by many as it did not explain how such species would gain flammability in the first place or how they will benefit from it (Snyder, 1984). In 1995, Bond and Midgley revisited this theory and proposed the “kill-thy-neighbour” hypothesis — an individual that is sufficiently flammable to kill its adjacent neighbour *and* have the ability for its offspring to fill the resulting gap would have greater fitness. Still, there has been criticism arguing that an individual would not adapt to promote its own death for fitness (Midgley, 2013; Schwilk and Kerr, 2002). The origins of flammability are still much debated, and this thesis does not directly aim to explore the origins. Rather it focuses on how flammability varies across space and time — specifically across a range of biomes and seasons with varying weather histories.

Research on plant flammability has been hampered by difficulties in measuring flammability at a meaningful scale. Many studies have investigated flammability at the scale of leaves (Alessio et al., 2008; Cornwell et al., 2015; Engber and Varner, 2012) and it is fairly intractable to experimentally study flammability at the scale of large trees or across landscapes. In between these scales, a recent study has developed an experimental design to measure branch-level flammability (Jaureguiberry et al., 2011). Branch-level measurement takes into consideration all of the properties of the leaves but expand on that by including branches, dead-leaf retention, leaf and twig density, and architecture. This method is a simple and standardised measurement, providing ecologists with the means to compare different components of a community and test which traits have a greater effect on plant-level flammability. Recently, Burger and Bond (2015) investigated the traits of certain plants and correlated this with their flammabilities. They found that percentage of dead material and fine fuels contributed to the biomass burnt. Though it does not provide sufficient evidence for flammability adapted traits, it does provide a starting point.

Heterogeneity is seen in the traits adapted by plants as they showcase a large array within a community and these can often be in the form microgeographic adaptations, a sub-topic

under local adaptation (Richardson et al., 2014). Here, plant species are influenced by their local environment; for example, within a species we are likely to find sun acclimated individuals with thicker but smaller (low surface-to-volume ratio) leaves when compared to shade acclimated individuals. Within these local adaptations, we see the impact that other factors can have on the flammability of individuals. If herbivory is high in an area, a single branch might have sparsely arranged leaves and twigs, reducing the likelihood of fire spread throughout the rest of the individual. Similarly, being in shade can result in higher moisture content that will reduce flammability. But, a plant exposed to drought conditions for an extended period will have lower moisture content and may have higher dead material — resulting in a greater chance of ignition. A less obvious factor is frost, which occurs frequently during the winter. Some plant species are adapted to frost by having small leaves and twigs, as such having low biomass making them less likely to be flammable.

Research pertaining to the internal properties of plants and flammability has been focussed mainly on moisture content. Though moisture content influences plant flammability (Chuvieco et al., 2004; Pellizzaro et al., 2007) directly, other research has also been conducted. Alessio et al. (2008) investigated how moisture and monoterpenes influenced flammability and found that, despite moisture being the dominant factor, monoterpenes negatively influenced flammability. Despite this, other work has suggested that the majority of volatile organic compounds formed as secondary metabolites increase flammability (Pausas et al., 2016). However, on the whole, research regarding volatiles and flammability is still limited. One of the most notable findings was that of the influence phosphorus (P) content has on flammability. Phosphorus as a chemical has been used in applications to suppress fire and is most commonly used in fire extinguishers. But, how might this relate to plant flammability? Plants require nutrients for survival in different quantities, with nitrogen and phosphorus availability being among the top influencers of growth and even species distribution. In the Fynbos, as with most of the Mediterranean-type systems, we find the soils to be particularly deficient in these two chemicals, while other biomes such as Forests often have considerably higher amounts of N and P. As phosphorus is a major constituent of fire extinguishers, there may be a link between phosphorus levels and vegetation' ability to suppress fire, however, this has never been tested as such. It was along these lines that Groom and Lamont (2010) investigated when they tested to see if P accumulation in seeds of a fire-prone system benefits fire survival. They found that serotinous plants have more P stored in

the seeds than plants with other reproductive strategies in the biome, though it only marginally decreased in reseeders. Serotiny is the reproductive strategy observed in fire-prone vegetation where species depend on the death of the adult plant before releasing seeds into the post-fire environment. Research in terms of chemical adaptations to fire is still very limited, but the opportunities to investigate are clearly there.

1.3. Data-driven review

Since the “Mutch” hypothesis was proposed, flammability as a theoretical research theme has blossomed; but nonetheless, there is a real challenge in finding literature that makes use of experimental designs or that are capable of linking the scales at which flammability applies. Here I provide a review of the literature to investigate different components of flammability and thereby determine how well questions are being answered. A literature search was conducted using the Web of Science with the following search criteria: “flamab” in the title or topic (i.e. to capture “flammable” or “flammability”), as well as “plant” in the topic. This search was then refined to specific categories: Ecology, Plant Sciences or Forestry, Environmental Sciences, Genetics Heredity or Evolutionary Biology and yielded 214 results. Using the first 150 articles, I screened how many of these pertained to flammability as a plant trait and found that only 38 (25%) were relevant. I further examined the relevant literature and found that only 23 of these utilized experiments as opposed to theories to elucidate flammability. With further investigation, I determined that the majority of studies (78%) used more than one species for experimentation (Fig. 1); with number of species ranging from 2 to 170. A single species was another popular choice with 22%, followed by 13% at community level. Of significance for this thesis is that none of the literature in this review looked at species from different vegetation types or biomes. Similar to the theories proposed by Mutch (1970), Bond and Midgley (1995), Schwilk and Kerr (2002), and Midgley (2013), the literature appears to focus on using only fire-dependent vegetation for flammability experiments rather than to compare what they find in fire-free biomes.

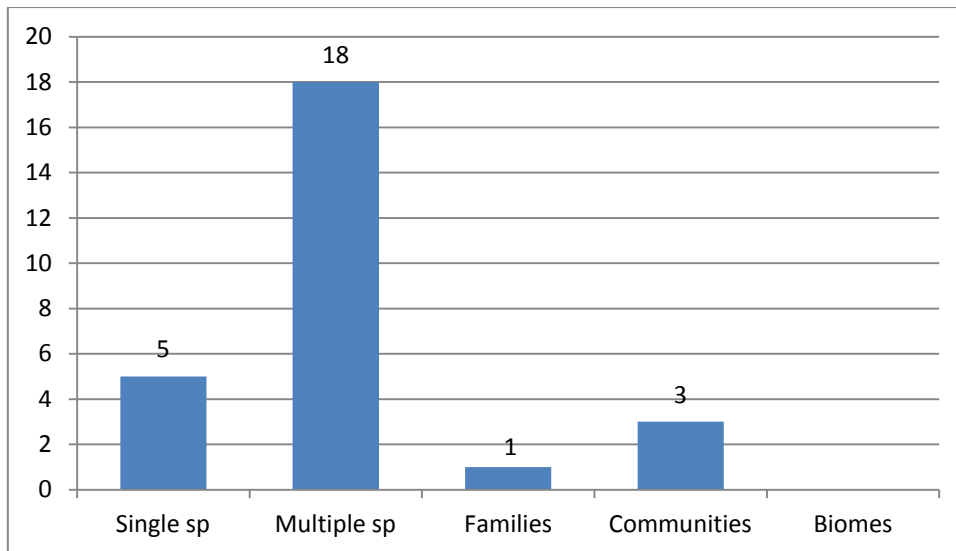


Fig. 1: Number of the experiments pertaining to different scales of study.

A secondary category investigated in the literature database was experiment type. This ranged from studies of chemical and molecular components to whole communities. Leaves and twigs (both living and dead) were the most commonly used (Fig. 2). Samples of these are easy to obtain and can be applied in an array of experiments. However, it is difficult to scale up results from this level, especially when looking at models. All other scales had relatively low publication numbers which raises concern about what we really know about flammability.

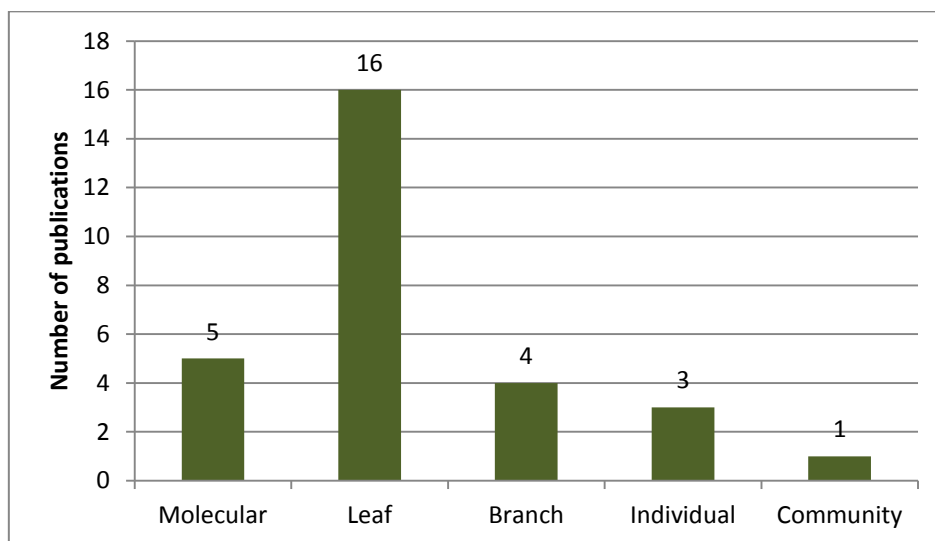


Fig. 2: Number of studies conducted at various scales.

Lastly, I explored which measures or elements of flammability previous research have used. Anderson (1970) and Martin et al. (1994) were among the first to discuss the different measures of flammability. These included ignitability (how quickly the sample takes flame), combustibility (the heat energy released), consumability (biomass loss), and sustainability (how well the sample carries a flame). These four measures form important components of flammability and were devised to measure the different energy outputs produced in a fire event. A major component of their development comes in the fact that no system has been designed to measure all of outputs and as such their individual measures were used to give insight into flammability (de Magalhães and Schwilk, 2012; Jaureguiberry et al., 2011; Kauf et al., 2015). Notable elements in the literature database include: research on genetics by Moreira et al. (2014) who looked at the genetic variation of a post-fire seeder, and models based on the flammability data of species (Santana and Marrs, 2014). Most studies investigated ignition and combustibility (Fig. 3), both of which involve different temperature ranges. Few of these have, however, looked at genetics and models (one study each) or a medley of the other measures in one experiment.

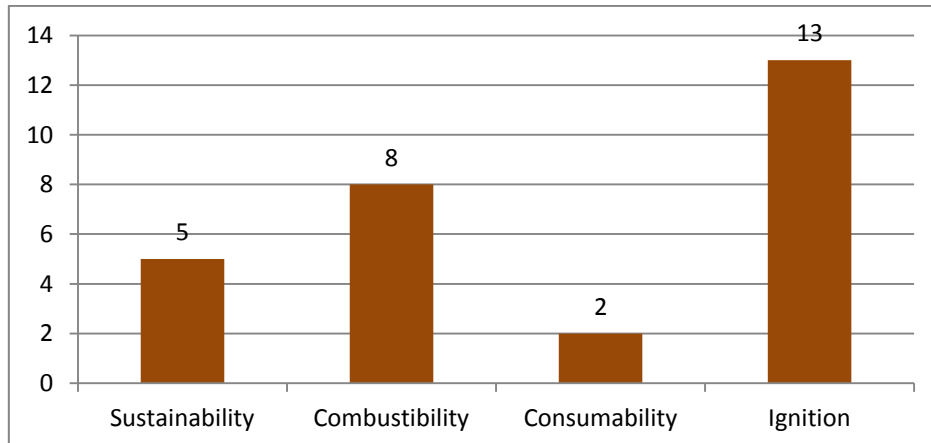


Fig. 3: Total count of measures used in study.

Fernandes and Cruz (2012) highlight a major limitation that was still evident in this review of the more recent literature — studies are limited to a select field or scale and thus findings are unable to extrapolate across scales to solve the evolutionary conundrum. The gap exists as we are unable to link flammability at leaf level to individual level and to community level. To approach this, one would have to evaluate flammability at the various scales and develop

models to incorporate the data from each scale and test it. The closest example to this was by Parsons et al. (2011) who linked fuels to three-dimensional models of fire spread through the canopy of an individual. Much of the reason for the limitations to the research has been the ability to measure all of the flammability components rather than just one (de Magalhães and Schwilk, 2012; Jaureguiberry et al., 2011; Kauf et al., 2015). In 2011, Jaureguiberry proposed a device for measuring flammability in a standardised and relatively inexpensive way. This device also allows for easy transport for in-field measurements. Using this measurement tool as the basis of my thesis, I set out to investigate the flammability of a host of species spanning biomes and across seasons.

1.4. Study focus

The gaps in the literature provide a framework of questions which this thesis can set out to answer. One of the major gaps is that research rarely cross spatial scales with none focussing on biomes. Secondly, most research only focussed on leaf flammability as opposed to testing across an individual's morphological scales. Much of the research has also been done in controlled environments, not compensating for change in prevailing weather. The last gap I focus on is that of a temporal component where seasonal climate has not been addressed directly. This investigation goes beyond current approaches by selecting a large array of species from a range of biomes — including non-flammable biomes. The first focus is to determine how flammability as a functional trait has evolved in relation to other functional traits and also to evaluate the flammable components of both fire-driven and fire-free biomes. This allows me to cover an array of spatial scales from individual to biome level, but also elucidate morphological aspects that influence flammability. Using selected species from each of the five biomes, I identify patterns pertaining to the temporal scale of weather with a focus on how prevailing conditions may influence flammability. My final data chapter will focus on how the external factors, in this case seasonal variation in temperature and precipitation, influence the flammability of species and biomes. In both chapter three and four, I will correlate flammability at various scales and identify any trends or noteworthy observation. This will be done using the same standardised method throughout my thesis across the two summers and two winters of 2014 and 2015.

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2. Investigating species-level flammability across five biomes in the Eastern Cape, South Africa.

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2.1. Abstract

The causes and consequences of plant flammability are a contested issue. In fire-prone ecosystems, high flammability is invoked as a trait (in combination with fire-survival traits) that enhances reproductive success and reduces competition in the post-fire environment. On the other hand, flammability may be a consequence of other selective forces, for example deterring herbivores. Here we use a standardised method for estimating the flammabilities of 99 species distributed across five biomes in a small area of the southwestern Cape Floristic Region, South Africa. The fire-prone Fynbos and Grassland biomes included many highly flammable species, notably among graminoids and small-leaved shrubs with densely packed, fine twigs. However, Fynbos included many weakly flammable species. In the fire-free biomes (Forest, Nama-Karoo and Thicket), most species had low flammability, especially succulents. However, flammable species also occurred in all three biomes, including species with traits normally attributed to non-flammable species (e.g. large leaves sparsely arranged on coarse twigs). Since these biomes are fire free, flammability in these species cannot be attributed to a fire-related selective regime.

2.2. Introduction

Interest in flammability at the species-level and how this translates to the community-level was initiated by Mutch (1970) who hypothesised that “if species have developed reproductive and anatomical mechanisms to survive periodic fires, then fire-dependent plants might also possess characteristics obtained through natural selection that actually enhance the flammability of these communities”. However, Mutch (1970) failed to explain how increasing flammability may increase individual fitness; selection would have to operate at the community (group) level for its predictions to hold (Snyder, 1984). Bond and Midgley (1995) provided an individual fitness argument by proposing that if individuals killed their neighbours via vigorous burning and also survived the fire – either by resprouting or reseedling – then this would increase post-fire recruitment, and thus also individual fitness. Furthermore, high flammability may have a selective advantage where it promotes recruitment of individuals post fire (Burger and Bond, 2015) via the germination of soiled-stored seeds (Bond et al., 1999; Pierce and Moll, 1994), the release of seeds from serotinous cones (Lamont and Cowling, 1984) or the recruitment of ramets from dormant buds (Bond and Midgley, 2003). Burger and Bond (2015) showed that that the proportions of dead and fine fuel are good predictors of flammability in a sample of Fynbos (fire-prone) and Forest (fire-free) species. Ericoid shrubs of Fynbos, with finely-packed fuel, much of which was dead, and which were obligate post-fire recruiters, had the highest flammability; Forest species that possessed sparsely arranged fuel of large, leathery (sclerophyllous) leaves, and which recruited in the intervals between fire, showed the lowest flammability.

