# Flammability traits of fynbos species with different post-fire regeneration strategies

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## Abstract

Wild fire is an important disturbance regime that shape global biome distributions and maintain the structure, function and biological diversity of plant communities in fire-prone environments. Physical, chemical and architectural properties are known to affect plant flammability, but few studies explore how these traits contribute to fire properties at the individual level and how flammability is influence by regeneration strategy. The flammability and traits that contribute to it is investigated in 15 co-occurring fynbos and forest species with burning experiments performed at Bain's Kloof Pass, Western Cape of South Africa. Eight species are characterised by fire-stimulated (mostly seeders) and seven by non-fire-stimulated recruitment (mostly resprouters). Results across all species are consistent with other studies which indicate that the proportion of dead and fine fuel is significant predictors of flammability. Significantly higher flame temperatures and values for % fuel burned were recorded for FSR's relative to NFSR's and these differences are attributed to significant differences in % fuel dead, fuel bed porosity and packing ratio. This is consistent with the hypothesis that flammability is most like to be selected for in fire-stimulated recruiters (first colonisers after fire) where a combination of increased flammability and recruitment success enhance their fitness in the fire-prone environment. This study indicates that cultivation of the highly flammable species *E. rhinocerotis, Stoebe sp., M. muricata, Erica sp.* and *P. amplexicaulus* on urban fringes should avoided to reduce fire-risk and thus increase human safety.

## Introduction

Natural or wild fires are recurring events in several ecosystem types, including savannas, Mediterranean shrublands and even boreal forests (Schwilk & Kerr, 2002), and have been so for millions of years helping to shape global biome distributions and maintain the structure, function and biological diversity of plant communities in fire-prone environments (Bond & Keeley, 2005). Different vegetation types can behave differently in their fuel properties and plant ecologists have long been intrigued by the striking adaptive responses of plants to fire. These typically comprise traits that promote survival from fires such as thick bark and resprouting from underground storage organs, and traits that cue reproduction to the post-fire environment such as heat or smoke-stimulated seed germination and serotiny (Schwilk & Ackerly, 2001; Schwilk & Kerr, 2002). Furthermore, flammable vegetation is often dominated by plants characterised by fire-promoting traits that encourage fire spread and increase fire intensity (Mutch, 1970; Zedler, 1995).

From laboratory combustion tests of litter fuels coupled with observations that fire-dependant plant communities resist invasion, are more flammable and burn more readily than non-fire-prone communities, Mutch (1970) proposed that natural selection has favoured the development of fire-promoting characteristics in flammable communities. However, critics of this hypothesis argue that natural selection does not act on communities, flammability traits may have evolved as a by-product of other adaptations that increase fitness, and it would be counter-productive for a species to evolve traits that would increase mortality by fire due to reduced individual survival and lifetime reproduction (Troumbis & Trabaud 1989; Snyder, 1984). Buckley (1984), Bond & Midgley (1995) and Schwilk (2002) have addressed these problems with individual-based arguments for the evolution of flammability traits in fire-prone environments. According to these authors, fire acts as an agent in interspecific competition and if by burning readily a species damages its competitors, and if the benefits it receives as a result of the damage to its competitors outweigh the damage it sustains itself, increased flammability can increase its fitness. Therefore, traits that increase the flammability of a particular species could be selected for if these traits are coupled with an increase in fitness regarding recruitment in the competition-free environment following fires. Fitness relating to recruitment success could include traits that would allow a given species to first occupy the newly formed,

competition-free environment such as rapid germination or fast seedling growth rates. More research on natural selection and the genes that code for flammability is needed since the evolution of flammability implies an entire paradigm shift regarding the relationship between fire and plants. Far from being passive responders to the physical phenomenon of fire, plants may be actively promoting (or reducing) the probability of burning through the evolution of traits that influence flammability.

Though there is a large literature on fuel and fire behaviour, very little of this deals with how traits of individual plants contribute to fire properties (e.g. Cowan & Ackerly, in press). From general considerations of vegetation as 'fuel', traits that might influence flammability include structural or architectural properties of plants such as the retention of dead material, leaf morphology and branching patterns which influence the spatial arrangement of fuels. These structural features influence the flammability and properties of the plant as 'fuel' by altering the air/fuel mix through changing surface area to volume ratios, fuel volume to canopy volume ratios, packing ratios, and the distribution of fuel in size-classes (fine/coarse fuels) (Rundel 1981; van Wilgen e al. 1990; Bond and Midgley 1995; Schwilk & Ackerly, 2001; Schwilk, 2003; Cochrane, 2009). Physiological or chemical properties that influence the flammability of plants include water content, presence and concentration of ether-extactive compounds such as volatile oils, fats, waxes, terpenes, cellulose, lignin, carbohydrates, and certain minerals (Mutch, 1970; Rundel, 1981; van Wilgen et al. 1990; Bond & Midgley, 1995; Schwilk & Ackerly, 2001; Schwilk, 2003; Cochrane, 2009; Ormeno et al., 2009). There are very few studies exploring how variation in putative 'flammability' enhancing traits influences fire behaviour at the whole plant level and even fewer exploring whether these traits influence local fire behaviour when a species forms part of a community and the 'fuel' of a fire (Schwilk 2003).

Plant populations persist through fire events either by resprouting, or through post-fire germination of a persistent seedbank, or both (Le Maitre and Midgley 1992; Bond & van Wilgen, 1995; Cowan & Ackerly, in press). Post-fire regeneration strategies (PFRS) applied by plants can broadly be classified into two categories. The first is that of seeders, propagule-forming species in which the population persists locally in the form of seeds and fruit following fire. This category includes obligate seeders, species that rely solely on regeneration from seed after fire, and facultative seeders, species that can both resprout

and recruit from seed after fire. The second PFRS is that of non-seeders, species whose propagules do not survive fires and owe their presence to seed dispersal from outside the fire-affected area (Saura-Mas et al., 2010). Some species in this category regenerate after fire by resprouting from underground or aerial components of the plant, which led to this category often confusingly being referred to as obligate resprouters (e.g. Keeley, 1991; Cowan & Ackerly, in press; Saura-Mas et al., 2010), which implies that the plant can only resprout, can not regenerate through seed at all, and must therefore have remained genetically identical over evolutionary time. Due to these complications regarding the proposed definitions of these categories, it is proposed in the current study to classify PFRS's as fire-stimulated recruiters (FSR), species that recruit immediately after fire either from seed alone (seeds resistant to or protected from fire) or by both seeding and resprouting, and non-fire stimulated recruiters (NFSR), species with typically fleshy, bird dispersed fruits that do not survive fire and recruit in the inter-fire interval, similarly either from seed alone or by both seeding and resprouting (see also LeMaitre & Midgley 1992; Bond & van Wilgen 1995; Pausas et al., 2004). Note however, the ratio of species that can resprout to those that can not is typically higher in the NFSR compared to the FSR, and that the referrals to the NFSR category as obligate resprouters by both Cowan & Ackerly (in press) and Saura-Mas et al. (2010) is most likely based on the fact that in the immediate post-fire environment, the species in this category can only regenerate by resprouting until reproductive maturity is reached to recruit by seeding, or adequate seed dispersal from in tact vegetation outside the fire boundary permits regeneration by seed and only if the micro-environment is favourable for light sensitive seedlings. This gives some support for the coining of the term 'obligate resprouters'.

