Research Square

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Does Seasonality of Leaf Terpene Content and Moisture Content Trigger Leaf Flammability Seasonal Variation?

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Research Article

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Abstract

Given the importance of terpenes and fuel moisture content (FMC) on flammability, this work aims at checking how these parameters affect leaf flammability of different native and Wildland-Urban Interfaces species (*Pinus halepensis, Cupressus sempervirens, Cupressocyparis leylandii*, and *Hesperocyparis arizonica*) across seasons in the French Mediterranean region. We found that the highest terpene diversity and content seasonally varied according to the species, with diterpene content being lower in spring for *C. leylandii*, while monoterpene and diterpene content being higher in summer and winter, respectively, for *P. halepensis*. Flammability and FMC varied according to the season but the pattern differed among species. A significant correlation between the latters was rarely observed and occurred in only one season, differing among species. The correlations between flammability and terpenes were mostly highlighted using single compounds, compared to subgroups, and they presented seasonal patterns varying among species. Checking the seasonal effect of groups of terpene compounds on flammability, there were seasonal differences in these groups according to the species and the variable tested. Mostly, these significant compounds were not the most concentrated. The best flammability drivers of each model, mostly diterpenes, except for *P. halepensis* whose flammability was mostly drove by mono- and sesquiterpenes, changed among seasons according to the flammability variable considered. When a best driver remained the same in different seasons, its effect on flammability could be opposite. In contrast, FMC was generally not a significant explanatory parameter of leaf flammability or did not improve the fit of models.

Introduction

Most plants in the Mediterranean basin are known to emit volatile (the least complex molecules with lower weight such as mono- or sesquiterpenes) or semi-volatile (heavier molecules such as diterpenes) terpenes (Llusià and Peñuelas 2000). Those plants emitting terpenes may or may not have specialized structures in which large pools of these compounds can be stored (Staudt et al. 1993; Seufert et al. 1995; Loreto et al. 1996; Llusià and Peñuelas 1998). In addition to leaf moisture and physical characteristics (such as leaf thickness, leaf density, leaf surface, or surface-to-volume ratio) largely known to influence leaf flammability (Ganteaume et al. 2018; Ormeno et al. 2020), these chemical organic compounds constitute another factor driving flammability. Indeed, given that most of them easily ignite (low flash and boiling point), they may thereby enhance plant flammability possibly affecting plants' fire behavior (White 1994; Cornelissen et al. 2003; Keeley et al. 2012). As the actual effects of these molecules on flammability have been found controversial (Cappelli et al. 1983; Alessio et al. 2008a), their role has often been neglected in studies on plant chemical ecology (e.g., Baluška 2013; Moore et al. 2014; Grootemaat et al. 2015). However, several works showed that leaf flammability was positively correlated with terpenes (e.g. monoterpene content in White 1994; Owens *et al*. 1998; Pausas *et al*. 2016) and these compounds were also found to affect litter flammability (Ormeño et al. 2009), their content (and composition) not varying significantly from green leaf to litter (Romero et al. 2019). Other studies demonstrated that the terpene content and composition affected differently the flammability components (Della Rocca et al.

2017; Romero et al. 2019) highlighting the importance of assessing flammability with different variables. Some studies also tempered the leading role of fuel moisture content (FMC) on flammability in favour of terpenes (Della Rocca et al. 2017; Ganteaume et al. 2021). Besides the obvious role of FMC in mitigating flammability by slowing down the heat transmission to the plant tissues (Pausas et al. 2016), this parameter has been shown to also interact with leaf-contained terpenes (Peñuelas and Lluisa 1997; Alessio et al. 2008b, De Lillis et al. 2009). Change in plant flammability according to the variation of hydration during the year has been demonstrated in numerous previous studies (e.g. Pellizzaro et al. 2007; Alessio et al. 2008b). However, the possible change in flammability could also be triggered by a seasonal change in terpene content which has been studied by several authors in the past (Peñuelas and Lluisá 1997; Lluisá and Peñuelas 2000; Alessio et al. 2008b; Lluisá et al. 2011), however, without linking both flammability and terpenes. This link becomes even more relevant given the importance of changes in fire activity and these compounds' dynamics due to global change factors (drought, warming and carbon dioxide emissions). The increase in temperature and decrease in water availability, on-going in a context of climate change, may produce an increase in flammability of species, especially in those that store terpenes.

Previous studies focusing on plant species commonly found in wildland-urban interfaces of SE France highlighted, for species containing terpenes, the composition and content of mono-, sesqui, and diterpenes as well as that of the single terpene compounds and their impact on flammability (Romero et al. 2019; Ganteaume et al. 2021). In any case, these studies did not assess the seasonal variation of such molecules and they also showed that species belonging to the same genus or to the same family differed in their terpene diversity and content highlighting these compounds as species-related traits.

The current work aimed at explaining the possible seasonal changes in four species' leaf flammability by the change in foliar hydration and terpene content throughout the year. In other terms, we are asking if the leaf flammability seasonal variation was triggered by a seasonal variation in terpene content and FMC and if the flammability drivers changed according to the season. It was also interesting to check if different species of the same genus (e.g. *Cupressus*) or family (e.g. Cupressacaea) presented the same pattern throughout the year, especially in terms of the seasonal variation in terpene content.

Materials And Methods

Species Studied and Sampling. The species studied in the current work, all conifers (one Pinacaea: *Pinus halepensis* Mill. 1768 and three Cupressacaea: *Cupressus sempervirens* L. 1753, *Hesperocyparis arizonica* Greene 1882 Bartel, (Adams *et al.* 2009), formerly *Cupressus arizonica*, and *Cupressocyparis leylandii* A.B. Jacks. and Dallim 1926) are common in the Wildland-Urban Interfaces (WUI) of the French Mediterranean region.

P. halepensis is the only species native to SE France while *H. arizonica* comes from the southwestern USA and *C. sempervirens* forms natural forest stands, mostly in the eastern part of the Mediterranean basin (in some parts of Tunisia, Italy, and Greece, for instance). The latter species can present two distinct varieties: var. *horizontalis* characterized by a broad pyramidal crown and horizontally spreading branches (constituting the natural stands) and var. *pyramidalis* (or *fastigata)* characterized by a compact conical crown and small angles between branches and trunk which is the variety studied in the current work. *C. leylandii* is an intergenic hybrid of the yellow cedar (*Callitropsis nootkatensis* D. Don 1824) native to northwestern America (the North American continent) and of the Monterey cypress (*Hesperocyparis macrocarpa* Hartw. 1847), a species endemic of Monterey Bay in California (USA). All of these species can be involved in fire propagation from wildland vegetation to nearby buildings, especially when they are used in ornamental hedges that provide a strong horizontal fuel continuity.