However, Schwilk and Kerr (2002), using a genetic population model, argued that there may not be explicit fitness benefits for traits that enhance flammability, but rather flammable characters are associated with other traits they are responsible for increased individual fitness. Therefore, high flammability may well be manifested in plants associated with fire-free biomes. Midgley (2013) argued that if flammability is a trait under selection then this can only occur when several unlikely contingencies coincide. He proposed that flammability is an emergent property that does not confer any selective advantages and that selection was more likely for traits that reduce flammability. Flammability and how this interacts with traits, selective pressures and individual fitness remains a contested topic (Hoffmann et al., 2012; Keeley et al., 2011; Midgley, 2013).

Flammability has been explored across a range of plant features, including leaf litter properties (Cornwell et al., 2015), leaf chemicals (Alessio et al., 2008), leaf traits (Engber and Varner, 2012), canopy architecture (Schwilk, 2003), and growth form (Jaureguiberry et al., 2011). In the South African context, van Wilgen et al. (1990) investigated both physical and chemical traits of species linked to flammability in Fynbos (fire-prone) and adjacent Afrotemperate Forest (fire-free) and found that Fynbos species are more flammable than Forest species. Using species from these same biomes, Burger and Bond (2015) obtained similar results using a standardised flammability experiment. These, and other, studies have dealt with the topic in a somewhat narrow context as they only examine one or two biomes and a small number of species. Here we use standardised flammability experiments (*sensu* Jaureguiberry et al., 2011) to investigate flammability across a large sample of species distributed across several biomes, some fire-prone and others fire-free.

The coastal plain of the southwestern part of South Africa's Eastern Cape Province offers excellent potential for investigating community-related variation in the flammability of plants owing to the juxtaposition of many fire-prone and fire-free biomes in small areas (Cowling, 1983; Cowling and Potts, 2015; Gibbs Russell and Robinson, 1981). Here we sampled 99 species from five biomes, namely Fynbos, Grassland, Nama-Karoo, Albany Thicket, and Forest. If flammability is an evolutionary selected trait (*sensu* Bond and Midgley, 1995; Burger and Bond, 2015; Mutch, 1970) then fire-prone biomes should have species with higher flammability than fire-free biomes. Specifically, Grassland and Fynbos should have a large proportion of highly flammable species while the Thicket, Nama-Karoo and Forest species should exhibit low flammability. We also investigated a range of functional traits that may be related to flammability. Species having a small-leaved, 'flammable' architecture (*i.e.* high twigginess and leaf density *sensu* Schwilk, 2003), should more flammable than sparsely branched plants with large, fleshy or soft leaves that are sparsely arranged (Burger and Bond, 2015; Fernandes and Cruz, 2012; Jaureguiberry et al., 2011; Pausas and Moreira, 2012).

2.3. Methods

2.3.1. Study area

Our study area comprises a ca. 3000 ha area of the Kaboega private reserve on the northern flanks of the Suurberg mountains in the Eastern Cape ($33^{\circ}15'44''S$; $25^{\circ}23'02''$; Fig. 1). The area supports five biomes, namely Fynbos, Grassland, Nama-Karoo, Albany Thicket, and Forest. Fire-prone biomes, Grassland and Fynbos, are associated with the infertile, sandy, quartzitic sandstone-derived soils of the Suurberg uplands; Fynbos occupies moist, poleward slopes while Grassland occupies dry, equator-facing slopes on the skeletal soils of the mountain ridges. Thicket and Nama-Karoo are associated with fine-grained and moderately fertile soils derived from shale and tillite deposits; Thicket occupies the steep slopes on the flanks of the Suurberg whereas Nama-Karoo is confined to the frost-prone valley floor (Duker et al., 2015). Small, linear patches of Forest (Southern Afrotropical Forest) occupy the deeply incised and fire-free canyons (kloofs) of perennial streams of the Suurberg. The study area falls within a region where rain may fall at any time of the year and there is no clear dry season, nonetheless consecutive dry months are not uncommon and may occur in any season (Kraaij et al., 2013; Schulze, 2008).

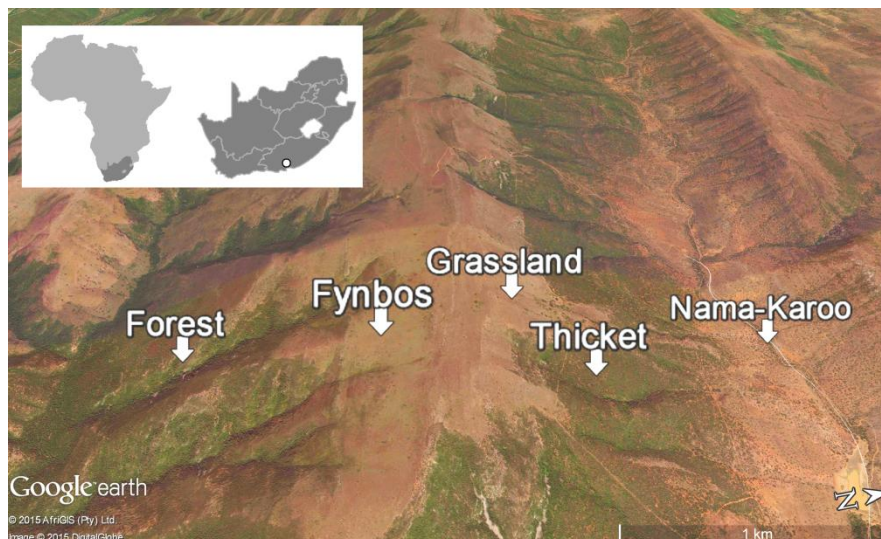


Figure 1. An example of the close juxtaposition in the study area of the five biomes used to sample species for flammability assessments. The majority of sites used for sampling were within 5 km of one another, but due to issues of accessibility in this difficult terrain some sites were up to 13 km apart.

2.3.2. Species sampling

We sampled a total of 99 species across the biomes with a minimum of 17 species per biome (Forest: 18; Fynbos: 21; Grassland: 17; Nama-Karoo: 20; Thicket: 23). Species were selected that best represented the biome in terms of abundance and cover. Of the selected species, two (*Diospyros scabrida* and *Polygala myrtifolia*) were found in more than one biome (Forest and Thicket). Following Jaureguiberry et al. (2011), samples were collected from six healthy-looking, sexually mature, randomly selected individuals of each species. The sampling and experiments were conducted between 10th to the 15th of March, 2014; all flammability measures were ascertained within three hours of sampling. The meteorological conditions leading up to and during the sampling period is expected to significantly influence flammability. There was no precipitation in the week prior to the start of and during the sampling except for a minor rainfall event (~1 mm) the evening and night before sampling commenced (Appendix A). There was no evidence that this had penetrated to the floor of the Forest vegetation and all branches and leaves were dry by the time of sampling.

2.3.3. Flammability

We used the equipment and methodology described in Jaureguiberry et al. (2011) for assessing species-level flammability. In brief, this involves placing a representative shoot sample (e.g. branch or grass/restio clump ~50 cm in length) on a grill above gas-driven flames at 150°C for two minutes (to simulate the drying effect caused by an approaching fire) before using a blowtorch for to ignite a small portion of the sample (if this had not already occurred). Three variables were recorded for each sample: maximum temperature of combustion (MT), burn rate (BR) and biomass burnt (BB). Each variable was relativized across all samples to a scale of 0-1; these were then summed to provide an overall flammability index from 0 (minimum flammability) to 3 (maximum flammability). Reference values were the observed maximum values of MT and BR: 800°C and 4 cm/s, respectively. These values are higher than those used by Jaureguiberry et al. (2011) (500°C and 1 cm/s, respectively) as we used a remote infrared thermometer (MT695, Major Tech, Isando, South Africa) with a capacity to measure higher temperatures (up to 850°C) and many of our samples had an MT greater than 500 °C (~55% of samples) and a BR greater than 1cm/s (~40%). Six replicate flammability assessments were conducted per species. In order to test the null hypothesis that there were no significant differences in flammability among biomes,

we used a Kruskal-Wallis one-way analysis of variance based on the median values per species within each biome. An accompanying conservative pairwise comparison based on the Bonferroni procedure was used to further explore the rejection of our null hypothesis; this used the `pair.kw` function from the `asbio` library version 1.1-5 (Aho, 2015) in R version 3.1.0 (R Development Core Team, 2015).

2.3.4. Functional traits

To explore relationships between flammability and functional traits, we collected the following categorical trait data for each non-graminoid species: growth form, leaf size, twiginess, leaf density and leaf texture (described in Table 1). These leaf and stem traits were not comparable between graminoids and other growth forms and so were not measured in graminoids. To compare traits in multivariate space with flammability and biome-association, we characterised the traits using a multiple correspondence analysis; this method is equivalent to a standard correspondence analysis performed on categorical data. Flammability and biome-association were then plotted onto the first two axes of the multiple correspondence analysis in order to identify relationships between flammability (or biome-association) with functional traits. This analysis was implemented in R version 3.1 (R Development Core Team, 2015) using the `ade4` library version 1.6-2 (Dray and Dufour, 2007).

2.4. Results

2.4.1. Biome-scale responses

A Kruskal-Wallis one-way analysis of variance rejected the hypothesis that there were no significant differences in species flammability between the biomes ($H=23.8$, $d.f.=4$, $p<0.001$; Fig. 2). An associated pairwise comparison based on a Bonferroni procedure found that Grassland significantly differed ($p<0.05$) from all fire-free biomes (Nama-Karoo; Thicket; Forest) but no other biomes differed significantly from one another (Fig. 2); note this test is considered conservative and may be prone to type two error (Kutner et al., 2005). The fire-prone biomes (Grassland and Fynbos) had a large proportion of highly and moderately flammable species and a small proportion of non-flammable species. Correspondingly, the

generally fire-free biomes (Thicket, Forest and Nama-Karoo) comprised a large proportion of non-flammable species. Grassland graminoids were highly flammable, but the two Fynbos graminoid species (restios) had moderate flammability.

However, there were several exceptions to these trends (Appendix B). Thus, we observed very low (< 1.0) flammability for two Fynbos shrubs (*Montinia caryophyllacea* and *Leucospermum cuneiforme*) and two Grassland shrubs (*Crassula ericoides* and *Hermannia flammea*). On the other hand, we recorded high (~2 or greater) flammability for four Nama-Karoo shrubs (*Asparagus capensis*, *Selago geniculata*, *Chrysocoma ciliata* and *Felicia muricata*), four Forest trees (*Buddleja salviifolia*, *Podocarpus falcatus*, *Loxostylis alata* and *Smelophyllum capense*) and several Thicket trees or tall shrubs (*Diospyros scabrida*, *Schotia afra*, *S. latifolia*, *Cussonia spicata*, *Ptaeroxylon obliquum* and *Olea europaea*).

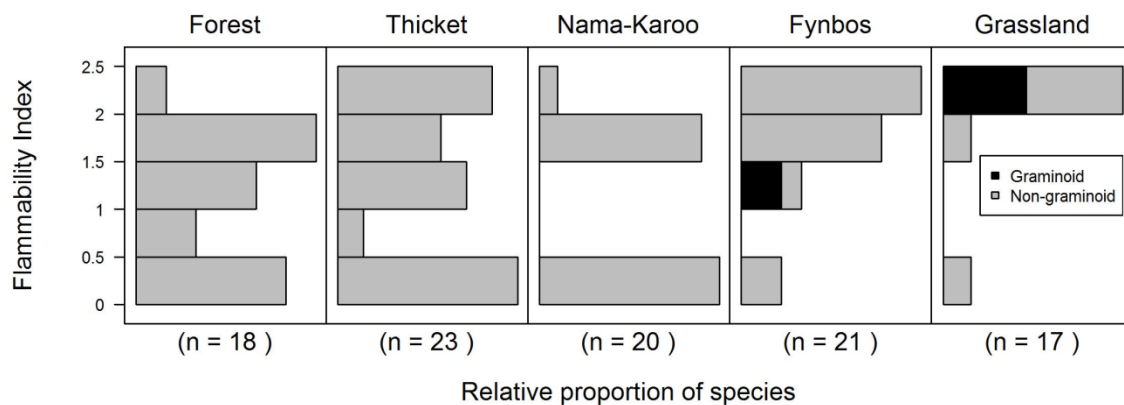


Figure 2. The distribution of the median flammability index values for each species within different biomes (six replicates per species per biome). A Kruskal-Wallis one-way analysis of variance rejected the hypothesis that there were no significant differences in species flammability between the biomes ($H=23.8$, $d.f.=4$, $p<0.0001$). Grassland significantly differed from all other biomes ($p<0.05$) and no other biomes differed significantly from one another. Graminoids from the Fynbos (i.e. restios; $n=2$) and Grassland (i.e. grasses; $n=6$) are highlighted in black.

2.4.2. Trait-based responses

A univariate breakdown of species per functional trait within each biome is reported in Appendix C. There were few clear relationships in multivariate space among traits and between traits and flammability or biome-association (Fig. 3); the two top panels in Figure 3 plot the flammability and biome-association along the first two component axes – these

categories were not included as data in the multiple correspondence analyses but plotted afterwards to judge any association with traits. Fleshy and succulent plants had low flammability overall. Large leaves were weakly associated with high flammability, while plants with small leaves and high twiginess had relatively high flammability. Finely branched Fynbos shrubs with densely packed, small leaves (*Erica* spp., *Elytropappus rhinocerotis*, *Phylica axillaris* and *Acmadenia obtusata*) had some of the highest flammabilities that we recorded.

Table 1: Trait descriptions

Variables	Description
FI	Flammability index = maximum temperature ¹ + burn rate ¹ + burnt biomass ¹ . For the multiple correspondence analysis (MCA; Fig. 3), FI was categorised into low (FI ≤ 1), moderate (1 < FI ≤ 2) and high (FI > 2).
Leaf size	Classified into small (≤15 mm), medium (15 mm to 45 mm), and large (>45 mm) in length.
Growth form	Classified into trees (>2.5 m in height), shrubs (0.3 m – 2.5 m), and subshrubs (<0.3 m); subshrubs included tall (but < 1 m) herbaceous species.
Twiginess	A visual estimation of the density of branches and twigs broken up into three categories: low (<5 branches per 20 cm × 25 cm grid), moderate (5-10), and high (>10).
Leaf density	A classification of the number of leaves found per 10 cm branch: dense (>40 leaves), moderate (30-40 leaves) and sparse. Sparse includes branches with <30 leaves per 10 cm, but also species with nodal growth where bare stem between nodes exceeded the length of the leaves.
Leaf texture	Determined by ‘feel’ (Cowling and Campbell, 1983)

¹Relativised to a scale of 0 to 1.