Research from both mediterranean-type ecosystems of California in the USA (Cowan & Ackerly, in press) and the Iberian Peninsula in Spain (Saura-Mas et al., 2010) has demonstrated a relationship between PFRS and plant flammability. These studies primarily found an increase in flammability associated with post-fire seeders such as a higher dead-to-live fuel ratio and fine fuel proportion, relative to 'obligate resprouters'. In the Mediterranean basin most seeders only emerged during the Quaternary with the onset of a highly fluctuating Mediterranean climate characterised by recurrent fires, leading Saura-Mas et al. (2010) to suggest that the plant features related to the combustibility and

flammability of seeder species may be a result of selective pressures associated with both fire and climate.

In this project, I studied a number of plant traits and their influence on flammability (measured experimentally) in a Mediterranean-type ecosystem, characterised by fire-prone shrublands (fynbos) with patches of associated Afromontane forest. From theoretical considerations, flammability is most likely to evolve where plants burn with sufficient intensity to kill their neighbours and where their seedlings are most likely to fill the gaps thus created (Bond and Midgley 1995; Scwhilk 2002). Plants with fire-stimulated recruitment must occupy a post-burn gap sooner than species that only recruit in mature unburnt stands. Consequently, FSR's are predicted to be more likely to have evolved increased flammability relative to NFSR's that do not recruit after fire and gain no advantage from burning. I focussed on whole plant responses rather than the more commonly studied flammability responses of particular organs such as leaves or stems (Mutch, 1970; Fonda et al., 1998; Dimitrakopoulos, 2001; Scarff & Westoby, 2006; Kane et al., 2008; Liodakis & Kakardakis, 2008; Ormeno et al., 2009; Saura-Mas et al., 2010). Identification of traits that best predict experimentally determined flammability is a necessary pre-requisite for exploring the possible evolution of flammability within a species or within a clade. Ideally I hoped to identify key traits so as to be able to compare plant phenotypes for relative flammability. As a second major objective, I tested whether flammability differed in fynbos species characterised by different post-fire regeneration strategies (PFRS's). Under the general heading of flammability, it is often useful to distinguish between the intensity at which a particular fuel burns and the ability of fuels to propagate and sustain a spreading flame (Scarff & Westoby, 2006). In this study, maximum temperature reached by the flames represents a parameter related to the energy or intensity of the flame, whereas % fuel burned is considered a proxy for flame sustenance. These two flammability parameters (maximum temperature and % biomass burned), centred around burning experiments, and six predicting parameters relating to plant flammability such as % dead material, fuel bed porosity, packing ratio, % water content and fuel size-classes, were measured in 15 species of which eight are FSR's and seven are NFSR's.

There are a limited number of studies relating to plant flammability in fynbos vegetation (e.g. van Wilgen et al., 1990), none of which directly addressed the relationship between

plant flammability and PFRS. Results from this study are important anthropogenically in terms of the fire-hazard posed by different species, ecologically with regards to the flammability of different PFRS's, and evolutionarily from the perspective that flammability can evolve in fire-prone habitats. If the latter is true, then positive feedbacks could develop between floristic composition and the environment, expressed as changes in the fire regime.

## Materials and methods

### Study region

The collection of plant species were carried out on Bain's Kloof Pass, located between Wellington and Ceres about 100km north-east of Cape Town in the Western Cape of South Africa (Fig. 1). A Mediterranean climate of warm, dry summers and cool-moderate, wet winters prevail in this region. The geographic co-ordinates of Bain's Kloof Pass are 33034'S and 19006'E, the area has an altitude of 1740m and mean annual rainfall of 730-850 mm (Witkowski & Mitchell, 1987).

The study region corresponds phytogeographically to the greater Cape Floristic Region (CFR), of which the species-rich Fynbos biome represents the major floristic constituent. Pockets of isolated forest occur in the CFR, scattered in the dominant fynbos matrix in habitats that ensures a prominent water source and protection from recurrent fires.

The dominant vegetation on the pass is characterised as mountain fynbos. Geologically the lower foothills on the eastern side of this mountainous area is typically granite-derived soils dominated by Boland Granite Fynbos, the intermediate regions by Malmesbury shale-derived soils giving rise to Swartland Shale Renosterveld, and the peak by soils derived from sandstone of the Table Mountain Group with thriving communities of Hawequas Sandstone Fynbos (Mucina & Rutherford, 2006).