Leaves of the different species were sampled in Le Tholonet (southeastern France) where the climate is typically Mediterranean. Leaf collection was carried out in three seasons in 2016: winter, spring, and summer (i.e. January-February, April-May, and August-September) in order to grasp the variability in terms of weather conditions over a year that could affect terpene and moisture content. We chose to work only on fresh green leaves from plant canopy as a previous work on these species (Romero et al. 2019) showed that their terpene content did not differ from that of litter leaves (i.e. entire leaves undergoing the first stage of decomposition on the ground).

For each species, a maximum of 25 g of mature green leaves was collected on five different individual plants, with at least 4 m distance between plants. For each plant sampled, 6 g were used for the burning experiments, 5 g for FMC measurements, and 1 g for terpene analysis. Sampling was conducted at least 48 h following a precipitation event to avoid any impact of recent rain on FMC. Collected leaves were placed in plastic bags that were stored in a cool box for immediate transportation to the laboratory, minimising changes in water content. The samples were burned the same day they were collected on returning to the laboratory.

Terpene Identification and Quantification. After sampling, leaves were stored at -80°C to avoid any metabolic transformation. Terpene content was analyzed once for each species, using 500 mg of leaves collected from the five different plants as presented in Romero et al. (2019). Terpenes were qualitatively and quantitatively analyzed using a gas chromatography coupled to a mass spectrometry (GC-MS, 7890B–Agilent Technologies®) as described in Romero et al. (2019). Terpene identification was achieved based on the molecule retention time (which was compared to that of the pure standard when available) as well as the molecule mass spectrum which was compared to available libraries (Adams 2007; Nist 2011). To complete this identification, experimental retention indexes were calculated for each molecule identified and compared to the theoretical retention indexes of these libraries. The terpene content - calculated following the methodology presented in Romero et al. (2019) - was expressed n mg g^{-1} of dry matter (DM).

For each plant species, the contribution of terpenes was investigated both, at the subgroup (comprising monoterpenes, sesquiterpenes, and diterpenes), and the single compound (within each subgroup) levels.

Flammability Experiments. For each species, thirty samples of 1 g leaf samples were burned using a 500 W epiradiator composed of a 10 cm radiant disc according to the methodology presented in Romero et al. (2019). The variation in temperature was recorded every second during burnings using a thermocouple (chromel-alumel, k type, 30 µm diameter) positioned 1 cm above the disc center. As soon as the fuel was in contact with the epiradiator surface, time and temperature recordings were started. Five flammability variables were measured during the burning experiments: (i) time-to-ignition, (TTI, s), defined as the time necessary for the fuel to ignite once laid on the radiant disc; (ii) ignition temperature (tTTI, °C), defined as the temperature recorded when the flame appeared; (iii) flaming duration (FD, s), time elapsed between the flame occurrence and its extinction; and (iv) the maximum temperature reached during the burning (Tmax, °C).

Just before the burning experiments, three samples of 5 g-leaf subsamples of each individual were oven-dried for 48 h at 60°C in order to measure their moisture content (i.e. FMC, calculated on a dry mass basis) at the time of burning.

Data Analyses. The statistical analyses were performed on each species' dataset taking into account the content of terpenes assessed at the subgroup, and single compound levels as well as FMC as explanatory factors of flammability. Although leaf thickness was an important driver of flammability (along with other structural leaf traits such as surface-to-volume ratio) and was taken into account in our previous work (Romero et al. 2019), it was not included in the present analyses as this parameter does not significantly change from one season to another. The different flammability variables (using a single mean value per individuals of each species) were used as dependent variables. All tests were performed using StatGraphics Centurion XVII – X64 software (StatPoint Technologies, Inc®).

First, we performed variance analyses (one-way ANOVA) to highlight the effect of season on FMC, terpene content and flammability for each species. In these analyses, the *Kruskal-Wallis* test was performed instead of the Fisher test because of the lower amount of data per season.

Then, for each species and season, simple linear regression analyses (*Fisher* test) were performed to highlight any significant correlations (positive or negative) existing between leaf parameters (FMC, terpenes) and flammability. When FMC explained a significant proportion of the variability of the relationship with a given flammability variable, we used the residuals of the regression as a moisture-corrected measure of this variable. This corrected variable was then regressed against the terpene content in order to only highlight the effect of terpenes avoiding the bias of the above-mentioned factors (see Pausas et al. 2016). In the simple linear regression analyses, the adjusted R^2 value was used to account for the variation in flammability.

Finally, partial least square (PLS) regression analyses were performed to determine the relative importance of the different fuel characteristics (first using terpene content only, then adding FMC in the models) on each flammability variable. These analyses allowed highlighting a pool of significant terpene compounds, along (or not) with FMC, affecting flammability as well as those being the best drivers according to the season. The significance of components in the models was determined according to uncertainty tests carried out within a full cross-validation. The scaled regression coefficients of the PLS models provided information on the effect (positive or negative) of each parameter on flammability metrics and its relative weight in the fitted model (absolute value) indicated the relative importance in predicting each flammability variable.

Results

Seasonal Variation of Terpenes and FMC. Analyses by GC-MS of the terpenes contained in leaves of the four species studied led to the identification of 55 different terpene compounds, *Cupressocyparis leylandii* presenting the highest terpene diversity (34 compounds identified: 11 monoterpenes, 12 diterpenes, and 11 sesquiterpenes) regardless of the season (Tab. 1). The season of the highest terpene diversity differed among species, summer for *C. leylandii* (displaying mostly diterpenes) as well as for *Heterocyparis arizonica* (displaying mostly sesquiterpenes), and winter and summer for *Cupressus sempervirens* (displaying mostly diterpenes and sesquiterpenes). For *Pinus halepensis,* the highest diversity was observed in the three seasons and concerned the monoterpenes. Overall, there was a low inter-individual variation of this number of compounds (<20%) regardless of the season (except for diterpenes for *H. arizonica* in winter and for *P. halepensis* in spring and summer).

Regarding the terpene subgroup, the monoterpene diversity did not significantly vary according to the season, except for *C. sempervirens* (*KW*= 10.29, p= 0.006) for which the number of molecules was the highest in winter and summer. Sesquiterpene diversity was significantly higher in summer for *H. arizonica* and in winter for *C. sempervirens*. Except for *H. arizonica*, the diterpene diversity seasonally varied and was significantly higher in summer for *C. leylandii* and *C. sempervirens* (*KW*= 14.0, p= 0.0009 and *KW*= 12.87, p= 0.0016, respectively) and in winter and spring for *P. halepensis* (*KW*= 10.96, p=0.0042). There was no seasonal variation in diversity of mono- and sesquiterpenes for *C. leylandii* as well as for *P. halepensis*, and of mono- and diterpenes for *H. arizonica*. For each species, the composition of the extracted compounds as well as the percentage of each family on the total amount of terpenes are presented in Suppl. Mat. 1.