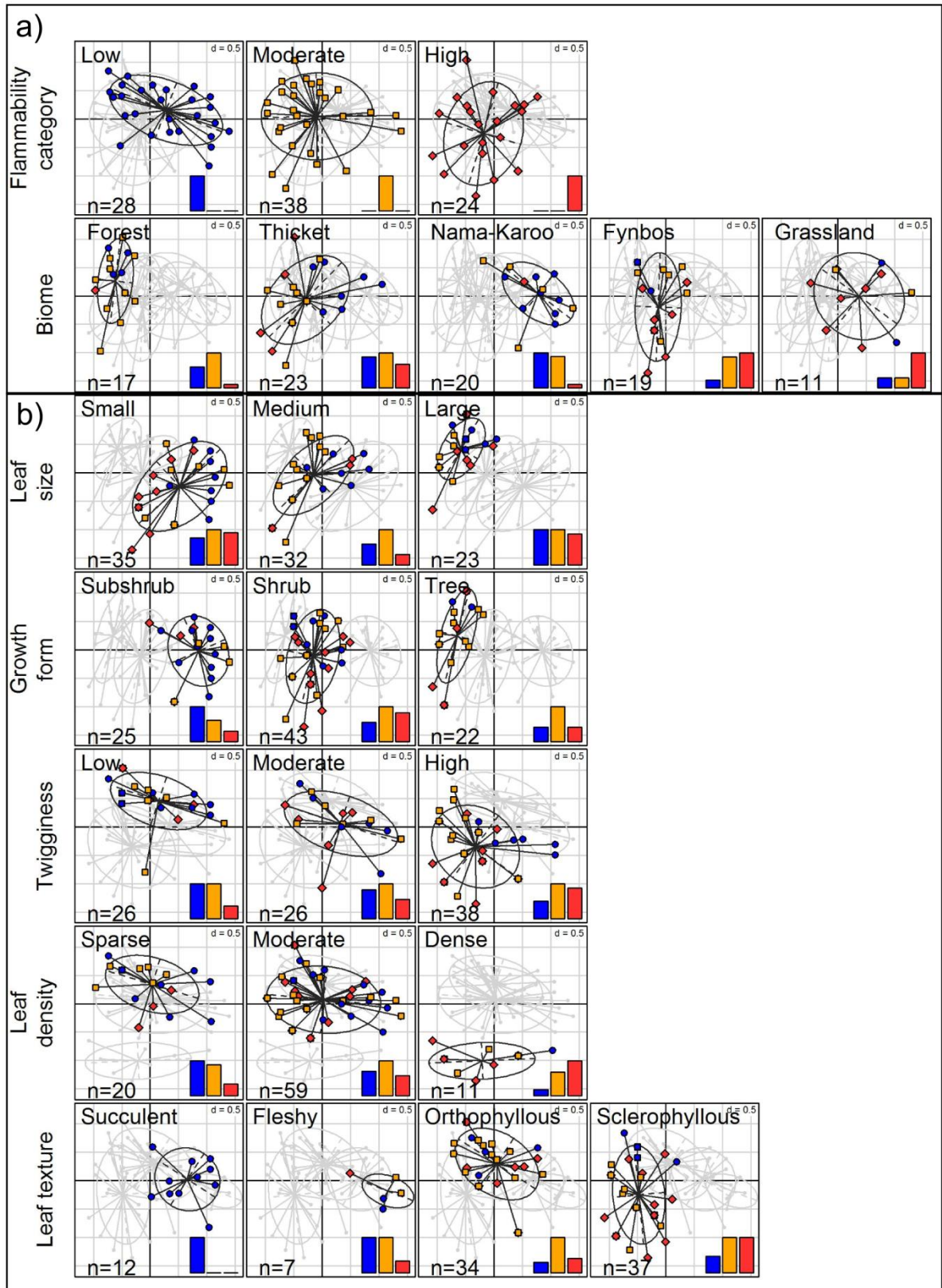


Figure 3. Multiple correspondence analysis of categorical functional traits for 88 non-graminoid species. (a) Biome-association and flammability categories. (b) Multivariate distribution of functional traits

summarised along two principle axes. Biome and flammability categories are independent variables that were not included in the multiple correspondence analysis; the post-analysis inclusion of these variables is used to determine possible associations between these categories and functional traits. Associations are visually judged by the degree of overlap in two-dimensional space between different panels. Each panel subfigure includes a histogram of the frequency of flammability categories (blue = low flammability; orange = moderate flammability; red = high flammability); this represents a breakdown of flammability for the species within a given trait category.

2.5. Discussion

2.5.1. Biome flammability patterns

As predicted, fire-prone biomes (Grassland and Fynbos) comprised a greater proportion of species with higher overall flammability than fire-free biomes (Nama-Karoo, Thicket and Forest). Interestingly, Grassland species were generally more flammable than Fynbos ones and only Grassland had a significantly greater proportion of flammable species than the fire-free biomes. While this may be a consequence of the higher number of flammable graminoids sampled in Grassland, many shrubs associated with this biome were also highly flammable. Fire-related traits in Fynbos species has been the subject of much research (Kraaij and van Wilgen, 2014; Le Maitre and Midgley, 1992), but this is not the case for Grassland species, especially shrubs and forbs. Most non-graminoid Grassland species resprout from fire (Uys et al., 2004; Zaloumis and Bond, 2011) but almost nothing is known about other fire-related traits.

Many Fynbos species – especially restioids and small-leaved (ericoid) shrubs – are highly flammable (Burger and Bond, 2015; van Wilgen et al., 1990). While intense canopy fire may provide the heat cue for the germination of poorly dispersed seeds of some of these species (Bond et al., 1999; Pierce and Moll, 1994), this adaptationist argument cannot apply to plants with small, wind-dispersed seeds such as the Ericaceae and many Asteraceae, which are dominant components of many Fynbos vegetation types. Furthermore, the “kill thy neighbour” argument (Bond and Midgley, 1995) is unlikely to have relevance for Fynbos shrubs in the more open, grassy Fynbos communities of the eastern Cape Floristic Region where overstorey proteoid shrubs are often sparsely distributed in the landscape (Heelemann et al., 2008). Interestingly, *Leucospermum cuneiforme*, a common shrub in eastern Fynbos, had very low flammability. This ecotype of *L. cuneiforme* sprouts from epicormic buds,

unlike the more common one which grows in much shrubbier Fynbos and sprouts from a lignotuber. Low flammability, largely a consequence of sparsely arranged leaves, may be advantageous where high fire intensities may harm epicormic buds. In the lignotuberous form, dormant buds are buried in the soil and, hence, protected from lethal temperatures (Bond and Midgley, 2003). We predict higher flammability for the lignotuberous ecotype. Indeed, a great deal about flammability could be learnt from detailed studies of variation within closely related clades, such as the *Aspalathus teres* complex which includes epicormic sprouters (Grassland), lignotuberous sprouters (moist grassy Fynbos) and non-sprouters (dry grassy Fynbos) which coexist at the landscape scale in the eastern Cape Floristic Region.

The remaining biomes in our study are not fire-prone; therefore, we would not expect high incidence of highly flammable species. Both Forest and Thicket are associated with fire-free sites (canyons, rock outcrops and scree slopes) when present in landscapes dominated by fire-prone Fynbos and Grassland (Cowling and Potts, 2015; Geldenhuys, 1994; Manders, 1990; Moll et al., 1980; Vlok et al., 2003; Watson and Cameron, 2001). Therefore, the incidence of highly flammable species in these two biomes was surprising. In the case of Forest, some of these species are associated with Forest margins (*Buddleja saligna*) and others, while also margin species, extend deep into fire-prone vegetation on rocky outcrops (*Loxostylis alata*, *Smelophyllum capense*). However, the most flammable Thicket species – *Schotia latifolia* and *Ptaeroxylon obliquum* – grow in dense Thicket that is seldom, if ever, exposed to fire. We have no explanation for the high flammabilities recorded in these species that are not associated with fire-prone environments, other than flammability is a consequence of other selective forces (Schwilk and Kerr, 2002) or is not under direct selection (Midgley, 2013).

The generally low flammability of Nama-Karoo species is not surprising, given that this open shrubland is largely incapable of supporting fire, owing to low biomass. Highly flammable species in this biome are finely-branched shrubs with densely-packed, small leaves (e.g. *Chrysocoma ciliata*, *Felicia muricata*) with wide distribution in semi-arid southern Africa and capable of growing in grassy shrublands that are subject to occasional fires (du Toit et al., 2014). Similarly, *Selago geniculata* is commonly found in drier forms of Fynbos and Grassland. Core Nama-Karoo species, especially succulents, had low flammabilities.

2.5.2. Trait-based responses

The general lack of robust relationships between measured traits and flammability suggests that either we failed to include critical flammability-related traits or that flammability is complex and influenced by a range of traits interacting in multifaceted ways that cannot be detected with the multivariate methods used here. We suspect both are likely to be true. Nonetheless, our results on trait-based responses are largely consistent with other studies: graminoids and highly twiggy shrubs with densely packed, small leaves showed higher flammability than species with succulent leaves or large, leaves that are sparsely arranged on coarse twigs (e.g. Burger and Bond, 2015; Cowan and Ackerly, 2010; Saura-Mas et al., 2010; Schwilk, 2003). Plants with the former traits are common in Fynbos and Grassland whereas plants with the latter traits are associated with Forest and Thicket. In fire-free Nama-Karoo, species fitting the flammable profile do show elevated levels of flammability relative to those with sparser and moist (succulent or fleshy-textured) fuel loads. In both Grassland and Fynbos, fire-prone biomes that support canopy fires, traits promoting high flammability may improve recruitment success in the post-fire environment (Keeley et al., 2011). This is not the case for other biomes where species' recruitment is not linked to fire disturbance (Cowling et al., 1997; Milton, 1995; Rahlao et al., 2009). However, there were interesting exceptions to this trend, notably among Forest and Thicket species that were highly flammable despite having architectural features not associated with these traits. This suggests that the selective pressures responsible for the high flammability of these species are not associated with fire-related benefits conferred upon individuals, such as enhanced post-fire recruitment. Indeed, the high flammabilities of these species may be an incidental consequence of other selective forces such as herbivore deterrence or, in the case of those from the Nama-Karoo, drought resistance (Schwilk and Kerr, 2002).

A future avenue to explore the role of fire in the evolution of flammability will be to identify the common traits among highly flammable species from fire-prone biomes and see whether these are observed in species from fire-free biomes. This, however, would require a more extensive trait investigation than presented here.

2.6. Conclusion

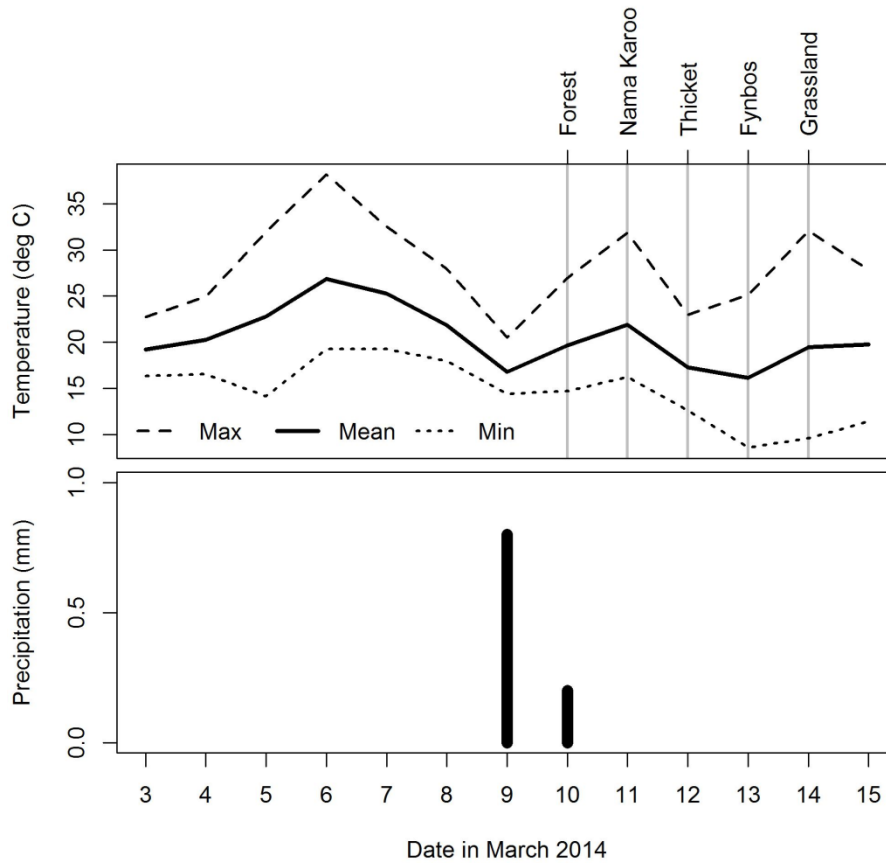
In this study we set out to identify patterns in flammability across a wide range of species and biomes. We found evidence to support the predictions deduced from the literature (Bond and Midgley, 1995; Mutch, 1970; Schwilk and Kerr, 2002), particularly in the fire-driven biomes, Fynbos and Grassland. However, we found great variation in flammability among the non-fire driven biomes and even several highly flammable species; this suggests other traits might cause flammability to emerge rather than it being selected (Midgley, 2013). If increased flammability is related to fire-embracing strategies rather than fire-surviving ones (Schwilk and Ackerly, 2001), why would species in non-fire driven systems be flammable? Though we found limited evidence to link observed traits to flammability, other factors such as drought, temperature or nutrient stress could potentially explain some of the phenomenon. Burger and Bond (2015) found clear relationships between flammability and recruitment strategy (a fire-tolerance trait); flammability only confers a selective advantage if there is an associated fire-tolerance trait. This still needs to be explored in this dataset. We emphasize that comprehensive research, such as the study by Burger and Bond (2015), are necessary if we are to broaden our knowledge on the topic. There is also a need to consider whole-plant architecture rather than assess this in terms of individual traits (Bowman et al., 2014; Burger and Bond, 2015), to determine how flammability scales between levels (e.g. branch-level to individual) and further expansion into the critical role of community composition on species-level flammability (Schwilk and Caprio, 2011).

2.7. Acknowledgments

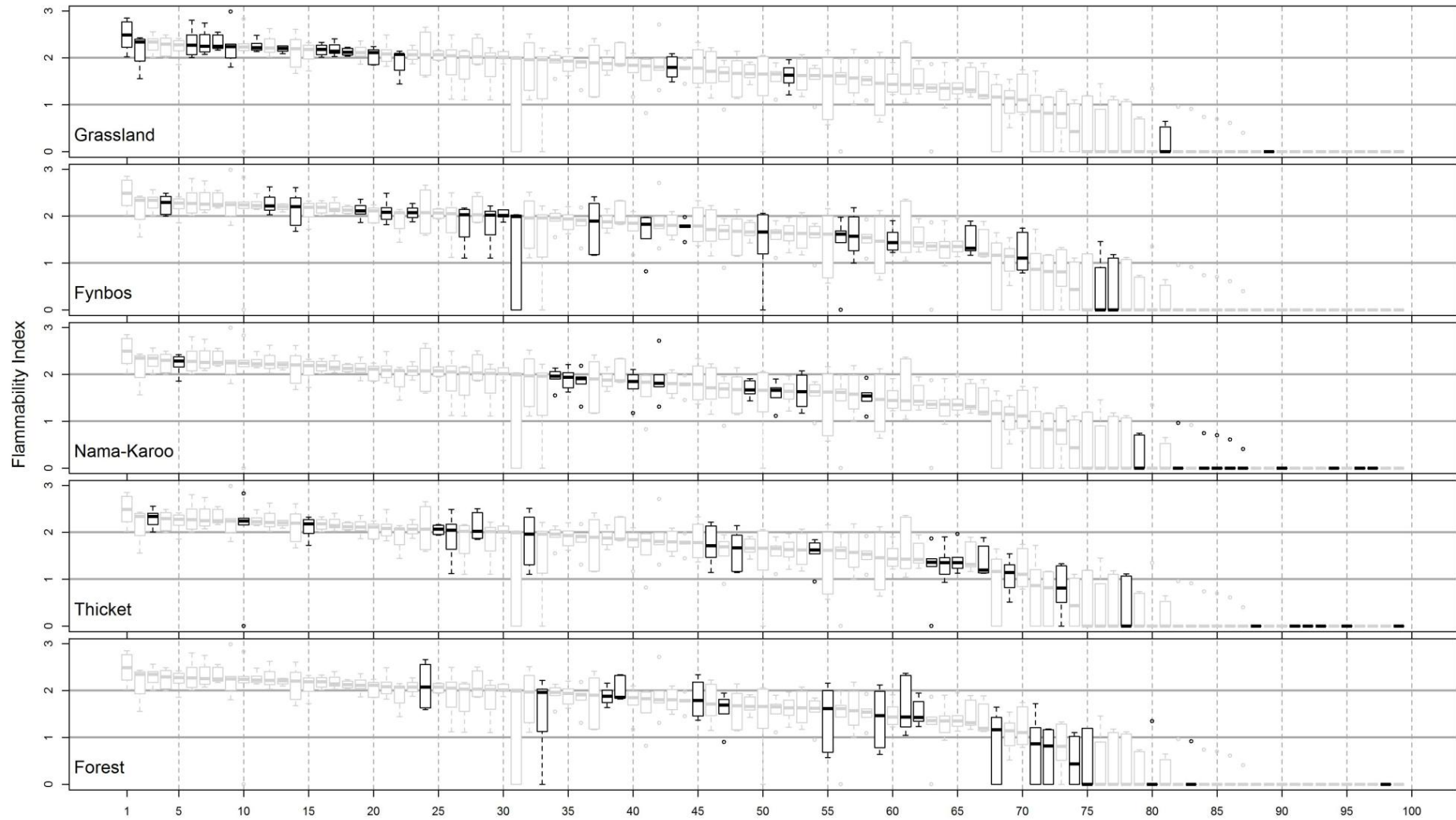
We thank Andre Bezuidenhout for allowing us to conduct our research on his property. We would also like to thank Ian and Sandra Ritchie for being extremely accommodating and helpful throughout the study period. Nelson Mandela Metropolitan University and the National Research Foundation provided support for equipment and funding. AJP received support from the National Research Foundation (RCA13091944022).