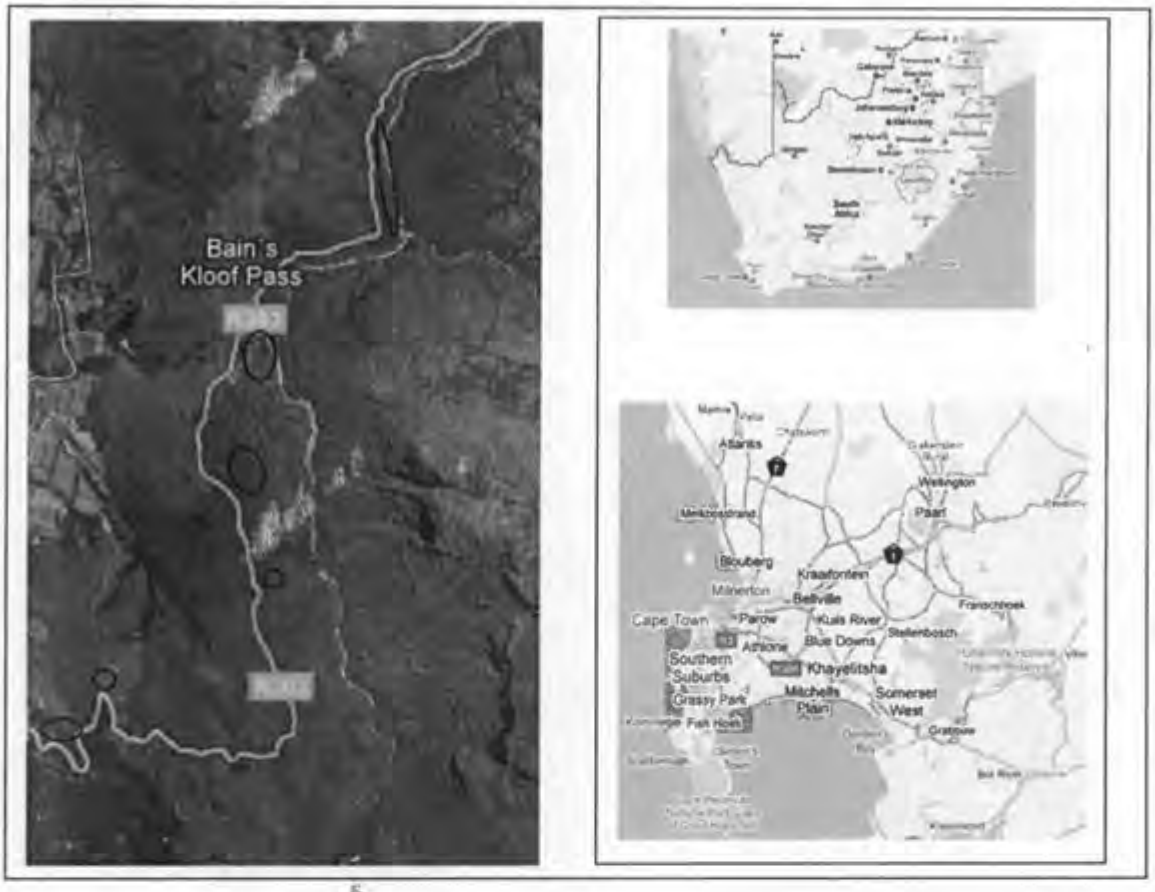


Fig. 1: A map of South Africa (top right), the location of the study region in the Western Cape (bottom right), and the circles representing the six sites A to F along the Bain's Kloof Pass from which the 15 species were collected on 23 October (left). Site A is at the bottom of the pass and map through to site F at the top.

**Species collection**

The circled areas on the map in Fig. 1 represent the six sites on the Bainskloof pass from which eight species in the FSR category and seven species in the NFSR category were collected. Due to the destructive nature of acquiring data during the flammability experiments and trait measurements, nine replicates of each species were collected. These comprised of nine healthy, sexually mature, randomly selected individuals. From the FSR category, *Elytropappus rhinocerotis* and *Metalasia muricata* were sampled from site A, *Leucadendron rubrum* and *Protea laurifolia* from site B, *Protea amplexicaulus* from site C,

*Cliffortia ruscifolia* and *Erica sp.* from site D, and *Stoebe sp.* from around the university accommodation at site E. Species in the NFSR category collected were Rhus *rehmanniana var. glabrata*, *Rhus stenophylla* (Rhus (old) = Searsia (new)) and *Olea europea ssp africana* from Site A, *Diospyros glabra* and *Heeria argentea* from site E, *Maytenus acuminata* and *Myrsine africana* from site F. In most species the entire individual was uprooted and the roots subsequently removed while still preserving canopy architecture, except for the larger shrubs or small trees where only a subset of the canopy were sampled, which comprised a branch of about 75cm that best represents the average architecture of the whole canopy. Similar sized individuals (or subsamples) were chosen from the field in order for the comparisons between the flammability experiments and trait measurements to be standardized and consistent among replicates.

**Flammability device**

Plants were exposed to flames using an apparatus devised specifically to measure flammability of whole plants. The apparatus is designed to measure the probability of a fire spreading through a canopy, and the test is based on the idea that If an individual plant is ignited and the fire fails to spread through its own canopy, then the plant will not be sufficiently flammable to spread the fire to kill its neighbours (cf Bond and Midgley 1995; Schwilk 2003). The intensity of the burn is also measured and can influence the likelihood of burning a neighbour so as to create a gap. The burning apparatus is based on the design proposed by Jaureguiberry et al. (unpublished article). It consists of an 85 × 60 cm metal barrel (standard 210L drum) cut in half along the length and placed horizontally. The two halves of the barrel are hinged with the top half acting as a removable wind-shield. Three parallel gas burners consisting of square tubing with a diameter of 2.5 cm and length of 80 cm are placed inside the barrel, seven cm from the bottom of the barrel and separated from each other by eight cm. An 85 × 55 cm grill with a mesh size of 2.5cm is placed above the burners at 22 cm from the bottom of the barrel. A 45 cm long thermocouple is attached to the grill and connected to a digital multi-meter on the outside of the barrel for temperature measurements of up to 600 °C.

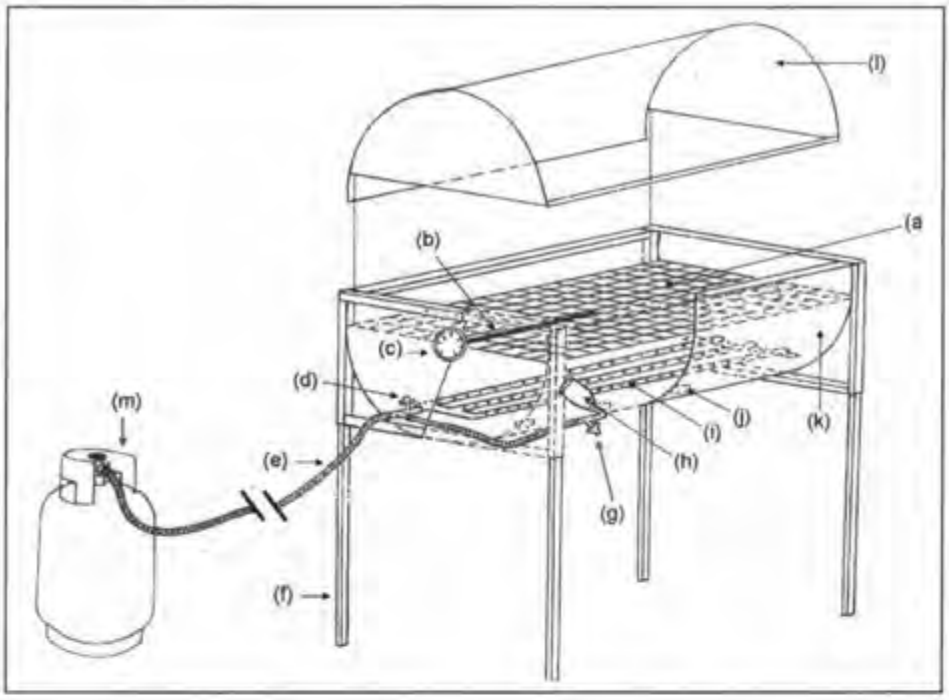


Fig. 2: General view of a device for measuring plant flammability in the field. (a) grill; (b) grill thermometer; (c) temperature gauge; (d) security valve; (e) connection to gas cylinder; (f) removable legs; (g) blowtorch valve; (h) blowtorch; (i) burners; (j) ventilation holes; (k) barrel; (l) removable wind protection; (m) gas cylinder. Diagram taken from Jaureguiberry et al. (unpublished article).