Regarding the single terpene compounds, the content of the most concentrated compounds characterizing each species were the sesquiterpenes β-caryophyllene for *P. halepensis* and cadina-1(6),4-diene <cis> for *H. arizonica*, the diterpene totarol for *C. sempervirens,* and the monoterpenes δ3-carene, α-pinene, and β-pinene for *C. leylandii*. It is worth noting that some compounds were not found all year round. Indeed, for *C. leyandii*, two diterpene compounds (abietal-4 epi and cembrene A) were detected only in summer (and were among the main compounds, i.e. content ≥ 0.1 mg g^{-1}: 0.34 and 0.14 mg g^{-1}, respectively) as well as the two sesquiterpenes muurol-5-en-4-one and muurol-5-en-beta-ol <cis> (both minor compounds) for *H. arizonica.* For *P. halepensis*, the diterpene cembrene was not detected in summer (but was among the main compound in winter: 0.34 mg g^{-1}). *C. sempervirens* presented the highest number of compounds (eight in total, one monoterpene, five sesquiterpenes, and two diterpenes) missing over a year (mostly in spring) but all of them were minor compounds (Suppl. Mat. 1).

Regardless of the species, the annual total terpene content did not vary according to the season but the species studied presented different seasonal patterns for the different terpene subgroups (Fig. 1). For *C. leylandii* (Fig. 1a), only diterpene content significantly varied among seasons, the content being lower in spring than in the other seasons. Regardless of the season, monoterpenes presented the highest values in this species. For *P. halepensis* (Fig. 1b), mono- and diterpene content seasonally varied but presented different patterns, the monoterpene subgroup being more concentrated in summer while that of diterpenes showed higher values in winter. Regardless of the season, the sesquiterpene subgroup presented the highest content, mostly due to β-caryophyllene (on average, 45% of the total content). *H. arizonica* and *C. sempervirens* did not present any seasonal variation in their terpene content, regardless of the subgroup (Fig. 1c, d).

The results obtained at the terpene subgroup level were confirmed by the analyses at the single compound level. For *C. leylandii*, only the content of six diterpene compounds differed among seasons, all of them among the main compounds in one season or another (cembrene being a major compound in winter and summer, isophyllocladene, manool oxide and manool oxide 4 epi only in winter while abietal 4 epi and cembrene A were detected in summer only). For this species, the most concentrated compounds were found in winter and were diterpenes. For *P. halepensis*, only the content of the diterpene cembrene varied seasonally and this molecule was not identified in summer; the most concentrated compounds were found in summer and belonged to the subgroup of monoterpenes. As for the subgroup level, the content of each single compound did not varied across seasons for *H. arizonica* and *C. sempervirens*. Even if in these species, some compounds were not present all year round (therefore presenting marked seasonal differences), all of them were minor compounds (Fig. 2). One of the explanations of the very low number of significant results was the high variability of content among seasons for most compounds, regardless of the species (e.g. the monoterpene myrcene for *P. halepensis*, the diterpene totarol for *C. sempervirens*, or the monoterpene β-pinene for *C. leylandii;* Suppl. Mat. 1).

The moisture content of the leaf samples of the different conifer species ranged from 91.41 (± 13.72) % (*P. halepensis*) to 125.95 (± 4.03) % (*H. arizonica*). Except for *H. arizonica* that presented the highest values regardless of the season, FMC varied according to the season but the pattern differed among species, opposing *C. leylandii* (increasing trend from winter to summer) to *C. sempervirens* and *P. halepensis* (highest values in winter and lower foliar hydration in spring and summer) (Fig. 3).

Role of Terpenes and FMC on Species' Flammability among Seasons. According to the variable tested, flammability could present or not a seasonal variation and the species studied differed in their seasonal pattern (Fig. 4). Except for tTTI which did not show a clear seasonal trend, all of the other variables varied seasonally for *C. leylandii*, flammability being the lowest in winter (but it is worth noting the long TTI in summer as well). Only Tmax varied according to the season for *H. arizonica* (highest values in spring) and tTTI for *C. sempervirens* (highest values in summer) while tTTI and TTI differed among seasons for *P. halepensis* (highest flammability in spring).

Surprisingly, a significant correlation between FMC and flammability was observed only in one season (which differed according to the species), except for *C. leylandii* for which the results were not significant throughout the year (Table 2). Only one flammability variable was significantly affected by FMC (which also differed according to the species): TTI for *H. arizonica* (in summer) and *C. sempervirens* (in winter) as well as Tmax for *P. halepensis* (in spring). These variables were therefore FMC-corrected when used in the univariate regression analyses linking flammability with terpenes. Regardless of the species, FMC decreased flammability.

The effect of the terpene subgroup content on flammability varied seasonally according to the species, except for *H. arizonica* (Table 3). Terpene content (diterpene) affected flammability (negatively, increasing TTI) only in summer for *C. leylandii* while, for *C. sempervirens*, this terpene subgroup enhanced flammability (increasing FD) in both spring and summer. For *P. halepensis*, the role of terpenes varied according to the season, diterpene and sesquiterpene content enhancing flammability (decreasing tTTI) in winter and summer, respectively, but presenting the opposite effect in spring. During this latter season, monoterpene content presented contrasting effects on flammability according to the variable considered (decreasing Tmax but also TTI).

When the same analyses were performed at the single compound level, taking into account both main and minor compounds, a higher number of significant correlations was highlighted between terpenes and flammability, the seasonal trend differing among species (Table 4). For *H. arizonica*, using the main compounds in the models, the correlations were not significant regardless of the flammability variable considered, as at the subgroup level. However, when the minor compounds were taken into account in the analyses, the correlations became significant in summer (only one compound affected flammability: the diterpene totarol, decreasing TTI) and in winter (four compounds, one sesquiterpene and three diterpenes differing from totarol, all enhancing flammability). For *C. leylandii*, significant relationships were highlighted in winter and summer but not in spring, regardless of the terpene subgroup. The main compounds involved were diterpenes and mostly mitigated flammability (all except manool oxide that presented the opposite effect on TTI and tTTI in winter). The minor compounds significantly affecting flammability, also in winter and summer, were diterpenes (still mostly mitigating flammability) and sesquiterpenes. The molecules differed between the two seasons but it is worth noting that one of the main compounds in winter, manool oxide, was found among the minor compounds in summer. For *C. sempervirens*, the significant molecules and their impact differed among seasons. They did not affect flammability in winter and only one compound (monoterpene δ3-carene) presented a significant effect (positive) on flammability in spring. Most significant correlations were highlighted in summer and involved the two main significant compounds, the diterpene totarol enhancing flammability in contrast to the monoterpene α-pinene. The significant minor compounds were all diterpenes and mitigated flammability except abietadiene. The role of the terpene compounds (both main and minor) on flammability was significant in the three seasons for *P. halepensis*, especially in winter and spring. The significant molecules (all sesquiterpenes or monoterpenes except one diterpene: manool oxide) and their impact differed among seasons (e.g. the monoterpene myrcene increasing flammability in winter in contrast to summer) except for the sesquiterpene germacrene (increasing FD in summer and winter) and the monoterpene α-pinene (mitigating flammability in winter and spring).

