Fire weather effects on flammability of indigenous and invasive alien plants in coastal fynbos and thicket shrublands (Cape Floristic Region)

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Background. Globally, and in the Cape Floristic Region of South Africa, extreme fires have become more common in recent years. Such fires pose societal and ecological threats and have *inter alia* been attributed to climate change and modification of fuels due to alien plant invasions. Understanding the flammability of different types of indigenous and invasive alien vegetation is essential to develop fire risk prevention and mitigation strategies. We aimed to assess the flammability of 30 species of indigenous and invasive alien plants commonly occurring in coastal fynbos and thicket shrublands in relation to varying fire weather conditions.

Methods. Fresh plant shoots were sampled and burnt experimentally across diverse fire weather conditions to measure flammability in relation to fire weather conditions, fuel moisture, fuel load and vegetation grouping (fynbos, thicket, and invasive alien plants). Flammability measures considered were burn intensity, completeness of burn, time-to-ignition, and the likelihood of spontaneous ignition. We also investigated whether the drying of plant shoots (simulating drought conditions) differentially affected the flammability of vegetation groups.

Results. Fire weather conditions enhanced all measures of flammability, whereas fuel moisture reduced burn intensity and completeness of burn. Live fuel moisture was not significantly correlated with fire weather, suggesting that the mechanism through which fire weather enhances flammability is not fuel moisture, but the ignition temperature of fuels. It furthermore implies that the importance of live fuel moisture for flammability of evergreen shrublands rests on inter-specific and inter-vegetation type differences in fuel moisture, rather than short-term intra-specific fluctuation in live fuel moisture in response to weather conditions. Fuel load significantly increased burn intensity, while reducing ignitability. Although fire weather, fuel moisture, and fuel load had significant effects on flammability measures, vegetation and species differences accounted for most of the variation. Flammability was generally highest in invasive alien plants, intermediate in fynbos, and lowest in thicket. Fynbos ignited rapidly and burnt completely, whereas thicket was slow to ignite and burnt incompletely. Invasive alien plants were slow to ignite, but burnt with the highest intensity, potentially due to volatile organic composition. The drying of samples resulted in increases in all measures of flammability that were comparable among vegetation groups. Flammability, and by implication fire risk, should thus not increase disproportionately in one vegetation group compared to another under drought conditions unless the production of dead fuels would be disproportionate among vegetation groups. Dead:live fuels potentially is a useful indicator of flammability of evergreen shrublands. Proxies for this ratio should thus be sought

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Abstract

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Keywords*:* burn intensity, completeness of burn, drought, fire danger indices, fire risk, fuel load, fuel moisture, time-to-ignition, spontaneous ignition, wildland-urban interface

Introduction

Flammability is the ability of vegetation (fuel) to burn (Fernandes and Cruz, 2012; Gill and Zylstra, 2005) and is a measure of fire behavior (fire intensity/severity) used in vegetation fire risk mitigation studies (Keeley, 2009). Vegetation flammability may result from climatic effects (Bond and Midgley, 1995; Calitz et al., 2015; Mutch, 1970; Snyder, 1984). For example, fires that are climate-driven may be limited when dry conditions reduce fuel production to sustain fires (Pausas and Bradstock, 2007), however dry conditions may also result in an increase in fire risk caused by the availability of dried fuels (Piñol et al., 1998). Fire-prone vegetation groups may furthermore have evolved traits that enhance their flammability and improve vegetation fitness in fire-dependent communities (Bond and Midgley, 1995). Correspondingly, species with high flammability traits would burn intensely, such that itself and the neighbour die, thereby facilitating recruitment – the ‘kill thy neighbour’ hypothesis (Bond and Midgley, 1995). Flammability traits may thus provide resilience associated with fire tolerance (Bond and Midgley, 1995; Calitz et al., 2015). Fire is accordingly one of the main determining factors of the ecology and distribution of ecosystems of the world, and is important for maintaining plant diversity (Bond, 1997; Bond et al., 2003; Bond and Keeley, 2005).