A blowtorch is placed between the grill and the burners, fixed to the front side and pointing upwards towards the grill. Both the burners and the blowtorch are connected to a propane-butane gas cylinder through a T-connection, each with a security/regulating valve. The bottom of the barrel has three ventilation holes, eight cm in diameter and evenly spaced from one another. The entire structure is mounted on four removable square tubing metal legs. Total weight of the device is about 22 kg, cost around 400$ for the construction and took two to three days to complete. Major benefits of the apparatus include its portability for field experiments, not relying on a power source other the gas cylinder, and incorporating the responses of whole individuals to fire thereby preserving the basic architectural arrangement of the plant components.

**Flammability experiments**

Three of the nine individuals collected for each species were used in collecting the flammability data. The burners were turned on until the grill thermometer reached a temperature of 150 °C and subsequently kept at this temperature throughout the entire experiment. This exposes the plants to pre-heating, which is considered an important aspect of the protocol simulating a natural fire when flames approach the vegetation exposing the plants to pre-heating and dehydration that increases their flammability. Each plant sample was placed on the grill and exposed to pre-heating for two minutes after which the blowtorch, which provides a source of flaming ignition at one end of the sample, is turned on for 10 seconds and subsequently turned off. The first parameter recorded for each sample relating to flammability was maximum temperature reached by the flames, measured at a distance of about 50cm from the burning plant with a remote infrared thermometer that can measure temperatures up to 1200 °C. The second flammability parameter measured was % biomass burned which was visually estimated after termination of the flame phase and subsequent glowing stage. This can be quantified as the length of the individual or sample remaining. However, there are difficulties in doing so where only the filamentous plant material burned and not the woody stems they were attached to, and where only one side of the plant burned along its longitudinal plane.

**Flammability traits**

The remaining six of the nine individuals collected for each species were used in collecting data on traits that could potentially be used in predicting the flammability of each species. Three individuals or samples from each species were separated according to live and dead material (twigs, branches and leaves) and subsequently weighed to determine the % dead material retained by each sample. The same sample was then used in the collection of the fuel size-class data. Each sample was separated based on stem diameter according to the following size-classes: 1) <3mm, 2) 3-6mm (both considered fine fuels), and >6mm (coarse fuels). Leaves were included in the stem diameter class of the stem size they were attached to and the biomass in each size-class was then weighed, thus utilizing the fresh mass. Each of the remaining three individuals of each of the 15 species collected were used to determine canopy volume, fresh mass, volume occupied by the plant/fuel through means of

volume displacement in a 5L measuring cylinder, and dry mass after oven-drying it at 72 °C for 48 hours. From this data variables that describe fuel properties and that might predict flammability (Rundel 1981; van Wilgen et al. 1990; Bond & Midgley, 1995; Schwilk & Ackerly, 2001; Schwilk, 2003; Cochrane, 2009) were derived: % fuel dead, fuel bed porosity, packing ratio, % water and the relative proportion of the three fuel size-classes.

1) % fuel dead = mass of dead material/dead mass + live mass
2) Fuel bed porosity = canopy volume/ fuel volume
3) Packing ratio = bulk density/specific gravity
4) % water = (fresh mass – dry mass/fresh mass) × 100
5) % fuel < 3mm = (< 3mm mass/total mass)
6) % fuel < 6mm = (<3mm mass + 3-6mm mass/total mass)

The canopy volume of each individual or subsample was determined using the formula for the volume of a cone, as this was the shape that best represented the dominant shape of individuals in the field, i.e. that of the branches spreading out from a singular point at the base. The cone was even congruent with the shape of the subsamples taken from the larger shrubs or trees. Bulk density in the formula for packing ratio is fresh mass of fuel/canopy volume, whereas specific gravity is mass of fuel/fuel volume.

**Statistical analyses**

Using the raw data (including all replicates) correlations were done in Statistica between the two flame parameters (maximum temperature and % biomass burned), and between the flame parameters and the measurements potentially influencing individual flammability. Regression lines were fitted to the scatterplots where a significant correlation was found. An analysis of variance (ANOVA) was performed to test for significant differences between FSR's and NFSR's in terms of all the parameters measured in this study (flame results and flammability traits). Significance was accepted at the 5% level. All graphs were created in Excel, except for the non-linear regressions done in Statistica.

## Results

### Correlations with flame parameters and flammability traits

With three replicates for each of the species, sample size (n) was 45 for all the correlations and comparisons between PFRS's. It is clear from Fig. 3 that a correlation between the two flame parameters maximum temperature and % fuel burned across all samples indicates a positive linear relationship. A high variation in the % fuel burned was found among the samples with the lowest value at 4% and the highest at 98%, whereas maximum temperature in this study did not exceed a maximum threshold (838 °C) and neither did any sample burn below a certain temperature (357 °C). This resulted in relatively less spread in the temperature relative to the % burned data. The correlation between maximum temperature and % fuel burned was significant ($t = 6.87$, $p < 0.001$, $R^2 = 0.52$).

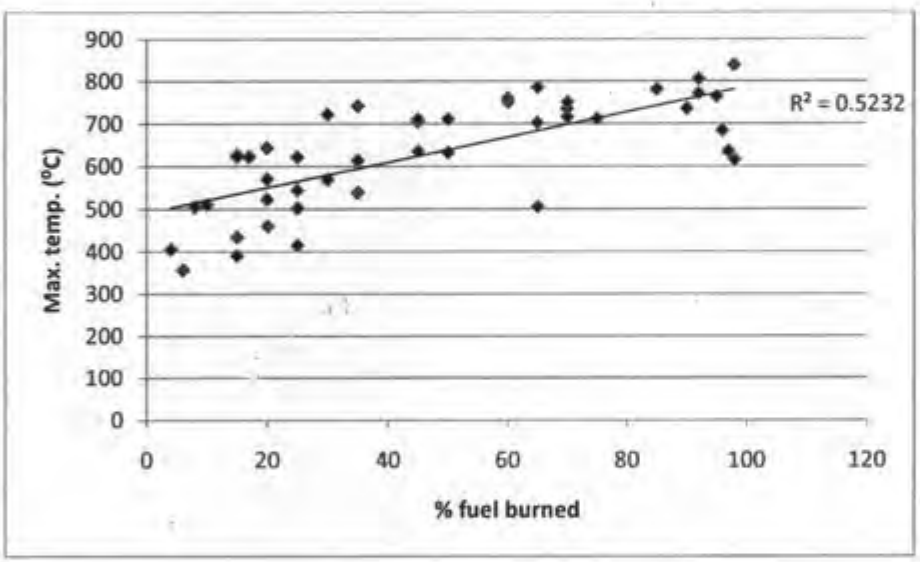


Fig. 3: Scatterplot of the two flame parameters maximum temperature reached and % fuel burned measured during the burn experiments at Baín's Kloof. The $R^2$-value indicates the strength of the relationship.

Fig. 4 shows the scatterplots of the correlations between one flame parameter, maximum temperature, and the six flammability traits. None of the relationships could be considered linear. The only significant correlations found was with % fuel dead ($t = 4.24$, $p < 0.001$, $R^2 = 0.29$) and % water ($t = -2.11$, $p = 0.04$, $R^2 = 0.09$). Although significant, note the low $R^2$-value for the correlation with % water. A logarithmic regression line was fitted to the scatterplot of % fuel dead (Fig. 5). The packing ratios determined in this study were generally low for all species.

