



Tree species flammability based on plant traits: A synthesis

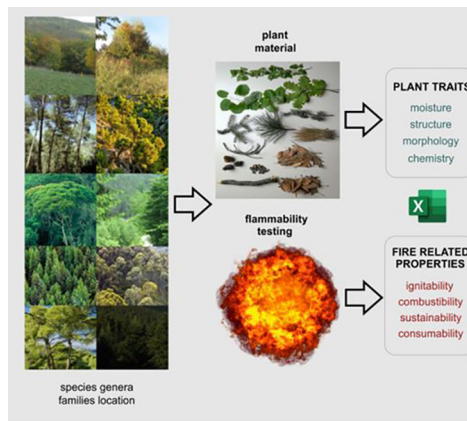
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HIGHLIGHTS

- Trait-based flammability studies yield scientific knowledge with wide applicability.
- Relevant plant traits determine the flammability-related differences between species.
- Environment-traits-flammability linkage by collecting more empirical data is needed.

GRAPHICAL ABSTRACT



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ABSTRACT

The occurrence of large and recurring forest fires has long been associated with fire-prone environments, but this perception has been shifted rapidly in recent decades as Earths' landscapes have become increasingly threatened by severe and unpredictable fires as a result of climate changes. In this regard, the flammability of trees is a topic of great interest for ecology, management, and the development of sustainable restoration and rehabilitation plans. Tree species differ in regard to flammability, and many plant functional traits contribute to flammability at species, community and vegetation level. The relationship between plant traits and flammability at species level is important for a broader understanding of the vegetation-fire dynamic at the local and landscape scales. This review summarizes the current state of knowledge regarding the impact of individual plant traits of tree species on flammability components. By keywords-based searching of academic databases, 85 research papers were collected and analyzed. The literature synthesis shows: i) main issues addressed in studies on plant trait-based tree flammability, ii) general research output and biogeographic regions studied, iii) inventory of tree taxa investigated, iv) relationships between plant traits and flammability components, v) the most relevant plant traits that determine the flammability-related differences between species.
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1. Introduction

Global climate change, landscape fragmentation, pollution, biological invasions, pest outbreaks, and wildfires, which are one of the most significant disturbances to the natural environment, all pose threats to forest ecosystems. Fire is an integral part of Earth System dynamics that had shaped ecosystems and affected their evolution since vegetation inhabited the land (Nichols and Jones, 1992; Falcon-Lang, 2000). Human impacts on fire dynamics are a widespread phenomenon (Pyne, 1997), considering the deep-rooted link between mankind and fire that dates back to the Holocene (Ohlson and Tryterud, 2000; Gavin et al., 2006; Jiang et al., 2008). Natural fire occurrence within a range of biomes that support a fire activity with substantial biomass and climate conditions is constantly being reshaped by a variety of anthropogenic-caused disturbances, ranging from land use and pollution to climate changes (Flannigan et al., 2000; Flannigan et al., 2009). Bond et al. (2005) suggested that the fire regime, not only climate distribution, determines the distribution and ecological features of several of the world's major biomes. Fires are a common and expected feature of the world's grasslands, savannas, Mediterranean shrublands and forests, as well as boreal forests (Archibold, 1995) and are considered to be a secondary control measure of vegetation distribution (Goldammer, 1993). According to Chapin et al. (2002), fire-prone vegetal associations cover 40% of the world's land surface. Fires decrease plant biomass by reducing aboveground plant parts (Costa et al., 2014; Vernes et al., 2004), resulting in the replacement of trees with shrublands or grasslands depending on the frequency and intensity of the fire (Slik et al., 2008; Barlow et al., 2003; Ryan and Williams, 2011). These processes can alter the distribution of flammable ecosystems beyond the physiognomic limitations determined by climate (Chapin et al., 2003; Bond et al., 2005; Pyne, 2019). The following direct and indirect evidence suggest that fire may be the primary factor in determining biomass distribution, supporting flammable ecosystems in forests-promoting climatic conditions (Bond et al., 2005): (i) patchy forest areas commonly occur in many landscapes dominated by fire-prone grasslands and shrublands, indicating a misalignment between climate and vegetation; (ii) experimenting with fire exclusion has frequently resulted in biome shifts from flammable formations to forested ecosystems; (iii) introducing anthropogenic fires to island ecosystems has resulted in the conversion of forests to flammable shrublands and grasslands; (iv) plantation forestry and the invasion of non-native trees into flammable grasslands and shrublands demonstrate that tree biomass in these ecosystems exceeds the climate-imposed limit.

Large trees account for about half of the world's mature forest biomass (Lutz et al., 2018), and their long lifespan is enabled with a variety of biophysical and ecophysiological traits that contribute to the capacity to adjust to both short-term seasonal changes and longer-scale climatic changes (Kelleher, 2018). Tree species distribution, interspecific interactions, forest community composition and spatiotemporal dynamics, as well as the response to various environmental disturbances such as wildfire, are all determined by a multitude of plant traits (Bond et al., 2005). Trade-offs between plant physiological adaptations to fire regimes, environmental pressures, and plant metabolic demands result in the development of fire response traits (de Dios, 2020). It is well established that tree flammability varies between and within species,

and that plant traits affect flammability and fire behavior (Dimitrakopoulos and Papaioannou, 2001; Kane et al., 2008; Engber and Varner, 2012; Wyse et al., 2016) and determine general plant flammability-related strategies in fire-prone ecosystems (Bond and Midgley, 1995; Pausas et al., 2017; Cui et al., 2020). Plant traits that contribute to species flammability are genetically determined, but they can be considerably modified by environmental and biotic factors (Rowe and Speck, 2005) and vary depending on tree size and forest succession (Babl et al., 2020). Overall fire behavior of plants can be altered by environmentally responsive changes in plant traits (Blackhall et al., 2012; Jolly et al., 2012; Page et al., 2012; Jolly et al., 2016; Page et al., 2014; Krix and Murray, 2018; Della Rocca et al., 2020; Michelaki et al., 2020).

According to commonly accepted definitions of flammability (capacity of plant biomass to burn), the process comprises four components: ignitability (the ability of a material to ignite); sustainability (the ability of a material to sustain combustion and produce energy); combustibility (the rate at which a substance burns into flame); and consumability (the proportion of biomass consumed during combustion) (Anderson, 1970; Martin et al., 1993; White and Zipperer, 2010). Flammability is determined by traits expressed at various biological and ecological levels (organ, species, population, community), and fire affects trait divergence, fire adaptations, and species persistence in fire-prone ecosystems (Pausas and Moreira, 2012). A review of the literature on the flammability of forest and woodland litter suggested that existing knowledge be better integrated with databases on plant traits (Varner et al., 2015). Species flammability is important for autecological and synecological considerations since it has been recognized as a function of the environment (Gill and Zylstra, 2005; Xanthopoulos et al., 2012). Generally, data on species flammability has been generated using species mean values from trait-based studies. However, without consideration of species-species interactions, habitat resource availability, between-species niche and trait overlap, and intraspecific trait variation, the predictive potential of mean-values-based data at the community and ecosystem scales is limited (Violle et al., 2012). Furthermore, the consistency of functional trait covariation from the individual to the ecosystem level, as well as the upscaling of trait-flammability relationships, is still poorly documented (Pausas, 2017; Alam et al., 2020).

Studies linking the plant traits to flammability components are important for better understanding fire-related ecological processes and provide information useful in restoration and reforestation programs. As models suggest that climate change will lead to more and more extreme fire events worldwide (Moritz et al., 2012), a synthesis of scientific evidence on this topic from various biogeographic regions can contribute to better understand fire-vegetation dynamics and expand this approach in fire-risk predictions. The purpose of this review was to identify and summarize studies that evaluated the relationships between plant traits and flammability of tree taxa with over-viewing the potential applications of knowledge on this topic.

2. Literature search and extraction of knowledge

This review of studies on tree species flammability related to plant traits has included all original research papers published on this topic in peer-reviewed scientific literature up to December 2020. The literature search was performed using the Scopus database (additional

search included the Web of Science and Google Scholar), with key words presented in the Title, Abstract and Keywords. The following queries were used: “flammability”, “forest”, “tree”, “species”, “trait”, “leaf”, “needle”, “bark” and “litter”. Papers were used to assess whether they provide the necessary information: biogeographical data, species taxonomic identification, and clear statement that research was aimed at the evaluation of the linkage between species' structural, physical, chemical, or ecophysiological traits and flammability. For this review we chose to focus on tree species, following the [FAO \(2005\)](#) definition of a tree, and to restrict to the medium-sized and large trees (meso- and megaphanerophytes sensu [Raunkiaer \(1934\)](#)). The nomenclature is confirmed according to The Plant List database (<http://www.theplantlist.org>). After compiling a database of 85 articles, the following parameters were extracted from publications: (i) bibliometric data, (ii) species investigated, (iii) plant material used for flammability testing, (iv) plant traits associated with flammability, (v) flammability testing method, (vi) flammability components measured, (vii) impact of a plant trait to a flammability component, (viii) location where the study was conducted. In further analysis, we added to these data (ix) grouping of species by botanical criteria: family, leaf habit, and leaf longevity, (x) forest type based on the ecoregion attributed following the study site description (WWF Terrestrial Ecoregions categories) (<https://www.worldwildlife.org>).

A database obtained provided sufficient information to assess the effect of specific plant traits on different flammability components. The effects of plant traits were categorized as either positive or negative, based on reported correlations between traits and flammability components. A trait with a neutral effect is described as one that did not affect a flammability component, or its effect showed high inter-species variability. All figures were produced in RStudio 1.3.1093.

3. The main issues addressed in studies on plant-trait-based tree flammability

The majority of studies aimed to assess the impact of plant traits on flammability components, in order to empirically rank trees from low to high flammable species. Most of the research findings contribute to science-based fire management by enhancing understanding of species fire behavior and promoting species selection for adequate forest management ([Núñez-Regueira et al., 1999](#); [Dimitrakopoulos and Papaioannou, 2001](#); [Xiaorui et al., 2001](#); [Bianchi et al., 2019](#); [Rasooli et al., 2021](#)). The risk of fire in the wildland-urban interface (WUI) area is a major concern in fire policy and this transitional zone is crucial for strategic vegetation planning. Plant-trait-based flammability approaches have been shown to provide relevant information on wildland fire behavior that can be implemented at the wildland-urban interface ([Simeoni et al., 2012](#); [Ganteaume, 2018](#)) and particularly for species selection for green firebreaks ([Krix et al., 2019](#)). Few studies have emphasized the importance of identifying the fire-sensitive species in WUI fire management ([Romero et al., 2019](#)) and establishing effective buffer zones based on suitable varieties ([Della Rocca et al., 2015](#)). A study of roadside vegetation indicated that trait-based flammability can be a useful component of road projects for fire spreading prevention ([Molina et al., 2019](#)). Differences in shoot-level flammability of a variety of indigenous and exotic plants revealed that some invasive species are highly flammable and increase the fire risk in the community, which is an important finding for fire managers to assess potential fire risk in landscapes ([Wyse et al., 2016](#)).

