

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Growth form and functional traits influence the shoot flammability of tropical rainforest species

Ebony Potts^{a,*}, David Tng^a, Deborah Apgaua^a, Timothy J. Curran^b, Jayden Engert^a, Susan G. W. Laurance^a

^a Centre for Tropical Environmental and Sustainability Science, College of Science and Engineering, James Cook University, 14-88 McGregor Rd, Smithfield, Qld 4878, Australia

^b Department of Pest-management and Conservation, Lincoln University, P.O. Box 85084, Lincoln, Canterbury 7647, New Zealand

ARTICLE INFO

Keywords:

Fire
Flammability
Functional Traits
Rainforest
Rainforest Restoration

ABSTRACT

Canopy fires are increasing globally with anthropogenic climate and land-use changes, even in fire-sensitive rainforest ecosystems. Identifying the ecological drivers that may be aiding canopy fires, such as species or growth form flammability, is crucial to recognising and mitigating fire risks. To address this, we quantified the shoot-flammability of 124 rainforest plant species using an experimental approach. We compared three flammability measures (burnt biomass, total burn time and maximum temperature reached) with plant functional traits across seven different growth forms (i.e., canopy, pioneer, and understory trees; pioneer, understory and invasive shrubs, and vines) and nine common plant families and other higher-level clades, such as conifers, hereafter abbreviated to families. From burning > 600 sun-exposed shoots, we found trees were higher in flammability than shrubs and vines, and the plant families: Sapindaceae, Proteaceae, Fabaceae, and Lauraceae, had especially high flammability, whereas Moraceae was very low. Of the functional traits examined, leaf dry matter content was consistently and significantly positively associated with species flammability. Invasive shrubs as a group were not particularly flammable, although there were exceptions, e.g., wild tobacco (*Solanum mauritianum*) was highly flammable. This study has two important implications for the management of fire in rainforests. First, we have demonstrated that many tropical rainforest trees may readily burn under severe fire conditions if fire were to reach the rainforest canopy. Second, a large proportion of the > 1 million rainforest trees planted in the Wet Tropics under restoration planting schemes are from our most flammable rainforest plant families, as these families are often recommended for their carbon sequestration potential. Hence, these plantings may be highly vulnerable to fire and if planted along the borders of primary forest they may carry fire into their canopies. Therefore, where fire risk is high, we recommend planting species with low flammability along borders of plantings and forests to act as 'green firebreaks' to reduce the risk of fire incursions.

1. Introduction

Globally, wildfires are increasing in severity in response to climate and land-use change (Jolly et al., 2015; Uhl & Kauffman, 1990). Rising temperatures, extreme weather events, and widespread droughts have been identified as key causes to changes in fire behaviour (Buis, 2019; Alam et al., 2020; Jolly et al., 2015; Wang et al., 2021). In addition, land conversion and fragmentation have been identified as key contributors to changes in local climates and ignition sources (Uhl & Kauffman, 1990; Briant et al., 2010). Such changes in climate have resulted in extended fire season lengths. For example, the frequency of longer fire seasons has

increased across 53.4 % of the globe and has doubled (108.1 %) the global burnable area per year (Jolly et al., 2015; Pausas et al., 2008). This is evident from the last three years alone, where the forests of Australia's east coast were engulfed by bushfires in a fire season that lasted for nearly-six months and burned over 10 million hectares of land (Gallagher et al., 2021). During this same time, severe wildfires also occurred in Greece, California, Canada, and in the Arctic Circle (Wang et al., 2021; NASA, 2021; Cal fire, 2021; Goss et al., 2020). However, it was not only temperate and Mediterranean biomes that were experiencing such intense wildfires, but also tropical and subtropical ecosystems. In fact, from 1997 to 2018 tropical forests and tropical savannas

* Corresponding author at: 179 Loridan Drive, Brinsmead, QLD 4870, Australia.

E-mail address: ebony.potts@my.jcu.edu.au (E. Potts).

<https://doi.org/10.1016/j.foreco.2022.120485>

Received 18 May 2022; Received in revised form 29 July 2022; Accepted 16 August 2022

Available online 22 August 2022

0378-1127/© 2022 Elsevier B.V. All rights reserved.

accounted for ~ 70–80 % of the global burned area interannual variability (Tang et al., 2021). In the years following, large out of control wildfires consumed > 760,000 ha of land in the Amazon rainforest in 2019, and another > 760,000 ha in 2020, while > 250,000 ha of rainforests were consumed in the Australian 2019/2020 megafires (Galagher et al., 2021; Bowman, 2020).

In general, fires are a rare phenomenon in rainforests (Bush et al., 2011). When they do occur, they are characterised as ground or low surface fires that follow clearings and forest debris (fuels) associated with logging and slash and burn agriculture (Cochrane and Laurance, 2008). Yet in recent years, fire regimes in rainforests have shifted and there have been more reports of canopy fires in these fire-sensitive ecosystems (Shlisky et al., 2007). Such intense canopy fires are often attributed to the climate and land-use changes discussed earlier, but also to human-mediated spread of invasive species (Cochrane, 2009). Invasive species spread rapidly in disturbed or cleared areas and can be found in high densities along rainforest edges (Cochrane, 2009; Goldammer, 1990). Some invasive species can produce large and constant amounts of fuels which can facilitate the ingress of fires into the rainforest (Cochrane, 2009). With that said, it is evident that these anthropogenic impacts are driving severe wildfire frequencies across nearly all biomes, even in characteristically wet biomes, however, less is known of the biological factors that influence flammability of tropical rainforest species.

Flammability is a core functional plant trait that is influenced by several chemical, structural, and functional plant traits (Pérez-Harguindeguy et al., 2016; Alam et al., 2020). By testing plant flammability, we can quantify how certain plant species may burn when exposed to fire and use this information to inform fire management or test plant evolutionary hypotheses (Cui et al., 2019, Cui et al., 2020ab). There are four components that determine the flammability of plant materials: (1) ignitability: time it takes for the plant to ignite, (2) combustibility: the maximum temperature the plant burns, (3) sustainability: total duration plant burns following ignition, (4) consumability: proportion of plant burned (Anderson, 1970; Martin et al., 1993). By taking these components into account, plant flammability can be investigated in a variety of ways, either looking at individual or whole plant components or different fuel types (live or dead), with all methods having advantages and disadvantages (Schwilk, 2015). Flammability studies are often used to understand different types of fires, such as ground, surface, or canopy (Ganteaume, 2018). Although all fire types are important to understand, canopy fires are the main types that are attributed to severe wildfires, thus need to be better investigated (Alam et al., 2020).

By quantifying the flammability of plant shoots, as well as certain tissue traits such as dry matter content and leaf mass per area, we can begin to understand how canopy-level fires might behave (Pérez-Harguindeguy et al., 2013; Wyse et al., 2016; Jaureguiberry et al., 2011; Alam et al., 2020). Plant shoots retain the architecture and finer fuels of the whole plant, thereby providing ecologically-informed results regarding canopy-level fire behaviour across a wide range of species (Jaureguiberry et al., 2011; Schwilk, 2015; Wyse et al., 2016). At the same time, by collecting additional plant trait measurements the relationships of plant traits and flammability can be determined and help to identify influences contributing to high or low plant flammability (Pérez-Harguindeguy et al., 2013; Wyse et al., 2016). Although the shoot flammability method is that it involves less precision compared to some other laboratory-based approaches, this method has been regarded as the most suitable, easily replicable, and cost-effective way to measure species flammability and understand how fire interacts within each ecosystem (Jaureguiberry et al., 2011; Schwilk, 2015; Wyse et al., 2016; Alam et al., 2020). However, while shoot flammability studies have been conducted in temperate (Wyse et al., 2016; Padulles Cubino et al., 2018; Cui et al., 2020ab; Alam et al., 2020) and Mediterranean environments (Burger & Bond, 2015; Calitz et al., 2015), they are yet to be carried out in tropical rainforest biomes.