-n?

Fig. 6 depicts the scatterplots between the second flame parameter, % fuel burned, and the six flammability traits. Although none of the relationships were very strong, a significant correlation was detected for % fuel dead ($t = 3.92$, $p < 0.001$, $R^2 = 0.26$), % fuel < 3mm in stem diameter ($t = 3.72$, $p < 0.001$, $R^2 = 0.24$), and % fuel < 6mm in stem diameter ($t = 2.26$, $p = 0.02$, $R^2 = 0.11$). A logarithmic regression line was fitted to the scatterplot of % fuel dead in Fig. 7.

n=?
You need to report dfs for the analyses. Based on your figs you see to have 45 points on each graph which is wrong according to your methods... descriptions... You are inflating the power of your analyses!

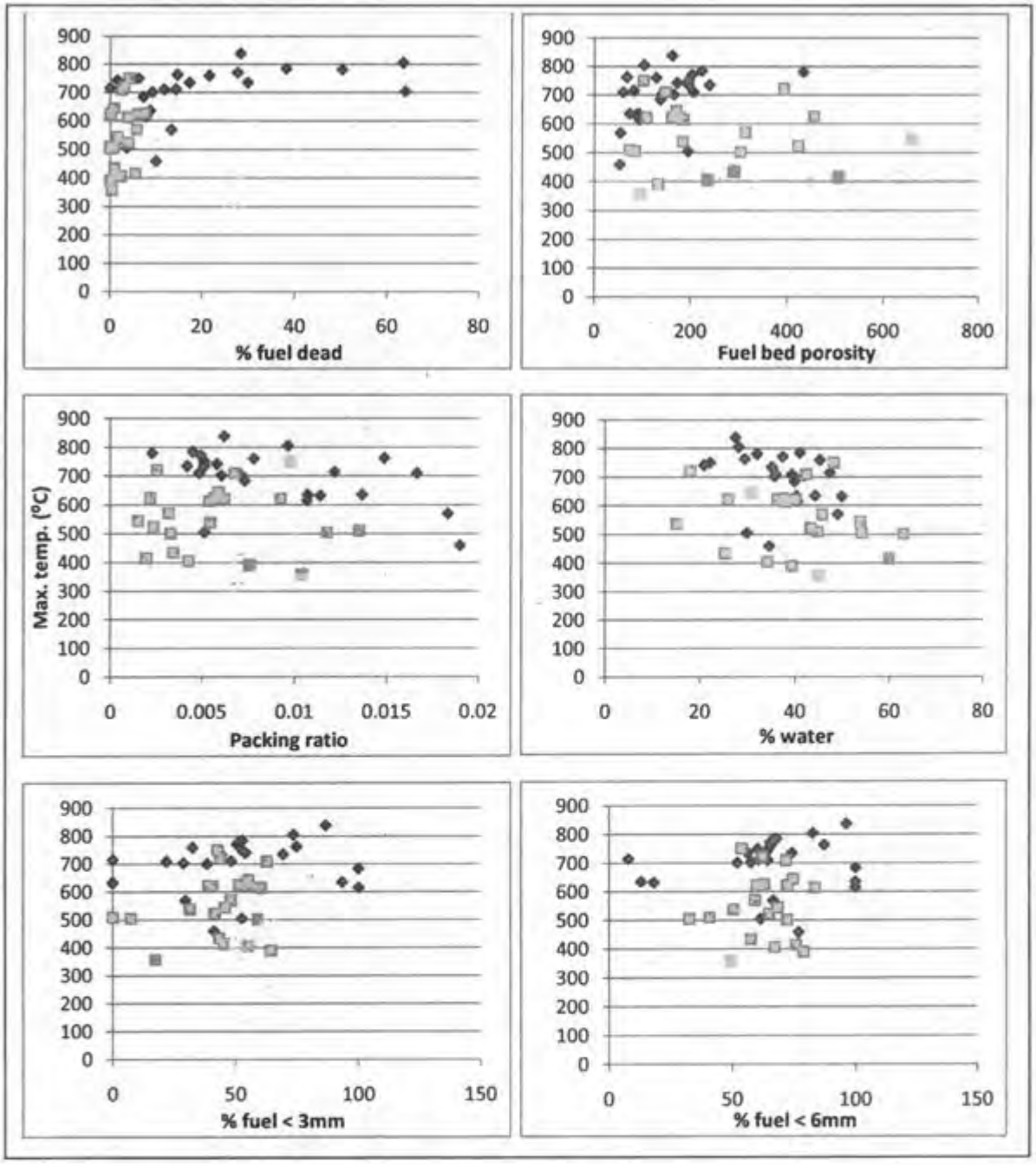


Fig. 4: Scatterplots of maximum temperature with each of the flammability traits of all FSR's and NFSR's collected from the study sites at Bain's Kloof.

surely points should be individual spp if you measured max temp on 3 indivs + traits on a different 6 indivs?