Flammability is also affected by weather conditions (Bond, 1997; Keeley and Syphard, 2017). To rate the fire-proneness of weather conditions, fire danger indices based on ambient temperature, relative humidity, wind speed, and rainfall are commonly used (Dowdy et al., 2009; Noble et al., 1980; Sirca et al., 2018). Ambient temperature and relative humidity also influence fuel moisture contents, thereby affecting flammability. For example, low fuel moisture facilitates the ease of ignition (Archibald et al., 2008; Baeza et al., 2002; Bond, 1997). Additionally, fuel properties such as the amount of flammable plant material (fuel load), packing ratio and chemical composition influence flammability (Brooks et al., 2004; Burger and Bond, 2015; Curran et al., 2017). For instance, greater fuel loads or volatile substances can increase fire intensity (Baeza et al., 2002; Saura-Mas et al., 2010).

Globally, extreme fires have become more common in recent years. Examples include the shrublands of California, Australia, Europe (Montenegro et al., 2004; San-Miguel-Ayanz et al., 2013), and more recently, South Africa (Kraaij et al., 2018). These fires have been accredited to the combinations of climate change (in the form of weather conditions more conducive to fire and extended droughts), increased ignitions, expanded wildland-urban interface areas linked to increasing human populations, changes in fuels that are often human-induced. (Archibald et al., 2008; Montenegro et al., 2004; Syphard et al., 2017; Turco et al., 2017; van Wilgen, 1984). Fuels accumulate excessively when humans suppress fires to safeguard assets, and due to invasion by invasive alien plants (hereafter IAPs) (Kraaij et al., 2018; Radeloff et al., 2005; Scott et al., 1998). The IAPs may affect flammability by altering the fuel structure, fuel distribution (horizontal or vertical fuel continuity), fuel moisture, chemical contents and fuel load (Brooks et al., 2004; Davies and Nafus, 2013; Richardson and van Wilgen, 2004). Extreme fires are also known to occur in shrublands after severe droughts due to the increase of dead (~dry) to live fuel ratios (Keeley et al., 2012; Keeley and Syphard, 2017; Kraaij et al., 2018).

Along the southern Cape coast of South Africa, fynbos and thicket shrublands occur interspersed despite displaying different fire dynamics and fuel structural traits (Campbell et al., 1981; Moll et al., 1984). Fynbos ecosystems commonly support canopy fires and comprise species that readily burn to open recruitment opportunities (gaps) post-fire (Buhk et al., 2007; Deacon et al., 1992). However, thicket mostly does not exhibit high flammability traits (Calitz et al., 2015), and recruitment from seed largely occurs in inter-fire periods (Pierce and Cowling, 1984). In 2017, extreme fires occurred in this region around the town of Knysna which burnt indigenous fynbos and thicket vegetation and further caused extensive damage to commercial plantations and residential properties (Fares et al., 2017; Kraaij et al., 2018). The extreme nature of these fires has been attributed to extensive IAP fuels, an expansive wildland-urban interface area, an unprecedented regional drought preceding the fires, and very high fire danger weather conditions at the time of the fires (Kraaij et al., 2018; Preston, 2017). The 2017 Knysna fires called for improved understanding of potential differences in flammability among vegetation groups, including IAPs occurring in this region. An analysis of satellite image derived proxies for burn severity showed to be higher, but completeness of burn lower, in IAPs than in indigenous fynbos and thicket vegetation (Kraaij et al. 2018). However, the findings have not been verified with field observations (Kraaij et al., 2018). Other studies have experimentally compared the flammability of species from several biomes (both fire-prone and fire-resistant) (Burger and Bond, 2015; Calitz et al., 2015), however, no study has compared the flammability of indigenous vegetation with that of IAPs, nor under varying fire weather conditions.