Rainforests are not only biologically and phylogenetically diverse

but are also comprised of structurally complex growth forms. This structural complexity of growth forms includes a dominant canopy layer made up of mostly trees and some woody vines and sub-canopy and understory layers made up of smaller trees and shrubs. Further, when rainforests become disturbed, recovery is led by pioneer species or, in human-dominated landscapes, by invasive species. For these reasons, we aim to quantify and compare the flammability of rainforest species across different growth forms and families to understand the structural and biological drivers of rainforest plant flammability. The outcomes of this study are intended to provide current tropical forest land-managers with nuanced fire mitigation methods that can be used to inform future fire-resistant restorations plans.

We asked four main questions: (1) Is there a difference in flammability among rainforest growth forms? (2) Are invasive shrubs the most flammable growth form? (3) Is there a difference in flammability among common rainforest families? and (4) Which plant functional traits influence flammability? We hypothesised that: (1) Shrubs will have higher flammability compared to trees and vines due to leaf traits that are related to lower plant moisture content and more combustible fuel; (2) Invasive shrubs will have the highest levels of flammability due to their leaf traits; (3) There will be taxonomic influences on leaf and twig traits that are phylogenetically conserved and influence flammability; and (4) Leaf traits related to lower plant moisture content and more combustible fuel, such as high dry matter content and leaf mass per area, will be related to a higher flammability.

2. Methodology

2.1. Species selection and collection

Woody plant species were collected from mid-elevation rainforest sites on the Atherton Tablelands in the Wet Tropics biogeographic region of north-eastern Australia (17°12'07" S, 145°40'34.5" E, ~750 m a.s.l.). The area experiences a tropical climate of cool, dry winters and hot, humid summers, with mean annual rainfall of approximately 1800 mm and average annual minimum and maximum temperatures of 15.3 °C and 25.6 °C (Bureau of Meteorology, 2021). The study locality is classified as moist uplands with complex rainforest structures on a basalt geology (Goosem and Tucker, 2013; Bureau of Meteorology, 2021).

We sampled a total of 124 species across seven different growth forms (Pioneer trees, Understory trees, Canopy trees, Pioneer shrubs, Understory shrubs, Invasive shrubs, and Vines) and 37 taxonomic families, encompassing three monocotyledons (two vines and one understory shrub), seven conifers, and the remainder dicotyledonous trees, shrubs, and vines (Supplementary table 1). Within this larger species pool, we examined a subset of 84 native species from common families which included two gymnosperm families (Araucariaceae and Podocarpaceae, hereafter referred to as 'Conifers'), and eight angiosperm families (Euphorbiaceae, Rutaceae, Fabaceae, Moraceae, Lauraceae, Sapindaceae, Myrtaceae, and Proteaceae) (Supplementary table1).

We collected 70 cm long sun-exposed terminal branches from healthy, reproductively mature individuals following an existing protocol (Jaureguiberry et al., 2011; Pérez-Harguindeguy et al., 2013; Wyse et al., 2016). Samples with compound leaves were treated the same way as those with simple leaves, even when compound leaves exceeded the 70 cm length. An additional 20 cm sample was collected from the same individual for leaf and twig functional trait measurements. Fresh shoot samples were weighed, placed horizontally on a concrete surface and dried under shelter for 24 h prior to flammability measurements (as per Wyse et al., 2016; Wyse et al., 2018). Sample collection generally commenced at 0700hrs with subsequent trait measurements and flammability tests from the previous days collection from 1200hrs. The following day flammability tests would occur from 0700hrs with subsequent collection and trait measurements from 1200hrs.

2.2. Flammability testing device

The flammability testing apparatus we used for the study was based on those described by Jaureguiberry et al. (2011) and Wyse et al. (2016). Due to state legal safety regulations regarding devices that connect with gas, we were unable to custom build the exact flammability testing apparatus, so we used a free standing five-burner BBQ (Beefeater 2000) for our purposes, which consists of the basic components present in the flammability testing apparatus described by Jaureguiberry et al. (2011). This apparatus consists of gas burners measuring 10 cm from grill mesh and 7 cm from the base. The apparatus was fitted with a hood and was positioned between windbreaks to create more homogeneous conditions for the experiment (Fig. 1).

2.3. Flammability measurements

We measured shoot flammability using three flammability traits of burnt biomass, burn time, and maximum temperature, following Wyse et al. (2016). Prior to flammability trait testing, ambient air temperature and relative humidity (Ozito ODT-100) were recorded. All five gas burners were set to the lowest setting, which maintained the device at 100–130 °C. Device temperatures were measured before each burn with two 2-input thermocouple thermometers (-50 °C–1300 °C), fitted with two K-type thermocouple probes per device (-5 °C – 250 °C [± 2.5 °C]). Shoots were weighed prior to burning and placed horizontally on the grill for two minutes to preheat and then a blowtorch flame was applied on the distal end of the shoot for 10 s. Once ignition occurred, we recorded the burn time with a stopwatch and the maximum temperature of the burning sampling with a Fluke 572–2 High Temperature Infrared Thermometer (-30 °C–900 °C, ± 1 °C). To record maximum temperature an Infrared Thermometer was held 50 cm away in front of the burning shoot (at roughly a 45° angle), acquiring the measurement by pointing the thermometer laser at the flames using an up and down ‘painting’ motion. Burnt biomass was visually estimated as a percentage by two observer’s post-burn. A metal grid was placed over the sample to facilitate estimating and before and after photos were taken. If the observers estimating burnt biomass suggested two different proportions, the mean of these values was recorded.

2.4. Functional trait measurements

Using 20 cm branches collected from the same individual plant, we measured leaf and twig plant functional trait following standardized methods (Pérez-Harguindeguy et al., 2013). Leaf Area (LA: cm²) was



Fig. 1. Shoot flammability apparatus positioned in sheltered area and fitted with four thermocouple probes to monitor average device temperatures.

estimated using photo editing software (Paint.net). Leaf dry matter content (LDMC: mg/g) and twig dry matter content (TDMC: mg/g) were measured by weighing fresh leaves and twigs, oven drying them at 75 °C for 48hrs and then weighing the dried leaf mass. Leaf mass per area (LMA: g/m²) was measured by dividing the dried leaf mass by the leaf area. Shoot moisture loss percent was calculated as: (shoot fresh mass - dry mass)/shoot fresh mass.

2.5. Statistical analyses

2.5.1. Mixed-effects models

We fitted separate models to examine differences in the flammability of plants among seven growth forms and nine common plant families using mixed-effects models in R (version 3.6.3; R Core Team, 2021). Models were developed for each of the three flammability response measures: Burnt biomass, burn time, and maximum temperature with fixed- and random-effect terms in packages lme4 and nlme (Bates et al., 2015; Pinheiro et al., 2021).

The response variable burnt biomass was examined using a binomial generalised linear mixed model (GLMM) via the *glmer()* function (link = “logit”) in package *lme4*. The GLMM modelling approaches accounted for non-normally distributions in proportional data (Bates et al., 2015). The fixed effects in each model were growth form or family, and leaf functional traits and shoot water loss, with data checked for normality and log transformations conducted if necessary. Models that examined growth form as an explanatory fixed factor included phylogenetic relatedness as a random effect by nesting species in genus in family, whereas family models included growth form as a random effect to account for the different proportions of tree and shrub species. Burn times and maximum temperatures were examined using linear mixed-effects model in package *nlme* with the *lme()* function (log-restricted likelihoods) with the same fixed and random effects. We used Estimated Marginal Means for post hoc analyses of fixed factor combination using the *emmeans* package (Lenth, 2021). All post hoc analyses examined pairwise comparisons with Bonferroni correction for multiple tests to establish a conservative threshold for significant Pearson Correlation values ($P < 0.005$). All data originally on logit scale were back transformed during post hoc tests.