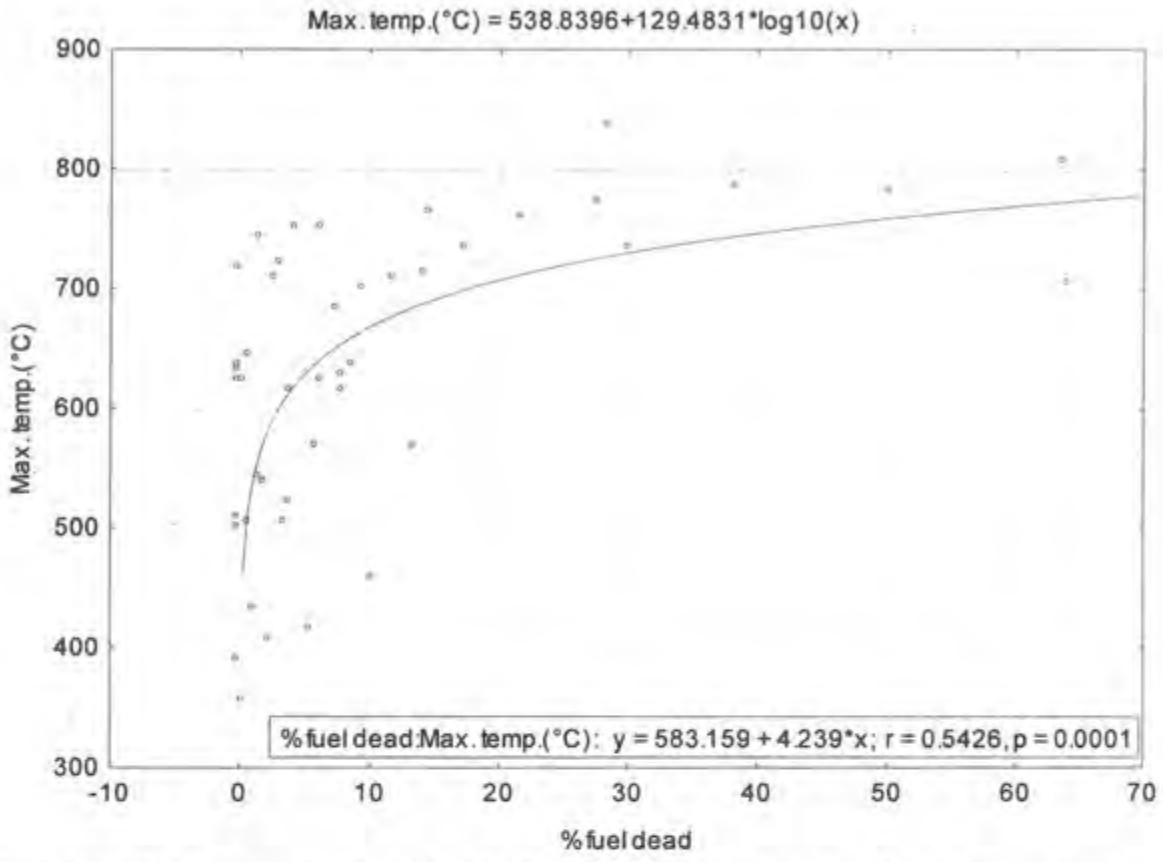


Fig. 5: Logarithmic regression line fitted to the relationship between maximum temperature and % fuel dead of all species collected at Bain's Kloof.

Why so many data points? 15 spp?

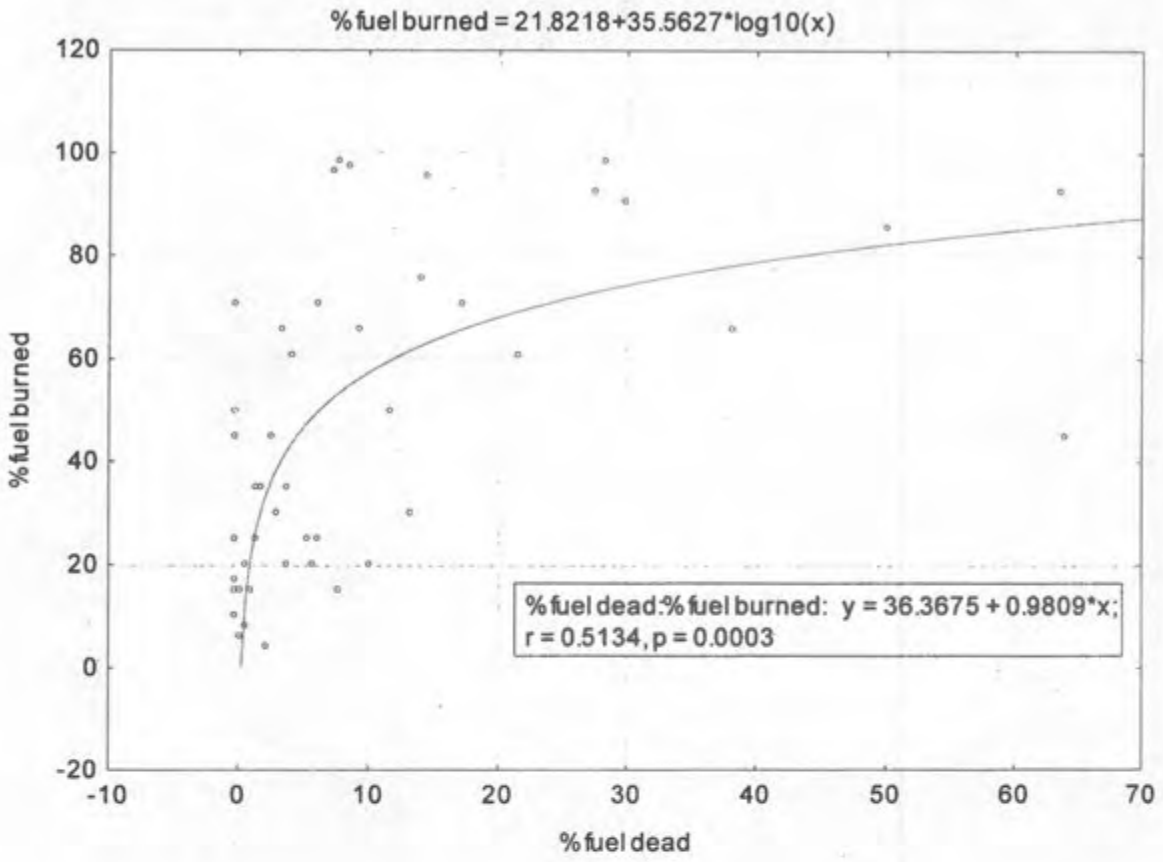


Fig. 7: Logarithmic regression line fitted to the relationship between % fuel burned and % fuel dead of all species collected at Bain's Kloof.

Main - you should include the Fig. as well in your analysis?

**Post-Fire Regenerative Strategy**

Although it is not so clear from the scatterplots in Fig. 4 and Fig. 6 that the two PFRS's shows a distinction from one another with respect to the six flammability traits, they do demonstrate the separation between PFRS's in terms of the flame parameters maximum temperature reached and % fuel burned. Significant differences were found between FSR's and NFSR's with respect to both flame parameters and three of the six flammability traits. Compared to NFSR's, FSR's burned at a significantly higher maximum temperature ($F = 22.19$, $p < 0.001$, $n = 45$), and was characterised by significantly larger proportion of the fuel being consumed during burning ($F = 64.42$, $p < 0.001$, $n = 45$). With respect to the flammability traits, FSR's were characterised by a significant larger proportion of dead material ($F = 6.65$, $p = 0.013$, $n = 45$), a lower fuel bed porosity ($F = 7.039$, $p = 0.011$, $n = 45$), and a higher packing ratio ($F = 6.00$, $p = 0,018$, $n = 45$), relative to NFSR's (see Table 1.).

Why ANOVA and not t-tests?

Table 1: Means and standard deviations of all the variables for the FSR's and NFSR's collected at Bain's Kloof. Means and standard deviations reported with one more decimal than the data.

| | FSR mean | FSR std. dev | NFSR mean | NFSR std. dev |
|---|---|---|---|---|
| Max. temp (°C) | 697.5 | 92.6 | 553.6 | 112.3 |
| % fuel burned | 69.1 | 23.5 | 22.4 | 13.3 |
| % fuel dead | 18.72 | 18.75 | 2.46 | 2.37 |
| Fuel bed porosity | 148.45 | 84.25 | 247.62 | 159.63 |
| Packing ratio | 0.0089 | 0.0047 | 0.0058 | 0.0034 |
| % water | 36.76 | 7.84 | 40.00 | 12.51 |
| % fuel < 3mm | 49.91 | 29.09 | 43.36 | 17.14 |
| % fuel < 6mm | 65.17 | 24.86 | 62.78 | 12.59 |

t? df?