2.8. Appendices

2.8.1 Appendix A: Temperature and precipitation for the week prior to and during the sampling period.

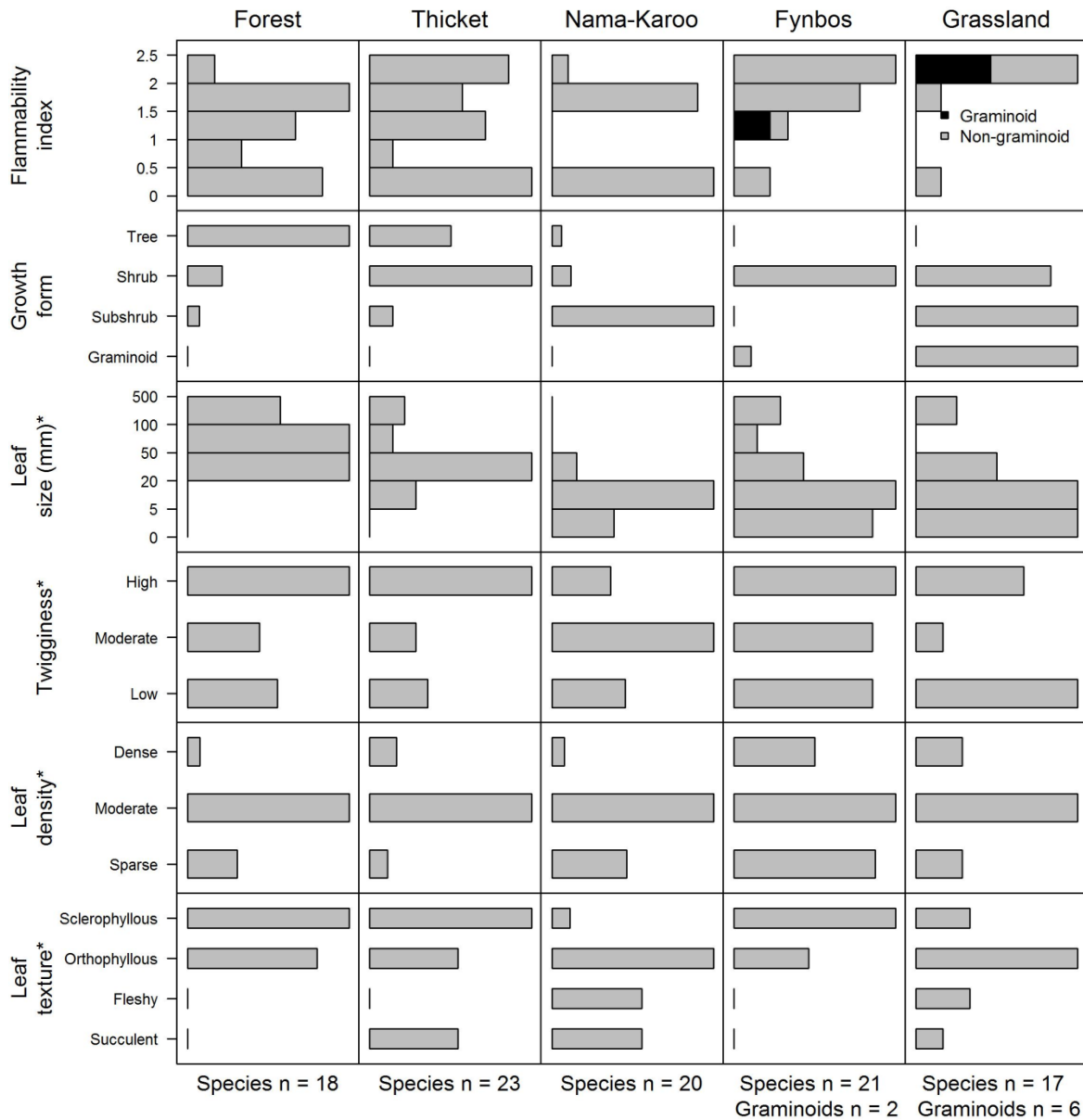


2.8.2. Appendix B: Flammability for 99 species from 5 biomes.



Species as listed (species in bold occur across more than one biome): 1 - *Heteropogon contortus* (Grs); 2 - *Themeda triandra* (Grs); 3 - *Ptaeroxylon obliquum* (Thi); 4 - *Acmadenia obtusata* (Fyn); 5 - *Asparagus capensis* (NK); 6 - Poaceae (Grs); 7 - *Euclea racemosa* (Grs); 8 - Cyperaceae (Grs); 9 - *Eragrostis* sp. (Grs); 10 - *Diospyros lycioides* (Thi); 11 - *Ehrharta* sp. (Grs); 12 - *Elytropappus rhinocerotis* (Fyn); 13 - *Aspalathus teres* (Grs); 14 - *Erica curviflora* (Fyn); 15 - *Schotia latifolia* (Thi); 16 - *Helichrysum nudifolium* (Grs); 17 - *Helichrysum oliganthus* (Grs); 18 - *Helichrysum rosum* (Grs); 19 - *Indigofera denudata* (Fyn); 20 - *Anthospermum herbaceum* (Grs); 21 - *Erica* sp 1 (Fyn); 22 - *Athanasia pinnata* (Grs); 23 - *Phyllica axillaris* (Fyn); 24 - *Loxostylis alata* (For); 25 - *Diospyros scabrida* (Thi); 26 - *Schotia afra* (Thi); 27 - *Metalasia muricata* (Fyn); 28 - *Cussonia spicata* (Thi); 29 - *Erica* sp 2 (Fyn); 30 - *Protea repens* (Fyn); 31 - *Protea lorifolia* (Fyn); 32 - *Olea europaea* (Thi); 33 - *Podocarpus falcatus* (For); 34 - *Chrysocoma ciliata* (NK); 35 - *Selago geniculata* (NK); 36 - *Felicia muricata* (NK); 37 - *Anthospermum aethiopicum* (Fyn); 38 - *Buddleja salviifolia* (For); 39 - *Smelophyllum capense* (For); 40 - *Rhigozum obovatum* (NK); 41 - *Erica pectinifolia* (Fyn); 42 - *Jamesbrittenia pinnatifida* (NK); 43 - *Selago* sp. 2 (Grs); 44 - *Selago corymbosa* (Fyn); 45 - *Polygala myrtifolia* (For); 46 - *Searsia longispina* (Thi); 47 - *Searsia* sp. (For); 48 - *Rhoicissus tridentata* (Thi); 49 - *Selago albida* (NK); 50 - *Hermannia salviifolia* (Fyn); 51 - *Aptosimum procumbens* (NK); 52 - *Indigofera* sp. (Grs); 53 - *Pentzia incana* (NK); 54 - *Polygala myrtifolia* (Thi); 55 - *Gonioma kamassi* (For); 56 - *Pelargonium* sp (Fyn); 57 - *Leucadendron salignum* (Fyn); 58 - *Vachellia karoo* (NK); 59 - *Diospyros scabrida* (For); 60 - *Helichrysum cymosum* (Fyn); 61 - *Pittosporum viridiflorum* (For); 62 - *Canthium inerme* (For); 63 - *Putterlickia pyracantha* (Thi); 64 - *Euclea undulata* (Thi); 65 - *Brachylaena ilicifolia* (Thi); 66 - *Restio* sp 1 (Fyn); 67 - *Pappea capensis* (Thi); 68 - *Grewia occidentalis* (For); 69 - *Boscia oleoides* (Thi); 70 - *Rhodocoma capensis* (Fyn); 71 - *Ficus sur* (For); 72 - *Rapanea melanophloeos* (For); 73 - *Gymnosporia capitata* (Thi); 74 - *Scolopia mundii* (For); 75 - *Cunonia capensis* (For); 76 - *Montinia caryophyllacea* (Fyn); 77 - *Leucospermum cuneiforme* (Fyn); 78 - *Plumbago auriculata* (Thi); 79 - *Atriplex semibaccata* (NK); 80 - *Colpoon compressum* (For); 81 - *Hermannia flammea* (Grs); 82 - *Aizoon* sp. (NK); 83 - *Todea barbara* (For); 84 - *Pachypodium subtingens* (NK); 85 - *Asparagus striata* (NK); 86 - *Crassula expansa* (NK); 87 - *Drosanthemum hispidum* (NK); 88 - *Cotyledon velutina* (Thi); 89 - *Crassula ericoides* (Grs); 90 - *Crassula mesembryanthemoides* (NK); 91 - *Crassula ovata* (Thi); 92 - *Crassula perforata* (Thi); 93 - *Crassula tetragona* (Thi); 94 - *Drosanthemum lique* (NK); 95 - *Euphorbia mauritanica* (Thi); 96 - *Lycium cinereum* (NK); 97 - *Mestoklema* sp. (NK); 98 - *Mikania capensis* (For); 99 - *Portulacaria afra* (Thi)

2.8.3. Appendix C: Univariate breakdown of species per functional trait within each biome. Graminoid species are not included in the leaf and stem traits (*).



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3. The influence of moisture on plant species flammability.

3.1. Abstract

This study investigates the relationship between moisture availability and plant flammability by exploring these traits across seasons, both within and across species found among five biomes in the Eastern Cape, South Africa. Three species from each biome were measured for moisture content and flammability during the summer and winter seasons of 2014 and 2015. Flammability was tested using the standard flammability measuring device. Comparing interspecies results suggests that moisture is not a strong predictor of plant flammability. Moisture availability when very high or very low indicated some correlation, but succulent species skewed results. In contrast, intraspecies correlations supported the concept that species respond to moisture in the environment differently due to adaptation and inherent traits. The results suggest that flammability is not strongly linked to moisture in the environment per se, but rather by species-level responses to moisture availability.

3.2. Introduction

The link between climatic conditions and fire regimes has been well documented, from research (Pausas and Fernández-Muñoz, 2011) to agricultural practices (Howden et al., 2007) and fire management (Whitlock et al., 2003). Temperature and moisture are two of the most important factors influencing fire regimes and are often coupled with the highest seasonal frequency of lightning events (Kraaij et al., 2013b; Mutch, 1970). Bond et al. (2005) highlight the importance of fire as a driver of the distribution of ecosystems, but still note the importance of climate for the continuation of fire regimes. An example of the impact climate has on fire regimes can be found in South Africa. The south-western tip of the country has a well-defined winter-rainfall system where fires are predominantly experienced in the dry summers. This is contrary to what we find to the north-east of the country, such as Limpopo or Mpumalanga, where summer-rainfall prevails with winter-drought (Cowling et al., 2004). The vegetation found in the respective systems reflects adaptation to these climates, and subsequent fire regimes, in the survival traits of species. Moisture, as with many other factors, varies across temporal and spatial scales. Temporally, precipitation may vary

seasonally, e.g. winter or summer rainfall regimes, and also annually in amount of rainfall. Spatially, precipitation conditions also differ — it is warmer and wetter around the equator than at the poles. Locally these spatial changes may be less dramatic, but are easily identified within the landscape. An example of this is the change in vegetation relating to orographic precipitation where precipitation on one side of the mountain is higher resulting in more moisture adapted vegetation such as forest compared to the more arid state over the mountain resulting in vegetation such as thicket (Roe, 2005).

In a seminal paper, Bond et al. (2003) discusses the link between climate and fire and specifically how shift in the regime can alter vegetation composition or spread. This is based on the concept that species respond to environmental conditions differently. Aronson and Shmida (1992) specifically looked at how vegetation over a vast rainfall gradient changes and was able to correlate the change to rainfall. They were also able to show that fluctuations in the rainfall can impact vegetation. Recently in the Southern Cape (2016-2017), several devastating fires occurred. Drought in the area has been acknowledged as the factor leading up to the fires as these conditions prevailed for more than 2 years. Similar to the effect of rainfall on the vegetation is the fire regime. Natural fire-dependant ecosystems are adapted to a certain fire regime and changes to that fire regime can cause drastic shifts to the ecosystem (Andersson et al., 2004; Hudak et al., 2004; Van Wilgen et al., 1992). The combination of rainfall season and fire consistency (or lack thereof) can be used to explain most of the South Africa's vegetation landscape. At the species level, however, plants show different inherent properties that may be reflected in their response to variability in the environment.

In this chapter I focus on how moisture availability can influence plant species flammability. Plant flammability has been suggested to be an adapted trait in fire-driven systems and as such we expect to find a correlation between flammability and moisture (Moreira et al., 2014). Midgley (2013) discusses moisture in relation to flammability briefly stating that flammable vegetation is likely to occur under arid conditions. In a recent study, Burger and Bond (2015) criticized this theory as Forests and Fynbos occur in the same seasonal regions and even the same soils. However, in their study they found that moisture content had an extremely low impact on individual flammability. van Wilgen (et al., 1990) measured moisture content between Forests and Fynbos in a fire-based correlation study and found that the Forest species had considerably and consistently higher moisture content. However,

beyond studies investigating the ignition point of vegetation, very little has been done on the link between moisture content and fire, specifically plant flammability. In Chapter 2 of this thesis I delve into the functional traits influencing plant species flammability but not moisture. As mentioned in literature (e.g. Sultan, 1995), the inherent ability of a species to manage water variability can be difficult to quantify. This is particularly true for determining adaptive plasticity or inevitable responses.

The literature suggests that species are adapted to the environment, in this particular case to fire in fire-driven systems. As moisture availability is said to be of key importance, I set out to investigate the relationship between plant moisture content and flammability. The main focus of this study is to determine if a species is adapted to climatic shifts, but also to investigate plant plasticity by acclimation to prevailing weather conditions. To reach this goal, species are selected from different biomes with certain species being present in more than one biome for comparing acclimation.