2.5.2. Ordination

We examined the overall flammability of the 124 individual plant species with a multivariate approach. Plant species were ordinated based on the three flammability measures (burnt biomass, burn time, and maximum temperature), with a non-metric multidimensional scaling (NMDS) ordination in the package PC-ORD 6.08 (McCune & Mefford, 2011). The ordination computed highly orthogonal principal axes in two dimensions using a Sorensen distance measure and a Monte Carlo randomization test to determine that the stress of the final solution was significantly lower than chance ($P < 0.019$). Ordination axes were correlated with the flammability measures and a secondary matrix of the growth form of plant species, using Bonferroni correction. A Multiple Response Permutation Procedure (MRPP) of the ordination examined pairwise dissimilarities between growth forms. Finally, to provide a useful fire management resource for land managers, the overall flammability of the 124 plant species was ranked and visualized in heatmaps (PCORD) based on ordination axes and compared with common rainforest plants from restoration plantings in the Wet Tropics (Engert et al., 2020).

3. Results

We sampled the shoot flammability of 611 individual plants from 124 species (Table S1). These species were categorised into seven growth forms, of which most (67 %) were considered as a type of tree species (canopy, pioneer, or understory), with the remainder recorded as shrubs (25 %) and vines (8 %). The higher representation of tree

species in our study reflects that typically more than half of the woody plant diversity of tropical forests is made up by trees (Croat 1978; Ribeiro et al 1999). We further examined if flammability had a phylogenetic relationship with a subset of nine families that had a good representation of species (n = 83 species).

3.1. Proportion of burnt shoot biomass

Total burnt biomass of the shoot samples ranged from 2 – 99.5 % (\bar{x} = 40) and was significantly associated with growth form, plant family, and leaf dry matter content (LDMC) (Fig. 2, Table S2). Leaf mass per area and the amount of moisture lost from the shoot in the 24 hr period prior to burning were not significant predictors of burnt biomass (Table S2). Of the growth forms studied, we found that a higher proportion of tree shoots were significantly more likely to be consumed by fire compared to shoots of shrubs and vines (Fig. 2a) and that LDMC was a highly significant predictor ($P < 0.0001$) of shoot burnt biomass (Table S2). The logistic regression curves of growth forms (Fig. 2a) illustrate that for canopy, pioneer, and understory trees there is a high probability that > 50 % of shoot biomass will burn when LDMC reaches 350–400 mg/g. Furthermore, when LDMC is 500 mg/g the logistic regression curves

predict that shoot biomass will burn between 30 and 60 % in vines and all shrubs and that > 70 % of shoot biomass will burn in canopy, pioneer, and understory trees. The estimated marginal means of the generalised mixed effects model comparing burnt biomass between growth forms shows the distinct difference in shoot consumption by fire between canopy, pioneer, and understory trees and the less flammable vines, pioneer, and understory shrubs (Fig. 2c, Table S2). Invasive shrubs showed a high variability among species compared to other shrubs with some having little burnt biomass (e.g., *Tithonia diversifolia* and *Montanoa hibiscifolia*) and others losing a high percentage of biomass (e.g., *Solanum mauritianum*). Pairwise comparisons between these growth forms with LDMC as an interaction term, found all trees (canopy, understory, and pioneer) were significantly different from vines and understory shrubs ($P < 0.02$, Table S3).

We observed a similar pattern among the nine common plant families although the logistic regression curves were more varied with the smaller sample size (Fig. 2b). Leaf dry matter content (LDMC) was significantly associated ($P < 0.0001$, Table S2) with the proportion of shoot biomass burnt (Fig. 2b & d) and varied between the plant families. The families Sapindaceae, Lauraceae, and Fabaceae lost > 60 % of shoot biomass with relatively low to moderate levels of LDMC (380 mg/g),

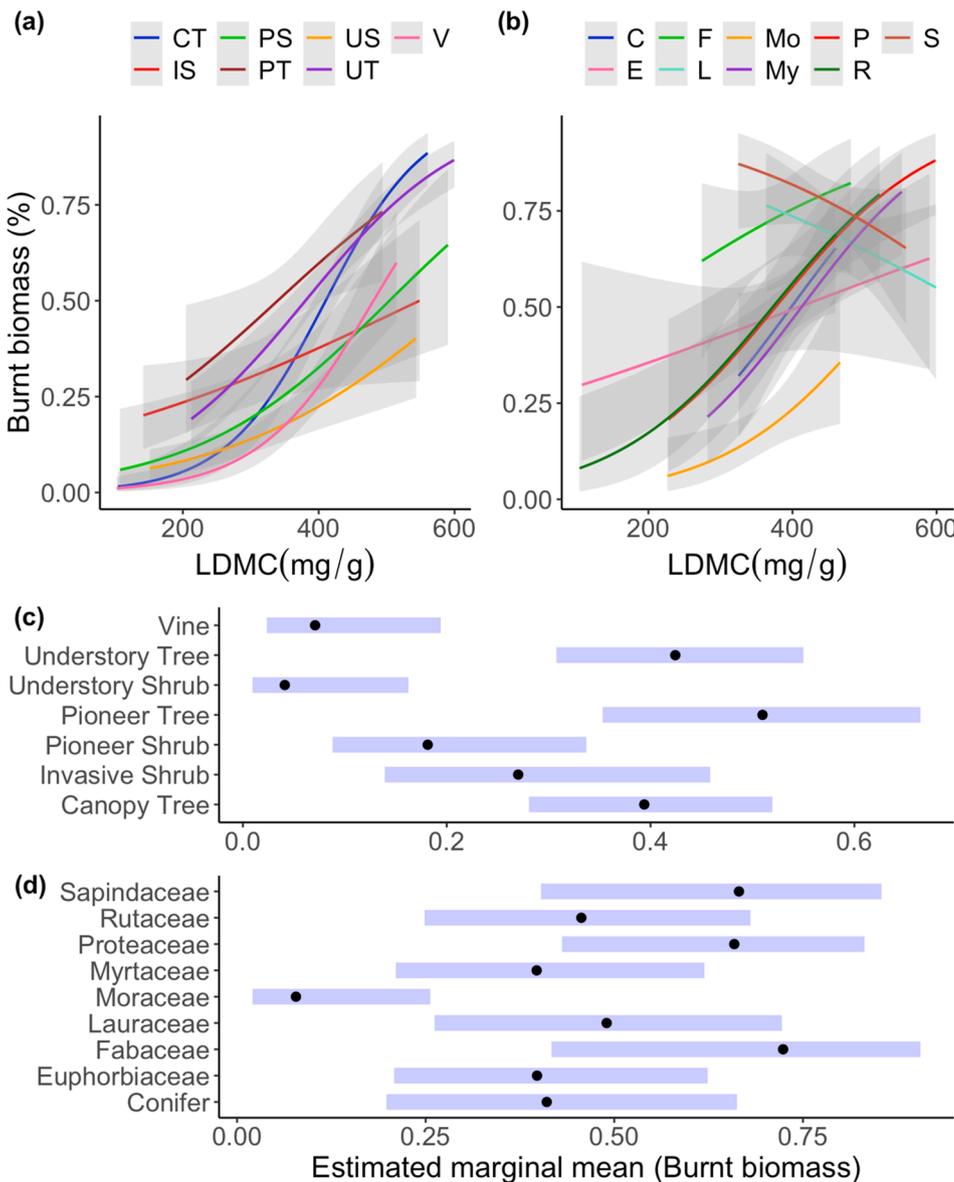


Fig. 2. Comparison of the amount of the % of shoot biomass burnt and LDMC of rainforest (a) growth forms (CT = Canopy Tree, PS = Pioneer Shrub, US = Understory Shrub, V = Vine, IS = Invasive shrub, PT = Pioneer Shrub, UT = Understory Tree), and (b) plant families (C = Conifer, F = Fabaceae, Mo = Moraceae, P = Proteaceae, S = Sapindaceae, E = Euphorbiaceae, L = Lauraceae, My = Myrtaceae, R = Rutaceae). Post hoc estimated marginal means plots show pairwise comparisons between (c) growth form and (d) plant family, both with LDMC interactions.