Seasonal Variation of Combined effects of Terpene Compounds and FMC on Flammability. Checking the possible seasonal patterns in the species studied, we found that there were seasonal differences in the groups of terpene compounds significantly explaining flammability and in their effects according to the species and the variable taken into account. The results were not significant in spring for *C. leylandii* (except for tTTI; Fig. 5), in winter, regardless of the variable considered for *C. sempervirens* (Fig. 6) and for *H. arizonica* (Fig. 7) regarding tTTI, and in summer regarding Tmax and tTTI for *P. halepensis* (Fig. 8). The significant compounds highlighted in summer mostly enhanced FD for *C. leylandii* and *H. arizonica* in contrast to other molecules mitigating flammability (regarding Tmax and tTTI) for the latter species and for *C. sempervirens* (regarding Tmax). Those identified in winter presented the opposite effect on flammability for *C. leylandii* as well as a positive effect for *H. arizonica* and *P. halepensis* (only the monoterpene terpinolene regarding TTI). The compounds identified in spring enhanced flammability for *C. sempervirens (*FD and Tmax) and *P. halepensis* (tTTI) while it was the opposite for *C. sempervirens* (TTI) and *P. halepensis* (FD and Tmax). Only three compounds were significant at the same time in winter and summer (e.g. the sesquiterpenes cedrol and β-elemene affecting Tmax with opposite effects) for *C. leylandii* and only one compound for *H. arizonica* (the diterpene nezukol correlated with TTI). Also three compounds were significant in spring and summer for *C. sempervirens* (e.g. the diterpene totarol correlated with FD), for *P. halepensis* (e.g. the monoterpene limonene correlated with Tmax), and for *H. arizonica* (e.g. the diterpene ferruginol correlated with Tmax, TTI, and tTTI). Two compounds were significant in winter and spring (e.g. the diterpene sempervirol correlated with FD, Tmax, and TTI) for *H. arizonica* and *P. halepensis* (e.g. the monoterpene terpinolene with TTI). The opposite effect could also occur between different variables (e.g. the monoterpene terpinen 4 ol with Tmax and Ttti for *C. leylandii*). Regarding this latter species, a compound significant in the three seasons was found (the sesquiterpene germacrene D presenting the opposite correlation with FD in winter-summer *vs* spring). Opposite correlations were also observed between different compounds of the same terpene subgroup accross different seasons (e.g. the diterpenes thunbergol *vs* totarol with Tmax for *C. sempervirens*) and sometimes within the same season (e.g. the monoterpenes α-pinene *vs* sabinene hydrate with FD in spring for *H. arizonica*).

When the significant compounds highlighted in each model were compared to the main terpene compounds (content ≥ 0.01 mg g^{-1}) identified for each species and season, it could be noted that significant compounds were not the most concentrated with a few exceptions. The following molecules mostly differed among species: the monoterpene α-pinene in spring and summer for *H. arizonica*, the monoterpene δ3-carene in winter for *C. leylandii,* the diterpene totarol as well as the monoterpene α-pinene in spring and summer *for C. sempervirens*, and the monoterpene myrcene in summer as well as the sesquiterpene β-caryophyllene in spring for *P. halepensis* (Fig. 4 and Suppl. Mat. 1).

Regardless of the species, the best drivers of each model (terpene compound presenting the highest regression coefficient explaining most of the flammability variation) changed among seasons according to the flammability variable considered (Tab. 5). When the best driver was the same at different seasons and for a given flammability variable, its effect on this variable could change (for instance, the monoterpene terpinolene positively affected TTI in winter but negatively in spring) or not (for example, the diterpene sempervirol positively affected FD in winter and in spring). The best drivers were most often diterpene compounds (displaying mostly a negative effect in winter and summer for *C. leylandii*, a positive effect in spring but the opposite in summer for *C. sempervirens*, and a positive effect regardless of the season *for H. arizonica*), regardless of the season and the variable, except for *P. halepensis.* For this latter species, flammability was mostly driven by mono- (with a positive effect in spring in contrast to the other seasons) and sesquiterpene (mostly with a positive effect on flammability) compounds (Tab. 5).

The seasonal variation of the proportion of flammability (R^2) explained by terpene compounds (Tab. 6) was highlighted in the different models. When the results were significant within a given species, the season in which the coefficient of determination, R^2, was the highest varied according to the flammability variable. The highest proportion of FD and TTI explained by terpenes occurred in the models run on the summer datasets except for *H. arizonica* and *P. halepensis* (spring datasets) while that of tTTI occurred in the models run on the spring dataset except for *P. halepensis* (winter dataset). The highest proportion of Tmax was found in the models run on the summer datasets for *C. sempervirens* and *H. arizonica*, on the winter dataset for *C. leylandii*, and on the spring dataset for *P. halepensis*.

Regarding the role of FMC in the explanation of flammability, in most cases, either FMC taken as parameter in the models or the results of the analyses were not significant, or the fit did not improve when FMC was added to the models (Suppl. Mat. 2). The fit improved when FMC was added to models in spring for *C. leylandii* (all results significant in contrast to the analyses taking into account only terpenes, except for tTTI for which the proportion of variation explained remaining the same) and for *P. halepensis* (regarding Tmax, FMC being the best driver). A better fit also occurred in winter for *H. arizonica* and *P. halepensis* (for both species, regarding TTI only) as well as for *C. sempervirens* (regarding TTI and tTTI), in contrast to the previous results, and in summer (for FD and tTTI). For the former species, FMC was the only best driver of TTI in summer and in winter for the latter.

Discussion

Seasonality of Traits and Flammability. A seasonal variation in flammability for Mediterranean species has already been reported by several authors (e.g. Rodriguez Añón et al. 1995; Alessio et al. 2008b). According to these previous studies, flammability - characterized by one (for *C. sempervirens* and *H. arizonica)* and up to three (for *C. leylandii*) significant variables – varied seasonally. A strong seasonality was found for TTI and Tmax (highest flammability in spring) only for *C. leylandii, P. halepensis* (for the former variable), and *H. arizonica* (for the latter) in contrast to *C. sempervirens* whose flammability was surprisingly higher in winter. Indeed, the driest seasons at the time of the sampling were spring and summer (Suppl.Mat.3).