3.3. Methods

The study area and sampling sites are described in Chapter 2; in brief, the area comprises a ca. 3000 ha area of the Kaboega private reserve on the northern flanks of the Suurberg mountains in the Eastern Cape (33°15'44"S; 25°23'02"). The area falls within an aseasonal rainfall region where it receives between 200mm and 800mm of rain per annum. Seasonal climatic can vary substantially as temperatures range from 25–45 °C in summer and -7–20 °C in winter. Climate data was collected by Robbert Duker using a weather station placed along an elevational gradient in the Kaboega reserve (Figure 1). Three species from each of the five biomes were selected based on morphological differences; one species, *Diospyros scabrida* was sampled from three biomes — Forest, Thicket and Grassland — to explore intra-species variation across biomes. Flammability was tested as per the standardised guidelines (Jaurequiberry et al., 2011) and was conducted during the summers and winters of 2014 and 2015 (Fig. 1). As described in Chapter 2, six replicates of each of the 15 species were used for the flammability experiment. Leaf material, and in some cases small twigs, were collected from individuals within the same population and subsequently weighed for wet weight. Where wet weight was not measured immediately, samples were placed in sealed plastic bags

and placed in a cool place, measured within 24 hours. A minimum of 50 g of biomass were collected per sample. These samples were dried for 48 hours at 60 °C in a drying oven and weighed again to calculate moisture content; the moisture content is calculated by subtracting the dry weight from the wet weight and dividing by the wet weight to produce a percentage. Data analyses were conducted using R version 3.1 (R Development Core Team, 2016) and the ade4 library version 1.6-2 (Dray and Dufour, 2007).

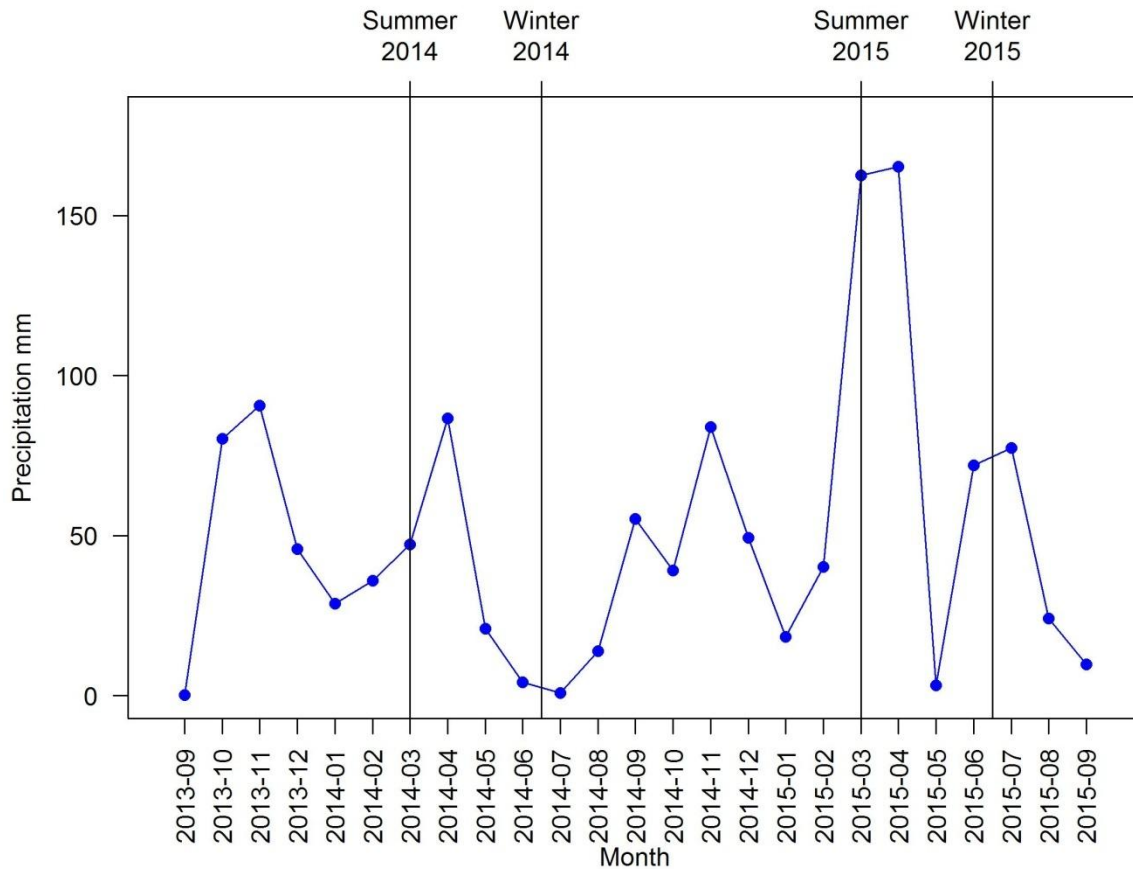


Figure 1: Sampling periods indicated in relation to monthly precipitation. Precipitation for the 2-year period stretching September 2013 to September 2015. (Data provided by Robbert Duker)

Of the four sampling events, the winter of 2014 was the driest, with the summer of 2014 having the highest amount of precipitation (Table 1). Although the summer of 2015 and winter of 2015 both received little rainfall in the few days before sampling, the moisture content of species suggests that the cooler winter climate allowed species to retain more moisture as seen in Figure 3. Looking at monthly rainfall (Fig 1) as well as the rainfall received prior to sampling events (Table 1), we see that a dry period occurred from May 2014 till March 2015.

Table 1: Cumulative precipitation in mm per days before sampling

Days prior to sampling	Summer 2014 (March)				Winter 2014 (June)			
	Total Prec	Mean Temp	Max Temp	Min Temp	Total Prec	Mean Temp	Max Temp	Min Temp
3	5.2	17.2	32.9	10.2	0	18.6	31.4	7.2
7	36.4	17.1	32.9	10.2	3	16.5	31.4	4.9
30	74.2	20.5	45	10.2	4.2	14.3	31.4	2.6
60	118.2	21.2	46.9	10.2	25.2	15.2	34.5	2.6
General description	Warm and Wet				Cool and Dry			
Days prior to sampling	Summer 2015 (March)				Winter (June)			
	Total Prec	Mean Temp	Max Temp	Min Temp	Total Prec	Mean Temp	Max Temp	Min Temp
3	1.8	21.6	35.4	16.7	0	13	22.5	7.4
7	2.2	22.6	39.4	16.7	0	12.7	22.5	5.1
30	23.4	21.2	41.3	9.8	67.6	12.3	26.2	5.1
60	64.8	20.9	45.3	9.8	75.2	14.1	30.2	5.1
General description	Warm and Dry				Cool and Wet			

3.4. Results & Discussion

3.4.1. Direct correlations

Figure 2 illustrates the relationship that existed between flammability and moisture content during the sampling times without labelling biomes or species. The regression line fitted for the summer and winter of 2014 accounted for 60% and 48% of the variance, respectively. In both of these, a significant correlation between flammability and moisture was found ($p=0.000$ and $p=0.002$). Visually, the general trend across all seasons is that moisture slightly influences the flammability of species. However, succulents clearly skew the results as seen during the drier seasons of 2014. The regression lines of the 2015 season account for far less variation (9% and 16%) than the 2014 seasons, indicating that when moisture levels are high, the flammability is influenced by other factors. The outliers causing the strong biases are the succulents, *Portulacaria afra* and *Drosanthemum lize* which occur in the Thicket and Nama-Karoo respectively. Removing the succulents changes the relationship between flammability and moisture — there is no significant correlation, irrespective of season (Figure 3) with the regression accounting for less than 8% of variance in all observed seasons. The argument made by Midgley (2013) comes to mind where he suggests that the environment plays a larger role in flammability than previous theories would suggest (Bond and Midgley, 1995; Mutch, 1970). Midgley (2013) argues that it is unlikely for an individual species to evolve flammability but rather that flammability emerges due to environmental conditions. One of these conditions may be drought which has been a common phenomenon in the southern Cape of South Africa. It has been well documented in the literature how plants adapt to water stress, particularly at the molecular level (Jones, 2006). As noted by Farooq et al. (2009), drought ultimately causes plants to reflect stress in their physical appearance. Plant growth is stunted as photosynthetic efficiency is reduced and chlorophyll molecules are lost resulting in plants appearing grey as opposed to normally being green. Continuous exposure to drought conditions leads to desiccation and, in many cases, increased proportion of dead material. As Keetch and Byram (1968) explains, this increases the likelihood of large and fierce crown fires occurring. As mentioned, the Southern Cape has been exposed to drought conditions since ~2015 with smaller drought conditions occurring even before that. During 2016 and 2017, severe fire events have occurred in this region from Cape Town to Port Elizabeth and a large fire event occurred at Kaboega as well in 2015. In these short periods, intense stress circumstances, plants aren't able to fully acclimate. However, over thousands and millions of years in decreased moisture environments, some

species adapt by having higher moisture storage capabilities as well as being efficient in water usage. Other than the succulents being non-flammable due to adaptation, the response of other species may be acclimation to prevailing weather conditions and requires further investigation.

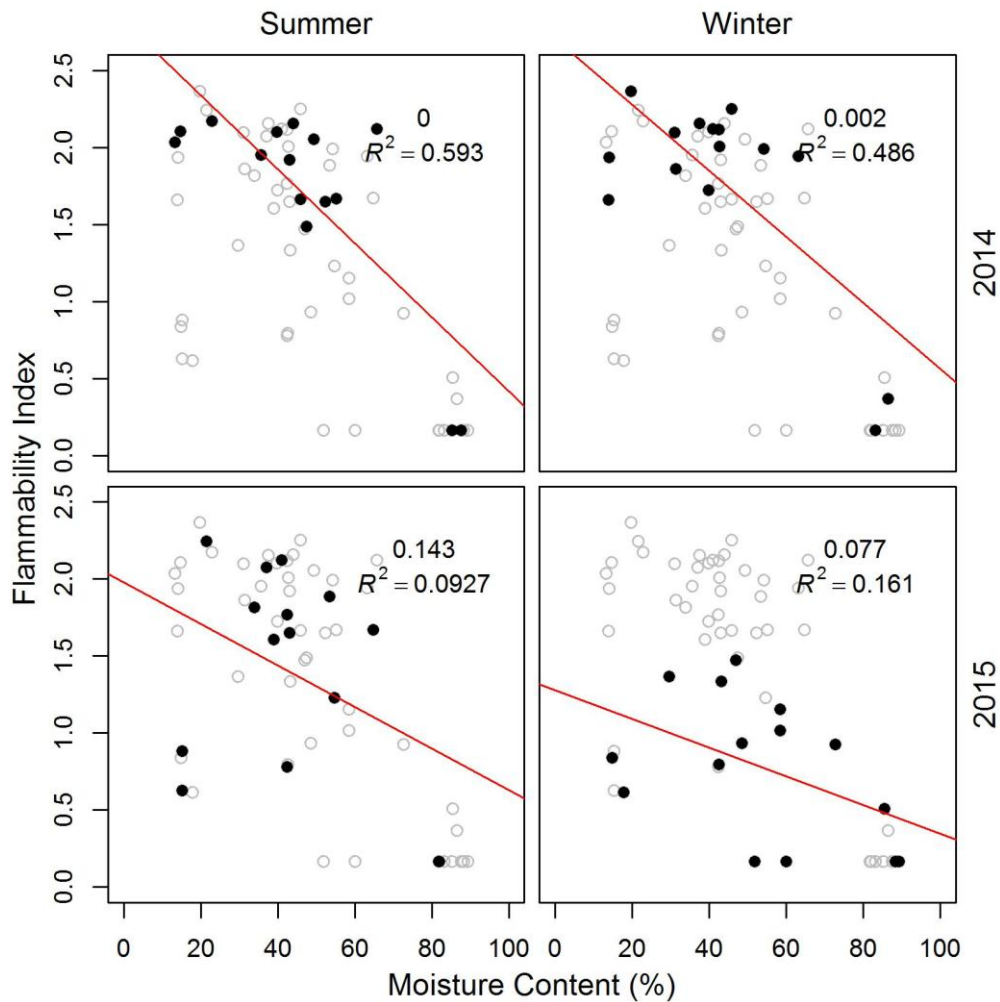


Figure 2: Seasonal correlation between species level flammability and moisture content with r^2 and p -values. Filled black circles represent the samples of the given season and greyed out open circles represent the samples from the other sampling periods.

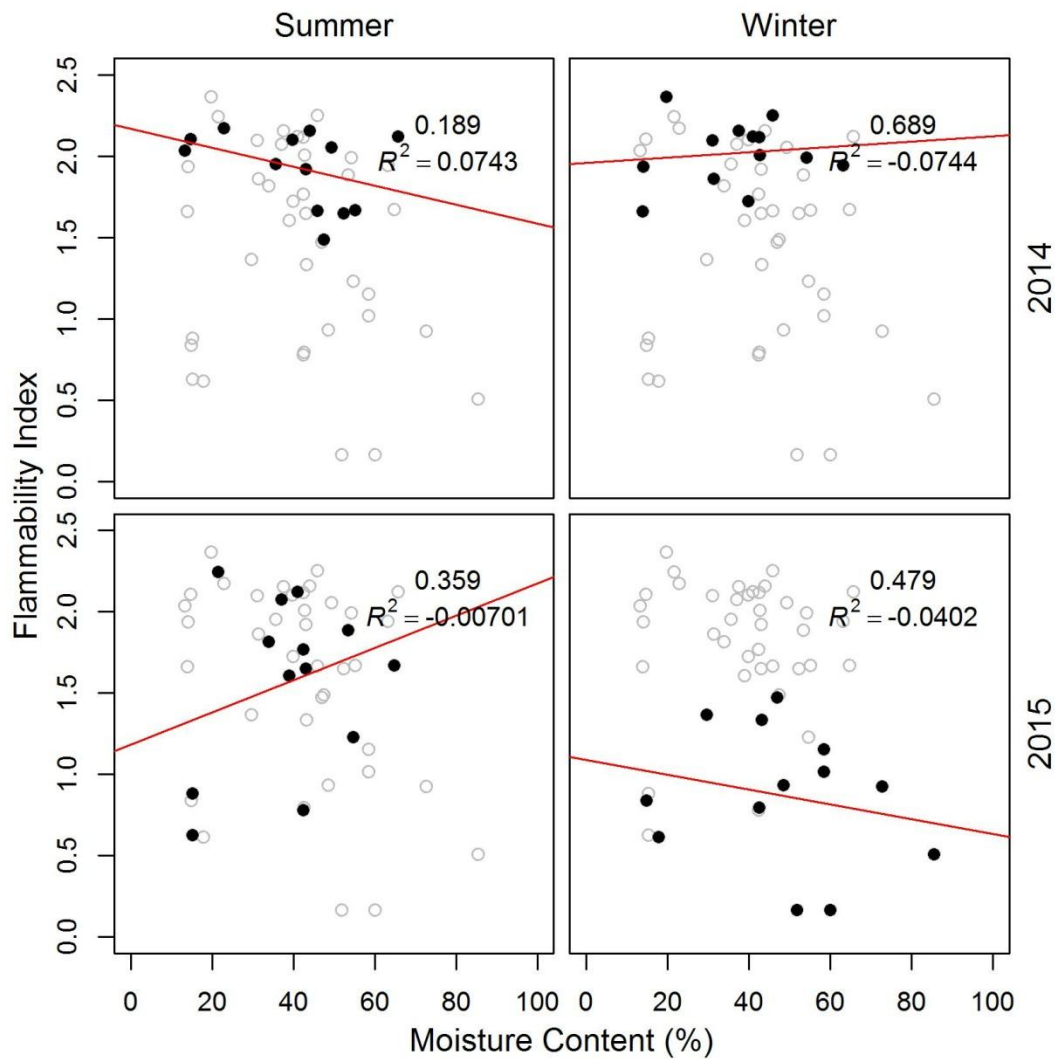


Figure 3: Seasonal correlation between species level flammability and moisture content with r^2 and p -values without succulents. Filled black circles represent the samples of the given season and greyed out open circles represent the samples from the other sampling periods.