whereas Rutaceae, Proteaceae, Euphorbiaceae, and Myrtaceae and Conifers burnt > 50 % of shoot biomass once LDMC reached 380–400 mg/g. Species in the family Moraceae demonstrated lower flammability, never burning > 40 % of shoot biomass irrespective of LDMC. Two of the most flammable families (Lauraceae and Sapindaceae) with respect to burnt biomass had declining logistic curves with increasing LDMC. In both families, all species recorded high leaf dry matter content values (from 380 to 600 mg/g), with burnt biomass values always being high ($\bar{x} = 54 - 96 \%$). In a pairwise comparison between families (and LDMC as an interaction term), all other families differed significantly from Moraceae except for Conifers and Myrtaceae (Table S3; all $P < 0.05$). Leaf mass per area and the amount of shoot moisture loss 24 hr prior to burning were not significant predictors of differences between these common families.

3.2. Burn time of shoots

The duration that shoots burned ($\bar{x} = 25$) varied from 2 – 140 s and was significantly associated with growth form, plant family, leaf dry matter content, and leaf mass per area (Fig. 3, Table S3). The length of time a shoot burns was correlated ($r_s = 0.76, P < 0.0001$) with the proportion of shoot biomass burnt. Hence, we observed some similar patterns in our comparisons of shoot burn time between growth forms (Fig. 3a) and burnt biomass. For example, all trees (canopy, pioneer, and understory) burned for significantly longer periods than vines ($P < 0.02$, Table S3) and canopy and pioneer trees burned significantly longer than understory and pioneer shrubs ($P < 0.02$, Table S3). Burn time among growth forms increased significantly with leaf dry matter content ($P < 0.0001$, Fig. 3c) and leaf mass per area ($P < 0.01$, Fig. 3e) but not with shoot water loss 24 hr prior to burning.

The correlation between burn time and burnt biomass was not as

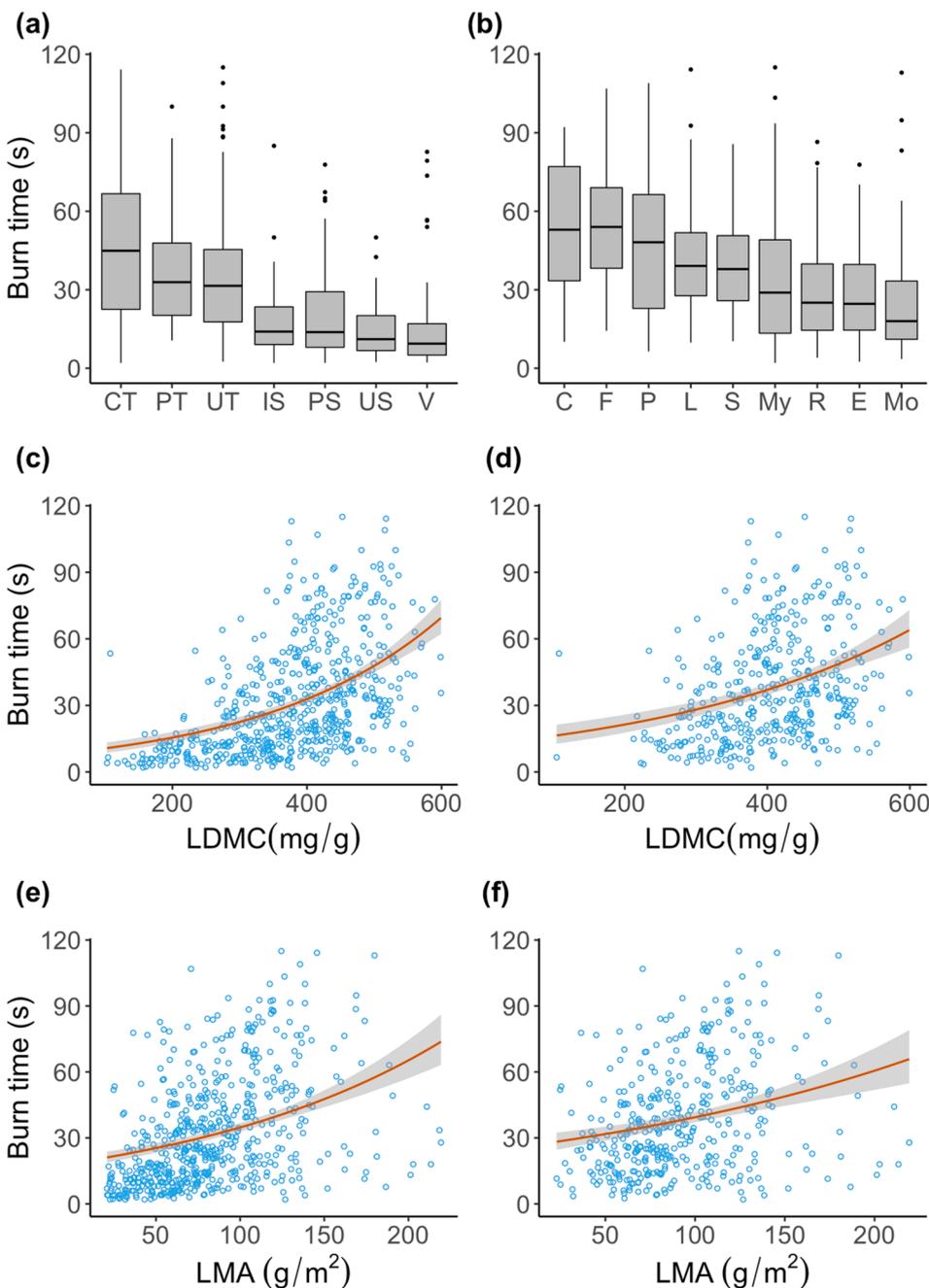


Fig. 3. An experimental comparison of the time taken for an ignited plant shoot to burn among rainforest (a) growth forms (CT = Canopy Tree, PS = Pioneer Shrub, US = Understory Shrub, V = Vine, IS = Invasive shrub, PT = Pioneer Shrub, UT = Understory Tree) and (b) plant families (C = Conifer, F = Fabaceae, Mo = Moraceae, P = Proteaceae, S = Sapindaceae, E = Euphorbiaceae, L = Lauraceae, My = Myrtaceae, R = Rutaceae). Relationship between (c) growth form burn time and leaf dry matter content, (d) family burn time and leaf dry matter content, (e) growth form burn time and leaf mass per area, and (f) family burn time and leaf mass per area. Outliers > 120 s have been excluded from figures (a), (b), (c), (d), (e), and (f).

significant for plant families ($r_s = 0.65$, $P < 0.0001$). We observed Conifers, Fabaceae and Proteaceae families burning for longer periods than Moraceae, Euphorbiaceae, and Rutaceae (Fig. 3b). Burn time among families increased significantly with leaf dry matter content ($P < 0.0001$, Fig. 3d), but not with leaf mass per area and shoot water loss 24 hr prior to burning. A pairwise comparison of families found the length of burn time was significantly different between both Moraceae and Myrtaceae and Conifers and Fabaceae ($P < 0.01$) and between Proteaceae and Moraceae ($P < 0.05$, Table S3). The estimated marginal means of the linear mixed effects model for burn time and plant family had a closer estimated mean between Moraceae and Myrtaceae as opposed to the medians represented in the boxplot (Fig. 3b), which shows Moraceae having closer medians to Euphorbiaceae and Rutaceae.