FMC also presented seasonal variations (except for *H. arizonica)* with differences among species. This result agreed with Pelizzaro et al. (2007) who showed that different Mediterranean species did not show the same seasonal pattern of FMC throughout the year and, in some of them, moisture content did not vary. Usually, for tree species, there is no pronounced decrease in FMC at the driest season, as found Viegas et al. (2001) for *P. halepensis*, the trees presenting deeper root systems than most Mediterranean shrubs (Kummerow 1981; Correia et al. 1992; Alessio et al. 2004). However, this result was in accordance with what we found for *H. arizonica* but not for *P. halepensis*. In some cases, FMC showed seasonal patterns that differed from those of flammability (e.g. for *C. sempervirens)*. *C. sempervirens* and *P. halepensis* presented lower moisture content in summer and spring, the driest seasons in 2016 (Suppl. Mat. 3), but the former was more flammable in winter according to tTTI only (the results for the other variables were not significant). This means that some species were more flammable during the most humid season (winter), as *C. leylandii.* This species presented the lowest FMC in winter in contrast to the other species despite the fact that they were all sampled from the same location and at the same time; therefore, they were subjected to the same weather conditions throughout the year. One explanation for this latter species' peculiar pattern would be that the plants sampled could have been watered during summer (as located not far from housing). According to several studies (Peñuelas and Lluisã 1997; Owens et al. 1998; Massari and Leopaldi 1998; McKenzie et al. 2004, Alessio et al. 2008b), the seasonal pattern of flammability is usually in accordance with the progressive increase in temperatures and water demand. This would also agree with the results obtained for *P. halepensis*. Indeed, in the current study, the seasons with the lowest leaf hydration regarding this species were spring and summer (to a lower extent), corresponding to the highest flammability. However, the effect of FMC (negative) on flammability was significant only in one season, which differed according to the species (higher FMC in summer for *H. arizonica* and in winter for *C. sempervirens,* affecting only TTI, as well as in spring affecting only Tmax for *P. halepensis*). We did not find, as Pelizzarro et al. (2007), that most species showed a maximum of moisture content and an increase in TTI in spring; but, as these authors highlighted, some of our species (*H. arizonica, C. sempervirens*) did not present any seasonal variation of TTI, or of FMC (for *H. arizonica*, only).

Terpene content and diversity also presented seasonal variations with patterns that could differ from those of flammability according to the species. Indeed, total terpene diversity was higher in summer for *C. leylandii* (due to higher diversity in diterpenes) and *H. arizonica* (due to higher diversity in sesquiterpenes) while *P. halepensis* and *C. sempervirens* presented the same pattern as flammability (high diversity and flammability in spring and winter respectively). The seasonal variation of terpene content also differed according to the level of terpene identification (i.e. subgroup and single compound) but was significant only in two species. Indeed, diterpene content was higher in winter and summer for *C. leylandii* and in winter for *P. halepensis* for which monoterpene content was higher in summer as well, which agreed with Alessio et al. (2008a). In contrast to our results regarding this latter species, Lluisiá and Peñuelas (2000) highlighted a drop in terpene content in spring, regardless of the compound. Seasonal variations in terpene concentrations (and emissions) have been reported in several previous studies and have confirmed that the season of peak concentrations seemed to be species-specific: in spring for Scots pine and some junipers (Adams, 1970), in summer for Douglas fir and other coniferous species (Wagner et al. 1990; Gambliel and Cates 1995; Zou and Cates 1995), in autumn-winter but with larger terpene concentrations also observed at the end of summer, for *P. halepensis* (Lluisá and Peñuelas 2000). In the current study, when a variation of the terpene subgroup content was highlighted, it was due to the seasonal variation of some terpene single compounds. However, most terpene single compounds did not present a significant seasonal variation (none for *C. sempervirens* and *H. arizonica*, only one for *P. halepensis,* and six for *C. leylandii*), for which only trends could be highlighted mostly due to the high inter-individual variation of their content (high standard deviation; Suppl. Mat. 1). Often, their seasonal trends could differ among species (e.g. monoterpene myrcene presented the highest content in spring for *C. leylandii* while it was in summer for *P. halepensis*). Previous studies also showed a spatial variation in terpene content resulting from differences in environmental conditions, such as drought stress or soil fertility (Gilmore 1977; Muzika et al. 1989; Kainulainen et al. 1992; Owens et al. 1998; Ormeño et al. 2008) but this was not the case in the current work since the studied species were collected from the same site.

Seasonal Variation of the Effect of Terpenes on Flammability. As already showed in Ganteaume et al. (2021), the number of significant results increased from the subgroup to the single compound level regardless of the season. Except for *H. arizonica* (no significant effect regardless of the season), the effect of the terpene subgroup content on flammability seasonally varied according to the species, *C. leylandii*'s and *C. sempervirens'* flammability being mainly affected by diterpenes (e.g. negative effect in summer for the former and positive effect in spring and summer for the latter) while *P.halepensis* was more affected by the other subgroups. Moreover, a same subgroup could present antagonist effects on flammability from one season to another (negative effect of diterpenes in winter becoming positive in spring). Regarding the single compound level, the seasonal trend also differed among species. The effect was positive mostly in winter for *H. arizonica* (two diterpenes) while it was negative mostly in winter (six diterpenes) for *C. leylandii* and mostly in summer (three diterpenes, one monoterpene) for *C. sempervirens*. Variable effects due to mono- and sesquiterpenes in the three seasons (between two and five compounds involved) occurred for *P halepensis*. This underlines the importance of searching for terpene effects at a more refined level than subgroup content, also using the minor compounds in the analyses (given some correlations became significant). Our results also showed that the effect of one single compound could differ among seasons, depending on the flammability variable considered, confirming the result at the subgroup level (the monoterpene myrcene presenting a positive effect on Tmax in winter and on TTI in summer for *P. halepensis*). This result stresses the importance of taking into account several components of flammability, as already highlighted by Ganteaume et al. (2021). It is worth noting that, in contrast to the results of Alessio et al. (2008), species with higher content in terpene volatiles were not the most flammable. Indeed, *P. halepensis*, the most flammable species in the current work, did not present the highest terpene content (as opposed to *C. leylandii)*. This could be due to the interaction between FMC and terpene content.

Seasonal Variation of the Combined Effect of Single Terpene Compounds and FMC on Flammability. We tested whether terpenes, as significant flammability drivers, varied according to the season and if FMC played a role in the seasonal variation of flammability. Indeed, several previous studies (Bernard-Degan

1988; Owens et al. 1998; Llusia and Penuelas 2000; Weise et al. 2005; Pellizzaro et al. 2009) dealt with the seasonal variation in flammability, FMC, or terpene content but few addressed the interactions between these parameters (Della Rocca et al. 2017; Ganteaume et al. 2021) but still, without tackling the effect of the season.

Checking the possible seasonal patterns in the species studied, we found that there were seasonal differences in the groups of terpene compounds significantly explaining flammability and their effects (positive or negative) contrasted according to the species and the variable taken into account. Only a few compounds were significant at the same time in two seasons, mostly for *H. arizonica* (only one in the three seasons, the sesquiterpene germacrene D for *P. halepensis*). Except for *H. arizonica*, these significant compounds could present an opposite effect on flammability among seasons according to the variable tested. These opposite effects could also occur between different variables and between different compounds of the same terpene subgroup in different seasons and sometimes in the same season, regardless of the species. Previous studies already showed that monoterpene content, for instance, presented the opposite effect on flammability according to the molecule considered (Owens et al. 1998). Except for a few significant compounds, which mostly differed among species and seasons, they were not the most concentrated molecules.