Few studies have investigated the decomposability and flammability of surface litter from a variety of tree species, providing data on carbon and nutrient fluxes that can be used to predict litter accumulation and model ecosystem processes ([Grootemaat et al., 2015](#); [Grootemaat et al., 2017a](#)). Study by [Wang et al. \(2009\)](#) developed a prediction model for plant flammability using species trait-based flammability variables which are significantly correlated with one another, suggesting that certain properties can be predicted from other known properties given their quantitative expressions.

Several studies focused on ecological conservation and restoration as a research objective. It has been demonstrated that the increasing presence of fire-facilitating species may alter the fire regime and endanger rare species in previously fire-safe habitats ([Mola et al., 2014](#)). In other cases, the extinction of a species with highly flammable litter resulted in the suppression of fire events and an increase in the abundance of mesophytic species ([Kane et al., 2019](#)). The fire suppression can result in a decrease in diversity and thus the suppression of fire-prone species ([Fournier et al., 2020](#)). Estimating forest floor moisture dynamics and species flammability in fire-excluded mesophytic forest communities is crucial for restoring understory diversity and ecosystem functions ([Kreye et al., 2018](#)). Differences in plant traits between species result in the production of charred litters with different degrees of aromatization/carbonization, which has a direct impact on soil properties and conservation ([Merino et al., 2015](#)). A study confirmed a wide range of trait-based flammability among phylogenetic groups, pointing to an evolutionary role of fire-suppressing traits ([Cornwell et al., 2015](#)). The trait-based flammability approach has also been shown to be appropriate for understanding the paleoecological impact of paleofires ([Belcher, 2016](#)).

Studies on the flammability of plant material derived from individual species and multiple-species mixtures revealed that the community composition is a crucial factor for fire dynamics in mixed forests ([de Magalhães and Schwilk, 2012](#); [Zhao et al., 2016](#); [Wyse et al., 2018](#)). The effect of the live foliage of different species on the flammability of mixtures is contrasting and non-additive ([Della Rocca et al., 2018](#)), and similar findings are reported for leaf and leaf-twig mixtures in the litter ([de Magalhães and Schwilk, 2012](#); [Zhao et al., 2019](#)). Plant-trait-related flammability testing of diverse species in the plant community has identified species that could increase the vulnerability of cork oak forests ([Dehane et al., 2017](#)) or those that could increase the spread of bushfires in dry sclerophyll forest ([Murray et al., 2013](#)). Pine species' susceptibility to different fire regimes can affect post-fire seedling survival ([Dewhurst et al., 2020](#)). Some studies combined a single species fire resistance score with community-weighted averaging to evaluate the fire resistance scores of different forest communities at a large regional scale, thereby contributing to a better understanding of ecosystem disturbance and community resistance ([Stevens et al., 2020](#)).

Given the variability of environmental conditions at the landscape scale, some studies attempted to link trait-based flammability to different forest habitats, weather conditions, or biotic pressures. It was shown that the variability of leaf flammability is related to the response of leaf traits to environmental variables ([Dickinson and Kirkpatrick, 1985](#); [Bianchi and Defossé, 2015](#); [Kauf et al., 2015](#); [Jolly et al., 2016](#); [Krix and Murray, 2018](#)) or site fire history ([Saura-Mas et al., 2010](#); [Blackhall et al., 2012](#); [Blackhall et al., 2017](#)). An experiment conducted under different watering regimes contributed to a better understanding of the relationship between environmental conditions, plant traits, and trait-related flammability ([Alessio et al., 2008a](#)), and it was implied that drought conditions may impact the flammability of some shrubland and forest species ([Alessio et al., 2008b](#)). Several studies reported that the flammability of trees can be significantly increased in diseased specimens ([Della Rocca et al., 2020](#)) and beetle-attacked trees ([Jolly et al., 2012](#); [Page et al., 2012](#); [Page et al., 2014](#)), whereas data related to altered flammability under grazing pressure were inconsistent ([Blackhall et al., 2012](#)). [Michelaki et al. \(2020\)](#) found that species with distinct resource-use strategies growing along environmental gradients have alternative leaf flammability syndromes with different ecological impacts that enhance their survival or reproduction in fire-prone areas.

The assessment of flammability was evaluated through the comparison of various approaches and methods. For instance, [Santacruz-García et al. \(2019\)](#) compared plant flammability assessments using two approaches (functional trait analysis and shoot-level device). To develop experimental models, some studies used a different number of samples ([Shan et al., 2008](#)) or different flammability testing devices ([Haurie et al., 2019](#)), while others proposed novel flammability classification

to include fuels with a high content of volatile flammable compounds (Essaghi et al., 2017). The combination of two different bench-scale devices (moisture analyzer and mass loss calorimeter or cone calorimeter) was used in an appropriate configuration for forest fuel to develop a new method for evaluating the flammability of live plant material (Madrigal et al., 2013). Several articles addressed the use of the cone calorimeter and the need to establish adequate protocols for obtaining comparable results (Weise et al., 2005; Dehane et al., 2015; Ramadhan et al., 2021). It has been reported that material with very low ignition frequency under certain testing conditions can be extremely flammable if testing conditions are slightly changed (Kauf et al., 2014). A study confirmed that some leaf litter beds can considerably lose previously established relationships between morphological traits and fire behavior after the 30-days exposure to outdoor winter conditions (Kauf et al., 2018).

A smaller number of studies were based on the one-species approach, providing results that can be applied in forest-fire modeling. It was shown that the effective heat of combustion is a function of moisture content in Douglas fir (Babrauskas, 2006) and that Douglas-fir trees do not produce firebrands if the moisture content is higher than 30% (Manzello et al., 2007). Similarly, the moisture content determined the flammability of live and dead Aleppo pine needles, with fresh live needles igniting about four times slower, and burning with much lower power and lower heat of combustion than dead needles (Jervis and Rein, 2016).

4. Global research output and locations of field studies

A total of 85 articles found to match the search criteria were published in academic journals from diverse subject categories. The most significant areas were Forestry, Ecology, Materials Science, Energy, and Chemistry. The International Journal of Wildfire research was considered as a leading journal in publishing articles on this topic (16 papers), followed by Forest Ecology and Management and Fire Safety Journal (6 and 5 papers, respectively). The number of publications showed a growing trend over the years (positive correlation between years and the number of publications, with half of the articles published from 2016 to 2020 (Fig. 1). The distribution of papers per country of production (including collaborative papers) shows that Spain and the USA had the most publications on this topic (15 papers per country). France

(11), Greece (9), and Australia (8) considerably contributed, and Italy and Argentina (5) showed an interest in tree flammability based on plant traits (Fig. 1). A map of locations is provided in Fig. 2 to show the phytogeographic diversity of field studies. In total, 98 locations were mapped using coordinates from study site descriptions (57 papers). Locations without coordinates (28 papers) are not included.

Considering the similarity of some ecosystems and forest types across the earth, several ecoregions can be assembled into the four main forest types studied. The studies related to Mediterranean forest type account for 51% of the published papers, followed by temperate-forest type, the tropical- and subtropical-forest type, and the boreal-forest type (Fig. 3).

5. Tree species, plant trait approach and methods used in flammability testing

The effects of plant traits on the flammability of 276 species were investigated (Table 1). All species belong to 122 genera (the most studied species were from: Pinus 42, Quercus 29, Eucalyptus 15). Out of the total number of representatives per family (51 families), 51.3% of species were members of four plant families: Pinaceae (63 species), Fagaceae (36), Cupressaceae (23), and Myrtaceae (21), and the number of species investigated per family was reported in Fig. 4. In terms of the total number of species studied, evergreen species accounted for 60%, deciduous species 33%, and semi-deciduous 7%, and broadleaved species outnumbered conifers (61% and 39%, respectively). The share of species with different leaf longevity and leaf habit per forest type was shown in Fig. 5. Considering the number of species investigated per forest type, temperate forest type had the highest diversity of species (148 species), followed by tropical and subtropical (64), Mediterranean (59), and boreal forest type (31) (Fig. 5).

Leaves and litter were the most commonly used plant material for determining plant traits and flammability (58 and 23 papers, respectively), followed by bark, branches, mixed material, and wood (9, 9, 4, and 3, respectively). Results showed that three main types of plant traits are associated with different components of flammability: ecophysiological (moisture content), structural and morphological (morphometric features of leaves, litter, bark, and wood), and chemical (chemical composition, elemental content, volatile and nonvolatile compound contents of leaves, litter, and bark).

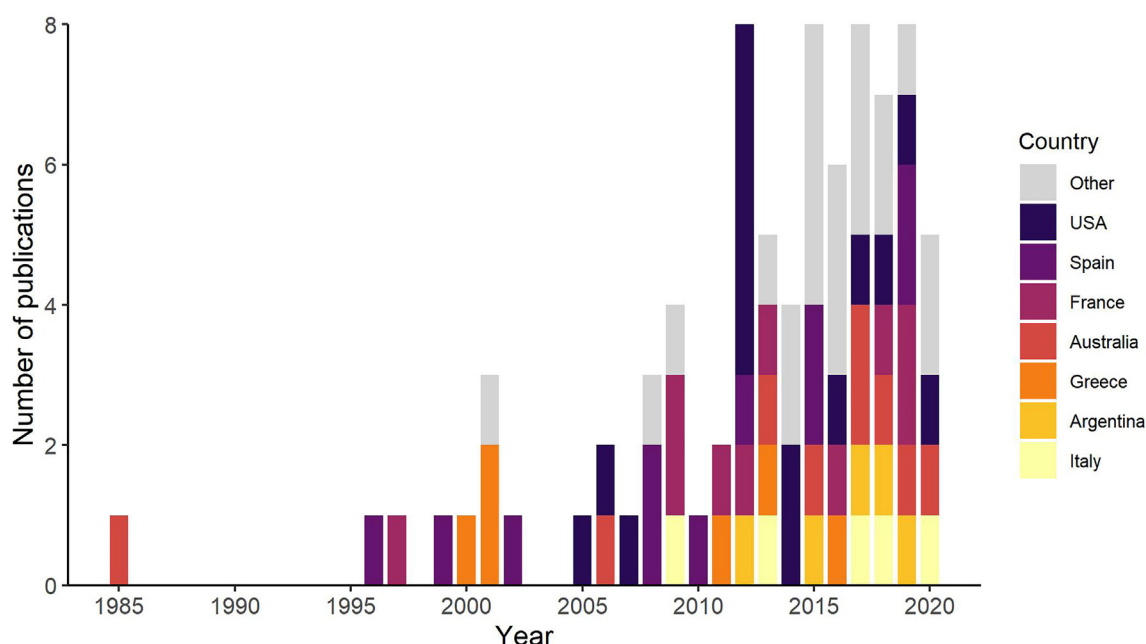


Fig. 1. Number of scientific articles on tree traits' based flammability published in academic journals grouped per country over the last 35 years.