3.3. Maximum temperature of burning shoots

The maximum temperature at which shoots burned ($\bar{x} = 712.9$) ranged from 259 to 900 °C was significantly associated with growth form, family, and leaf dry matter content (Fig. 4, Table S4). On average trees and pioneer shrubs burnt hotter than shrubs and vines but there were less distinct differences between function groups for this measure compared to the amount of shoot biomass burnt or for burn time. Leaf dry matter content was significantly associated ($P < 0.0001$, Table S4) with the maximum temperature reached for burning shoots. Among the common families, shoots from Sapindaceae, Lauraceae and Fabaceae burned hotter than Euphorbiaceae, Conifers and Rutaceae. In a pairwise comparison, the maximum temperatures for burning shoots of Sapindaceae were significantly hotter than for Conifers and Rutaceae ($P < 0.05$, Fig. 4B, Table S4).

3.4. Overall flammability

The ordination of overall flammability of 124 species was resolved into a two-dimensional solution that explained 99.4 % of the data variation. Of the two axes recommended in the final solution, Axis 1 explained most of the data variability ($R^2 = 0.96$) and was strongly and positively correlated with all three flammability measures (Fig. 5a, Table 1). Axis 2 explained only a small amount ($R^2 = 0.028$) of the overall data variability and ranked species only according to the length of burn times (Fig. 5a, Table 1). More tree species were positively associated with Axis 1, but there was no significant distinction between all seven growth forms (Fig. 5a, Table 1). The MRPP analysis of the growth form groupings in the ordination found the group mean distances ($\delta = 0.540$) for understory trees was below the actual δ mean distance ($\delta = 0.645$) threshold for all groups, signifying that species in this group showed more similar flammability responses than all the other growth forms. Canopy ($\delta = 0.663$) and pioneer ($\delta = 0.648$) trees, invasive shrubs ($\delta = 0.678$) and vines ($\delta = 0.665$), all had δ mean values above this threshold but below the Expected δ ($\delta = 0.734$) value, which is a predicted mean distance if there were no species grouping in categories. Pioneer ($\delta = 0.79$) and understory shrubs (0.788) were above this expected value suggesting that as groups there was more variability among species than expected by chance.

3.5. Fire risk in rainforest restoration plantings

We qualitatively applied our species' flammability rankings from Axis 1 rank ordination heat map (Fig. S1) to the plant species commonly used in rainforest restoration in the Wet Tropics region, Australia, from 2012 to 2017 (Engert et al., 2020). There were 75 of our species reported from the two studies that encompassed 151,227 seedlings planted out at 8300 sites over the five-year period between 2012 and 2017. We

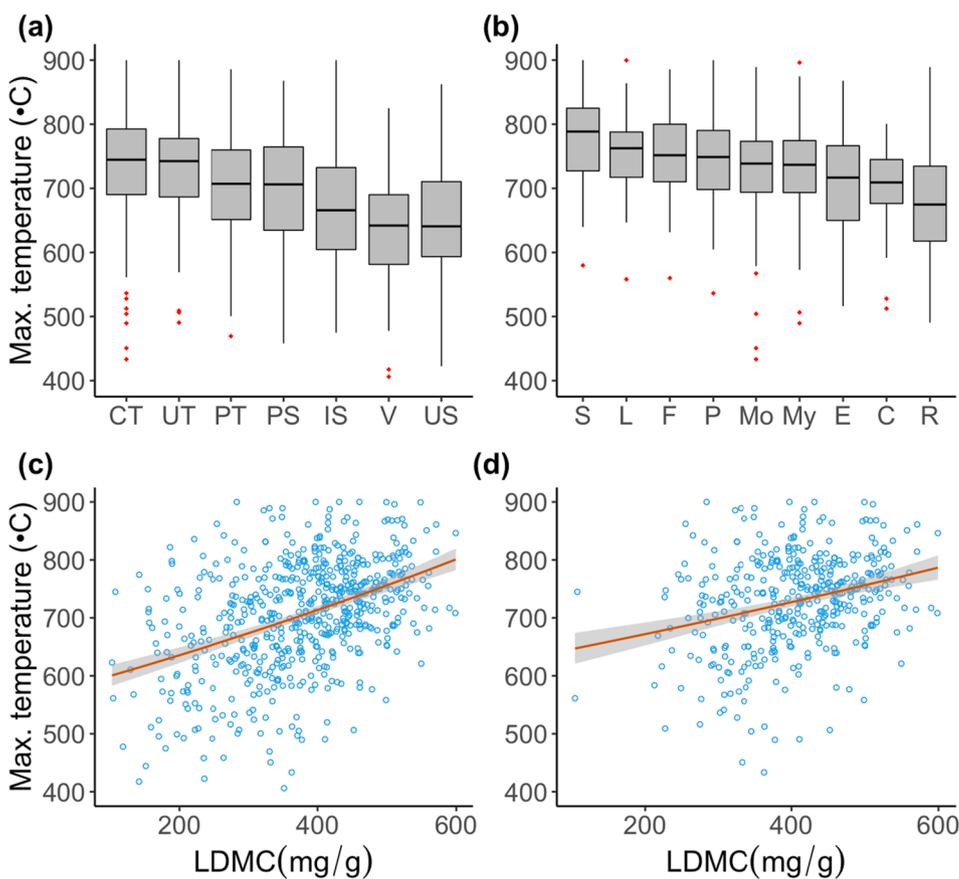


Fig. 4. Comparison of the maximum temperatures that shoots burn among (a) growth forms (CT = Canopy Tree, PS = Pioneer Shrub, US = Understory Shrub, V = Vine, IS = Invasive shrub, PT = Pioneer Shrub, UT = Understory Tree) and (b) plant families (C = Conifer, F = Fabaceae, Mo = Moraceae, P = Proteaceae, S = Sapindaceae, E = Euphorbiaceae, L = Lauraceae, My = Myrtaceae, R = Rutaceae). Relationship between (c) growth form burn time and leaf dry matter content, and (d) family burn time and leaf dry matter content. Outliers < 400 °C were excluded from figures (a), (b), (c), and (d).