In this study, the primary aim was to assess flammability of live plant material of IAPs, fynbos, and thicket in relation to fire weather conditions, fuel moisture, and fuel load. Flammability measures considered were: burn intensity, completeness of burn, and ignitability (time-to-ignition and likelihood of spontaneous ignition). We hypothesized that (H_1) fuel moisture would have negative effects on flammability; (H_2) fire weather conditions would have positive effects on flammability, and (H_3) fuel load would positively affect burn intensity. A secondary aim was to assess the flammability of partially dried plant material as a crude proxy for drought effects, to ascertain whether drying of fuels (~drought) would differentially affect the flammability of the vegetation groups of interest. Study results will inform fire risk management in the southern Cape landscapes and elsewhere with similar fuel traits and characteristics.

Materials & Methods

Study area

This study was conducted along the southern Cape coast of South Africa within the Cape Floristic Region close to the city of George (33.964°S, 22.534°E). The climate is moderated by the maritime influence with average minimum and maximum temperatures ranging from 7–19ºC in June and 15–26ºC in January an annual average rainfall of approximately 800 mm throughout the year (Bond, 1981). The area experiences weather conditions suitable for fires at any time of the year and fires are often associated with hot, dry katabatic (‘berg’) winds (Kraaij et al., 2013; van Wilgen, 1984).

The vegetation of the study area is classified as Southern Cape Dune Fynbos (Mucina and Rutherford, 2006; Pierce and Cowling, 1984) consists of medium-dense sclerophyllous fynbos (~fine-leaved) shrublands up to 2 m in height, interspersed with dense clumps of subtropical mesophyllous thicket shrubs or trees up to 4 m in height (Campbell et al., 1981; Kraaij et al., 2011; Pierce and Cowling, 1984). Both fynbos and thicket are evergreen. Fynbos shrublands are fire-prone and flammable while smaller areas of thicket vegetation seldom burn (Geldenhuys, 1994). The persistence of fynbos-thicket mosaics requires fire at appropriate intervals (15–25 years) since thicket becomes dominant in the prolonged absence of fire (Kraaij and van Wilgen, 2014; Strydom et al., submitted). The area contains extensive invasions of IAPs, commonly of the genera *Acacia, Eucalyptus,* and *Pinus* (Baard and Kraaij, 2014; van Wilgen et al., 2016).

Data collection

Live plant samples

We experimentally measured the flammability of species from three vegetation groups, namely IAPs, fynbos, and thicket. Plant shoots (hereafter samples) are generally the most flammable structures since leaves are the first fuel source to ignite during fire, subsequently spreading fire to other plant structures (Murray et al., 2013). Sampling was done over 21 occasions (February – November 2018) that were specifically selected to represent varying fire weather conditions. On each occasion, we collected two live plant samples of 30 species across three vegetation groups (10 species per vegetation group; details in Supplementary 1) common in the study area. One sample was used for flammability experiments, while the other for fuel moisture measurements. For each species, samples of approximately 70 cm in length that were representative of the fuel structure characteristic of the species were sourced. On each of the sampling occasion, samples from all 30 species were collected and burnt to ensure that flammability was measured under comparable conditions. Sample collection either started at 9h00 and subsequent burning at 12h00 or at 11h00 and 14h00 (respectively) to incorporate additional variation in fire weather conditions. For each occasion, the Canadian fire weather index was computed based on the temperature, relative humidity, rainfall (over the past 24 hours), and wind speed (Bedia et al., 2015; Dowdy et al., 2009) at the time that burning commenced. These weather measurements were obtained from a weather station located on the George Campus of Nelson Mandela University (‘Saasveld NMMU CW373’ on the Vital Weather online platform: www.vitalweather.co.za) where the experimental burning was conducted.