3.4.2. Species-level responses

The correlations between flammability and moisture for species (Figure 2 & 3) do not necessarily reflect the impact of moisture content per se, but rather moisture in the environment. The general trend of these results suggests that moisture content does not strongly influence flammability. However, species are adapted to different environmental conditions and will respond to environmental variations based on inherent and reflex traits (Sultan, 1995). The Forest species all had strong negative correlations ($r^2=0.807, 0.873,$

0.918) and above 80% of the variation could be explained by the regression. When comparing the *Diospyros* species (found in Fynbos, Forest, Grassland, and Thicket), it is noted that there is considerable variation in the results. The regression is able to account for at least 80% of the variance among the Fynbos and Forest with negative correlations of 0.95 and 0.807 respectively. Whereas the Grassland and Thicket had no correlation and a maximum of 50% of variance was explained by the regression. *Diospyros scabrida* was found in three of the biomes and the results varied considerably among them. Despite arguments made that species have inherent ability to adapt, the results of this species strongly suggest that there is adaptive plasticity taking place. Plants have been shown to acclimate to temporal changes in moisture (Picotte et al., 2007), and the variation in flammability may well be correlated to morphological changes taking place in response to moisture availability. These results are in agreement with Midgley (2013), in that flammability emerges as a result of the environment rather than inherently adapting flammability. However, the *Diospyros* genus is not strongly correlated to fire driven systems, despite its representation within them. When we look at species typical of fire-driven systems, we find that there were strong correlations between flammability and moisture. The *Erica* sp (Ericoid), *Leacadendron salignum* (Proteoid), and *Themeda triandra* (Graminoid) all had strong negative correlations ($r^2=0.709$, 0.914, and 0.975 respectively) and more than 70% of variance was explained by the regression. In all three of these species we see that a small amount of moisture could strongly influence flammability. This fits the general expectations that species of fire-driven systems (particularly those of strong seasonal rainfall) may have adapted flammability in response to climatic conditions.

Despite observing correlation between moisture content and flammability, the results appear to be very species-specific and require further evaluation. As seen in Figure 4, *Pentzia* has higher moisture content than some of the *Diospyros* and the *Erica* species, although it exists in an environment typically described as dry and even arid. *Pentzia incana* is found in the Nama-Karoo, which experiences extreme climate shift throughout the year when compared to some other biomes (Rutherford et al., 2006). The species, as observed at Kaboega, has dense architecture and small leaves. The small leaves can be attributed as an adaptation to the arid conditions to conserve moisture while the dense architecture is likely caused by herbivory. The architecture could potentially allow moisture from precipitation to be trapped within the matrix of branches and leaves in which case the environment has control over the

flammability. Another species that can reiterate the importance of architecture is *Themeda triandra* (Plate 1). This grass species was found to be considerably flammable but at the same time showed the highest correlation between flammability and moisture with 98% variance being accounted for in the regression ($r^2=0.975$). The grass species has both trichomes and is found in small clumps. Trichomes has been documented to be a adaptation for moisture retention (Farooq et al., 2009; Picotte et al., 2007). It should be mentioned however, that small individuals like *Pentzia* and *Chrysocoma* may include small branches in the analyses of their moisture, which may potentially influence the results. The data used for the correlation statistic is also based on only four points which falls below statistical recommendations.

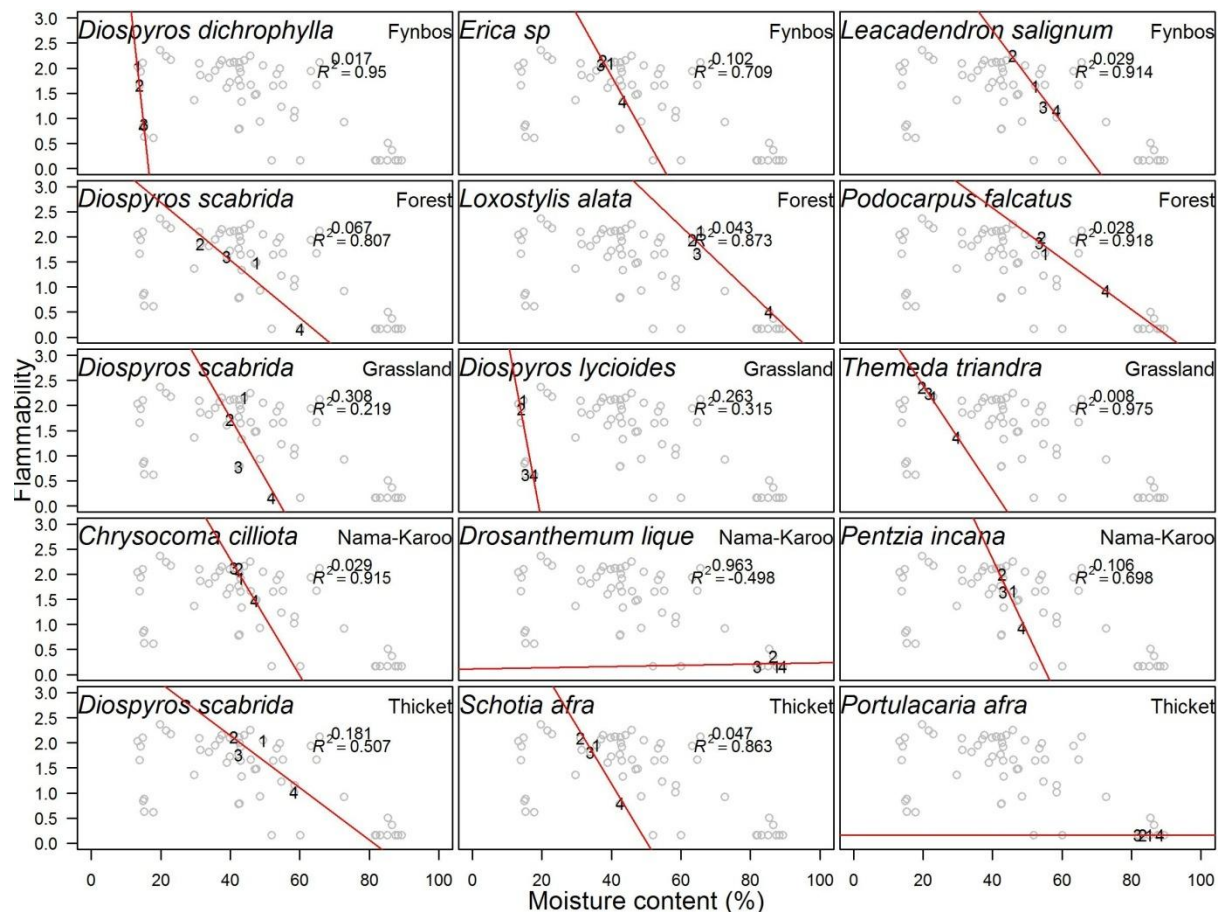


Figure 4: Species-level flammability vs moisture content (1-Summer 2014; 2-Winter 2014; 3-Summer 2015; 4-Winter 2015).

There were other observations in this test that should also be mentioned. The succulents indicated no correlation at all with *Drosanthemum lique* having a significance of 0.963 and *Portulacaria afra* producing a perfect 1 which is invalid as true correlation is not possible. The consistently high moisture and low flammability found in these species cannot be correlated. It should also be pointed out that large trees such as *Loxostylis alata*, *Podocarpus falcatus*, and *Schotia afra* all had strong correlations ($r^2 > 0.85$). All three are large evergreen trees found in fire-free systems. They would strongly argue for the theory that flammability emerges due to environmental conditions (Midgley, 2013) as one would expect them to have lower flammability throughout. Considering the range of significance observed in the correlation test, it appears as though species may have inherently different moisture retaining capabilities which may be irrelevant to the fact that they are fire-prone or fire-free. Despite the environment having the overarching impact on flammability and moisture, individual or species' traits may ultimately dictate how they respond to environmental triggers.

3.5. Conclusion

The study was aimed at determining the impact prevailing weather has on plant flammability by comparing it to moisture content. I find that species with strong inherent adaptation to climate skews the results to conform to the expectations of moisture negatively affecting plant flammability. When these biases are removed, there is no significant correlations which probes further evaluation. Observations at the species-level illustrate that there is no consistent response across all species, but rather that species have inherent adaptation to climate or they acclimate to the prevailing weather conditions. Unfortunately this study was a very small snapshot of the relationship between moisture and flammability with a limited number of species and replication. To further this research, studies will need to cover a larger array of traits from various species with increased replication.

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4. The impact of climate variation on plant flammability.

4.1. Abstract

Plants acclimate to the natural environment they are frequently exposed to. Climate, as temperature and precipitation, can greatly influence how species a species evolves over long periods of time. Certain species have been documented to develop traits associated with fire regimes, which in many cases are linked to the environment. In this study, I focus on comparing flammability of species across seasons and hypothesise that plants will be more flammable in the summer than winter. I also hypothesise that flammability will be similar between the same season in different years. Ninety-nine plant species, from five distinct biomes were used in the experiment to incorporate fire-driven and fire-free species. The results were compared between seasons and these indicated that factors other than climate also impacts flammability. Similar seasons also proved to have different flammabilities as drought and annual rainfall were strong drivers. Looking at biome-scale comparisons, I find that inherent properties that are unlikely fire-driven may influence the results. From this I can infer that species-level responses vary considerably between and among communities. Subsequent studies will need to focus on measuring a range of functional traits over temporal and spatial scales.

4.2. Introduction

Flammability heterogeneity is mainly driven by climate, but also by prevailing weather conditions. As discussed in the previous chapter, moisture from precipitation can influence species flammability. However, temperature also forms part of the climate story which impacts the flammable character of individuals. A plant community might receive sufficient rainfall to decrease flammability, but if high temperatures persist, the evaporation can again increase flammability due to moisture loss. Both of these can vary considerably throughout the year in any given area. Seasons, an example of climatic heterogeneity, can strongly influence the landscape, vegetation and biodiversity. Regions experiencing strong seasonal change often showcase a range of species adapted to the change. A global example of this is the Mediterranean systems that experience warm, dry summers and cool, wet winters — plant species found here generally set seed in the summers and seeds germinate in the winters after

some rainfall (Bradshaw et al., 2011). Coupled with this seasonal change, is the occurrence of fire events, which for the most part occur in the dry summers. Many plant species, such as the Proteoids, are adapted to the frequency of fire events. To elaborate, it has been suggested that species can adapt to frequent fire events over thousands of years as opposed to a single fire event that occurred once in a century or more (Lamont et al., 2013). The climate of the Cape Floristic Region (CFR) where many Proteoids occur, receives sufficient rainfall in the winter to promote biomass build-up while the warm dry summers desiccate plants while also increasing dead material which then results in a higher likelihood of fire occurring (Barker et al., 2004; Cowling et al., 1996). Droughts and flood conditions can strongly impact on these season, particularly when it is over an extended period of time. It should also be noted that it takes several seasons (usually) for biomass to accumulate. As mentioned, flammability is said to be a trait formed as an adaptation to these fire-driven systems. The parent plant is likely to burn to create the nutrient-rich, competition-free environment for the benefit of its offspring. In Chapter 1 and 2, I explored flammability in the literature and as a functional trait respectively. This is to discover our knowledge limitations as well as to bridge certain gaps in the knowledge base. To further explore flammability, I look at the standardised flammability protocol to determine how choice of season and conditions leading up to sampling play a role in determining the results.

Within the guidelines for the standardised flammability protocol, Jaureguiberry et al. (2011) list several concerns regarding experimenting on temporal and spatial scales. Firstly, they elaborate on the effect that precipitation may have on the flammability results. As discussed in the previous chapter, I explore the relationship between moisture and flammability. In the study I found that moisture as a factor can influence the result, particularly when temperature correlates with precipitation (i.e. cold and wet vs. warm and dry). The study however was subject to low sample size and replication and longer period of study should be used to test feasibility of protocol. Another recommendation by Jaureguiberry et al. (2011) is to standardise the season of experimentation as species acclimated to seasonal variation may alter findings. Their reasoning is that seasonal phenology may influence results. Using the example of the CFR again, many species flower in the spring before the summer fires, while in the winter resprouting and germinating is associated with the rainfall (Cowling et al., 1997). A specific example of this is the presence or absence of flowers that may bring new properties to the flammability measures. Phenology however, is still a product of climate and the influence of climate heterogeneity on flammability is the main focus. I hypothesize that

(1) plant flammability will be significantly different between summer and winter seasons and
(2) not significant different among consecutive summer or winter seasons. Here I conduct the standardised flammability protocol across seasons and across different biomes.

4.3. Methods

The exact same procedure for sampling species was conducted as discussed in Chapter 2. Ninety-nine different species from five different biomes in the Kaboega reserve were used. Six replicates of each species were measure at each of the sampling dates. The total number of observations equates to over 2500 with replication occurring at sample level, vegetation level and across seasons making this study one of the largest regarding flammability. The precipitation and temperature data was measured using a weather station placed along a topographic transect at Kaboega and regularly collected by Robbert Duker. The flammability experiment was conducted 2 weeks in the summers and winters of 2014 and 2015. A repeated measures ANOVA was done to compare the variation in flammability between biomes and seasons. This is to determine how responsive different vegetation is to prevailing weather conditions, in particular seasonal drought. Multcomp 1.4-7 (Hothorn et al., 2009) and nlme 3.1-131 ((Pinheiro et al., 2017)) was used in R version 3.1 (R Development Core Team, 2016). A post-hoc test was done to further compare the biomes within each season.

Temperature data as seen in Figure 1 indicates the strong difference in maximum temperature between summer and winter seasons. The rainfall data (Fig. 2) is not indicative of a strong seasonal region, but rather one that has aseasonal rainfall. This is expected and this portion of the Eastern Cape falls within an aseasonal rainfall regime. To the north and east the climate is that of a summer rainfall while the west receives winter rainfall. However, the argument could be made that it also fits a summer rainfall pattern to a small extent. The summer sampling took place roughly one month after the temperature peak while winter sampling was done near the coldest temperature.

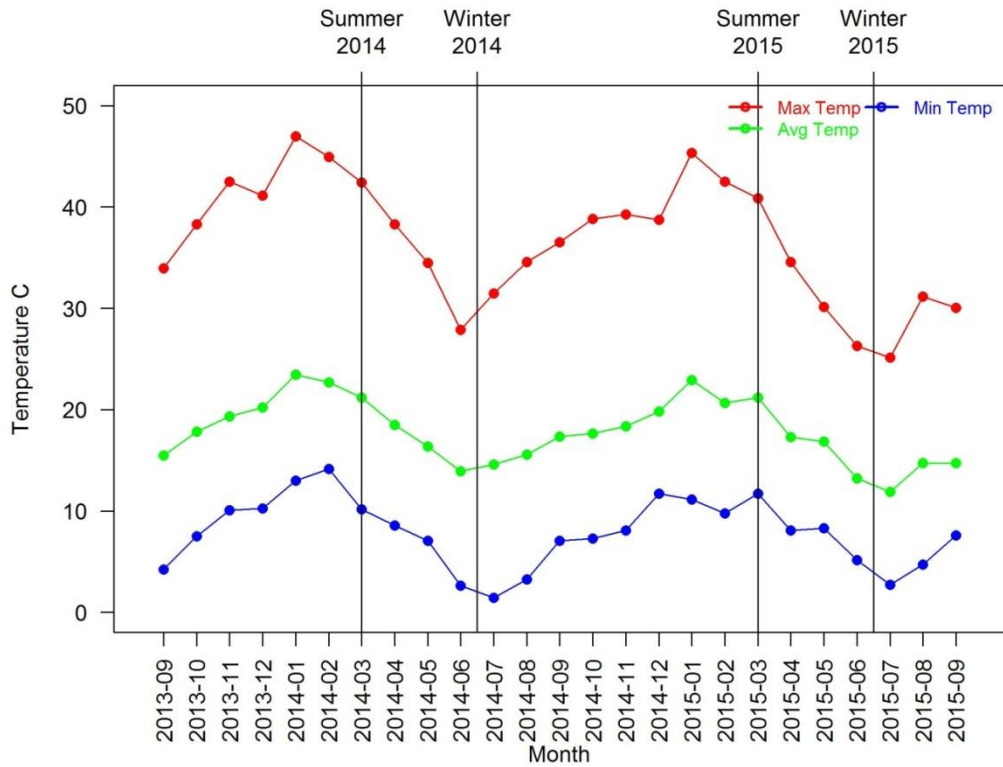


Figure 1: Monthly temperatures for Kaboega reserve (absolute maximum and minimum temperature observed for Max temp and Min Temp respectively).