Regardless of the species, the best drivers of each model mostly changed among seasons according to the flammability variable considered. When the best driver was the same accross different seasons, the effect on the variable could change in some cases. These compounds were mostly diterpenes (with variable effects according to the species and the season), except for *P. halepensis* mostly driven by monoterpenes (variable effect in spring) and sesquiterpenes (positive effect on flammability) compounds. For a given species, the seasonal variation of the proportion of flammability (R^2) explained by terpene compounds varied according to the flammability variable (in spring and summer for *H. arizonica* and *C. sempervirens*, winter and spring for *P. halepensis*, and in the three seasons for *C. leylandii*.

Despite the fact that some studies showed that flammability strictly depends on leaf water availability for a given species, the moisture content and the plant structure interact and indirectly influence the fire behaviour (Alessio et al. 2008b; Fernandes and Cruz 2012; Zhao et al. 2014). Previous laboratory-scale studies identified leaf moisture content as a key flammability variable (Pausas et al. 2016), that interacts with the terpenes contained in the leaves (Alessio et al. 2008b, De Lillis et al. 2009). However, Della Rocca et al. (2017) and Ganteaume et al (2021) confirmed that flammability was not always driven by FMC but also by the terpene content and that, in some cases, there was an interaction between both leaf parameters. In the current study, we also highlighted that each species presented its own seasonal pattern regarding the different parameters. Regarding the role of FMC in the explanation of flammability, most of the time, FMC was not significant or did not improve the fit of the models (most changes occurred in spring for *C. leylandii*, when the terpene content was the lowest, as well as in winter and summer for *C. sempervirens*, but at a lower extent). Other fuel parameters could play a more important role in the explanation of flammability in the seasons for which the fits were the poorest.

Conclusions

The aim of this work as to assess what part of terpene content and FMC played on the seasonal variation of flammability of different conifer species found in the WUI of SE France (*Pinus halepensis, Cupressus sempervirens, Cupressocyparis leylandii,* and *Hesperocyparis arizonica*) and if the flammability drivers varied seasonally. The season of the highest terpene diversity (diterpene composition for *C. leylandii* as well as *P. halepensis*, and sesquiterpene composition for *H. arizonica*) and the terpene subgroup content differed among species, presenting different seasonal patterns (diterpene content lower in spring for *C. leylandii*, while monoterpene and diterpene content higher in summer and in winter, respectively for *P. halepensis*). FMC varied according to the season but the pattern differed among species and could also differ from that of flammability according to the variable tested.

Significant correlations between FMC and flammability were rarely observed (solely in one season, for only one flammability variable, differing among species) in contrast to those with terpene content (however, more frequent at the single compound level than for the terpene subgroup), the seasonal trend differing among species. Checking the seasonal variation of groups of terpene compounds on flammability, we found that there were seasonal differences in these groups according to the species and the variable tested, the molecules often displaying opposite effects (among flammability variables or seasons). As a whole, these significant compounds were not the most concentrated, except for a few molecules. The best drivers of each model, mostly diterpenes, except for *P. halepensis* (mono- and sesquiterpenes), changed among seasons according to the flammability variable considered. When the best driver was the same at different seasons, for a given flammability variable, its effect on this variable could change. In contrast, mostly, FMC was not a significant parameter or did not improve the fit of models.

Even if *Pinus halepensis* is the most flammable species, the flammability of the others studied species could also be enhanced by some terpene single compounds, especially in spring and summer (while it is in winter and summer for *P. halepensis*), meaning that these species can act on the fire risk not just in summer, as it is commonly assumed in the Mediterranean regions, and this has to be taken into consideration in the forest and wildland-urban interfaces management in this area.

Declarations

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Tables

Table 1 Terpene diversity (number of compounds) according to the terpene subgroup in the four species studied

Terpene subgroup/Season	Winter	Spring	Summer
Cupressocyparis leylandii			
MT	11	11	11
ST	11	11	11
DT	10	10	12
Total	32	32	34
Hesperocyparis arizonica			
MT	6	6	6
ST	8	8	9
DT	7	7	7
Total	21	21	22
Cupressus sempervirens			
MT	6	5	6
ST	8	6	6
DT	7	5	8
Total	21	16	20
Pinus halepensis			
MT	7	7	7
ST	6	6	6
DT	5	5	4
Total	18	18	17

MT: monoterpenes, ST: sesquiterpenes, DT: diterpenes

Table 2 Correlations between fuel moisture content (FMC) and flammability (TTI: time-to-ignition, Tmax: maximum temperature) throughout the year in the four species studied

Species/Season	Winter	Spring	Summer
Hesperocyparis arizonica	NS	NS	TTI_FMC: F=58.57, p=0.0046, R^2=0.94, positive effect
Cupressocyparis leylandii	NS	NS	NS
Cupressus sempervirens	TTI_FMC: F=288.96, p=0.0004, R^2=0.99, positive effect	NS	NS
Pinus halepensis	NS	Tmax_FMC: F=14.2, p=0.033, R^2=0.77, negative effect	NS

Simple linear regression, *F*: *Fisher* test, p: probability, R^2: adjusted coefficient of determination, NS: not significant). N=xx

Table 3 Correlations between terpene subgroup content (MT: monoterpenes, ST: sesquiterpens, DT: diterpenes) and flammability (TTI: time-to-ignition, FD: flaming duration, Tmax: maximum temperature, tTTI: ignition temperature; in italic: FMC-corrected variables) according to the season for the four species studied

Species/Season	Winter	Spring	Summer
Hesperocyparis arizonica	NS	NS	NS
Cupressocyparis leylandii	NS	NS	DT_TTI: *F*=30.86, p=0.0115, R^2=0.88, positive effect
Cupressus sempervirens	NS	DT_FD: *F*=12.02, p=0.04, R^2=0.73, positive effect	DT_FD: *F*=121.38, p=0.0081, R^2=0.98, positive effect
Pinus halepensis	DT_tTTI: *F*=17.67, p=0.0246, R^2=0.81, negative effect	MT_TTI: *F*=16.72, p=0.0264, R^2=0.80, negative effect	ST_tTTI: *F*=16.52, p=0.0269, R^2=0.79, negative effect
		DT_tTTI: *F*=22.18, p=0.0181, R^2=0.84, positive effect	
		MT_*Tmax*: *F*= 10.49, p=0.048, R^2=0.70, negative effect	
		ST_tTTI: *F*=18.22, p=0.0236, R^2=0.81, positive effect	

Simple linear regression, *F*: *Fisher* test, p: probability, R^2: adjusted coefficient of determination, NS: non-significant

Table 4 Correlations between terpene compound content (divided into main content: ≥ 0.05mg g^{-1} and minor content: < 0.05mg g^{-1}; normal font: monoterpenes, italic font: sesquiterpenes, and bold font: diterpenes) and flammability (TTI: time-to-ignition, FD: flaming duration, Tmax: maximum temperature, tTTI: ignition temperature; in italic: FMC-corrected variables) according to the season