Samples used for flammability were burnt using an approach similar to that of Calitz et al. (2015) and Curran et al. (2017). Plant flammability was measured using the method and equipment described by Jaureguiberry et al. (2011), the apparatus comprises a metal barrel (85 cm x 60 cm) that is horizontally orientated with the top removable half that is used for wind protection (Baeza et al., 2002). The metal barrel is connected to a grill thermometer, removable gas cylinder and a blowtorch (Curran et al., 2017; Jaureguiberry et al., 2011). Each sample was placed on the barrel cavity grill to pre-heat at 230°C for two minutes to imitate the heating and drying effect of an approaching fire. If the samples had not spontaneously ignited within two minutes, it was ignited at the top of the shoot by exposing it to the blow torch for a period of five seconds (Calitz et al., 2015). Advantages of using this apparatus are that it preserves the architectural arrangement of plant material (Jaureguiberry et al., 2011). It further enables a more realistic comparison of relative canopy flammability among species than methods that use only smaller plant components (i.e. twigs or leaves) (Burger and Bond, 2015; Jaureguiberry et al., 2011).

Four aspects associated with species-level flammability were measured and recorded (largely after Calitz et al., 2015 and Jaureguiberry et al., 2011). Firstly, burn intensity taken as the maximum temperature (cf. Keeley, 2009) reached by a sample while burning, measured using an infrared thermometer (Major Tech 695; maximum recordable temperature: 800°C). Secondly, the completeness of burn, calculated as the proportion of the pre-burn wet mass of the samples that was consumed by the fire (mass was measured using an electronic scale). Thirdly, time-to-ignition, measured as the time elapsed between placement of the samples on the grill and spontaneous ignition (appearance of the first flame); samples that required to be ignited with the blow torch were therefore excluded from this measures' dataset. For every sample, we recorded whether it spontaneously ignited within the two minutes (pre-heating duration was consistent as there were many samples) of pre-heating or not, this binomial response comprising the fourth measure termed 'spontaneous ignition'.

Fuel moisture was calculated on a sample shoot similar in dimensions to that of flammability measurements. The fresh material was stored in sealed containers (of known mass) until these were weighed (within less than 3 hours of collection) to obtain wet fuel mass. Samples were then oven-dried at 80ºC for 48 hours and weighed again to obtain dry fuel mass (Ruffault et al., 2018; Teie, 2009). The fuel moisture was calculated as the percentage of wet mass comprised of water. Although sample size (shoot length) was standardized, samples nevertheless presented different fuel loads which is known to influence burn intensity (Keeley, 2009). Therefore, for each sample, dry plant mass (as a measure of fuel load) was estimated from pre-burn wet mass and thus provided the variable termed fuel load.

Dried plant samples

To investigate whether simulated drought conditions differentially affected the flammability of the vegetation groups, additional samples (similar to that collected for the flammability experiment's live samples described above) were collected and left to dry under ambient conditions, out of direct sunlight, for a minimum of two weeks but not until leaf loss occurred. Sampling was conducted over five occasions (during February – March 2019) of high fire weather conditions. The drying duration was standardized for all species to avoid the loss of leaves since certain plants would drop leaves due to drought stress (Clarke and McCaig, 1982). Flammability experiments and pre-burn estimations of fuel moisture were undertaken on these dried samples as described above for live (undried) samples.

Data analysis

Live plant samples

We assessed flammability (of live samples) in terms of four response variables (burn intensity, completeness of burn, time-to-ignition, and spontaneous ignition) respectively, in relation to the predictor variables (i) fire weather (continuous), (ii) fuel moisture (continuous), (iii) fuel load (dry plant mass; continuous), (iv) vegetation groups (IAPs, fynbos, thicket; categorical) and (v) species (30 species; categorical) using generalized linear mixed-effects models (Bates, 2010; O'Hara, 2009). Detailed species-level comparisons were not the primary focus of the study and species was therefore included as a random factor, whereas the other predictor variables were included as fixed factors. To test for potential collinearity between fire weather and fuel moisture, we ran the Spearman-rank correlation test for each respective species which showed that these variables were not significantly correlated (see Results) and could both be retained in subsequent analyses. We ran generalized linear mixed-effects models using the *lme4* package (Bates, 2010) in the open-source R software version 3.6.1 (R Development Core Team 2019) with burn intensity log-transformed (to correct right-skewed distribution), completeness of burn arcsine-transformed (as it was expressed as proportions), time-to-ignition square root-transformed (to correct left-skewed distribution), and assessed spontaneous ignition using logistic regression (binomial family, logit link function). Subsequently, Type II Wald chi-square test (Hastie and Pregibon, 1992) was computed to determine the significance of fixed factors on the specific models. We incorporated the scale function to the generalized linear mixed-effects models and logistic regression model (using transformed data) to standardize variables of different scales and obtain the relative influence of fixed factors (Becker et al., 1988).