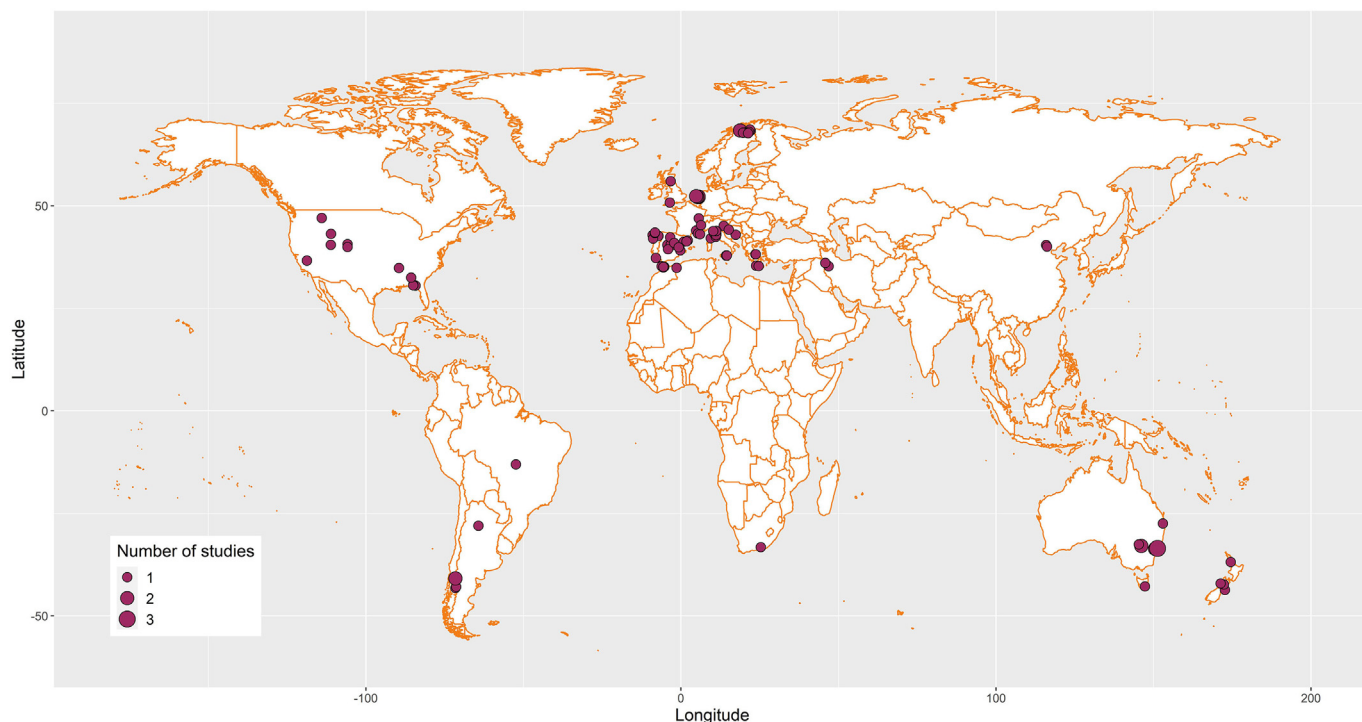


Fig. 2. Map of locations studied in 57 papers published in Academic journals since 1985 referring to tree traits' based flammability.

Most of the articles (78%) reported the effect of moisture content on species' flammability (in particular on ignitability). The FMC (fuel moisture content) of live or dead plant material, expressed on a dry-mass basis, was the relevant parameter. Of the total number of articles applying FMC measurements (58), 41% investigated a single effect of FMC on species flammability; the remaining articles reported on the combined effects of FMC and structural/morphological traits (33%), FMC and chemical traits (19%), FMC, chemical and structural/morphological traits (7%) on different components of flammability. Out of the total number of reviewed papers, 40 aimed to correlate structural and morphological traits of tree species with flammability components, and

the morpho-structural traits of leaves (56 species) and litter (47 species) were the most frequently determined. The relationship between flammability components and bark structure, wood structure, and morphology of branches was estimated for a smaller number of species (23, 10, and 4 species, respectively). The chemical traits of the leaves, bark, and litter of tree species (54, 11, and 8 species, respectively) were assessed in 22 papers using different analytical approaches (elemental analysis, gas chromatography, calorimetry, and spectrophotometry).

Experimental flammability tests were conducted in the laboratory by using different test devices: epiradiator (33%), designed burner devices (31%), calorimeters (19%), muffle furnace (6%), thermogravimetric analyzer (5%), ignition apparatus (4%), and combustion analyzer (2%). Four studies used a device designed for flammability measurements in the field, but the authors stated that the method is still laboratory-based rather than field-based, which should be considered when interpreting the results (Wyse et al., 2018). One study included information on both laboratory and field flammability testing (Molina et al., 2018). The most frequently determined flammability component was ignitability (time to ignition, critical heat flux, critical temperature, ignition frequency), and a large percentage of papers reported data for two or more flammability components. The wide range of methods used for flammability testing resulted in different evaluations of the same parameter, e.g. ignition timing was evaluated either visually or based on heat rate criteria.

6. Effects of plant traits on flammability components

The moisture content of both live and dead plant parts, expressed on a dry mass basis (FMC), was the most frequently reported flammability-related plant trait and was found to be directly related to flammability components (Table 2). The majority of studies found that higher FMC of leaves, twigs, terminal branches, litter, wood, and bark decreases biomass's ability to ignite, i.e. correlates positively with a prolonged ignition time and negatively with ignition frequency. FMC has been shown to have a negative effect on combustibility, sustainability, and consumability in a smaller number of papers, and few studies reported that FMC of plant material does not affect ignition.

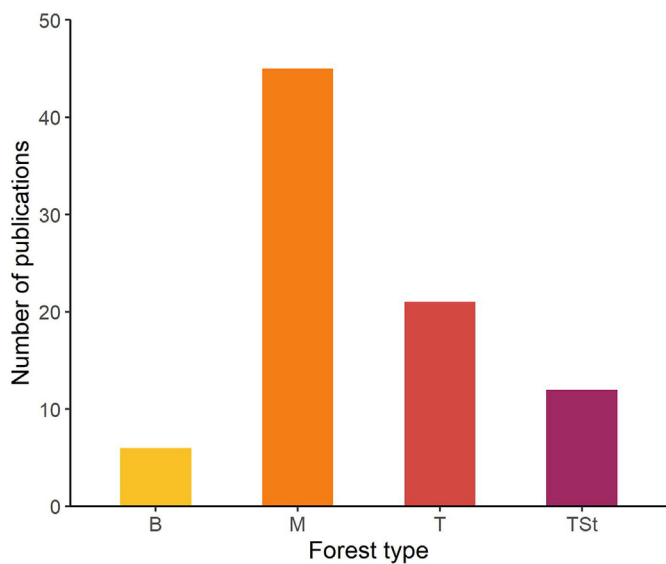


Fig. 3. The number of papers published in Academic journals since 1985 concerning tree traits' based flammability divided by forest type. B, boreal; M, Mediterranean; T, temperate; TSt, tropical and subtropical.

Table 1
List of species studied, plant traits associated with flammability and relevant publications.

Species	Plant trait associated with flammability	Reference
<i>Abies alba</i> Mill.	Bark structure, wood structure	Frejville et al. (2013)
<i>Abies amabilis</i> Douglas ex J.Forbes	Bark structure	Stevens et al. (2020)
<i>Abies cephalonica</i> Loudon	Foliage chemistry	Ntoufas et al. (2016)
<i>Abies concolor</i> (Gordon) Lindl. ex Hildebr.	Foliage morphology, bark structure	de Magalhães and Schwilk (2012); Belcher (2016); Stevens et al. (2020)
<i>Abies grandis</i> (Douglas ex D. Don) Lindley	Bark structure	Stevens et al. (2020)
<i>Abies lasiocarpa</i> (Hooker) Nuttall	Bark structure	Stevens et al. (2020)
<i>Abies magnifica</i> A. Murray	Foliage morphology, bark structure	de Magalhães and Schwilk (2012); Stevens et al. (2020)
<i>Abies nephrolepis</i> (Trautv. ex Maxim.) Maxim.	Foliage MC	Shan et al. (2008)
<i>Abies procera</i> Rehder	Bark structure	Stevens et al. (2020)
<i>Abies recurvata</i> Mast.	Foliage morphology	Belcher (2016)
<i>Abies veitchii</i> Lindl.	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Acacia aneura</i> F. Muell. ex Benth.	Foliage morphology, litter morphology	Scarff and Westoby (2006)
<i>Acer mono</i> Maxim.	Foliage MC, foliage chemistry	Shan et al. (2008); Wang et al. (2009)
<i>Acer pseudoplatanus</i> L.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts	Núñez-Regueira et al. (1996); Núñez-Regueira et al. (1999) 43
<i>Acer rubrum</i> L.	Litter MC, litter structure	Kreye et al. (2018)
<i>Acer saccharum</i> Marshall	Foliage MC	Shan et al. (2008)
<i>Acer tegmentosum</i> Maxim.	Foliage MC	Shan et al. (2008)
<i>Acer ukurunduense</i> Trautv. et C.A.Mey.	Foliage MC	Shan et al. (2008)
<i>Afrocarpus falcatus</i> (Thunb.) C.N.Page	Foliage morphology	Calitz et al. (2015)
<i>Agathis australis</i> (D.Don) Lindl. ex Loudon	Foliage morphology, terminal branches MC	Belcher (2016); Wyse et al. (2016)
<i>Ailanthus altissima</i> (Mill.) Swingle	Foliage MC, foliage chemistry	Wang et al. (2009); Molina et al. (2019)
<i>Alectryon excelsus</i> Gaertn.	Terminal branches MC	Wyse et al. (2016); Molina et al. (2017)
<i>Alnus hirsuta</i> (Spach) Rupr.	Foliage MC	Shan et al. (2008)
<i>Alnus incana</i> (L.) Moench	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Alnus mandshurica</i> (Callier) Hand.-Mazz.	Foliage MC	Shan et al. (2008)
<i>Angophora costata</i> (Gaertn.) Hochr. ex Britten	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Grootemaat et al. (2017a)
<i>Aspidosperma excelsum</i> Benth.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Aspidosperma quebracho-blanco</i> Schltldl.	Foliar and twig MC, foliar and twig DMC	Santacruz-García et al. (2019)
<i>Athrotaxis cupressoides</i> D.Don	Foliage morphology	Belcher (2016)
<i>Athrotaxis × laxifolia</i> Hook.	Foliage morphology	Belcher (2016)
<i>Austrocedrus chilensis</i> (D. Don) Pic.Serm. & Bizzarri	Foliage MC	Bianchi and Defossé (2015); Bianchi et al. (2019)
<i>Banksia marginata</i> Cav.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Murray et al. (2013); Grootemaat et al. (2017a)
<i>Beilschmiedia tarairi</i> (A. Cunn.) Kirk	Terminal branches MC	Wyse et al. (2016)
<i>Beilschmiedia tawa</i> (A. Cunn.) Kirk	Terminal branches MC	Wyse et al. (2016)
<i>Betula costata</i> Trautv.	Foliage MC	Shan et al. (2008)
<i>Betula nigra</i> L.	Foliage MC	Shan et al. (2008)
<i>Betula pendula</i> Roth	Bark structure, wood structure, litter MC, litter morphology, litter structure	Frejville et al. (2009); Zhao et al. (2019)
<i>Betula platyphylla</i> Sukaczew	Foliage MC	Shan et al. (2008)
<i>Betula pubescens</i> Ehrh.	Litter morphology, low branches MC and chemistry	van Altena et al. (2012); Blauw et al. (2017)
<i>Brachychiton populneus</i> (Schott & Endl.) R.Br.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure, litter morphology	Scarff and Westoby (2006); Calitz et al. (2015); Grootemaat et al. (2017a)
<i>Callitris columellaris</i> F. Muell.	Foliage morphology, litter morphology	Scarff and Westoby (2006)
<i>Calocedrus decurrens</i> (Torr.) Florin	Foliage morphology	de Magalhães and Schwilk (2012)
<i>Carya alba</i> (L.) Nutt. ex	Litter MC, litter structure	Kreye et al. (2018)