Heterocyparis arizonica	Winter	Spring	Summer
main compounds	NS	NS	NS
minor compounds	TTI_**sempervirol**	NS	TTI_**totarol**
	F=43.29, p=0.0071, R^2=0.91, negative effect		*F*=12.36, p=0.039, R^2=0.74, negative effect
	FD_**sempervirol**		
	F=63.00, p=0.0042, R^2=0.94, positive effect		
	FD_*α aconerol*		
	F=17.66, p=0.025, R^2=0.81, positive effect		
	Tmax_**nezukol**		
	F=38.34, p=0.0085, R^2=0.90, positive effect		
Cupressocyparis leylandii	Winter	Spring	Summer
main compounds	TTI_**manool oxide**	NS	TTI_**cembrene**
	F=13.53, p=0.035, R^2=0.76, negative effect		*F*=219.13, p=0.0007, R^2=0.98, positive effect
	Tmax_**nezukol**		
	F=11.00, p=0.045, R^2=0.71, negative effect		
	FD_**nezukol**		
	F=20.73, p=0.020, R^2=0.83, negative effect		
	tTTI_**manool oxide**		
	F=14.14, p=0.033, R^2=0.77, positive effect		
	tTTI_**totarol**		

	F=16.83, p=0.026, R^2=0.80, positive effect		
minor compounds	Tmax_*β-elemene*	NS	FD_*copaene*
	F=12.81, p=0.037, R^2=0.75, negative effect		*F*=10.98, p=0.045, R^2=0.71, positive effect
	Tmax_*cedrol*		TTI_*elemol*
	F=13.21, p=0.036, R^2=0.75, positive effect		*F*=44.33, p=0.0069, R^2=0.91, positive effect
	TTI_**isopimara**		TTI_**isophyllocladene**
	F=22.96, p=0.017, R^2=0.85, negative effect		*F*=23.82, p=0.016, R^2=0.85, positive effect
			TTI_**manool oxide**
			F=46.18, p=0.0065, R^2=0.92, positive effect
			TTI_**manool oxide 13 epi**
			F=1580.47, p<0.0001, R^2=0.99, positive effect
Cupressus sempervirens	Winter	Spring	Summer
main compounds	NS	TTI_δ 3 carene	TTI_α pinene
		F=13.93, p=0.033, R^2=0.76, negative effect	*F*=55.14, p=0.018, R^2=0.95, positive effect
			FD_**totarol**
			F=209.06, p=0.0047, R^2=0.99, positive effect
minor compounds	NS	NS	FD_**abietadiene**
			F=19.89, p=0.047, R^2=0.86, positive effect

			Tmax_**sclarene**
			F=19.81, p=0.047, R^2=0.86, negative effect
			Tmax_**thunbergol**
			F=52.24, p=0.019, R^2=0.94, negative effect
			TTI_**sandaracopimarinal**
			F=34.28, p=0.028, R^2=0.92, positive effect
Pinus halepensis	Winter	Spring	Summer
main compounds	FD_α pinene	*Tmax* _α pinene	FD_*germacrene*
	F=15.79, p=0.028, R^2=0.79, negative effect	*F*=63.80, p=0.0041, R^2=0.94, negative effect	*F*=15.45, p=0.029, R^2=0.78, positive effect
	FD_β pinene	*Tmax*_β pinene	TTI_myrcene
	F=18.35, p=0.023, R^2=0.81, positive effect	*F*=20.39, p=0.020, R^2=0.83, negative effect	*F*=13.61, p=0.034, R^2=0.76, positive effect
	FD_*germacrene*	TTI_β pinene	
	F=61.95, p=0.0043, R^2=0.94, positive effect	*F*=16.83, p=0.026, R^2=0.80, negative effect	
	Tmax_myrcene	tTTI_*α humulene*	
	F=10.51, p=0.048, R^2=0.70, positive effect	*F*=16.62, p=0.027, R^2=0.80, positive effect	
	tTTI_*β caryophyllene*		
	F=17.04, p=0.026, R^2=0.80, positive effect		
minor compounds	FD_limonene	*Tmax*_α thujene	FD_*cadinene*
	F=14.62, p=0.031, R^2=0.77, positive effect	*F*=11.89, p=0.041, R^2=0.73, negative effect	*F*=22.08, p=0.018, R^2=0.84, positive effect
	TTI_terpinolene	*Tmax*_limonene	FD_*cubebol*

	F=12.39, p=0.039, R^2=0.74, positive effect	F=13.39, p=0.039, R^2=0.76, negative effect	F=29.25, p=0.012, R^2=0.88, positive effect
	tTTI_*cadinene*	TTI_limonene	
	F=10.71, p=0.047, R^2=0.71, negative effect	F=13.36, p=0.035, R^2=0.76, negative effect	
	tTTI_**manool oxide**	TTI_terpinolene	
	F=24.50, p=0.016, R^2=0.85, positive effect	F=16.96, p=0.026, R^2=0.80, negative effect	

Simple linear regression: F= *Fisher* test, p= probability, R^2= adjusted coefficient of determination, NS= non-significant

Table 5 Main driving terpene compounds and their effect (+: positive, -: negative) on flammability according to the season for the four species studied

		Winter	**Spring**	**Summer**
Cupressocyparis leylandii	FD	DT nezukol (-)		MT sabinene hydrate (+)
	Tmax	DT cedrol (+), ST β elemene (-), ST nerodiol (-), DT nezukol (-)		
	TTI	DT isopimara (-)		DT manool oxide 13 epi (+), DT cembrene (+)
	tTTI	DT manool oxide (+), DT totarol (+)	MT terpinene 4 ol (-)	ST elemol (+)
Cupressus sempervirens	FD		DT sclarene (+)	DT totarol (+)
	Tmax		DT abienol (+)	DT sclarene (-)
	TTI		MT δ 3 carene (-)	MT α pinene (+), DT sandaracopimarinal (+)
	tTTI		DT sandaracopimarinal (-)	MT limonene (-), DT sandaracopimarinol (+)
Hesperocyparis arizonica	FD	DT sempervirol (+)	DT sempervirol (+)	DT abietal 4 epi (+)
	Tmax	DT nezukol (+)	DT sempervirol (+)	MT sabinene hydrate (-)
	TTI	DT sempervirol (-)	DT Ferruginol (+)	DT totarol (-)
	tTTI		MT α pinene (-)	DT Ferruginol (+)
Pinus halepensis	FD	ST germacrene D (+)	DT cembrene (-)	ST cadinene (+), ST cubebol (+)
	Tmax	MT myrcene (+)	MT α pinene (-)	
	TTI	MT terpinolene (+)	MT β pinene (-), MT terpinolene (-)	MT myrcene (+)
	tTTI	DT manool oxide (+)	ST α humulene (+), ST β caryophyllene (+)	

MT: monoterpene, ST: sesquiterpene, DT: diterpene, FD: flaming duration, Tmax: maximum temperature, TTI: time-to-ignition, tTTI: ignition temperature