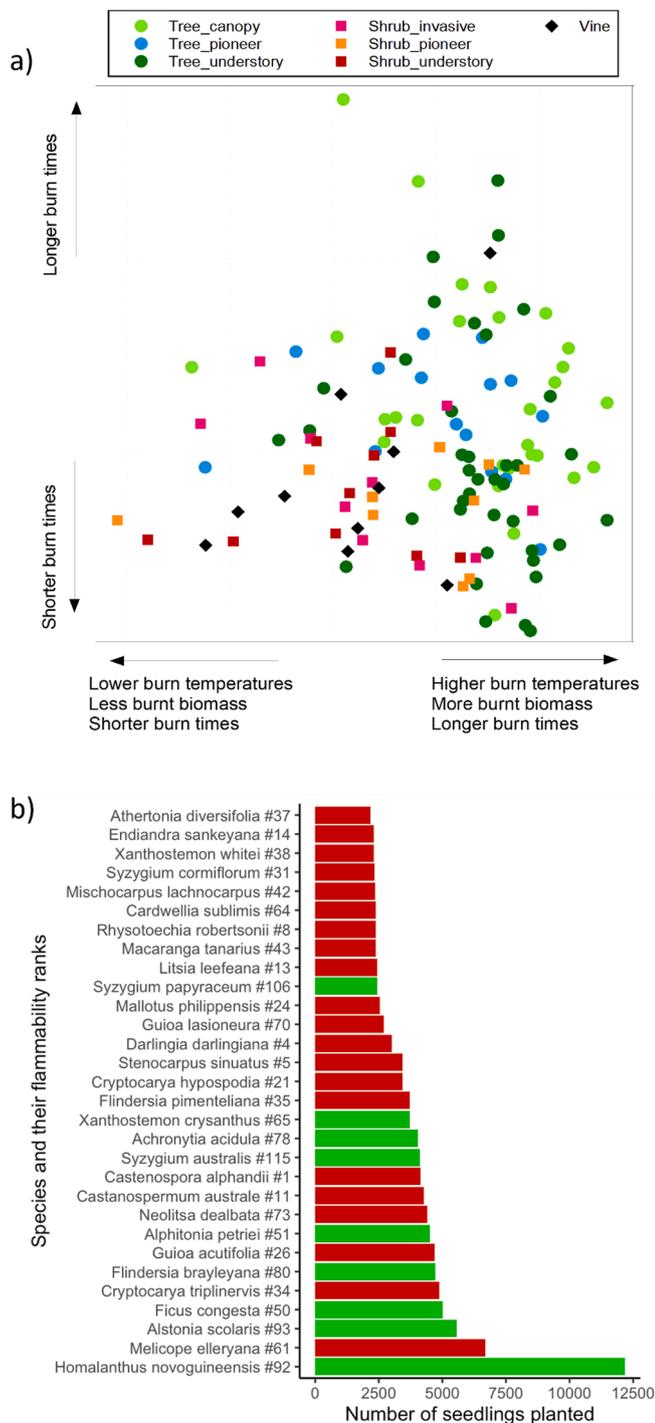


Fig. 5. (a) Two-dimensional ordination of 124 species showing how each growth form interacts with flammability components and (b) bar plot showing the top 30 most planted species in Wet Tropics Bioregion species from 2012 to 2017, alongside that species' flammability ranking found in this study (represented by the # notation). Red colouration represents the species that are high in flammability and green bars represents those low in flammability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

assessed the top 30 most planted species in Australian Wet Tropics restoration projects against our species flammability ranks (Fig. 5b). *Homalanthus novoguineensis* was the most planted species with 12,176 seedlings planted across 375 sites and was ranked 92/124 in flammability, suggesting a lower-than-average flammability (Fig. 5b). Alternatively, *Castanospora alphanthii* was the most flammable species (1/124 in

Table 1

Pearson correlations of flammability measures and growth forms with ordination axes.

Measure	Axis 1	Axis 2
Burnt biomass	0.485**	0.027(NS)
Burn time	0.432**	0.292*
Maximum temperature	0.977**	-0.106 (NS)
<u>Second matrix</u>		
Growth form	0.196 (NS)	0.058 (NS)

Bonferroni-corrected $\alpha = 0.0125$ **P < 0.00001, *P < 0.001.

flammability ranking; Fig. 5b) and was the 11th most planted species in the Wet Tropics with 4152 individuals planted across 237 sites.

4. Discussion

In a shoot flammability study of rainforest plants, we found significant differences between plant growth forms and among common rainforest families. In particular, shoots of trees were more flammable than vines and shrubs—including even invasive shrubs. Additionally, shoots of Sapindaceae, Lauraceae, Fabaceae, and Proteaceae were notably more flammable than Moraceae. In terms of the functional trait drivers of shoot flammability, we observed that leaf dry matter content significantly influenced all three flammability measures for both growth forms and families. Leaf mass per area significantly influenced burn time among growth forms but not common families whereas shoot moisture loss in the 24 h prior to burning had no significant effect on any of the flammability measures.

In similar experimental studies from temperate ecosystems trees have been found to have a lower flammability than shrubs, forbs and grasses (Burger and Bond 2015) or have a similar flammability to shrubs (Cui et al. 2020). One mechanism that may be influencing the higher flammability of trees compared to shrubs and vines in these rainforests is the effects of different environmental conditions on leaf traits and architecture that occur along the vertical forest profile. Rainforests experience steep gradients in temperature, solar radiation, humidity and wind from the canopy to the understory (Barker 1996, Anhuif and Rollenbeck 2001). For example, when temperatures are measured in Celsius, tree canopies may experience almost double the temperatures to which understory plants are exposed (Leahy et al. 2021). Despite the fact that all of our shoot samples were sunlit branches collected from the understory, we expect that trees have adapted to the relatively harsher environmental conditions of rainforest canopies by having leaves that are denser, tougher or thicker and as a consequence they often have higher levels of leaf dry matter content (Cornelissen et al. 2003).

We found that leaf dry matter content was positively correlated with shoot flammability in rainforest plants. Species with higher leaf dry matter content often have higher flammability (Pérez-Harguindeguy et al. 2013, Alam et al. 2020), with other factors such as leaf drying rate, branch architecture and leaf surface-to-volume ratio also found to affect flammability (Pérez-Harguindeguy et al. 2013). Our study's measure of shoot drying rate (shoot-moisture loss in the 24-hour-period prior to burning) did not correlate with flammability, although we did note that thinner leaves on pioneer trees did visibly wilt overnight whereas the thicker leaves on fig species (Moraceae) did not. Shoot moisture loss was included in this study because the leaves of rainforest species are relatively thin and may lose moisture at higher rates than sclerophyll species. Hence, this variable might be associated with higher flammability through greater ignitability and longer burn times.

We were surprised to discover that, as a group, the shoots of invasive shrubs were not highly flammable compared to other growth forms; a finding contrary to other studies and popular opinion among land managers (Msweli et al. 2020). For example, a comparison of the flammability of plant species in coastal South Africa found that the flammability of invasive species exceeded that of fynbos and thicket

shrublands (Msweli et al. 2020). Similarly, among 60 plant species examined in New Zealand the exotic shrub species *Ulex europaeus* ranked the highest in terms of flammability (Wyse et al. 2016), though other exotic species had low flammability. In our study, the shoots for most invasive shrubs only lost < 50 % of their biomass and on average burned for only 30 s. One exception was wild tobacco (*Solanum mauritianum*), otherwise known as kerosene plant, which ranked among our highest species in terms of maximum temperature when burning. The disparity between our study's results and land managers' observations may be due to other factors that contribute to fire spread and intensity, such the quantity of woody plant biomass and the location of that biomass with respect to surface fires. For example, scrambling invasive shrubs like *Lantana camara* (Ranking 97/124 in this study and being low in flammability) often produce dense thickets in dry rainforest or degraded forest areas (Fensham et al. 1994, Berry et al. 2011). These thickets are made up of many fine branches of light wood that are close to the ground compared to trees which support live biomass high up in the canopy, where it is normally inaccessible to ground fires (Berry et al. 2011).

Vine shoots ranked very low with respect to flammability. However, we think this is in part due to a limitation in the experimental approach. In most cases, a 70 cm-sample of vine had few branches and leaves were widely spaced, making fire propagation across the shoot less likely. Given the shoot architecture of vines and woody lianas, we think the 70 cm shoot length was inadequate and not representative of the long branching structure associated with this growth form. Woody lianas for instance, grow in large, dense clumps often associated with the high-light conditions of tree canopies whereas, vines like the *Piper* spp. grow on long thin branches, but with more succulent leaves associated with the shaded conditions of the forest interiors. It should also be noted, that while we found the fronds of the rattan species (*Calamus australis*) to be relatively low in flammability, the spines along the stems were very flammable, and when exposed to a flame, the rattan stem ignited and burned like a fuse. In such a case, the shoot flammability measurement may provide little information on the potential candlewick effect these species can have for transporting fire into rainforest canopies. Importantly with respect to fire fuel, rattans, unlike most other tropical rainforest plants, also retain dead leaves along their stem. Holding dead biomass in forest canopies and a stem that acts as a wick when burning suggests that this species could have an important role in carrying fires into rainforest canopies.