Table 1 (continued)

Species	Plant trait associated with flammability	Reference
Elliott <i>Carya glabra</i> (Mill.) Sweet	Litter MC, litter structure	Kreye et al. (2018)
<i>Castanea dentata</i> (Marshall) Borkh.	Foliage morphology, litter MC	Kane et al. (2019)
<i>Castanea mollissima</i> Blume	Foliage morphology, litter MC	Kane et al. (2019)
<i>Castanea sativa</i> Mill.	Foliage MC, MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts	Núñez-Regueira et al. (1996); Núñez-Regueira et al. (1999); Dimitrakopoulos and Papaioannou (2001)
<i>Castanopsis hystrix</i> Hook. f. & Thomson ex A.DC.	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Casuarina cristata</i> Miq.	Foliage morphology, litter morphology	Scarff and Westoby (2006)
<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière	Terminal branches MC	Wyse et al. (2016)
<i>Cedrus deodara</i> (Roxb. ex D.Don) G.Don	Foliage MC	Molina et al. (2017)
<i>Ceratonia siliqua</i> L.	Foliage MC, litter MC, litter morphology	Dimitrakopoulos and Papaioannou (2001); Kauf et al. (2015); Essaghi et al. (2017); Molina et al. (2017) Stevens et al. (2020)
<i>Chamaecyparis lawsoniana</i> (A. Murray) Parl.	Bark structure	
<i>Cinnamomum camphora</i> (L.) J.Presl	Foliage MC, foliage morphology	Murray et al. (2013)
<i>Calocedrus decurrens</i> (Torr.) Florin	Bark structure	Stevens et al. (2020)
<i>Coprosma arborea</i> Kirk	Terminal branches MC	Wyse et al. (2016)
<i>Cordyline australis</i> (G. Forst.) Endl.	Terminal branches MC	Wyse et al. (2016)
<i>Corymbia gummifera</i> (Gaertn.) K.D.Hill & L.A.S.Johnson	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure, litter mass loss	Murray et al. (2013); Grootemaat et al. (2015); Grootemaat et al. (2017a); Krix and Murray (2018)
<i>Corynocarpus laevigatus</i> J.R.Forst. & G.Forst.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Grootemaat et al. (2017a)
<i>Cryptomeria japonica</i> (Thunb. ex L.f.) D.Don	Litter morphology, terminal branches MC	Cornwell et al. (2015); Wyse et al. (2016)
<i>Cunninghamia lanceolata</i> (Lamb.) Hook.	Foliage morphology, litter MC, litter morphology, litter structure	Cornwell et al. (2015); Belcher (2016); Zhao et al. (2016)
<i>Cupressus macrocarpa</i> Hartw.	Foliage and twig MC, foliage and twig chemistry, foliage morphology	Xiaorui et al. (2001); (Belcher, 2016)
<i>Cupressus nootkatensis</i> D. Don	Bark structure	Stevens et al. (2020)
<i>Cupressus arizonica</i> Greene	Foliage MC	Dimitrakopoulos and Papaioannou (2001); Molina et al. (2017)
<i>Cupressus sempervirens</i> L.	Foliage MC, foliage morphology, foliage chemistry, twigs with foliage morphology and chemistry, terminal branches MC, branches morphology, bark structure, wood structure, litter MC, litter chemistry, litter structure	Dimitrakopoulos and Papaioannou (2001); Dimitrakopoulos and Panov (2001); Ganteaume et al. (2012); Mola et al. (2014); Wyse et al. (2016); Della Rocca et al. (2015); Della Rocca et al. (2017); Molina et al. (2017); Della Rocca et al. (2018); Ganteaume (2018); Romero et al. (2019); Della Rocca et al. (2020) Calitz et al. (2015) Belcher (2016)
<i>Cussonia spicata</i> Thunb.	Foliage morphology	
<i>Dacrycarpus imbricatus</i> (Blume) de Laub.	Foliage morphology	Belcher (2016)
<i>Dacrydium cupressinum</i> Sol. ex G.Forst.	Terminal branches MC	Wyse et al. (2016)
<i>Dacryodes microcarpa</i> Cuatrec.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Dysoxylum spectabile</i> (G. Forst.) Hook.f.	Terminal branches MC	Wyse et al. (2016)
<i>Elaeocarpus reticulatus</i> Sm.	Foliage MC, foliage morphology	Murray et al. (2013)
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Wood FMC, wood morphology, wood chemistry	Haurie et al. (2019)
<i>Enterolobium schomburgkii</i> (Benth.) Benth.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Eucalyptus amygdalina</i> Labill.	Foliage, twigs and litter MC and chemistry	Dickinson and Kirkpatrick (1985)
<i>Eucalyptus camaldulensis</i> Dehnh.	Foliage MC, terminal branches MC	Dimitrakopoulos and Papaioannou (2001); Wyse et al. (2016); Molina et al. (2017); Molina et al. (2019)
<i>Eucalyptus eugenioides</i> Sieber ex Spreng.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark structure, bark chemistry	Grootemaat et al. (2017a)
<i>Eucalyptus globulus</i> Labill.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts, litter MC, litter chemistry, litter structure	Núñez-Regueira et al. (1996); Ganteaume et al. (2010); Merino et al. (2015)
<i>Eucalyptus intertexta</i> R.T.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark structure,	Scarff and Westoby (2006); Grootemaat et al. (2015); Grootemaat

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Table 1 (continued)

Species	Plant trait associated with flammability	Reference
Baker	bark chemistry, litter morphology, litter mass loss	et al. (2017b)
<i>Eucalyptus oblonga</i> A. Cunn. ex DC.	Foliage MC, foliage morphology	Krix and Murray (2018)
<i>Eucalyptus obliqua</i> L'Hér.	Foliage, twigs and litter MC and chemistry	Dickinson and Kirkpatrick (1985)
<i>Eucalyptus pilularis</i> Sm.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Grootemaat et al. (2017a)
<i>Eucalyptus piperita</i> Sm.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Grootemaat et al. (2017a); Krix and Murray (2018)
<i>Eucalyptus populnea</i> F. Muell.	Foliage morphology, litter morphology	Scarff and Westoby (2006)
<i>Eucalyptus pulchella</i> Desf.	Foliage, twigs and litter MC and chemistry	Dickinson and Kirkpatrick (1985)
<i>Eucalyptus punctata</i> A. Cunn. ex DC.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure	Grootemaat et al. (2017a); Krix et al. (2019)
<i>Eucalyptus saligna</i> Sm.	Foliage MC, foliage chemistry	Ramadhan et al. (2021)
<i>Eucalyptus umbra</i> F. Muell. ex R.T.Baker	Foliage MC, foliage morphology, foliage chemistry, litter mass loss	Grootemaat et al. (2015)
<i>Eucalyptus viminalis</i> Labill.	Terminal branches MC	Wyse et al. (2016)
<i>Fagus grandifolia</i> Ehrh.	Litter MC	Mola et al. (2014)
<i>Fagus sylvatica</i> L.	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Fraxinus chinensis</i> Roxb.	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Fraxinus chinensis</i> subsp. <i>rhynchophylla</i> (Hance) A.E.Murray	Foliage MC	Shan et al. (2008)
<i>Fraxinus excelsior</i> L.	Litter morphology	Kauf et al. (2018)
<i>Fraxinus mandshurica</i> Rupr.	Foliage MC, litter morphology	Shan et al. (2008); Kauf et al. (2018)
<i>Fraxinus ornus</i> L.	Foliage MC	Molina et al. (2017)
<i>Fraxinus rotundifolia</i> Vahl	Foliage morphology, wood and bark MC, wood and bark structure	Rasooli et al. (2021)
<i>Fuchsia excorticata</i> (G. Forst.) L.f.	Terminal branches MC	Wyse et al. (2016)
<i>Handroanthus chrysanthus</i> (Jacq.) S.O. Grose	Wood FMC, wood morphology, wood chemistry	Haurie et al. (2019)
<i>Ilex opaca</i> Aiton	Litter MC	Mola et al. (2014)
<i>Juglans mandshurica</i> Maxim.	Foliage MC	Shan et al. (2008)
<i>Juniperus thurifera</i> L.	Terminal branches MC	Wyse et al. (2016)
<i>Juniperis scopulorum</i> Sarg.	Bark structure	Stevens et al. (2020)
<i>Juniperus occidentalis</i> Hook.	Bark structure	Stevens et al. (2020)
<i>Knightia excelsa</i> R.Br.	Terminal branches MC	Wyse et al. (2016)
<i>Kunzea robusta</i> de Lange & Toelken	Terminal branches MC, DMC, structure	Wyse et al. (2018)
<i>Larix decidua</i> Mill.	Bark structure, wood structure	Frejaville et al. (2013)
<i>Larix × eurolepis</i> A.Henry ^a	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Larix gmelinii</i> (Rupr.) Kuzen.	Foliage MC	Shan et al. (2008)
<i>Larix gmelinii</i> var. <i>olgensis</i> (A.Henry) Ostenf. & Syrach	Foliage MC	Shan et al. (2008)
<i>Larix kaempferi</i> (Lamb.) Carrière	Litter MC, litter morphology, litter structure	Zhao et al. (2019)
<i>Larix occidentalis</i> Mill.	Bark structure	Stevens et al. (2020)
<i>Laurus nobilis</i> L.	Foliage MC	Dimitrakopoulos and Papaioannou (2001); Molina et al. (2017)
<i>Liquidambar styraciflua</i> L.	Litter MC	Mola et al. (2014)
<i>Liriodendron tulipifera</i> L.	Litter MC, litter structure	Mola et al. (2014); Kreye et al. (2018)
<i>Lithocarpus thalassicus</i> (Hance) Rehder	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Lysiloma acapulcense</i> (Kunth) Benth.	Wood FMC, wood morphology, wood chemistry	Haurie et al. (2019)
<i>Maackia amurensis</i> Rupr.	Foliage MC	Shan et al. (2008)
<i>Machilus pauhoi</i> Kaneh.	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Magnolia champaca</i> (L.) Baill. ex Pierre	Foliage MC	Shan et al. (2008)
<i>Magnolia conifera</i> var. <i>chingii</i> (Dandy) V.S. Kumar	Foliage MC	Bianchi et al. (2019)
<i>Magnolia grandiflora</i> L.	Foliage MC, litter MC	Mola et al. (2014)
<i>Magnolia macclurei</i> (Dandy) Figlar	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Malus baccata</i> (L.) Borkh.	Terminal branches MC	Wyse et al. (2016)
<i>Metrosideros excelsa</i> Sol.	Terminal branches MC	Wyse et al. (2016)