It is clear from the results that the most important findings of the current study was 1) the relative consistency of the flammability device in detecting differences in maximum

You don't demonstrate this

temperature reached by the flames and % fuel burned between species and PFRS's, and 2) the significant relationship between the two flammability traits (proportion of dead material retained by the plant and the fine fuel proportion) and the actual flammability of the plant, i.e. maximum temperature reached by the flames and % fuel burned.

## Discussion

### Flammability device

Although highly standardised results are derived from flammability experiments that involve thermogravimetric laboratory experiments in combustion chambers (see Dimitrakopoulos, 2001, Liodakis & Kakardakis, 2008), these typically small plant fragments does not scale up well to that of whole shoots in a natural landscape. Jaureguiberry et al. (unpublished article) illustrated the potential of the flammability device used here with the burning results of 34 species from central Argentina, characterised by different growthforms and thus different architectures. The variability in their data was mostly accounted for by differences between growthforms and species rather than between replicates, leading the authors to suggest that the device is sensitive enough to detect differences among plants with different functional traits, yet robust enough to produce consistent results among samples with similar traits. The results from this study seems to support these findings in that the variation in the flame parameters maximum temperature and % fuel burned within a particular species is less than between species (see Table 1). This indicates that the device and protocol is adequate for the acquisition of comparable flammability data over large numbers of species from different floras and ecosystems.

You have NOT shown this at all ?

### Correlations with flame parameters and flammability traits

The results from this study indicate that % dead fuel is one of the most important plant traits influencing individual plant flammability. An increase in % dead material is associated with increased flame temperatures and % fuel burned. Various studies have reported that the retention of dead plant material as opposed to self-pruning significantly affects plant flammability. Schwilk (2003) performed a large-scale prescribed burning experiment on

different vegetation treatments that were manipulated with regards to dead fuel amount and arrangement, and concluded that dead branch retention may indeed increase local fire temperatures and heat release rates. Furthermore, other Mediterranean ecosystems show an increased proportion of dead material being associated with post-fire seeder species that often depend on and promote fire (Saura-Mas et al., 2010; Cowan & Ackerly, in press). However, Saura-Mas et al. (2010) used whole plants for acquiring flammability trait data, but performed burning tests only on the leaves, whereas Cowan & Ackerly performed no direct burning experiments. These authors primarily used the fact that post-fire seeders occur in fire-prone environments (indicated by fire regime) as a proxy for being more flammable. In contrast, this study reports results from both burning experiments and flammability traits of 15 co-existing species and indicates that % dead material directly influences maximum temperature reached and % fuel burned.

A second plant trait that significantly affected individual plant flammability in this study was fine fuel proportion. This result is evident in the fact that increased % fuel < 3mm or/and % fuel < 6mm in diameter was associated with an increase in % fuel burned. Similar to the dead fuel propotion, Saura-Mas et al. (2010) and Cowan & Ackerly (in press) showed that the fine fuel proportion (stems < 6mm in diameter) was notably higher in flammable post-fire seeders compared to the relatively non-flammable resprouters.

Lastly, the relatively weak but significant negative correlation between maximum temperature and % water found in the plant tissues indicates that a higher water content is responsible to some degree for lower flame temperatures and thus flammability. In a comparison between fynbos and forest vegetation in relation to their fire regime, van Wilgen et al. (1990) found that fynbos had an average of 50-100% more water than forest species thus increasing the flammability of fynbos vegetation. However, the scatter observed in the data regarding water content from this study implies that it is a relatively weak predictor of plant flammability and the differences in flammability detected between species or PFRS's is likely caused or dominated by differences in other flammability traits. The % dead material and fine fuel proportion could potentially be used as relatively good predictors of plant flammability at the individual or species level.

Packing ratios were generally low compared to other studies (see Scarff & Westoby, 2006). Packing ratio generally refers to the ratio of bulk density (fuel mass/ canopy volume) to specific gravity (fuel mass/fuel volume) which implies that it is a ratio of a ratio. However, it is sometimes referred to a single ratio, that of fuel volume/canopy (bed) volume, reflecting the proportion of the bed volume occupied by fuel (see Scarff & Westoby, 2006). Note that if the mass term used in both bulk density and specific gravity is based on the mass of a whole individual, mass cancels out transforming the formula for packing ratio to a single ratio, i.e. that of fuel volume/canopy volume. Therefore, packing ratio in this study is not a unique character as it is the inverse of fuel bed porosity (canopy volume/fuel volume) which reflects how sparse the canopy is.

A disadvantage of using whole individuals in a flammability study is that it is highly impractical to determine surface area of the different plant organs. Most flammability studies focus on either the shoots or the leaves, and although the scaling up from these components to whole individuals in the field might be questionable, measuring surface area of leaves can be done with relative ease. In the current study, it was impractical to calculate surface area from stem diameters that constantly change from the base to the tips, or from the masses of filamentous leaves and highly branched growthforms that characterise several genera in this fire-prone region including *Elytropappus* and *Stoebe*.

**Post-fire regenerative strategy**

The increased flammability both in terms of maximum temperature reached and % fuel burned associated with FSR' relative to NFSR's supports the prediction of flammability being more likely to evolve in species that needs to occupy the gap first following disturbance by fire. This finding in fynbos vegetation is consistent with the results from other Mediterranean ecosystems such as California in the USA (Cowan & Ackerly, in press) and the Iberian Peninsula in Spain (Saura-Mas et al., 2010) where increased flammability in post-fire seeders relative to resprouters have been reported. However, note that during the leaf burning experiments carried out by Saura-Mas et al. (2010), lower flame temperatures in post-fire seeders relative to resprouters were interpreted as increased flammability based on the notion that less energy is required to result in combustion, resulting in a reduced time to ignition i.e. "post-fire seeders burst into flame at lower temperatures". In contrast,

time to ignition was not measured in this study and increased flame temperatures were interpreted as higher flammability. This was based on the fact that increased fire temperature or intensity increases the chance of neighbouring fuel particles in the vicinity of the flame to ignite and burn with enough energy to spread the flame. This demonstrates how controversial results from flammability experiments can be and indicates the importance of knowing which component of flammability is measured, how this component is influenced during burning, and what it signifies in relation to the actual flammability of the plant.