We also examined if the shoot traits that increase flammability of rainforest species were phylogenetically conserved, by testing the responses of 84 species from nine common families. We found species in Sapindaceae, Lauraceae, Fabaceae, and Proteaceae were highly flammable compared to moderate responses from Myrtaceae, low responses from Rutaceae and Euphorbiaceae, and very low for Moraceae. Interestingly, we found that conifers sustained the longest burn times but did not burn particularly hot nor thoroughly. We expected conifers, Myrtaceae and Rutaceae to be more flammable because they often contain resins, leaf oils, or aromatic volatiles (Popović et al. 2021). It has been demonstrated in temperate ecosystems that phylogeny, growth form and occurrence in fire-prone habitats influences shoot flammability (Burger and Bond 2015, Cui et al. 2020), with more flammable plants occurring in fire-prone ecosystems. In these fire-prone ecosystems, phylogenetically conserved plant traits may increase flammability and evolutionary fitness (Pausas et al., 2017), however in fire-sensitive ecosystems like rainforests, the traits associated with flammability are likely contemporaneous with responses to other abiotic and biotic drivers. For example, leaf defenses to avoid insect attack may result in an increase in the highly flammable lignin (Popović et al. 2021) or leaf chemicals such as terpenes (Sardans et al. 2015). We suggest future studies that consider these factors could provide a better understanding of the vulnerability of rainforest plants to fire.

The recovery of tropical rainforests via tree plantings and secondary forest regeneration are crucial to global aspirations for biodiversity conservation and carbon sequestration (Goosem and Tucker 1995,

Goosem et al. 2016, Engert et al. 2020). Our findings that many plant species used in restoration are highly flammable in our region has important implications to these programs. It signifies potential need for physical or green fire breaks (Curran et al. 2018). We recommend that in vulnerable landscapes the planting edges should avoid big timber species (and carbon sequestrers) in the families Sapindaceae, Proteaceae, Fabaceae, and Lauraceae or "edge closers" (e.g. acacias). Instead, where fire incursion is a clear threat, we would suggest the inclusion of low flammability species such as the figs in the Moraceae family. Tropical forests are becoming increasingly threatened by wildfires driven by climate and land-use pressures. Understanding how plants burn within these ecosystems is therefore imperative due to the environmental values these systems support.

Future climate and land use changes may increase the risk of wildfire incursions in rainforests, which is why understanding how plants burn within these ecosystems is imperative due to the environmental values these systems support. In this novel tropical rainforest flammability study, we have demonstrated that under experimental conditions rainforest trees and plant families Sapindaceae, Fabaceae, Lauraceae and Proteaceae are very high in flammability and that shrubs, vines and plant family Moraceae are quite low in flammability. Furthermore, we have shown that the functional trait leaf dry matter content influences shoot flammability and that leaf mass per area influences growth form burn times. We have also demonstrated that with rattan presence there is a potential fire wicking effect to the rainforest canopy that may occur. The outcomes of this research are valuable as they equip land managers with knowledge that can be applied when planning restoration projects. By using this information land managers will be able to plant green firebreaks comprised of native rainforest species to better mitigate the risks of future rainforest fire incursions.

CRedit authorship contribution statement

Ebony Potts: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **David Tng:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision. **Deborah Appaua:** Conceptualization, Methodology, Writing – review & editing. **Timothy J. Curran:** Conceptualization, Methodology, Writing – review & editing. **Jayden Engert:** Investigation, Data curation. **Susan G. W. Laurance:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We would like to thank Skyrail Rainforest Foundation and Ecological Society of Australia's 2021 Applied Forest Ecology award for funding this project. We would also like to thank The School for Field Studies, Yungaburra for hosting the project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120485>.