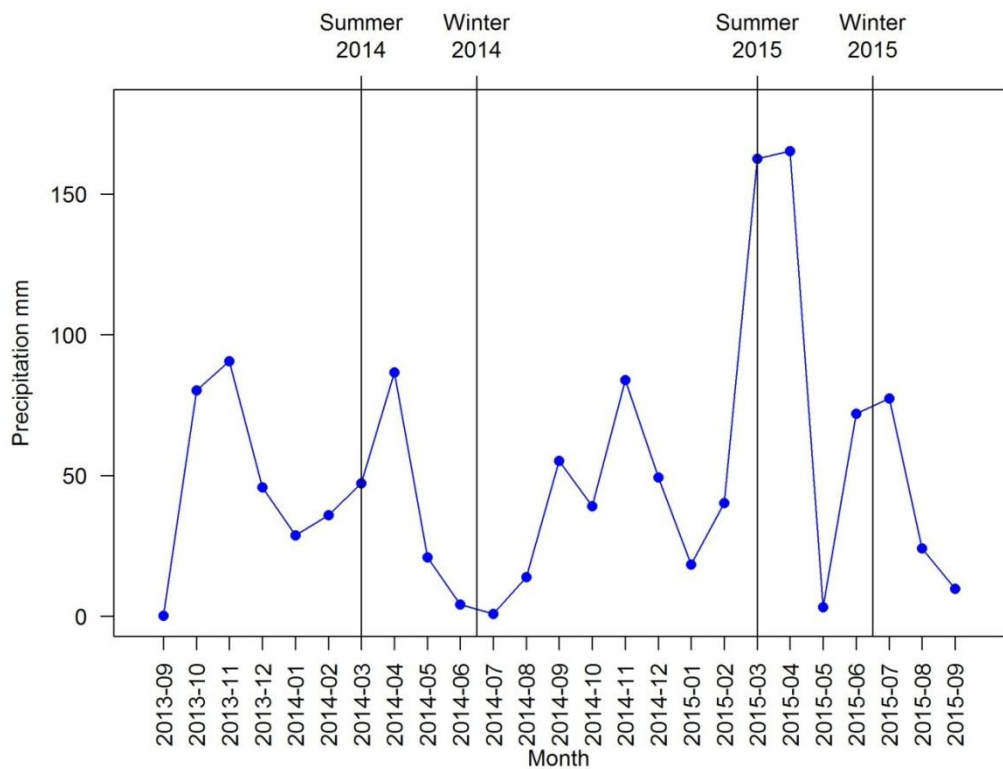


Figure 2: Monthly precipitation

4.4. Results & Discussion

4.4.1. Seasonal comparisons

In Chapter 2, I focussed on the functional traits of species and how they may affect flammability. The study was a snapshot in time, however, and as discussed I wanted to expand the observations across time scales. Figure 3 shows how plant flammability in different biomes was affected by environmental conditions across different sampling times. Figure 3 demonstrates that the winter 2015 data showed the lowest flammability across all biomes while the other seasons still had relatively similar means. The only major exception to this is the Nama-Karoo in winter 2014 where it had much higher flammability. When looking at Figures 1 & 2 we can see that it was extremely cold and very dry. Both of these can cause stress in the plant and the lower moisture content boosted the flammability even more. Significant variance was noted within the summer 2014 and winter 2015 data with both having $p < 0.001$. A post-hoc test reaffirmed the graphical interpretation of winter 2015 as it was significantly different from all three of the other seasons ($p < 0.001$). This season had the lowest maximum and average temperatures as well as receiving a reasonable amount of precipitation. The only other significant difference noted was between winter 2014 and summer 2015 ($p = 0.044$). The winter of 2014 indicated the highest overall flammability across all biomes. This suggests that temperature might not strongly correlate to flammability. The cold temperatures observed in the winter 2014 data can cause plant stress evident as desiccation or increased dead material. Within the forest biome, many tree species had browned leaves due to the cold conditions, most notably *Ficus sur* (Wild fig). Browned leaves are observed when photosynthetic efficiency drops which reflect plant stress. Further analysis of the data is required as biomes occur within the landscape they are adapted to and thus different responses may occur when comparing biomes (Mucina and Rutherford, 2006).

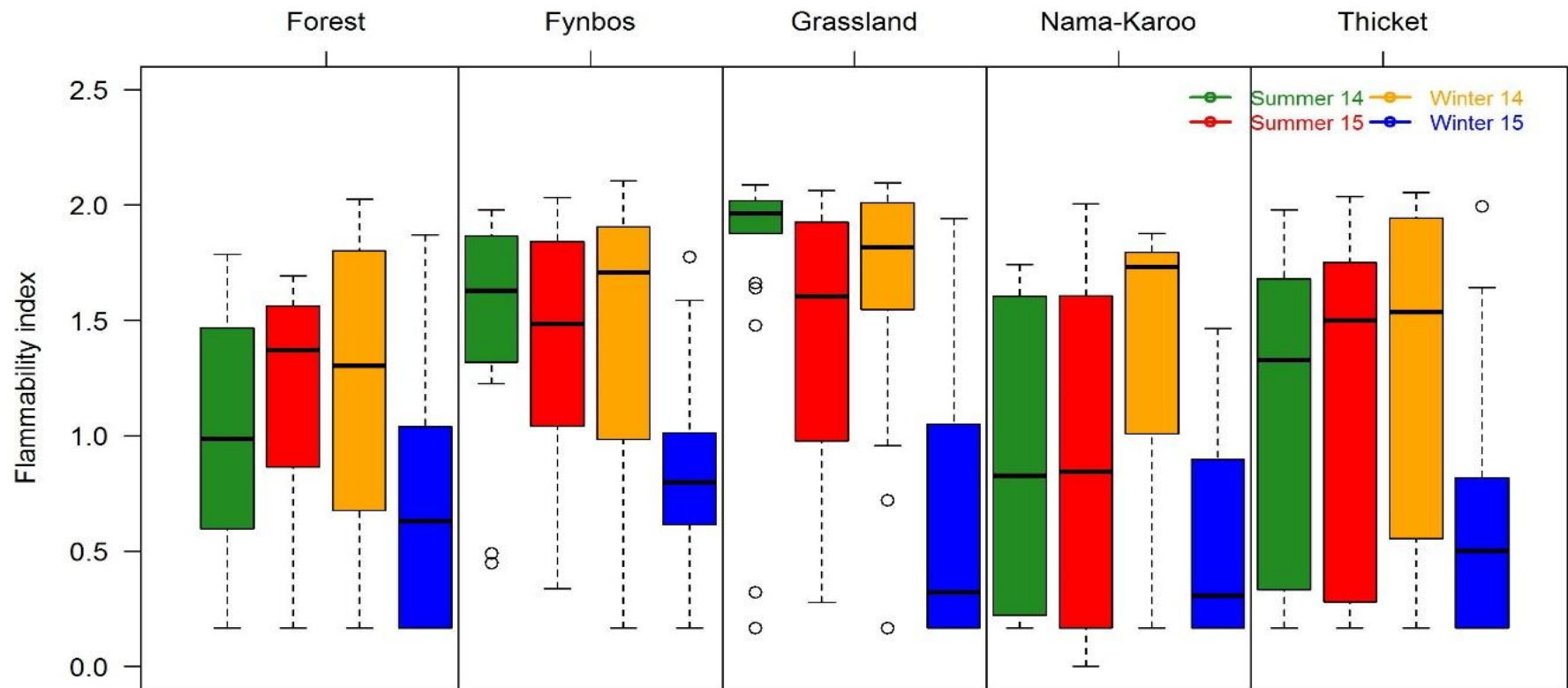


Figure 3: Species-level flammability represented as biomes per season. Seasons coded by year of sampling (e.g. Summer 14 of 2014 and Summer 15 of 2015).

4.4.2. Snapshot interpretations / Biome comparisons

In the Nama-Karoo, some species show stronger seasonal change as frost in the valley bottoms, where this vegetation occurs, is regular during winter. For examples, species such as *Pentzia incana*, *Chrysocoma ciliata*, and *Jamesbrittenia pinnatifida* (plates 1-3) are small herbaceous shrubs with small leaves and twigs in an often-dense matrix and during extended drought conditions, these plants shrivel, becoming denser. Interestingly, the variance of species flammability in the Nama-Karoo is much lower in the winter compared to the summer. In both summer seasons, precipitation was relatively high. In 2014 the winter received the lowest amount of precipitation while the 2015 winter had reasonably high precipitation. It appears the two semi-extremes observed resulted in the variance being smaller while moderate summer rainfall allows greater variance. Similarly, the Grassland species showed greater variance in the higher precipitation yielded 2015 compared to 2014.

In the Fynbos and Grassland, the moisture appears to impact species flammability more. In both cases, the summer of 2014 had higher flammability than the 2015 summer, despite having similar temperatures. In the case of Grassland however, aspect may explain some variance as the biome receives much more sunlight (and thus heat) resulting in the lower variance with higher flammability in summer 2014. Based on field observations, moisture retention in the branch matrix of plants (as water on leaves or twigs) is much higher in these two biomes, relative to the other examined biomes. In both cases, species are (in general) more flammable in the summers than in the winter of 2015, does however illustrate that temperature cannot be excluded from the reasoning. The warmer conditions of summer allow higher evaporation to take place compared to the cold winters (Chuvieco et al., 2004). If one could standardize the experiment to test temperature and moisture individually, one can create powerful indices to be used in fire prediction modules.

Further observations of phenology whilst conducting sampling, indicated that certain inflorescence features may impact on the flammability of a species. An example of this is the Fynbos species, *Protea lorifolia*. The Fynbos biome predominantly occurs in the winter-rainfall region of South Africa with fires mostly occurring in the dry warm summers. The species is serotinous, meaning it releases the seeds in the post-fire environment after the individual dies (Bond, 1984). During the summer sampling events, some individuals had flowers present. It was noted that these flowers encouraged ignition as the hairs were clearly

very flammable (plate 5). Thus, the individual becomes more flammable due to higher burn rate and burnt biomass (Pausas et al., 2016). Other phenological anomalies were noted in the Grassland and Thicket as well. In the Grassland, species such as *Helichrysum nudiflorum* (plate 6 & 7) had a large proportion of dead leaves present in the summer sampling which again increases flammability as opposed to the green, moisture-rich leaves seen in winter.

Table 1. Significant differences between biomes (established using a TukeyHSD test) per season (summer or winter). Lower diagonal is the 2014 comparisons, and upper diagonal is the 2015 . * p<0.001, ** p<0.01, * p<0.05. The p-values are reported in Appendix B.**

Summer	Forest	Fynbos	Grassland	Nama-Karoo	Thicket
Forest	-	<i>ns</i>	<i>ns</i>	<i>ns</i>	**
Fynbos	***	-	<i>ns</i>	<i>ns</i>	<i>ns</i>
Grassland	***	<i>ns</i>	-	<i>ns</i>	***
Nama-Karoo	<i>ns</i>	**	***	-	**
Thicket	*	<i>ns</i>	***	<i>ns</i>	-
Winter	Forest	Fynbos	Grassland	Nama-Karoo	Thicket
Forest	-	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Fynbos	<i>ns</i>	-	<i>ns</i>	<i>ns</i>	<i>ns</i>
Grassland	<i>ns</i>	<i>ns</i>	-	<i>ns</i>	<i>ns</i>
Nama-Karoo	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	<i>ns</i>
Thicket	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	-

Reviewing the interbiome comparisons, we find some interesting values. In summer 2014, the Forest biome was significantly different to all biome except Nama-Karoo where it had extremely low significance (p=0.999). In summer 2015, the Forest was only significantly different to Thicket (p=0.003) and in both winters showed no significant differences. Following a similar trend to the Forest, is Fynbos which was significantly different to all biomes in summer 2014 except Grassland. This is expected as these occur in similar landscape with the main difference being aspect and then they also share traits as fire driven systems (Cowling and Campbell, 1983). However, in all of the other seasons, Fynbos showed no significant differences. Grassland showed great difference to Nama-Karoo in summer 2014 (p<0.001) which, in itself would not be surprising until one compared it to summer 2015 (p=0.996) where they appear to be very similar. If the significant change was observed between a summer and a winter, one could suggest that the seasonal climate was the main

driver. But, as it is between summers, there has to be more to the story. I suspect that moisture availability is one of the major factors to consider here. Looking at the temperatures we see that the summers had similar values, however the precipitation was much higher during the summer 2015. In Figure 3 we see that Nama-Karoo had similar variance in both summers, but Grassland clearly had much higher flammabilities during summer 2014. This observation hints to what was mentioned in Chapter 3, whereby species may have functional traits adapted for surviving in their niche which can influence flammability without any clear association. It reflects the importance of moisture availability in fire prediction (Santana and Marrs, 2014). The statistics gathered here also alludes to the importance of temperature. I have listed some of the significant differences observed during the summer sampling dates, however none were observed during winter dates. No significant difference is also an important result as in this particularly case suggests we look at all the results. The precipitation was variable among all sampling dates and the amounts prior to sampling similarly. Temperature on the other hand showed clear distinction between summer and winter months. Although temperature does play a role in the amount of moisture available as well as evaporation rates, it can also influence plant morphology (Picotte et al., 2007). As mentioned, some plants shrivel up during cold periods while some go brown and then again some desiccate during warm periods or produce more dead material.

4.4.3. Intrabiome comparisons

To further investigate this, I look at the difference in responses in flammability between individual biomes sampled over the two years. Within the Forest biome, summer 2014 was not significantly different to any of the other season, including the winter of 2015. Winter 2014 and summer 2015 were also not significantly different, but both were significantly different to winter 2015 ($p=0.002$ and <0.001 respectively). The different correlations between the seasons reflect the concept of species responding to climate differently within the Forest biome. The Fynbos biome shows a different result. Summer 2014, 2015, and the winter of 2014 were not significantly different from each other, but all were from winter 2015.. The biome performs similarly when exposed to different climate combinations (warm and wet; cold and dry; warm and wet), but the combination of cold and wet significantly decreases flammability. As the Fynbos, in general, is known to be adapted to a winter rainfall regime with fires in summer, we expect flammability to be lower in winter (Bond, 1984).

Some literature argues that species may have adapted the flammable trait in response to regular fires (Bond et al., 2003; Mutch, 1970) while others suggest flammability emerges due to the environment (Midgley, 2013). I believe that a community of species that have adapted to fire will showcase similar variation in flammability across seasons while those that are vastly different represent traits that can influence flammability by coincidence but their flammability ultimately reflects acclimation to the environmental conditions at the time. Similar to the Fynbos, Grassland had significantly different results in all seasons compared to winter 2015. However, summer 2015 was very dissimilar to both summer 2014 and winter 2014 ($p=0.003$ and 0.068 respectively), while summer and winter 2014 were not dissimilar ($p=0.723$). This variability reflects a combination of plants that are consistently flammable along with some that vary, suggesting the species have different coping mechanisms to climate and also that climate is a stronger driver in this biome (Breman et al., 2011). The Thicket biome was very similar in summer and winter 2014 and summer 2015 with all seasons significantly different to the winter sampling. The Thicket found at Kaboega is a mixture of Arid and Mesic Thicket. The Arid Thicket would be expected to cope well with the increased aridity when compared to the Mesic. The significant difference between the sampling dates was the increased precipitation that preceded the winter 2015 sampling. Thus, Thicket species show similar responses to arid conditions, but when moisture increases considerably, the flammability is much lower. The Nama-Karoo was the only biome to fit expected results. Both summer seasons were significantly different to the winter seasons, and in both cases no significance among same seasons. This biome is fire-free and strongly adapted to cold temperatures in winter and warm in summer under arid conditions (Rutherford et al., 2006). Considering these results, it seems as if the inherent properties for surviving here are coincidentally influencing flammability. Thus, in the case of this biome, flammability emerges and is not inherent (Midgley, 2013).