Dried plant samples

We compared the flammability (in terms of burn intensity, completeness of burn, and time-to-ignition, respectively) of the dried samples with that of live samples of the same species that was measured on five occasions under comparable fire weather conditions. We calculated the change in flammability between live and dried samples by subtracting the flammability measure of each live sample from that of its dried counterpart. We then used this derived variable as response variable and employed Kruskal Wallis to test whether the difference in flammability between live and dried samples varied among vegetation groups.

Results

Live plant samples

Fire weather and fuel moisture were not significantly correlated within any of the study species (Supplementary 1). Increasing severity of fire weather significantly increased flammability through increasing burn intensity, increasing completeness of burn, increasing the likelihood of spontaneous ignition, and reducing time-to-ignition (Table 1, Fig. 1). Increasing fuel moisture significantly decreased burn intensity, completeness of burn, and the likelihood of spontaneous ignition. Fuel load significantly increased burn intensity and time-to-ignition.

In considering vegetation groups, flammability was generally highest in IAPs, intermediate in fynbos, and lowest in thicket (Table 1, Fig. 1). IAPs burnt at significantly higher intensity than fynbos and thicket. IAPs and fynbos showed significantly higher ignitability (shorter time-to-ignition and a greater likelihood of spontaneous ignition) than thicket.

Amongst the different fixed factors, vegetation groups consistently had the largest influence (i.e. the largest scaled estimates; Table 1) on all flammability measures. Fire weather had the second largest influence on ignitability, while fuel moisture had the second largest influence on burn intensity and completeness of burn.

The total variance in the flammability measures explained by the models was generally low (24 - 40%; conditional R^2 values, Table 1). The fixed factors combined explained less variation (8 - 22%; marginal R^2 values, Table 1) than species as random factor by itself (12 - 20%), except in terms of spontaneous ignition where vegetation groups and fire weather were most influential.

Dried plant samples

Drying out of samples under ambient conditions for two weeks resulted in an average reduction in fuel moisture contents of approximately 30% (Fig. 2 A), and the extent of this reduction did not differ significantly among vegetation groups (H_2=1.4, p=0.505). Dried samples exhibited increased flammability compared to their live counterparts, i.e. an average increase in burn intensity of 115°C; an 11% increase in completeness of burn; and a 46 seconds reduction in time-to-ignition (Fig. 2 B - D). However, this differential response in flammability between dried and live samples was comparable among the vegetation groups in terms of burn intensity (H_2=0.8, p=0.666), completeness of burn (H_2=1.8, p=0.410), and time-to-ignition (H_2=0.6, p=0.741).

Discussion

Effects of fuel moisture, fire weather, and fuel load on live fuels

Fuel moisture content is widely regarded to be a major determinant of flammability in grassland, shrubland and forested ecosystems with sufficient evidence of its dampening effects on fire behaviour and flammability (Bianchi and Defossé, 2015; Fares et al., 2017; Pausas and Paula, 2012). Live fuel moisture has furthermore been shown to respond closely to fire weather, particularly in grassland ecosystems (Bianchi and Defossé, 2015; Bowman et al., 2014; Chuvieco et al., 2004). That is why several fire danger indices attempt to account for fuel moisture to improve fire danger forecasting (Madula, 2013; Rothermel, 1983; Ruffault et al., 2018; Sirca et al., 2018). This concept assumes that the mechanism behind the enhancing effects of fire weather on flammability is through short-term (i.e. daily) variation in fuel moisture in response to weather conditions. However, contrary to expectation, fuel moisture in this study was not significantly correlated with fire weather in any of the study species. Fuel moisture did significantly correlate to burn intensity and completeness of burn as hypothesized (H_1), but the magnitude of its influence on flammability relative to the other factors investigated was generally low.