References

- Alam, M.A., Wyse, S.V., Buckley, H.L., Perry, G.L.W., Sullivan, J.J., Mason, N.W.H., Buxton, R., Richardson, S.J., Curran, T.J., Gilliam, F., 2020. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *J. Ecol.* 108 (2), 641–653.
- Anhuf, D., Rollenbeck, R., 2001. Canopy structure of the Rio Surumoni rain forest (Venezuela) and its influence on microclimate. *Ecotropica* 7 (1–2), 21–32.
- Barker, M.G., 1996. Vertical profiles in Brunei rainforest: I. microclimate associated with a canopy tree. *J. Trop. For. Sci.* 8 (4), 505–519. <http://www.jstor.org/stable/43582174>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Berry, Z.C., Wevill, K., Curran, T.J., 2011. The invasive weed *Lantana camara* increases fire risk in dry rainforest by altering fuel beds. *Weed Res.* 51 (5), 525–533. <https://doi.org/10.1111/j.1365-3180.2011.00869.x>.
- Bowman, K.W., 2020. Historic rainforest fires threaten climate and raise risk of new diseases. Retrieved from <https://theconversation.com/historic-amazon-rainforest-fires-threaten-climate-and-raise-risk-of-new-diseases-146720>.
- Briant, G., Gond, V., Laurance, S.G.W., 2010. Habitat fragmentation and the desiccation of forest canopies: a case study from eastern Amazonia. *Biol. Conserv.* 143 (11), 2763–2769. <https://doi.org/10.1016/j.biocon.2010.07.024>.
- Buis, A. (2019). A degree of concern: Why global temperature matter. Retrieved from <https://climate.nasa.gov/news/2865/a-degree-of-concern-why-global-temperatures-matter/>.
- Bureau of Meteorology, 2021. Climate statistics. Retrieved from http://www.bom.gov.au/climate/averages/tables/cw_031193_All.shtml.
- Burger, N., Bond, W.J., 2015. Flammability traits of Cape shrubland species with different post-fire recruitment strategies. *S. Afr. J. Bot.* 101, 40–48. <https://doi.org/10.1016/j.sajb.2015.05.026>.
- Bush, M. B., Flenley, J. R., & Gosling, W. D. (2011). *Tropical Rainforest Responses to Climatic Change (Second Edition)* (2nd ed.). Springer Heidelberg Dordrecht. <https://doi.org/10.1007/978-3-642-05383-2>.
- Cal fire. (2021). Stats and events. Retrieved from <https://www.fire.ca.gov/stats-events/>.
- Calitz, W., Potts, A.J., Cowling, R.M., 2015. Investigating species-level flammability across five biomes in the Eastern Cape, South Africa. *S. Afr. J. Bot.* 101, 32–39. <https://doi.org/10.1016/j.sajb.2015.07.005>.
- Cochrane, M.A., 2009. *Tropical Fire Ecology. Climate Change, Land Use, and Ecosystem Dynamics*. Springer International Publishing.
- Cochrane, M. A., & Laurance, W. F., (2008). Synergisms among Fire, Land Use, and Climate Change in the Amazon. *Ambio*, 37(7/8). 522-527. <https://www.jstor.org/stable/25547943>.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurrich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., Van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51 (4), 335–380. <https://doi.org/10.1071/BT02124>.
- Croat, T.B., 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford USA.
- Cui, X., Paterson, A.M., Alam, M.A., Wyse, S., Marshall, K., Perry, G.L.W., Curran, T.J., 2020a. Shoot-level flammability across the Dracophyllum (Ericaceae) phylogeny: evidence for flammability being an emergent property in a land with little fire. *New Phytol.* 228 (1), 95–105. <https://doi.org/10.1111/nph.16651>.
- Cui, X., Paterson, A.M., Wyse, S.V., Alam, M.A., Maurin, K.J.L., Pieper, R., Padullés Cubino, J., O'Connell, D.M., Donkers, D., Bréda, J., Buckley, H.L., Perry, G.L.W., Curran, T.J., 2020b. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nat. Plants* 6 (4), 355–359.
- Curran, T.J., Perry, G.L., Wyse, S.V., Alam, M.A., 2018. Managing fire and biodiversity in the wildland-urban interface: a role for green firebreaks. *Fire* 1 (1), 1–3. <https://doi.org/10.3390/fire1010003>.
- Engert, J.E., Vogado, N.O., Freebody, K., Byrne, B., Murphy, J., Sheather, G., Snodgrass, P., Nugent, L., Lloyd, D., Laurance, S.G.W., 2020. Functional trait representation differs between restoration plantings and mature tropical rainforest. *For. Ecol. Manage.* 473, 118304.
- Fensham, R.J., Fairfax, R.J., Cannell, R.J., 1994. The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, north Queensland. *Aust. J. Ecol.* 19 (3), 297–305. <https://doi.org/10.1111/j.1442-9993.1994.tb00493.x>.
- Gallagher, R.V., Allen, S., Mackenzie, B.D.E., Yates, C.J., Gosper, C.R., Keith, D.A., Merow, C., White, M.D., Wenk, E., Maitner, B.S., He, K., Adams, V.M., Auld, T.D., Nimmo, D., 2021. High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. *Divers. Distrib.* 27 (7), 1166–1179.
- Ganteaume, A., 2018. Does plant flammability differ between leaf and litter bed scale? Role of fuel characteristics and consequences for flammability assessment. *International Journal of Wildland Fire* 27 (5), 342–352. <https://doi.org/10.1071/WF17001>.
- Goldammer, J.G., 1990. *Fire in Tropical Biota: Ecosystem Processes and Global Challenges*. Springer-Verlag, New York.
- Goosem, M., Paz, C., Fensham, R., Preece, N., Goosem, S., Laurance, S.G.W., Zobel, M., 2016. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. *J. Veg. Sci.* 27 (3), 504–514.
- Goosem, S., Tucker, N.I.J., 2013. *Repairing the Rainforest*, second edition. Wet Tropics Management Authority and Biotropica Australia Pty. Ltd., Cairns. <https://www.wettropics.gov.au/flipbook/files/inc/73edf6105e.pdf>.
- Goss, M., Swain, D.L., Abatzoglou, J.T., Sarhadi, A., Kolden, C.A., Williams, A.P., Diffenbaugh, N.S., 2020. Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. *Environ. Res. Lett.* 15 (9), 094016.
- Jaureguiberry, P., Bertone, G., Díaz, S., 2011. Device for the standard measurement of shoot flammability in the field. *Austral Ecol.* 36 (7), 821–829. <https://doi.org/10.1111/j.1442-9993.2010.02222.x>.
- Jolly, W.M., Cochrane, M.A., Freeborn, P.H., Holden, Z.A., Brown, T.J., Williamson, G.J., Bowman, D.M.J.S., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat. Commun.* 6 (5), 1–11. <https://doi.org/10.1038/ncomms8537>.
- Leahy, L., Scheffers, B.R., Andersen, A.N., Hirsch, B.T., Williams, S.E., Barnes, A., 2021. Vertical niche and elevation range size in tropical ants: Implications for climate resilience. *Divers. Distrib.* 27 (3), 485–496.
- Lenth, R. V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.3. Retrieved from <https://CRAN.R-project.org/package=emmeans>.
- McCune, B., & Mefford, M. J. (2011). PC-ORD. Multivariate analysis of ecological data. Glendened Beach, Oregon: MjM Software. Retrieved from [https://www.scrip.org/\(S\(i43dyn45teexjx455qit3d2q\)\)/reference/ReferencesPapers.aspx?ReferenceID=493849](https://www.scrip.org/(S(i43dyn45teexjx455qit3d2q))/reference/ReferencesPapers.aspx?ReferenceID=493849).
- Msweli, S.T., Potts, A.J., Fritz, H., Kraaij, T., 2020. Fire weather effects on flammability of indigenous and invasive alien plants in coastal fynbos and thicket shrublands (Cape Floristic Region). *PeerJ* 8, 1–18. <https://doi.org/10.7717/peerj.10161>.
- Nasa NASA. (2021). Fire consumes large swaths of Greece. Retrieved from <https://earthobservatory.nasa.gov/images/148682/fire-consumes-large-swaths-of-greece>.
- Padullés Cubino, J., Buckley, H.L., Day, N.J., Pieper, R., Curran, T.J., 2018. Community-level flammability declines over 25 years of plant invasion in grasslands. *J. Ecol.* 106 (4), 1582–1594. <https://doi.org/10.1111/1365-2745.12933>.
- Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? A review. *International Journal of Wildland Fire* 17 (6), 713–723. <https://doi.org/10.1071/WF07151>.
- Pausas, J.G., Keeley, J.E., Schwilk, D.W., Rees, M., 2017. Flammability as an ecological and evolutionary driver. *J. Ecol.* 105 (2), 289–297.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurrich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Cornelissen, J.H.C., 2016. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 64 (8), 715. <https://doi.org/10.1071/bt12225.co>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. (2021). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-152. Retrieved from <https://CRAN.R-project.org/package=nlme>.
- Popović, Z., Bojović, S., Marković, M., Čerđić, A., 2021. Tree species flammability based on plant traits: A synthesis. *Sci. Total Environ.* 800, 149625.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>.
- Riberio, J.E., Hopkins, M.J., Vicentini, A., Sothers, C., Costa, M.A., Brito, J., de Souza, A. A., Martins, L.H., Lohmann, L., Assuncao, P., Pereira, E., Silva, A., Mesquita, M., Procopio, L., 1999. *Flora of Reserva Ducke, INPA/DFID*. Midas Printing, Brazil.
- Sardans, J., Llusa, J., Owen, S., Niinemets, U., Penuelas, J., 2015. Screening Study of Leaf Terpene Concentration of 75 Borneo Rainforest Plant Species: Relationships with Leaf Elemental Concentrations and Morphology. *Rec. Nat. Prod.* 9 (1), 19–40.
- Schwilk, D.W., 2015. Dimensions of plant flammability. *New Phytol.* 206 (2), 486–488. <https://doi.org/10.1111/nph.13372>.
- Shlisky, A., Waugh, J., Gonzalez, P., Gonzalez, M., Manta, M., Santos, H., Alvarado, E., Ainuddin Nuruddin, A., Rodriguez-Trejo, D.A., R. Swaty, Swaty, R., Schmidt, D., Kaufmann, M., Myers, R., Alencar, A., Kearns, F., Johnson, D., Smith, J., & Zollner, D. (2007). *Fire, Ecosystems and People: Threats and Strategies for Global Biodiversity Conservation*. Global Fire Initiative Technical Report 2007-2. The Nature Conservancy. Arlington, VA.
- Tang, R., Mao, J., Jin, M., Chen, A., Yu, Y., Shi, X., Zhang, Y., Hoffman, F.M., Xu, M., Wang, Y., 2021. Interannual variability and climatic sensitivity of global wildfire activity. *Adv. Clim. Change Res.* 12 (5), 686–695. <https://doi.org/10.1016/j.accre.2021.07.001>.
- Uhl, C., Kauffman, J.B., 1990. Deforestation, Fire Susceptibility, and Potential Tree Responses to Fire in the Eastern. *Ecology* 71 (2), 437–449. <https://doi.org/10.2307/1940299>.
- Wang, H.H., Finney, M.A., Song, Z.L., Wang, Z.S., Li, X.C., 2021. Ecological techniques for wildfire mitigation: Two distinct fuelbreak approaches and their fusion. *For. Ecol. Manage.* 495 (5), 119376 <https://doi.org/10.1016/j.foreco.2021.119376>.
- Wyse, S., Perry, G.L.W., O'Connell, D.M., Holland, P.S., Wright, M.J., Hosted, C.L., Whitelock, S.L., Geary, L.J., Maurin, K.J.L., Curran, T.J., 2016. A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. *International Journal of Wildland Fire* 25 (4), 466–477. <https://doi.org/10.1071/WF15047>.
- Wyse, S., Perry, G.L.W., Curran, T.J., 2018. Shoot-Level Flammability of Species Mixtures is Driven by the Most Flammable Species: Implications for Vegetation-Fire Feedbacks Favouring Invasive Species. *Ecosystems* 21 (5), 886–900. <https://doi.org/10.1007/s10021-017-0195-z>.