Table 1 (continued)

Species	Plant trait associated with flammability	Reference
ex Gaertn.		
<i>Micropholis egensis</i> (A. DC.) Pierre	Litter morphology, litter structure	Parsons et al. (2015)
<i>Myrica rubra</i> (Lour.) Siebold & Zucc.	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Mytilaria laosensis</i> Lecomte	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Nestegis lanceolata</i> (Hook. f.) L.A.S.Johnson	Terminal branches MC	Wyse et al. (2016)
<i>Nothofagus antarctica</i> (G. Forst.) Oerst.	Foliage MC, foliage morphology	Blackhall et al. (2012); Bianchi and Defossé (2015); Bianchi et al. (2019)
<i>Nothofagus dombeyi</i> (Mirb.) Oerst.	Foliage MC	Bianchi et al. (2019)
<i>Nothofagus fusca</i> (Hook. f.) Oerst.	Terminal branches MC	Wyse et al. (2016)
<i>Nothofagus menziesii</i> (Hook.f.) Oerst.	terminal branches MC	Wyse et al. (2016)
<i>Nothofagus pumilio</i> (Poepp. & Endl.) Krasser	Foliage MC	Blackhall et al. (2017); Bianchi et al. (2019)
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> (Hook.f.) Poole	Terminal branches MC	Wyse et al. (2016)
<i>Nyssa sylvatica</i> Marshall	Litter MC, litter structure	Kreye et al. (2018)
<i>Ocotea acutangula</i> (Miq.) Mez	Litter morphology, litter structure	Parsons et al. (2015)
<i>Ocotea guianensis</i> Aubl.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Olea europaea</i> L.	Foliage MC, foliage morphology, foliage chemistry, terminal branches MC, litter MC, litter morphology, life form, regenerative strategy	Dimitrakopoulos and Papaioannou (2001); Weise et al. (2005); Saura-Mas et al. (2010); Murray et al. (2013); Calitz et al. (2015); Kauf et al. (2015); Wyse et al. (2016); Molina et al. (2017); Molina et al. (2019)
<i>Ostrya virginiana</i> (Mill.) K.Koch	Litter MC	Mola et al. (2014)
<i>Pappea capensis</i> Eckl. & Zeyh.	Foliage morphology	Calitz et al. (2015)
<i>Phellodendron amurense</i> Rupr.	Foliage MC	Shan et al. (2008)
<i>Phyllocladus toatoa</i> Molloy	Foliage morphology	Belcher (2016)
<i>Picea abies</i> (L.) H.Karst.	Foliage MC, low branches MC and chemistry, bark structure, wood structure, litter MC, litter morphology, litter structure	Frejaville et al. (2013); Zhao et al. (2016); Blauw et al. (2017); Bianchi et al. (2019)
<i>Picea engelmannii</i> Parry ex Engelm.	Foliage MC, foliage chemistry, bark structure	Page et al. (2014); Stevens et al. (2020)
<i>Picea glauca</i> (Moench) Voss	Bark structure	Stevens et al. (2020)
<i>Picea koraiensis</i> Nakai	Foliage MC	Shan et al. (2008)
<i>Picea sitchensis</i> (Bong.) Carr.	Bark structure	Stevens et al. (2020)
<i>Pinus albicaulis</i> Engelm.	Bark structure	Stevens et al. (2020)
<i>Pinus armandii</i> Franch.	Foliage MC, foliage chemistry, litter MC, litter morphology, litter structure	Wang et al. (2009); Zhao et al. (2016)
<i>Pinus ayacahuite</i> Ehrenb. ex Schltldl.	Foliage MC, foliage chemistry, litter MC, litter morphology, litter structure	Wang et al. (2009); Zhao et al. (2016)
<i>Pinus banksiana</i> Lamb.	Foliage MC, foliage chemistry, foliage structure	Jolly et al. (2016); Dewhirst et al. (2020)
<i>Pinus brutia</i> Ten.	Foliage MC, foliage morphology, foliage and twigs chemistry, terminal branches MC, branches morphology	Dimitrakopoulos and Papaioannou (2001); Dimitrakopoulos and Panov (2001); Wyse et al. (2016); Michelaki et al., 2020
<i>Pinus canariensis</i> C.Sm.	Foliage MC, terminal branches MC	Wyse et al. (2016); Essaghi et al. (2017)
<i>Pinus cembra</i> L.	Bark structure, wood structure	Frejaville et al. (2013)
<i>Pinus clausa</i> (Chapm. ex Engelm.) Vasey ex Sarg.	Foliage MC	McAllister and Weise (2017)
<i>Pinus contorta</i> Douglas ex Loudon	Foliage MC, foliage chemistry, twig and litter MC, bark structure	Jolly et al. (2012); Page et al. (2012); McAllister and Weise (2017); Bianchi et al. (2019); Stevens et al. (2020)
<i>Pinus coulteri</i> D.Don	Terminal branches MC	Wyse et al. (2016)
<i>Pinus densiflora</i> Siebold & Zucc.	Foliage chemistry	Dewhirst et al. (2020)
<i>Pinus edulis</i> Engelm.	Bark structure	Stevens et al. (2020)
<i>Pinus engelmannii</i> Carr.	Foliage chemistry	Dewhirst et al. (2020)
<i>Pinus flexilis</i> E.James	Foliage chemistry	Dewhirst et al. (2020); Stevens et al. (2020)
<i>Pinus glabra</i> Walter	Litter MC	Mola et al. (2014)
<i>Pinus greggii</i> Engelm. ex Parl.	Foliage chemistry	Dewhirst et al. (2020)
<i>Pinus halepensis</i> Mill.	Foliage MC, foliage morphology, foliage chemistry, foliage and twigs MC, foliage and twigs chemistry, terminal branches MC, branches morphology, litter MC, litter morphology, litter chemistry, litter structure	Pappa et al. (2000); Dimitrakopoulos and Papaioannou (2001); Dimitrakopoulos and Panov (2001); Liidakis et al. (2011); Alessio et al. (2008b); De Lillis et al. (2009); Ormeño et al. (2009); Simeoni et al. (2012); Mola et al. (2014); Kauf et al. (2015); Jervis and Rein

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Table 1 (continued)

Species	Plant trait associated with flammability	Reference
<i>Pinus jeffreyi</i> A.Murray bis	Foliage morphology	(2016); 111 Ntoufas et al. (2016); Wyse et al. (2016); Dehane et al. (2017); Molina et al. (2017); Romero et al. (2019); Michelaki et al., 2020
<i>Pinus koraiensis</i> Siebold & Zucc.	Foliage MC	de Magalhães and Schwilk (2012); Stevens et al. (2020) Shan et al. (2008)
<i>Pinus krempfii</i> Lecomte	Foliage morphology	Belcher (2016)
<i>Pinus lambertiana</i> Douglas	Foliage morphology, bark structure	de Magalhães and Schwilk (2012); Stevens et al. (2020)
<i>Pinus massoniana</i> Lamb.	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Pinus monticola</i> Douglas ex D. Don	Foliage chemistry, bark structure	Dewhurst et al. (2020); Stevens et al. (2020)
<i>Pinus muricata</i> D.Don	Foliage chemistry	Dewhurst et al. (2020)
<i>Pinus nigra</i> Arnold	Foliage chemistry, litter MC, litter chemistry, litter structure	Simeoni et al. (2012); Merino et al. (2015); Dewhurst et al. (2020)
<i>Pinus patula</i> Schiede ex Schldl. & Cham.	Foliage chemistry	Dewhurst et al. (2020)
<i>Pinus pinaster</i> Aiton	Foliage MC, foliage chemistry, terminal branches MC, MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts, litter MC, litter chemistry, litter structure	Núñez-Regueira et al. (1996); Ganteaume et al. (2010); Madrigal et al. (2013); Simeoni et al. (2012); Merino et al. (2015); Wyse et al. (2016); Della Rocca et al. (2017); Essaghi et al. (2017); Molina et al. (2017)
<i>Pinus pinea</i> L.	Foliage MC, foliage chemistry, bark structure, litter MC, litter chemistry, litter structure	Ganteaume et al. (2010); Ormeño et al. (2009); Courty et al. (2012); Della Rocca et al. (2017); Essaghi et al. (2017); Molina et al. (2017); Madrigal et al. (2019); Molina et al. (2019)
<i>Pinus ponderosa</i> Douglas ex C.Lawson	Foliage MC, foliage morphology, bark structure	de Magalhães and Schwilk (2012); Bianchi et al. (2019); Stevens et al. (2020)
<i>Pinus pumila</i> (Pall.) Regel	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Pinus radiata</i> D.Don	Foliage MC, foliage chemistry, terminal branches MC, DMC and structure, MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts	Núñez-Regueira et al. (1999); Wyse et al. (2016); Bianchi et al. (2019); Wyse et al. (2018); Dewhurst et al. (2020)
<i>Pinus resinosa</i> Aiton	Foliage MC, foliage chemistry, foliage structure	Jolly et al. (2016)
<i>Pinus strobus</i> L.	Foliage chemistry, litter MC, litter morphology, litter structure	Simeoni et al. (2012); Zhao et al. (2016); Dewhurst et al. (2020)
<i>Pinus sylvestris</i> L.	Foliage MC, foliage chemistry, low branches MC and chemistry, MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts, wood chemistry, litter MC, litter morphology, litter structure	Núñez-Regueira et al. (1999); Shan et al. (2008); Liodakis et al. (2013); Zhao et al. (2016); Blauw et al. (2017); Zhao et al. (2019); Dewhurst et al. (2020)
<i>Pinus tabuliformis</i> Carrière	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Pinus uncinata</i> Ramond ex DC.	Bark structure, wood structure	Frejaville et al. (2013)
<i>Pinus wallichiana</i> A. B. Jacks.	Foliage chemistry	Dewhurst et al. (2020)
<i>Pittosporum undulatum</i> Vent.	Foliage MC, foliage morphology	Murray et al. (2013)
<i>Platanus orientalis</i> L.	Foliage MC	Dimitrakopoulos and Papaioannou (2001)
<i>Platycladus orientalis</i> (L.) Franco	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Podocarpus totara</i> G.Benn. ex D.Don	Terminal branches MC	Wyse et al. (2016)
<i>Populus alba</i> L.	Foliage MC	Molina et al. (2019)
<i>Populus canadensis</i> Moench	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Populus nigra</i> L.	Foliage MC, terminal branches MC	Wyse et al. (2016); Bianchi et al. (2019)
<i>Populus suaveolens</i> Fisch. ex Loudon	Foliage MC	Shan et al. (2008)
<i>Populus tremula</i> L.	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Populus tremula</i> var. <i> davidiana</i> (Dode) C.K. Schneid.	Foliage MC	Shan et al. (2008)
<i>Pouteria ramiflora</i> (Mart.) Radlk.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Protium guianense</i> (Aubl.) Marchand	Litter morphology, litter structure	Parsons et al. (2015)
<i>Prumnopitys ferruginea</i> (G.Benn. ex D.Don) de Laub.	Terminal branches MC	Wyse et al. (2016)
<i>Prunus armeniaca</i> L.	Foliage MC	Shan et al. (2008)
<i>Prunus davidiana</i> (CarriŠre) Franch.	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Prunus padus</i> L.	Foliage MC	Shan et al. (2008)
<i>Prunus serotina</i> Ehrh.	Litter MC, litter structure	Kreye et al. (2018)
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Foliage MC, branches MC, tree MC, tree structure, bark thicknesses	Babrauskas (2006); Manzello et al. (2007); McAllister and Weise (2017); Bianchi et al. (2019); Stevens et al. (2020)
<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk.	Foliage morphology	Calitz et al. (2015)
<i>Pyrus ussuriensis</i> Maxim. ex Rupr.	Foliage MC	Shan et al. (2008)