Fire weather significantly enhanced all measures of flammability as hypothesized (H_2), however the lack of response of live plant moisture contents to fire weather suggests that the mechanism through which fire weather enhances flammability may not be fuel moisture. Instead, the mechanism may involve the effect of fire weather on fuel temperature in relation to ignition temperature (Bedia et al., 2015; Pausas and Paula, 2012; Piñol et al., 1998). Other studies that have investigated fuel moisture–flammability relations (e.g., Bianchi et al., 2018) have not evidently assessed the effects of fire weather or have manipulated fuel moisture through drying out of fuels beyond natural levels of fluctuation in live fuels (Dimitrakopoulos and Papaioannou, 2001). We argue that the importance of live fuel moisture for flammability of evergreen shrublands rests on inter-specific and inter-vegetation type differences in fuel moisture contents (cf. Chuvieco et al., 2004), rather than short-term intra-specific fluctuation in live fuel moisture in response to weather conditions. The incorporation of satellite-derived proxies for live fuel moisture into fire danger indices is therefore unlikely to be useful in these systems. Although fire weather increased all measures of flammability (and particularly ignitability), it was less influential than vegetation groups. The contribution of short-term weather conditions to the severity of the 2017 Knysna fires was regarded to have been secondary to that of the long-term drought preceding these fires that would have caused a buildup of dead fuels (Kraaij et al., 2018). Fire weather is expected to increase in importance in its effects on flammability if cognizance is taken of dry or dead fuels (see below) and when considering stand level fire behaviour. Although plant shoot flammability experiments were an improvement on laboratory assessments of the flammability of excised leaves, the scale of experimentation relative to stand or landscape level fire was still inadequate. For instance, particular aspects of fire weather, such as wind speed, greatly influence wildfire spread and spotting behavior (Forsyth et al., 2019). Such dynamics could not be considered in the current study thereby likely leading to an underestimation of the importance of fire weather on flammability and, by implication, fire behavior.

Fuel load had varying effects on flammability, depending on the measure considered; it increased burn intensity as hypothesized (H_3), but reduced ignitability. These findings support other evidence for positive correlations between the amount of biomass (~fuel load) that vegetation presents and fire intensity or severity (Baeza et al., 2002; Keeley, 2009; Saura-Mas et al., 2010), but negative correlations between fuel load and completeness of burn (Kraaij et al., 2018; van Wilgen et al., 1990). Such contrasting effects on the different aspects of flammability emphasize the need to consider flammability in terms of its constituent measures rather than treating it as a composite measure (Engber and Varner, 2012; Pausas et al., 2012; Santana and Marrs, 2014).

Although fuel moisture content, fire weather conditions, and fuel load had significant effects on some of the flammability measures, these factors did not explain a large portion of variability in the flammability response. Species, which was assessed as a random factor, often accounted for more variation in flammability than the fixed factors combined. This suggests important species effects on flammability, which warrant more detailed investigation.

Vegetation group effects in relation to fire risk

Vegetation group comparisons showed that the flammability of IAPs exceeded that of thicket in terms of all flammability measures and exceeded that of fynbos in terms of burn intensity. These findings support claims (Forsyth et al., 2019; Stander, 2019) and other evidence (Brooks et al., 2004; Kraaij et al., 2018; Richardson and Rejmánek, 2011) that invasions by alien plants can add to the severity, intensity, and difficulty of control of wildfires. Fynbos and IAPs were more ignitable than thicket, and thus present higher risks under moderate and high fire weather conditions, whereas thicket presents lower risks under low and moderate fire weather conditions. Accordingly observations from the 2017 Knysna fires indicated that thicket only becomes ignitable under very high or extreme fire weather conditions but may then burn at intensities exceeding that in fynbos but not that of IAPs (Kraaij et al., 2018) presumably on account of disparate fuel loads (Keeley, 2009; Mandle et al., 2011). There were no significant differences between the flammability of fynbos and IAPs but completeness of burn appeared to be the highest in fynbos which suggests that the risk of recurring fire in fynbos will be almost zero for some period post-fire, whereas incomplete burning of IAPs and thicket will not afford the same level of risk reduction shortly post-fire.