Based on the significant differences between FSR's and NFSR's in terms of the flammability traits, this study indicates that the flammability differences found with respect to PFRS can most likely be attributed to % fuel dead, fuel bed porosity and packing ratio. The relatively more flammable FSR's retain on average more than three times as mush dead material (Table 1) than NFSR's. This is supported by Cowan & Ackerly (in press) who reported that the variation in proportion of dead material among species is significantly different between PFRS's, with the average proportion of dead fuel for the two post-fire seeding species 3,5 times that of the two resprouters. Since the FSR's and NFSR's examined in this study is often found in similar conditions with respect to climate and the geology of the substrata, environmental effects such as drought or stress is assumed to have a minimal contribution to the observed differences in % dead fuel. This implies that the retention of dead plant material may have been selected for to a higher degree in the FSR's compared to the NFSR's. The lower fuel bed porosity values observed in FSR's compared to NFSR's (factor of 1.7, Table 1) reflects the relative sparse nature of the crowns of NFSR (typically forest) species. A similar finding was reported by Van Wilgen et al. (1990) who used fuel volume/canopy volume (= inverse of fuel bed porosity and = packing ratio in this study) as an indication of the sparseness of the crowns and found this ratio in forest to be half that in species. Both fuel bed porosity and packing ratio therefore indicates that the continuity of fuel is much increased in FSR's, subsequently increasing the flammability of most species with this recruitment mode.

*P. laurifolia* and *L. rubrum* burnt at similar temperatures and were characterised by similar percentages fuel burned compared to species in the NFSR category. This can be explained by the extremely low proportion of dead and fine fuel, coupled with the tough and

sclerophyllous leaves in these two species relative to the rest of the FSR's, which reduced their flammability to values similar to those of NFSR's. *P. laurifolia* and *L. rubrum* are serotinous and although almost always found in fire-prone fynbos, these species, along with the NFSR's, do not seem to actively promote flammability. In contrast, P. amplexicaulus, which retains a large proportion of dead leaves that drastically increases its flammability, along with the rest of the species in the FSR category, appear to actively promote fire.

Fire has widely been neglected as an evolutionary force (Bond & Midgley, 1995; Bond & Keeley, 2005). In fire-prone environments, co-occurring vegetation states is maintained by different self-reinforcing feedback with fire in that sclerophyll vegetation that depend on fire is more flammable and occurs in regions with the highest fire severity and frequency, whereas forest vegetation is less flammable and characterised by lower fire severity and longer fire-free periods (Odion et al., 2010). Similarly, the prolonged absence of fire in the Cape is known to result in the gradual replacement of fire-dependant fynbos by thicket and forest species through ecological succession (Cowling et al. 1997). Alteration of the fire regime through the evolution of flammability results in the selective exclusion or admission of other species to a fire-prone ecosystem depending on their pre-existing traits with fire (Bond & Midgley, 1995). These studies, along with the results from this study, therefore show that positive feedbacks can evolve between floristic composition and fire, expressed as changes in the fire regime. If the flammability of a species coincides with its optimum disturbance regime, a positive feedback between population growth and fire regime can be expected (Bond & Midgley, 1995; Schwilk & Kerr, 2002). FSR's are not only more flammable than NFSR's, they frequently occur in areas characterised by higher fire frequencies in the CFR. If it is accepted that succession occurs from fynbos to forest, the increased flammability observed in FSR's (fynbos species) compared to NFSR's (forest species) contrasts with the general finding of increased fuel loads and subsequent fire risk with an increase in time since the last fire. This finding therefore renders the act of prescribed burning for the purpose of reducing fuel loads and fire severity in the fynbos biome unnecessary, supporting the conclusions regarding this fire management practise of van Wilgen (2009) and van Wilgen et al. (2010).

From a fire-hazard perspective for urban fringes in fire-prone fynbos, and based on the burning temperature and % fuel burned reported from this study, cultivation of the highly

flammable species *E. rhinocerotis, Stoebe sp., M. muricata, Erica sp.* and *P. amplexicaulus* in gardens should be avoided. Planting of the less flammable species, including P. laurifolia, L. rubrum, and all the species in the NFSR category, should reduce probability of ignition and fire spread thus decreasing the risk of fire. This information could be incorporated into city and residential development sectors in order to increase the safety of the human environment within ecosystems that depend on fire for their long-term persistence and conservation.

It is worthy to note that subset sampling of larger shrubs and trees results in inaccurate estimates of flammability traits such as not including the whole architecture and also not the dead material often found at base of the shrub. The season and meteorological conditions during the few days prior to sampling is expected to significantly influence flammability. The rain received prior to and during the weekend of the burning experiments is may therefore have affected the results from this study, and although all plant samples were exposed to the same conditions leading one to think that the results might still be consistent in terms of their relative differences in flammability, different species absorb or lose water at different rates due to different stem diameters, different relative proportions of the different constituent tissues, and the relative differences in tissue densities that influence the rate of water movement in and out of the plant. Nevertheless, despite these 'limitations', the results from this study is adequate for indicating the general trends in flammability of different species and PFRS's.

Future research in this field could include additional flame parameters in the analysis such as flame length (Mutch, 1970) as an alternative measure of fire intensity, some measure of the burning rate (Jareguiberry et al., unpublished article) or the spread of fire as an additional measure of fire sustenance, and time to ignition (Saura-Mas et al., 2010) as a reflection of the heat energy required for combustion. Although time-consuming, the flammability device used here could be adapted to incorporate these additional flame parameters with relative ease. Flammability traits not considered in this study could include surface to volume ratios as this would most likely be a good predictor of flammability in some of the highly branched species in particular, and the presence and concentration of volatile fats and oils that is likely to affect flammability. Since auto-correlation between some variables is likely, I suggest using as much flame parameters and flammability traits as

possible in a multivariate model in order to determine which variables best explain the overall variation in flammability. In order to test whether a particular species can evolve flammability and whether it is able to invade fire-free habitats subsequently constructing its own 'fire niche' and maintaining a particular fire regime that favours itself (see Schwilk, 2003; Rahlao et al., 2009), information is required regarding its flammability, coupled with data on some increase in fitness with respect to post-fire recruitment such as increased germination or growth rates. Suitable species for such a study based on the results from this study include *Stoebe sp, E. rhinocerotis, Erica sp* and *M. muricata*.

## Conclusion

The flammability device used in this study proved to be fairly consistent in the detection of flammability differences between species and PFRS and is thus considered adequate for the acquisition of comparable flammability data across various ecosystems. The flammability traits % dead fuel and the proportion of fine fuel turned out to be relatively good predictors of individual plant flammability across all species, whereas differences in flammability between FSR's and NFSR's can most likely be attributed to % fuel dead, fuel bed porosity and packing ratio. The increased flammability associated with FSR'S relative to NFSR's is consistent with the theory that the evolution of flammability is most likely to occur FSR's that depend on the rapidity of colonization on post-fire environments for persistence in the landscape. This results in positive feedbacks between floristic composition and fire disturbance regime in fire-prone fynbos regions of the CFR. The flammability traits found to be significant in this study can easily be measured in the field and used in on-site field assessments of flammability of individual species in a community, and evaluations of the fire-risk posed by these species. This could aid in the selection of particular species to be cultivated on urban fringes so as to reduce the likelihood of these plants burning and causing damage or to reduce the predicted fire frequency in particular regions.

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