Table 1 (continued)

Species	Plant trait associated with flammability	Reference
<i>Quercus brantii</i> Lindl.	Foliage morphology, wood and bark MC, wood and bark structure	Rasooli et al. (2021)
<i>Quercus chrysolepis</i> Liebm.	Litter MC, litter structure	Kreye et al. (2018)
<i>Quercus douglasii</i> Hook. & Arn.	Litter morphology	Engber and Varner (2012)
<i>Quercus engelmannii</i> Greene	Litter MC, litter structure	Kreye et al. (2018)
<i>Quercus faginea</i> Lam.	Foliage MC, foliage chemistry, foliage and twigs MC, terminal branches MC, bark structure, wood structure, litter MC, litter chemistry, litter structure	Ganteaume et al. (2010); Wyse et al. (2016); Dehane et al. (2017); Della Rocca et al. (2017); Della Rocca et al. (2018)
<i>Quercus falcata</i> Michx.	Litter MC, litter structure	Mola et al. (2014); Kreye et al. (2018)
<i>Quercus garryana</i> Douglas ex Hook.	Litter morphology	Engber and Varner (2012)
<i>Quercus hemisphaerica</i> Bartram ex Willd.	Litter MC	Mola et al. (2014)
<i>Quercus ilex</i> L.	Foliage MC	Dehane et al. (2017); Molina et al. (2017)
<i>Quercus imbicaria</i> Michx.	Litter morphology	Kauf et al. (2018)
<i>Quercus incana</i> Bartram	Foliage MC, foliage morphology, foliage chemistry, foliage and twigs MC, foliage and twigs chemistry, branches morphology, bark structure, wood structure, litter MC, litter morphology, litter chemistry, litter structure, life form, regenerative strategy	Massari and Leopaldi (1998); Dimitrakopoulos and Papaioannou (2001); Dimitrakopoulos and Panov (2001); Alessio et al. (2008a); De Lillis et al. (2009); Saura-Mas et al. (2010); Curt et al. (2011); Kauf et al. (2015); Dehane et al. (2017); Della Rocca et al. (2017)
<i>Quercus kelloggii</i> Newb.	Litter MC	Mola et al. (2014)
<i>Quercus laevis</i> Walter	Foliage morphology, litter morphology	de Magalhães and Schwilk (2012); Engber and Varner (2012)
<i>Quercus libani</i> Olivier	Foliage morphology, litter morphology, wood and bark MC, wood and bark structure	Kauf et al. (2018); Rasooli et al. (2021)
<i>Quercus lobata</i> Née	Litter MC	Mola et al. (2014)
<i>Quercus margarettae</i> (Ashe) Small	Litter MC	Mola et al. (2014)
<i>Quercus mongolica</i> Fisch. ex Ledeb.	Foliage MC	Shan et al. (2008)
<i>Quercus nigra</i> L.	Litter MC	Mola et al. (2014)
<i>Quercus palustris</i> Münchh.	Litter morphology	Kauf et al. (2018)
<i>Quercus pubescens</i> Willd.	Foliage MC, foliage chemistry, litter MC, litter structure	Dimitrakopoulos and Papaioannou (2001); Curt et al. (2011); De Lillis et al. (2009); Ganteaume et al. (2010)
<i>Quercus pyrenaica</i> Willd.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts	Núñez-Regueira et al. (1999)
<i>Quercus robur</i> L.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts, litter MC, litter morphology, litter structure	Núñez-Regueira et al. (1996); Núñez-Regueira et al. (1999); Zhao et al. (2019)
<i>Quercus shumardii</i> Buckland	Litter morphology	Kauf et al. (2018)
<i>Quercus stellata</i> Wangenh.	Litter MC, litter structure	Mola et al. (2014); Kreye et al. (2018)
<i>Quercus suber</i> L.	Foliage MC, foliage chemistry, foliage and twigs MC, terminal branches MC, bark structure, litter structure	Massari and Leopaldi (1998); De Lillis et al. (2009); Curt et al. (2011); Wyse et al. (2016); Dehane et al. (2015); Essaghi et al. (2017); Molina et al. (2017); Molina et al. (2018)
<i>Quercus variabilis</i> Blume	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Quercus velutina</i> Lam.	Litter MC, litter structure	Kreye et al. (2018)
<i>Quercus virginiana</i> Mill.	Litter MC	Mola et al. (2014)
<i>Quercus wislizeni</i> A.DC.	Litter morphology	Engber and Varner (2012)
<i>Rhamnus davarica</i> Pall.	Foliage MC	Shan et al. (2008)
<i>Robinia pseudoacacia</i> L.	Foliage MC, foliage chemistry, foliage morphology, wood and bark MC, wood and bark structure	Shan et al. (2008); Wang et al. (2009); Rasooli et al. (2021)
<i>Salix pierottii</i> Miq.	Foliage MC	Shan et al. (2008)
<i>Salix rorida</i> Laksch.	Foliage MC	Shan et al. (2008)
<i>Sapium glandulosum</i> (L.) Morong	Foliage MC, foliage morphology, foliage chemistry, litter mass loss	Grootemaat et al. (2015)
<i>Schinopsis lorentzii</i> (Griseb.) Engl.	Foliage and twig MC, foliage and twig DMC	Santacruz-García et al. (2019)
<i>Sequoia sempervirens</i> (D. Don) Endl.	Foliage morphology; bark structure	Belcher (2016); Stevens et al. (2020)
<i>Sequoiadendron giganteum</i> (Lindl.) J. Buchholz	Foliage morphology, litter MC, litter morphology, litter structure, bark structure	de Magalhães and Schwilk (2012); Belcher (2016); Zhao et al. (2016); Stevens et al. (2020)
<i>Schima superba</i> Gardner & Champ.	Foliage and twig MC, foliage and twig chemistry	Xiaorui et al. (2001)
<i>Sloanea eichleri</i> K.Schum.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Sorbus aucuparia</i> L.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts, bark structure, wood structure	Núñez-Regueira et al. (1999); Frejaville et al. (2013)
<i>Sorbus domestica</i> L.	Litter morphology	Kauf et al. (2018)
<i>Styphnolobium japonicum</i> (L.) Schott	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Swietenia humilis</i> Zucc.	Wood FMC, wood morphology, wood chemistry	Haurie et al. (2019)
<i>Syncarpia glomulifera</i> (Sm.) Nied.	Foliage MC, foliage morphology, foliage chemistry, bark MC, bark chemistry, bark structure, litter mass loss	Grootemaat et al. (2015); Grootemaat et al. (2017a)

(continued on next page)

Table 1 (continued)

Species	Plant trait associated with flammability	Reference
<i>Tabebuia rosea</i> (Bertol.) Bertero ex A.DC.	Wood FMC, wood morphology, wood chemistry	Haurie et al. (2019)
<i>Tamarix smyrnensis</i> Bunge	Foliage MC	Dimitrakopoulos and Papaioannou (2001)
<i>Tapirira guianensis</i> Aubl.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Taxodium distichum</i> (L.) Rich.	Foliage morphology	Belcher (2016)
<i>Taxodium huegelii</i> C. Lawson	Litter MC, litter morphology, litter structure	Zhao et al. (2016)
<i>Taxus baccata</i> L.	MC in mixed sample of all living tree parts, chemistry of mixed sample of all living tree parts	Núñez-Regueira et al. (1999)
<i>Taxus floridana</i> Nutt. ex Chapm.	Litter MC	Mola et al. (2014)
<i>Tetraclinis articulata</i> (Vahl) Mast.	Foliage and twigs MC, terminal branches MC	Wyse et al. (2016); Dehane et al. (2017)
<i>Thuja occidentalis</i> L.	Foliage MC, foliage morphology, litter MC, litter structure	Molina et al. (2017); Ganteaume (2018)
<i>Thuja plicata</i> Donn ex D. Don	Bark structure	Stevens et al. (2020)
<i>Tilia amurensis</i> Rupr.	Foliage MC	Shan et al. (2008)
<i>Tilia mandshurica</i> Rupr. & Maxim.	Foliage MC	Shan et al. (2008)
<i>Torreya taxifolia</i> Arn.	Litter MC	Mola et al. (2014)
<i>Trattinnickia boliviana</i> (Swart) Daly	Litter morphology, litter structure	Parsons et al. (2015)
<i>Trattinnickia glaziovii</i> Swart	Litter morphology, litter structure	Parsons et al. (2015)
<i>Trattinnickia rhoifolia</i> Willd.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Tristaniopsis laurina</i> (Sm.) Peter G. Wilson & J.T. Waterh.	Foliage MC, foliage morphology	Murray et al. (2013)
<i>Tsuga heterophylla</i> (Raf.) Sarg.	Foliage morphology, bark structure	Belcher (2016); Stevens et al. (2020)
<i>Tsuga mertensiana</i> (Bong.) Carr.	Bark structure	Stevens et al. (2020)
<i>Ulmus alata</i> Michx.	Litter MC, litter structure	Kreye et al. (2018)
<i>Ulmus davidiana</i> var. <i>japonica</i> (Rehder) Nakai	Foliage MC	Shan et al. (2008)
<i>Ulmus laciniata</i> (Trautv.) Mayr	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Ulmus macrocarpa</i> Hance	Foliage MC	Shan et al. (2008)
<i>Ulmus pumila</i> L.	Foliage MC, foliage chemistry	Wang et al. (2009)
<i>Vitex lucens</i> Kirk	Terminal branches MC	Wyse et al. (2016)
<i>Vochysia vismiifolia</i> Spruce ex Warm.	Litter morphology, litter structure	Parsons et al. (2015)
<i>Xylopia amazonica</i> R.E.Fr.	Litter morphology, litter structure	Parsons et al. (2015)

^a Taxa with unsolved name or ambiguous taxonomic status.