Simulated drought conditions

Extremely large and severe fires, including the 2017 Knysna fires, are often associated with preceding droughts (Kraaij et al., 2018; Quinn, 1994; San-Miguel-Ayanz et al., 2013; Williams, 2013) and the resultant increase in dead fuels (Keeley, 2009). The extent and severity to which thicket, normally regarded as a fire-resistant (~poorly ignitable) vegetation (Calitz et al., 2015; Cowling and Potts, 2015), burnt in the 2017 Knysna fires, was attributed to extreme fire weather conditions and to the preceding severe drought (Kraaij et al., 2018). In this study, we confirmed that the drying of fuels as a crude proxy for severe drought effects considerably increased flammability. However, the magnitude of the increase in flammability in response to drying of fuels was consistent across vegetation groups. Flammability, and by implication fire risk, is thus unlikely to increase disproportionately in one vegetation group compared to another under extended drought unless the production of dead fuels due to drought would be disproportionate among the vegetation groups. We concede that the proxy for drought conditions could not realistically simulate all potential effects of drought on fuel modification and flammability, and in particular on the dying off of fuels and resultant increase in litter component. Detailed consideration of this aspect was beyond the scope of this study and warrants further investigation. Given that dead fuels respond more rapidly to weather conditions than live fuels, the ratio of dead to live fuels are likely to be a useful indicator of fire risk in evergreen shrublands (Keeley, 2009). Proxies for this ratio should, therefore, be sought for incorporation into fire danger indices.

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Table 1(on next page)

Output of generalized linear mixed-effects models and logistic regression model that assessed flammability in terms of burn intensity, completeness of burn, time-to-ignition and spontaneous ignition.

Fixed factors included in the generalized linear mixed-effects models (gaussian family, identity function; details in Supplementary 2) and logistic regression model (binomial family, logit link function) were fire weather, fuel moisture, fuel load, and vegetation groups (IAPs, invasive alien plants; Fyn, fynbos; and Thi, thicket), while species was included as a random factor. Significance codes: *p <0.05, **p <0.01, ***p <0.001 [a]Chisq statistics and significance levels were obtained from deviance tables (Type II Wald chi-square tests). [b]Scaled estimates were derived from incorporating the scale function in the generalized linear mixed-effects models and logistic regression model. [c]R^2 values were derived using the r.squaredGLMM function, where conditional R^2 indicates the proportion of variance explained by fixed and random factors combined, marginal R^2 indicates the proportion of variance explained by fixed factors alone and R^2(1|Species) indicates variance explained by the random factor alone.

Factors	Burn intensity			Completeness of burn			Time-to-ignition			Spontaneous ignition		
	Estimate	Chisq [a]	Scaled estimate [b]	Estimate	Chisq [a]	Scaled estimate [b]	Estimate	Chisq [a]	Scaled estimate [b]	Estimate	Chisq [a]	Scaled estimat [b]
Fire weather	0.0007	4.1 *	0.06731	0.1300	11.0 ***	0.1175	-0.0339	21.0 ***	0.19471	0.0650	23.8 ***	0.6671
Fuel moisture	-0.0015	4.4 *	0.11524	-0.1616	4.6 *	0.1225	0.0271	2.8	0.09747	-0.0379	4.5 *	0.3265
Fuel load	0.0004	5.6 *	0.10090	-0.0180	1.1	0.0477	0.0121	9.3 *	0.16529	-0.0063	2.6	0.1900
Veg group [IAP and Fyn]	-0.0427	8.1 *	0.39141	-1.1895	5.7	0.1048	-0.7575	9.6 **	0.36388	0.2156	16.3 ***	0.2156
Veg group [IAP and Thi]	-0.0648		0.59446	-5.2832		0.4657	0.8838		0.42458	-1.5563		1.5564
Conditional R^2 [c]		0.2961			0.2442			0.3983			0.3459	
Marginal R^2 [c]		0.0942			0.0798			0.1935			0.2258	
R^2 (1|Species) [c]		0.2019			0.1644			0.2048			0.1201	