4.5. Conclusion

This chapter has set out to be a multifaceted approach to determine flammability response to climate heterogeneity. Flammability has to date only been analysed in a snapshot in both time and space. Heterogeneity however tells us that things will change over temporal and spatial scales and thus the need for such an investigation was paramount (Pausas et al., 2017). Geographically, the study is still narrow, but it encompasses a large array of biomes and their

species which I believe compensates for spatial aspect to some extent. At the temporal scale I looked at four seasons spread over two years. This timeline can also be considered narrow, but it still allows for the variation I was looking for in climate. I set out hypotheses to test and found that: (1) flammability is only significantly different between summer and winter seasons when a drastic change in the environment conditions has occurred, such as a drought or high precipitation; and (2) that said drastic events can influence flammability among the same season. This is not to say that climate variation does not impact flammability directly. From the data we can see that different combinations of temperature and moisture can strongly impact flammability. The particular study area has aseasonal rainfall and as such the variation in climate may be different from what one might find in a strongly seasonal rainfall area. My recommendation would be to have this study done in strongly seasonal regions as well as over a longer time period. Greater variance will provide a better narrative regarding flammability in response to climate.

4.6. Appendices

4.6.1. Appendix A: Seasonal comparisons by ANOVA (blue) and TukeyHSD post-hoc (clear).

Season	Summer 2014	Winter 2014	Summer 2015	Winter 2015
Summer 2014	<0.001	0.309	0.810	<0.001
Winter 2014	0.309	0.795	0.044	<0.001
Summer 2015	0.810	0.044	0.254	<0.001
Winter 2015	<0.001	<0.001	<0.001	<0.001

4.6.2. Appendix B: Biome comparisons by per (established using a TukeyHSD test).

Lower diagonal is the 2014 comparisons, and upper diagonal is the 2015.

Summer	Forest	Fynbos	Grassland	Nama-Karoo	Thicket
Forest	-	0.514	0.238	0.569	0.003
Fynbos	<0.001	-	0.44	0.095	0.795
Grassland	<0.001	0.986	-	0.996	<0.001
Nama-Karoo	0.999	0.001	<0.001	-	0.004
Thicket	0.033	0.072	<0.001	0.328	-
Winter	Forest	Fynbos	Grassland	Nama-Karoo	Thicket
Forest	-	0.968	0.628	0.397	0.741
Fynbos	1	-	0.984	0.787	0.993
Grassland	0.961	0.983	-	0.959	1
Nama-Karoo	0.999	0.998	1	-	0.934
Thicket	0.201	0.52	0.554	0.89	-

4.6.3. Appendix C: Intra-biome comparisons across seasons (established using a TukeyHSD test).

Fynbos	Summer 2014	Winter 2014	Summer 2015	Winter 2015	Grassland	Summer 2014	Winter 2014	Summer 2015	Winter 2015
Summer 2014	-	0.979	0.438	<0.001	Summer 2014	-	0.723	0.003	<0.001
Winter 2014	0.979	-	0.686	<0.001	Winter 2014	0.723	-	0.068	<0.001
Summer 2015	0.438	0.686	-	<0.001	Summer 2015	0.003	0.068	-	<0.001
Winter 2015	<0.001	<0.001	<0.001	-	Winter 2015	<0.001	<0.001	<0.001	-
Forest	Summer 2014	Winter 2014	Summer 2015	Winter 2015	Thicket	Summer 2014	Winter 2014	Summer 2015	Winter 2015
Summer 2014	-	0.297	0.551	0.100	Summer 2014	-	0.262	0.998	<0.001
Winter 2014	0.297	-	0.973	0.002	Winter 2014	0.262	-	0.347	<0.001
Summer 2015	0.551	0.973	-	<0.001	Summer 2015	0.998	0.347	-	<0.001
Winter 2015	0.100	0.002	<0.001	-	Winter 2015	<0.001	0.001	<0.001	-
Nama-Karoo	Summer 2014	Winter 2014	Summer 2015	Winter 2015					
Summer 2014	-	0.003	0.997	0.039					
Winter 2014	0.003	-	<0.001	0.067					
Summer 2015	0.997	<0.001	-	<0.001					
Winter 2015	0.039	0.067	<0.001	-					

4.6.4. Appendix D: Plates

Plates 1-3 from Nama-Karoo, 4 & 5 from Fynbos, 6 & 7 from Grassland.



Plate 1: *Pentzia incana* (Dense shrubs with large open spaces inbetween).



Plate 2: *Chrysocoma ciliata* (Dense shrub, often in between *P. incana*).



Plate 3: *Jamesbrittenia pinnatifida* (Small, dense and very sparsely spread).



Plate 4: *Protea lorifolia*



Plate 5: *Protea lorifolia* inflorescence (Trichomes on petals and sepals).



Plate 6: *Helichrysum nudifolium*



Plate 6: *Helichrysum nudifolium*

4.7. References

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5. General discussion

5.1. Background of study

Since the Mutch hypothesis (1970), interest in understanding plant flammability has increased. In the years following this theory, many have criticized its standing on flammability being an adapted functional trait (Midgley, 2013; Schwilk et al., 1997; Zedler, 1995), while others suggested alternate theories to substantiate this plant trait (Bond and Midgley, 1995). Despite the growing interest, few have attempted to directly experiment on and measure flammability. This is largely due to the number of factors influencing flammability and different scales to consider (Bowman et al., 2014). The properties of flammability have been described to be consumability, combustibility, sustainability, and ignitability (de Magalhães and Schwilk, 2012). Individually, these measures have been investigated (Schwilk and Ackerly, 2001), but few have attempted to include several measures as experimental design is of key importance. In 2011, Jaureguiberry et al. proposed a device that was able to measure plant flammability in near entirety in a standardised manner that was both time and financially efficient. Since the development of this approach, several studies have used it for research (Arganaraz et al., 2015; Burger and Bond, 2015; Schwilk, 2015; Wyse et al., 2016). However, many of these studies, and even those fire studies predating flammability experiments, focus on species found in a fire-prone environments. Similarly, few studies experiment on fire temporally, thus producing snapshot studies. I believed that to move forward our understanding of flammability, a standardised measurement of flammability should be used to consider as trait adaptation is heterogeneous in the natural environment. Thus, using the standardised flammability device as a base for my experimentation, I set out to investigate flammability across different spatial and temporal scales.

5.2. Main results

My first focus was on flammability as a functional trait and to which of the proposed theories it fits best (Bond and Midgley, 1995; Midgley, 2013; Mutch, 1970; Schwilk and Kerr, 2002). At the biome-level, the results conform slightly to expectation with fire-driven systems having higher overall flammability compared to fire-free systems. At species-level however,

there were several cases of fire-driven species (Fynbos and Grassland) having low flammability while many species from fire-free biomes had high flammabilities (Forest, Nama-Karoo, and Thicket). Certain flammable species had traits normally attributed to non-flammable species (e.g. large leaves sparsely arranged on coarse twigs) which strongly suggests that flammability may not be inherent, but rather surfaces when exposed to sufficient fire. Still, many of the traits associated to fire-driven systems correlated to high flammability (e.g. dense architecture and sclerophyllous leaves) (Kraaij and van Wilgen, 2014; Le Maitre and Midgley, 1992).

As the results proved inconclusive in explaining flammability as a functional trait, I look at rainfall, keeping in mind that fire-driven systems have fire-regimes that strongly correlate to rainfall (Govender et al., 2006; Kraaij et al., 2013a). I correlate observed flammabilities with plant moisture content, and use climate data to better understand the relationship. I find that moisture at a landscape scale does not drive flammability at the species scale directly — it is rather a product of the species' inherent ability to retain moisture or a result of inevitable response (Farooq et al., 2009; Picotte et al., 2007). However, this is not to say that regional precipitation is irrelevant as droughts or high rainfall is shown to also influence flammability as expected (Pausas and Fernández-Muñoz, 2011).

Using only a select number of species and with the focus solely placed on moisture still gives a snapshot view on flammability. With this in mind I expanded the experiment to the same range of species used in Chapter 2 and sampled over two consecutive summers and two consecutive winters. This places the focus on flammability's relationship with climate as both temperature and precipitation are known to be a driver of fire-regimes (Bond et al., 2005, 2003). Here I find that high rainfall in the month(s) leading up to sampling can significantly influence the flammability results, to the degree where overall differences amongst biomes shift. I also note that different combinations of temperature and moisture can cause variation in observed flammability. However, this still fits with the previous chapter's results in that climate at extremes (e.g. cold and very wet) influence flammability more. At the species-level, we see that plants show different responses to the climatic changes, much of which can be attributed to phenology (Heelemann et al., 2008; Steenkamp et al., 2000). There were also cases that reflect the inherent ability of a species to respond to the environment. One example is the trichomes found on *Themeda triandra*, a clumped Graminoid, which retained moisture and is said to cool the plant (Picotte et al., 2007), but also increased its flammability. Another example would be the increase in dead material on shrubs following a period of drought.

Finally, I looked at individual biome responses across the seasons. Intriguingly, in cases like the fire-driven Fynbos, there was great variation in flammability between seasons. This suggested that some species have inherently different mechanisms of response towards climatic changes while others reflect plastic responses. This is fascinating as it argues for and against flammability being adapted to the environment. Fynbos and Thicket were both only significantly different to the winter that received abundant rainfall. My argument is that a community of species that have adapted to fire will showcase similar variation in flammability across seasons while those that are vastly different represent traits that can influence flammability by coincidence but their flammability ultimately reflects the environmental conditions at the time.

5.3. Limitations

Chapter two focussed on flammability as a functional trait by comparing it to other traits, both fire-driven and fire-free. Although this study included a 99 species from different habitats, it still only looked at flammability at a single point in time and measured but a few traits. Burger and Bond (2015) did a similar study but had a stronger focus on traits with limited number of species. Although they showed interesting findings, there was no distinct correlation to flammability and they suggested that phenology should be considered. My chapters following this looked at climate and I noted that there are a vast variety of responses by plants to environmental conditions. None of the results can conclusively demonstrate that flammability is as an evolutionary trait, however it does hint at where links may exist. The study area for this thesis falls within a non-seasonal rainfall region. As such, many endemics of the area, whether fire-driven or not, may not reflect strong correlation between flammability and season.

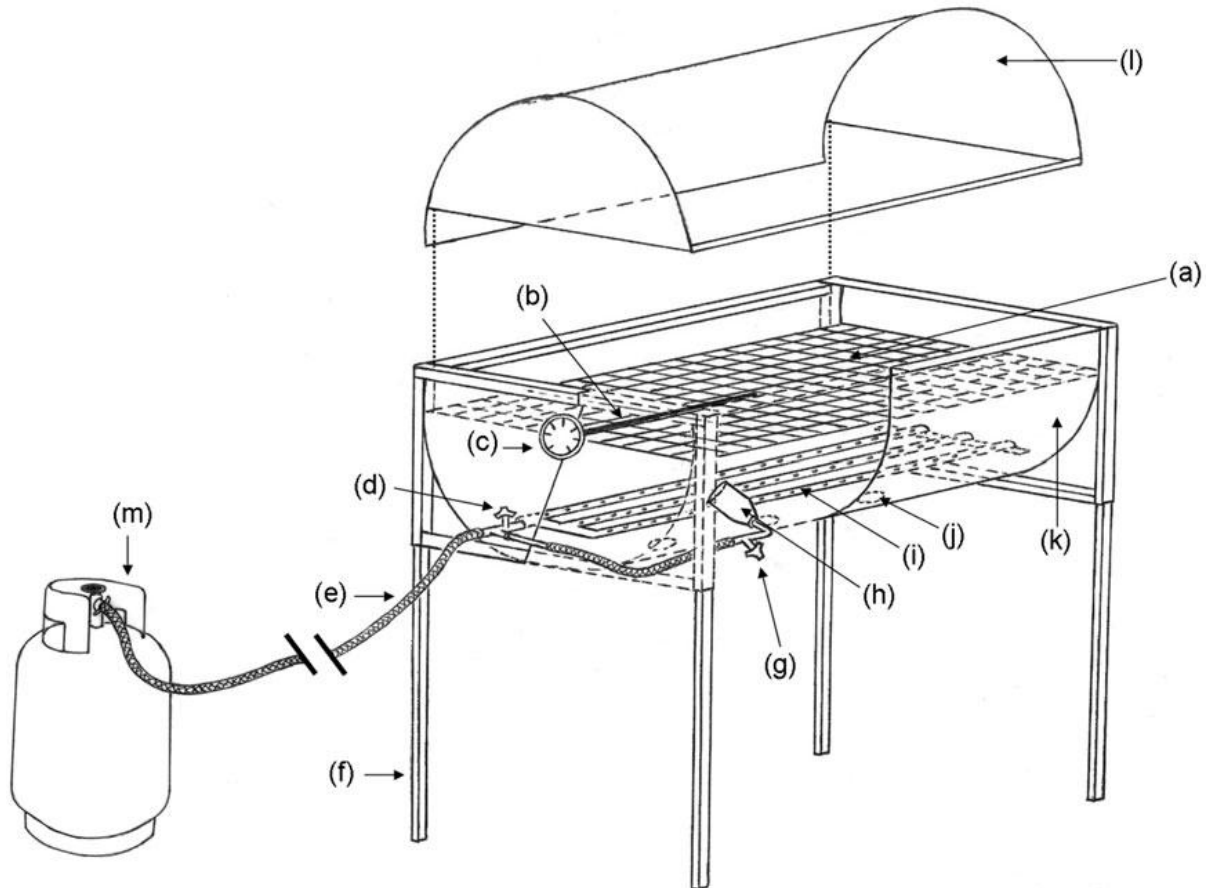
5.4. Future research

I believe this research to be novel and further development of the standardised approach will prove useful. The guidelines set out by Jaureguiberry et al. (2011) for measuring standardised flammability suggest that season and meteorological conditions may strongly influence the results and recommend standardising the sampling time and conditions where possible. Despite this, I strongly suggest that future research will have to look at the heterogeneity of

fire as a whole and its implications for flammability (Pausas and Ribeiro, 2017). Using species from different vegetation types should be of utmost importance as only using fire-driven species will influence results. I also suggest comparing across regions with differing rainfall season, but using similar species for reference. The last suggestion based on my results would be to expand on a temporal scale, preferably more than two years as drought or flood conditions will hamper results. My suggestions correlate with Pausas et al. (2017), who describes the importance of considering heterogeneity in the environment and thus include multiple scales when investigating flammability. If this approach to flammability can be adapted to where a standard is used, one can create a meta-analysis anywhere in the world (e.g. comparing the different Mediterranean shrublands). The data gathered on flammability can be used in prediction modelling for fire management (Santana and Marrs, 2014), particularly when data on moisture content is included. A more modern use of this data would be 3D modelling, whereby individual plants are modelled to show fire spread throughout the canopy and subsequently to neighbouring plants (Parsons et al., 2011).

5.5. Appendix

5.5.1. Appendix A: Excerpt from guidelines for the standardised flammability device (Jaureguiberry et al., 2011).



General view of a device for measuring plant flammability in the field. (a) grill; (b) grill thermometer; (c) temperature gauge; (d) security valve; (e) connection to gas cylinder; (f) removable legs; (g) blowtorch valve; (h) blowtorch; (i) burners; (j) ventilation holes; (k) barrel; (l) removable wind protection; (m) gas cylinder. See main text for technical details.

5.5.2. Appendix B: Image of the device produced for this study.



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