The surface leaf area-to-volume ratio (SA/V) was found to be the most important for flammability among the various parameters of foliage structure and morphology (Table 3). This parameter describes the particle geometry and relative dimensions of fuel-complex elements (Fernandes and Rego, 1998) and has a significant impact on the components of flammability (Anderson, 1970). Its higher values are associated with higher rates of energy and mass exchange, resulting in shorter ignition delays and faster fire spread (Anderson, 1970; Chandler et al., 1983; Dimitrakopoulos and Panov, 2001; Weise et al., 2005; Sauramas et al., 2010; Engber and Varner, 2012; Simeoni et al., 2012). Leaf and litter-leaf area, as well as specific leaf area (SLA), were found to be significant predictors of flammability, with broader and wider leaves having a lower time-to-ignition (Murray et al., 2013; Ganteaume, 2018). Also, larger leaf area was found to be significantly related to high spread rate and combustibility (de Magalhães and Schwilk, 2012; Krix et al., 2019) and to have a negative relationship with sustainability (de Magalhães and Schwilk, 2012). Leaf thickness, on the other hand, had a negative effect on ignitability (prolonged time-to-ignition) but a positive effect on sustainability (Grootemaat et al., 2017a; Ganteaume, 2018; Romero et al., 2019). Bark thickness was found to be inversely related to burning rate and the mass loss rate (Frejaville et al., 2013) and

corkbark thickness was found to be a good predictor of sustainability and consumability (Dehane et al., 2015). Litter bulk density, particle density and porosity, calculated from the ratio of the weight and volume of a sample, are indicators of the ability for heat absorption prior to ignition, radiation attenuation, combustion dynamics, and mass losses (low density/high flammability) (Simeoni et al., 2012). Considering the morphology traits, litter composed of large, long, or curled leaves provides an open litter-bed structure that is more conducive to oxygen flow and thus stimulates flammability (Scarff and Westoby, 2006; Engber and Varner, 2012; Della Rocca et al., 2018). A meta-analysis of data from seven experimental studies on leaf traits, litter structure, and flammability showed that leaf curl, SA/V, and SLA were more strongly related to flammability than leaf thickness, length, area, and tissue density (Burton et al., 2021).

A high lignin and tannin content in bark (Grootemaat et al., 2017b), leaves (Pappa et al., 2000; Grootemaat et al., 2015), and litter (Grootemaat et al., 2015) showed a positive relationship with sustainability (Table 4). The contents of non-fiber carbohydrates and crude fat in leaves had a negative correlation with the temperature at ignition, and positive linear relationships with the duration of flaming and the high heats of combustion (Page et al., 2012). Also, the concentrations

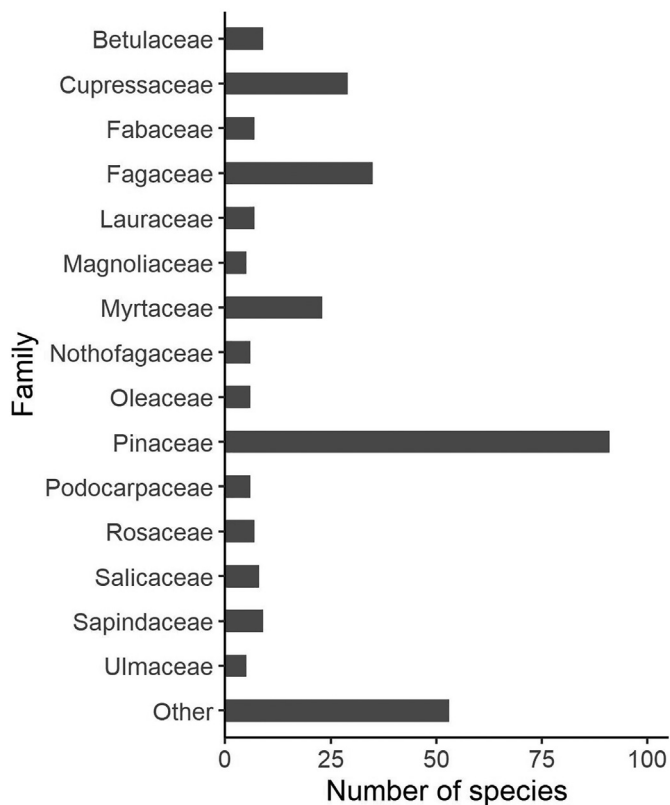


Fig. 4. The number of tree species investigated for tree traits' based flammability grouped per plant family. Families with at least 5 species are represented, and the rest of the families are collectively shown as Others.

of some elements in leaves affected the flammability components (higher [Ca] and [Mg] have a positive relationship with the duration of flaming) (Page et al., 2012), as did the concentrations of the same elements in the bark (higher [Ca] and [Mg] lowered combustibility) (Grootemaat et al., 2017b). Studies have shown that foliar terpenoid concentration was not clearly correlated with flammability and its effect was estimated to be much smaller than the effect of moisture content (MC) (Alessio et al., 2008a, 2008b) (Table 4). Terpenoid (highly flammable volatiles) occurrence in leaf and litter was differently correlated with flammability components (Ormeño et al., 2009). Not only the content, but also the diversity of these compounds that are considered to be the first compounds to ignite and are also responsible for forest-fire spreading (De Lillis et al., 2009; Courty et al., 2012) can affect the flammability of plant material, and different subclasses of terpenoids exhibit different, sometimes contrasting, effects at certain stages of fire induction and development (Della Rocca et al., 2017; Romero et al., 2019).

Studies that included a range of tree species provided evidence which plant traits determine interspecific differences and categorized species based on their flammability. Regression models were developed and used to rank the relative flammability of tree species based on the leaves' moisture content and the time to ignition (Dimitrakopoulos and Papaioannou, 2001). Bianchi et al. (2019) used an inverse relationship between leaf MC and ignition to rank species varying from the most ignitable conifers with low MC to the least ignitable native species. The MC and water retention of leaf litter contributed to interspecific differences in leaf litter flammability. Conifer species had high moisture retention and short flame heights, as well as the brief flaming, smoldering duration, and low consumption rate, whereas deciduous hardwood trees with low moisture retention burned with tall flames, durable flame and smoldering, and a high consumption rate (Mola et al., 2014). McAllister and Weise (2017) demonstrated that trends in the trait-flammability component differ in live and dead plant material and that between-species variation represents a major issue. This

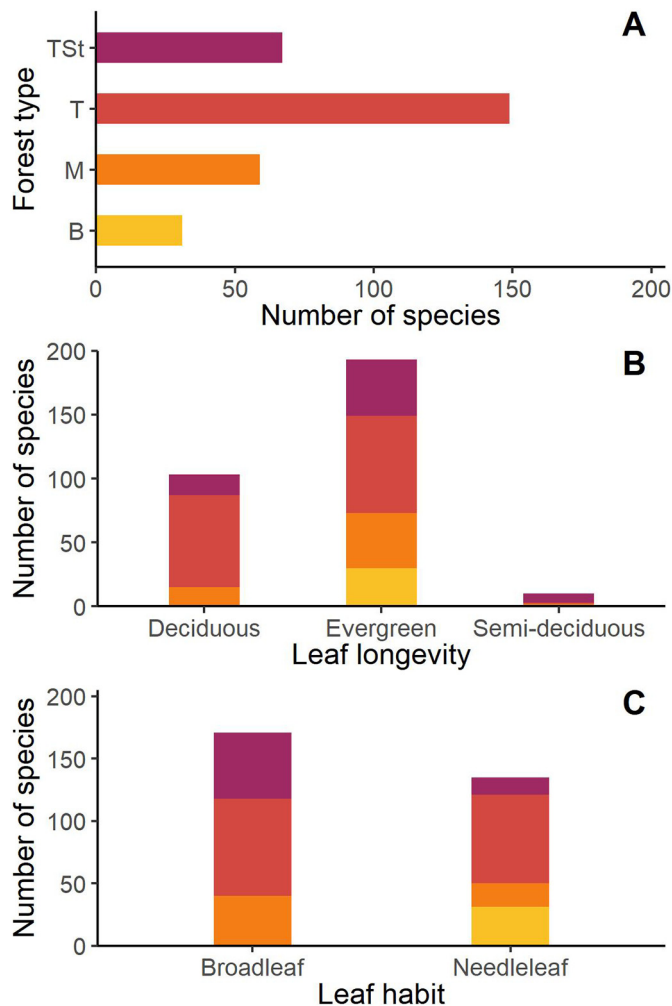


Fig. 5. The number of species per forest type (A), number of species with different leaf longevity per forest type (B), and number of species with different leaf habits per forest type (C). TSt, tropical-subtropical forest type; T, temperate forest type; M, Mediterranean forest type; B, boreal forest type.

study reported that moisture content is not the most relevant trait for predicting the ignition behavior of live fuels and suggested that other physical and chemical traits be considered as better predictors of ignition behavior (McAllister and Weise, 2017).

The main traits that contributed to interspecific variation in time-to-ignition were leaf moisture content and specific leaf area, while leaf dry mass and to a lesser extent leaf chemistry (N, P, and tannin concentrations) explained differences in flame duration and smolder duration (Grootemaat et al., 2015). Except for leaf thickness, all measures of leaf size contributed to species ranking on a flammability spectrum, with larger leaves igniting faster (Murray et al., 2013). Also, leaf size determined between-species differences in heat-release and scaled species from large-leaved trees that created an open litter-bed structure and burned faster to small-leaved conifers that burned with smaller gas-flow rates (Scarff and Westoby, 2006). Smaller and thickened leaves produced longer flaming and smoldering but intermediate flame height and mass loss, whereas large and thin leaves produced tall flames, a high consumption rate, and brief flaming and smoldering (Engber and Varner, 2012). Several species studied differed significantly in all flammability components, with leaf size and litter density being more important than SLA in explaining these differences (de Magalhães and Schwilk, 2012). Litterbed packing density (a function of litter tissue density and litterbed packing ratio) determined between-species differences and the flammability of mixtures by affecting the sustainability (by increasing total burning time and decreased fire front spread)

Table 2
The relationship between moisture content and flammability components.