Figure 1

Predicted effects of fixed factors on the flammability measures, (A – D) burn intensity, (E – H) completeness of burn, (I – L) time-to-ignition, and the probability of (M – P) spontaneous ignition.

Fixed factors were fire weather, fuel moisture, fuel load, and vegetation group (IAPs, invasive alien plants; Fyn, fynbos; and Thi, thicket). The effects shown here were based on the model outputs shown in Table 1 (shaded bands depict standard errors and whiskers show 95% confidence intervals).

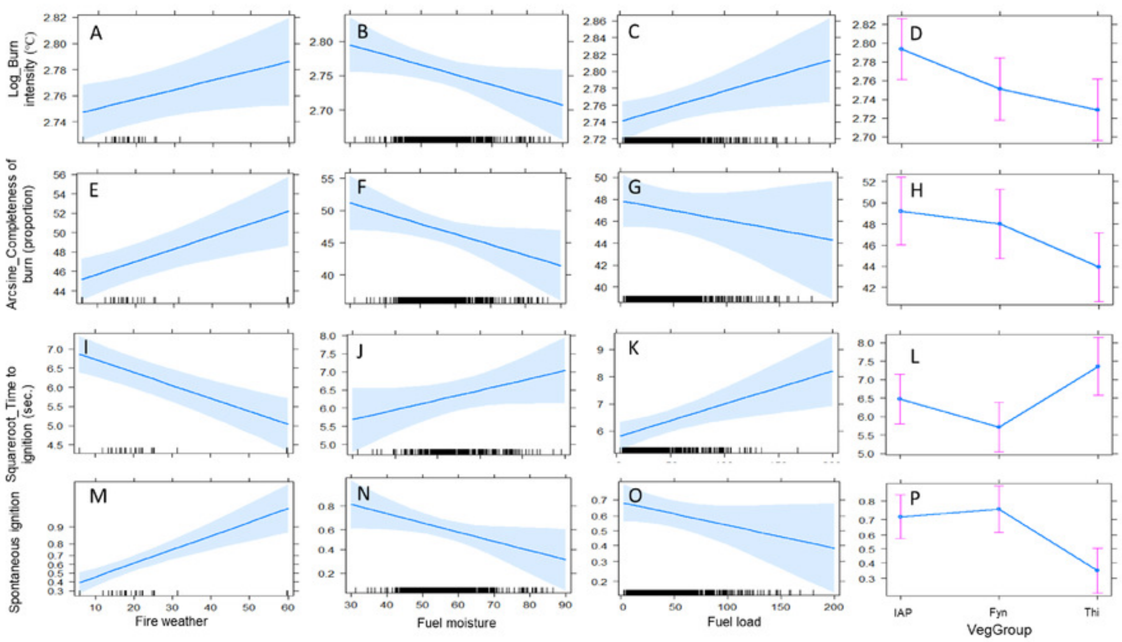

Figure 2

The change (Δ) between live and dried samples in (A) fuel moisture, (B) burn intensity, (C) completeness of burn, and (D) time-to-ignition, compared among vegetation groups.

Live and dried samples were of the same species under comparable fire weather conditions. Vegetation groups were IAPs, invasive alien plants; Fyn, fynbos; and Thi, thicket. Medians (lines), 25–75 quantile ranges (boxes), 1.5 * interquartile ranges (whiskers), and outliers (dots) are shown.