



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



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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.

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1. 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 reseeding—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-in this issue](#)) via the germination of soil-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 \(2015-in this issue\)](#) showed 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 that 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 Afrotropical Forest (fire-free) and found that Fynbos species are more flammable than Forest species. Using species from these same biomes, [Burger and Bond \(2015-in this issue\)](#) 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-in this issue; 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 evolutionarily selected trait (sensu Bond and Midgley, 1995; Burger and Bond, 2015-in this issue; 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 twiginess and leaf density sensu Schwilk, 2003), should be more flammable than sparsely branched plants with large, fleshy or soft leaves that are sparsely arranged (Burger and Bond, 2015-in this issue; Fernandes and Cruz, 2012; Jaureguiberry et al., 2011; Pausas and Moreira, 2012).

2. Methods

2.1. 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°15'44"S; 25°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 Afrotemperate Forest) occupy the deeply incised and fire-free canyons (*kloofs*) of perennial streams of the Suurberg. The study area is 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).

2.2. 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 the 10th and 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. 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 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 1 cm/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

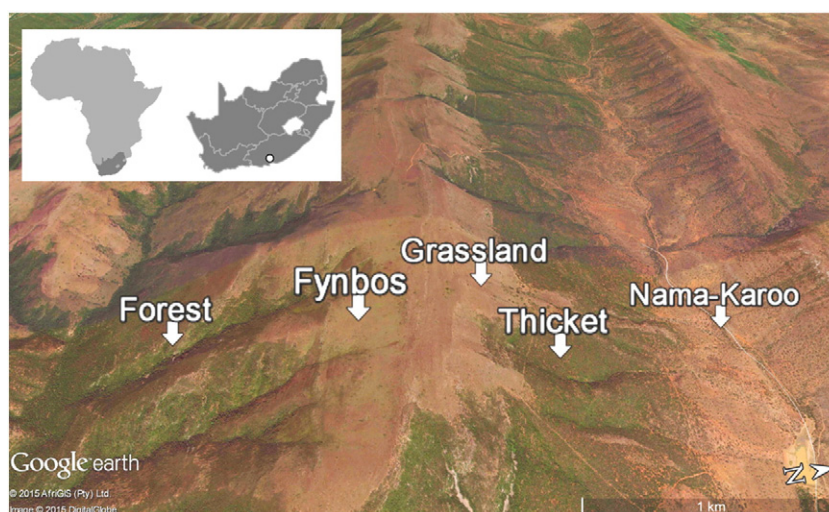


Fig. 1. An example of the close juxtaposition in the study area of the five biomes used to sample species for flammability assessments. The majority of sites used for sampling were within 5 km of one another, but due to issues of accessibility in this difficult terrain, some sites were up to 13 km apart.

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