Plant trait	IGNI	COMB	SUST	CONS
Leaf FMC	●●●●●●●●	●●●●●●	●●	●
	●●●●●●●●			
	●●●●●●●●			
	●●●●●●●●			
Litter FMC	●●●●●●●●	●●●●	●●	●●
	●●			
Terminal branches FMC	●●●●			
Leaves + twigs FMC	●●●●	●●	●●	●
Bark FMC	●●●●			●
Wood FMC	●			
Mixed material FMC	●●	●●		

Dots represent the number of papers reporting negative (●) or neutral (●) relationship among tree traits and flammability components (IGNI, ignitability; COMB, combustibility; SUST, sustainability; CONS, consumability).

(Zhao et al., 2016). Surface area and volume were found to account for 78% of between-species variability, such as thin, lightweight, and loosely packed leaves burned rapidly with a high consumption rate (Parsons et al., 2015). A study by Michelaki et al. (2020) identified relationships between leaf flammability syndromes and trade-offs in resource allocation. Smaller leaves sustained combustion for a longer time, whereas larger leaves had a higher combustion rate and extinguished fire more rapidly. Leaves with high SLA and nutrient concentrations ignited faster and sustained fire for longer, whereas leaves with low SLA and low dry matter content had a higher consumption rate realizing more heat (Michelaki et al., 2020).

The stored terpenoids explained 19% to 50% of the total flammability of both leaves and litter for species with the same fuel moisture content, and the relationship between FMC and the ignition probability varied across the studied species, being different at the same FMC value (Della Rocca et al., 2017). Broadleaved monoterpene-emitting species differed in their temperature of flame appearance, which depended on leaf water content for 65%, while monoterpene emissions explained 35% of the dependency (De Lillis et al., 2009).

A high N concentration was the strongest driver of interspecific bark ignitability, while Cu and P concentrations explained interspecific variation in flame duration per bark mass (Grootemaat et al., 2017b). Thin-barked species had higher bark flammability (Frejaville et al., 2013; Stevens et al., 2020), and denser-wood species had a slightly higher peak heat release rate or higher smoke release and peak heat release rate (Haurie et al., 2019).

Although the differences in flammability of tree species are evident, both from observational and from empirical data, there are many open questions for understanding plant functional traits that contribute to species, community and vegetation flammability, both on the local and wider landscape scales (Schwilk and Caprio, 2011). A specific plant trait can be important for an adaptive value of a species in specific stand conditions, regardless if it is an advantage or disadvantage in relation to flammability. The linkage of environment and set of plant traits is

usually consistent within the plant functional types, and the fire is one of the many environmental challenges that need to be resolved. Therefore, a single-trait contribution to overall species' fire behavior cannot not be evaluated separately from other traits (Schwilk, 2015; Tumino et al., 2019). However, trait-flammability relationships should be considered in terms of individual flammability components as well, because different components have different importance in species-specific responses to local environment, which is why the transferring species-related flammability information from one area to another deserves a particular caution (Kauf et al., 2015).

It is well established that certain plant traits are correlated with all components of flammability, i.e. MC is negatively correlated with ignition, combustion and sustainability (reviewed by Fares et al., 2017). A plant trait can affect only one of the flammability components, while others may be stimulating for some stages of fire development but suppressing in others (particle density, leaf mass fraction, leaf area and thickness, twig and stem diameter) (de Magalhães and Schwilk, 2012). Covariation of traits at the species level may produce either their synergistic effect to flammability (e.g. specific leaf area and bulk density), or traits may not be consistently synergistic in terms of species' flammability (e.g. high MC and large leaf area, which oppositely affect ignitability) (Tumino et al., 2019).

Collection of data on flammability-related species-specific plant traits enables the ranking of a number of species with regard to their fire behavior and using these findings in the restoration of pyrophytic woodlands and forests (Mola et al., 2014; Kreye et al., 2018; Kane et al., 2019) and in wildland-urban interfaces (White and Zipperer, 2010). The cumulative effect of species' traits that stimulate or suppress wildfires becomes more complex in mixed stands, where coexisting species show different fire responses and their individual traits exhibit non-additive effects in overall flammability (de Magalhães and Schwilk, 2012; Van Altena et al., 2012; Zhao et al., 2016; Della Rocca et al., 2018; Wyse et al., 2018; Zhao et al., 2019).

Laboratory flammability studies have certain constraints regarding the complexity of factors in wildfire conditions (Fernandes and Cruz, 2012), and it has been demonstrated that bench-scale flammability experiments cannot simulate the real heat spread and presence of highly volatile isoprenoids (Molina et al., 2018). However, the study of Tumino et al. (2019) showed that some traits known to influence flammability in the laboratory can be associated with field-scale flammability metrics. Certainly, more laboratory flammability studies can provide an insight into interspecific differences and intraspecific variability in standardized conditions, and more empiric data in this field are needed to improve the approaches of plant flammability studies towards full-scale fire simulations and modeling.

Out of the total number of tree species investigated for their trait-based flammability, a considerable number of species have been evaluated solely based on moisture content (of foliage, terminal branches, or litter; 43, 22, and 12 species, respectively). For a smaller number of species, information on flammability refers to either morphological (foliage or litter; 10 and 29 species, respectively) or chemical traits (8 species). For the rest of the species, there is more data on the effect of diverse species-specific traits on flammability, and this data is provided from the same case studies (90 species) or collected from different studies (54 species). The complexity of the impact of individual and multiple plant traits on the flammability components, as well as species-specific interrelationships among plant traits, highlight the need for a comprehensive evaluation of species plant-trait based flammability and provide a rationale for further research on this topic. It was emphasized that the standardization of flammability test methods is needed for obtaining comparable data (White and Zipperer, 2010) as well as the harmonization of sampling protocols and methods, consistency of terminology, and linkage of laboratory and field studies that should lead to a better understanding of species, community and vegetation fire behavior (Varner et al., 2015). More research in

Table 3
The relationship between structural and morphological tree traits and flammability components.

Plant trait	IGNI	COMB	SUST	CONS
Leaf SA/V	●●●●	●●	●	●
Leaf SLA	●●●●●		●	
Leaf area	●●●	●●	●	
LMA	●●●	●	●	●
Leaf thickness	●●●●	●	●●	●
Leaf tissue density	●●	●●		
Leaf curliness	●●		●●	
LDM, LDMC		●	●●	
Leaf length	●	●●		
Leaf size	●●	●		
Leaf width	●			
Leaf volume		●		
Leaf bulk density	●			
Litter SA/V	●●●●●	●●		
Litter SLA	●●	●●●●	●●	●
Litter leaf area	●●●			
Litter dry mass			●	
Litter leaf thickness			●	
Litter bulk density	●●●●●	●	●●	●
TDMC		●		
Bark thickness	●●●●	●●●		●●
Bark roughness	●	●		●
BAM	●			
Cork thickness	●	●		
Cork density	●			
Wood density	●●			

Dots represent the number of papers reporting positive (●), negative (●), or neutral (●) relationship among tree traits and flammability components (IGNI, ignitability; COMB, combustibility; SUST, sustainability; CONS, consumability). SLA, specific leaf area; SA/V, surface-to-volume ratio; LMA, leaf mass per area; LDM, leaf dry matter; LDMC, leaf dry matter content; TDMC, twig dry matter content; BAM, bark area per mass.

this field from different ecosystems and biogeographic regions is required for a comprehensive consideration of the global fire phenomenon, which can contribute to the long-term preservation of both the ecological and socio-cultural values of all forest types on Earth (Moritz et al., 2014).

Table 4
The relationship between chemical traits and flammability components.

Plant trait	IGNI	COMB	SUST	CONS
Leaf terpenoids content	●●●●●●●●	●●●●●●●●	●●●●●	●
Leaf ADF	●●	●●	●	
Leaf NDF	●●	●		
Leaf NCF	●●	●		
Leaf crude fat	●●	●		
Leaf ash content	●●			
Leaf protein content	●			
Leaf tannin content			●	
Leaf [K]			●	
Leaf [Ca]			●	
Leaf [Mg]			●	
Leaf [N]			●	
Leaf [P]			●	
Litter terpenoids content	●●	●●	●●●●●	●
Litter C:N	●	●		
Litter lignin content		●	●	
Litter [N]			●	
Litter [P]			●	
Bark lignin content			●●	
Bark tannin content			●	
Bark [Ca]	●	●●		
Bark [Cu]			●●	
Bark [Mg]		●		
Bark [N]	●			
Bark [P]			●	
Mixed mat. ash content	●			
Mixed mat. lignin content	●			
Mixed mat. rough grease content	●			
Mixed mat. [K]		●●		

Dots represent the number of papers reporting positive (●), negative (●), or neutral (●) relationship among tree traits and flammability components (IGNI, ignitability; COMB, combustibility; SUST, sustainability; CONS, consumability). ADF, Acid detergent fiber; NDF, Neutral detergent fiber; NCF, Nonfiber carbohydrates.

7. Conclusion

Fires have a global impact on forest ecosystems, including those that were not previously thought to be fire-prone. Knowledge of the species-level flammability of trees is required for understanding the vegetation-

fire dynamics and is crucial in fire prevention and post-fire restoration efforts. A review of the literature confirms that plant-trait-based studies have expanded comprehension of the role of plant traits in tree flammability and have implications for both ecological and management issues. The overall research output reveals a growing trend in the publication of findings on this topic, which represents a nexus of several scientific disciplines, including Plant Science, Ecology, Forestry, Plant Pathology, Materials Science, and Energy.

Regarding the wide biogeographic distribution of field surveys, a variety of local studies provided valuable insights into the local perspectives and issues related to tree flammability. Most studies are located in the Mediterranean region and related to the Mediterranean-forest type worldwide, which corresponds to a perception of fire-prone regions and vegetation types. However, large forest fires occur in diverse ecological/climatic conditions, in tropical forests (Amazonia, Central Africa, SE Asia), boreal regions (North America, Siberian Far East), temperate to boreal forests (northern Eurasia), and with the current climate changes, in temperate deciduous forests (Central and Eastern Europe, North America, East Asia). To the best of our knowledge, many fire-affected regions which are inhabited with various tree taxa have remained underexplored in this regard.

An overview of the influence of individual plant traits on flammability components is provided using the dataset obtained by extracting knowledge from the reviewed articles. As a more detailed approach to this topic, the contribution of individual plant traits in interspecific variability related to flammability is demonstrated. A synthesis of tree species investigated so far based on the plant trait-flammability approach revealed that a smaller number of species have been investigated comprehensively, i.e. with a greater number of plant traits and flammability components included. This opens the space for further research on the relationship between environment-plant traits-flammability by collecting more empirical data and considering the specific environmental and biotic pressures that affect plant trait variability and species flammability.

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.

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