Table 6 Results of Partial Least Squares regression analyses showing the proportion of flammability (FD: flaming duration, TTI: time-to-ignition, Tmax: maximum temperature, tTTI: ignition temperature) explained by the different terpene compounds according to the models run on the four species' datasets

		Winter	Spring	Summer
C. leylandii	FD	p=0.010; R^2=0.92 ; 1 component	NS	p=0.0002; R^2=0.99 ; 1 component
	Tmax	p=0.007; R^2=0.93 ; 1 component	NS	p=0.034; R^2=0.82 ; 1 component
	TTI	p=0.034; R^2=0.82 ; 1 component	NS	p=0.0009; R^2=0.98 ; 1 component
	tTTI	p=0.047; R^2=0.78 ; 1 component	p=0.018; R^2=0.99 ; 3 components	p=0.002; R^2=0.97 ; 1 component
C. sempervirens	FD	NS	p=0.013; R^2=0.90 ; 1 component	p=0.023; R^2=0.95 ; 1 component
	Tmax	NS	p=0.028; R^2=0.84 ; 1 component	p=0.002; R^2=0.99 ; 2 components
	TTI	*NS*	p=0.048; R^2=0.78 ; 1 component	p=0.019; R^2=0.96 ; 1 component
	tTTI	NS	p=0.001; R^2=0.98 ; 1 component	p=0.023; R^2=0.95 ; 1 component
H. arizonica	FD	p=0.002; R^2=0.97 ; 1 component	p=0.0003; R^2=0.99 ; 2 components	p=0.010; R^2=0.92 ; 1 component
	Tmax	p=0.031; R^2=0.83 ; 1 component	p=0.046; R^2=0.78 ; 1 component	p=0.013; R^2=0.90 ; 2 components
	TTI	p=0.015; R^2=0.89 ; 1 component	p=0.003; R^2=0.96 ; 1 component	*p=0.010; R^2=0.98 ; 1 component*
	tTTI	NS	p=0.018; R^2=0.88 ; 1 component	p=0.044; R^2=0.79 ; 1 component
P. halepensis	FD	p=0.006; R^2=0.94 ; 1 component	p=0.049; R^2=0.77 ; 1 component	p=0.0007; R^2=0.99 ; 1 component
	Tmax	p=0.043; R^2=0.79 ; 1 component	*p=0.018; R^2=0.88 ; 1 component*	NS
	TTI	p=0.039; R^2=0.81 ; 1 component	p=0.0006; R^2=0.99 ; 1 component	p=0.002; R^2=0.98 ; 1 component
	tTTI	p=0.002; R^2=0.98 ; 1 component	p=0.002; R^2=0.97 ; 1 component	NS

R^2: coefficient of determination, p: probability, NS: non-significant). Italic font when the variables were FMC-corrected

Figures

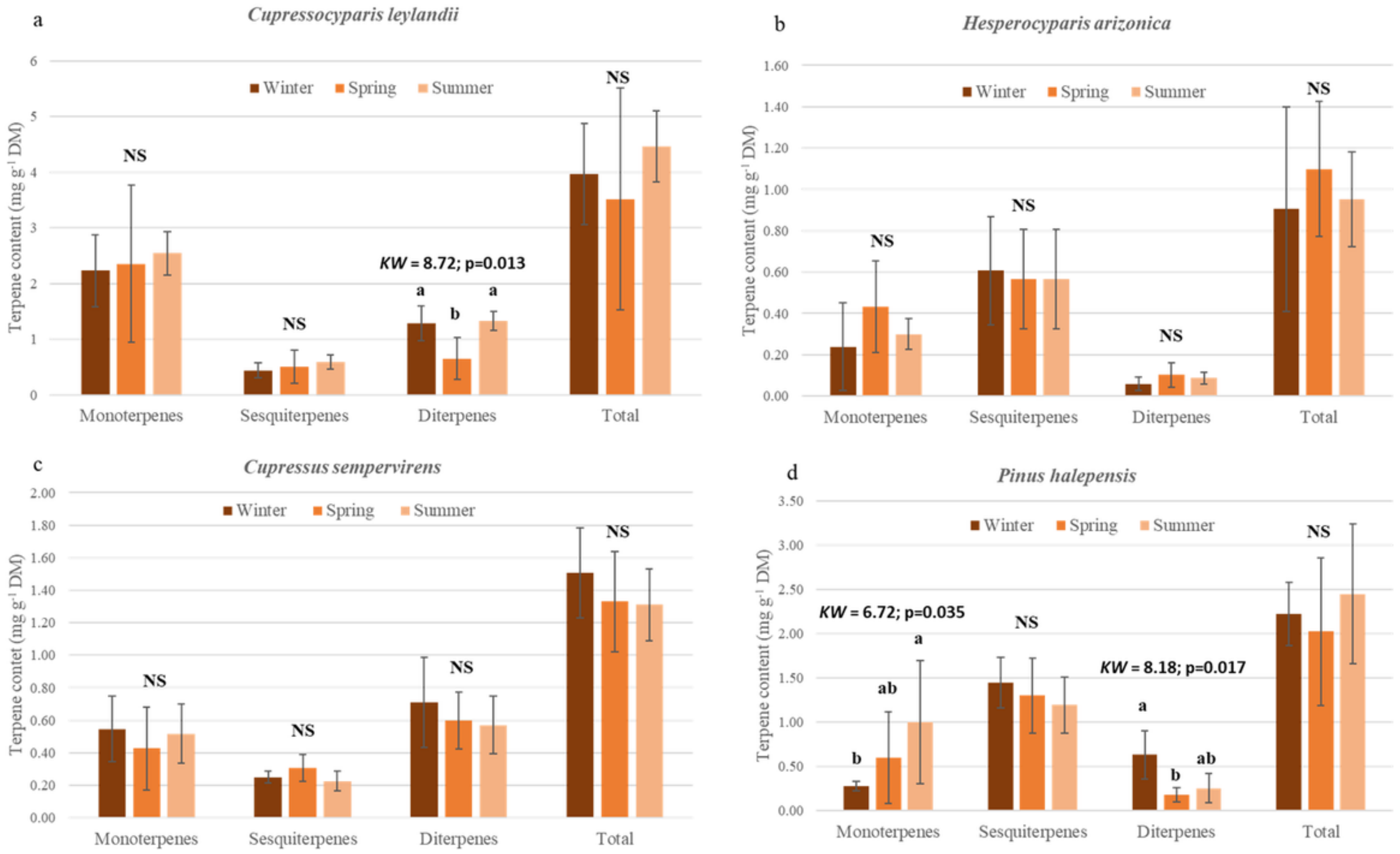

Figure 1

Variation of the terpene seasonal content (subgroups and total) for the four species studied (when significant, the results of the test are shown: KW: Kruskal-Wallis test, p: probability). Lowercase letters indicate significant differences among seasons for each terpene subgroup with a>b>). Values shown refer to the average for n=6

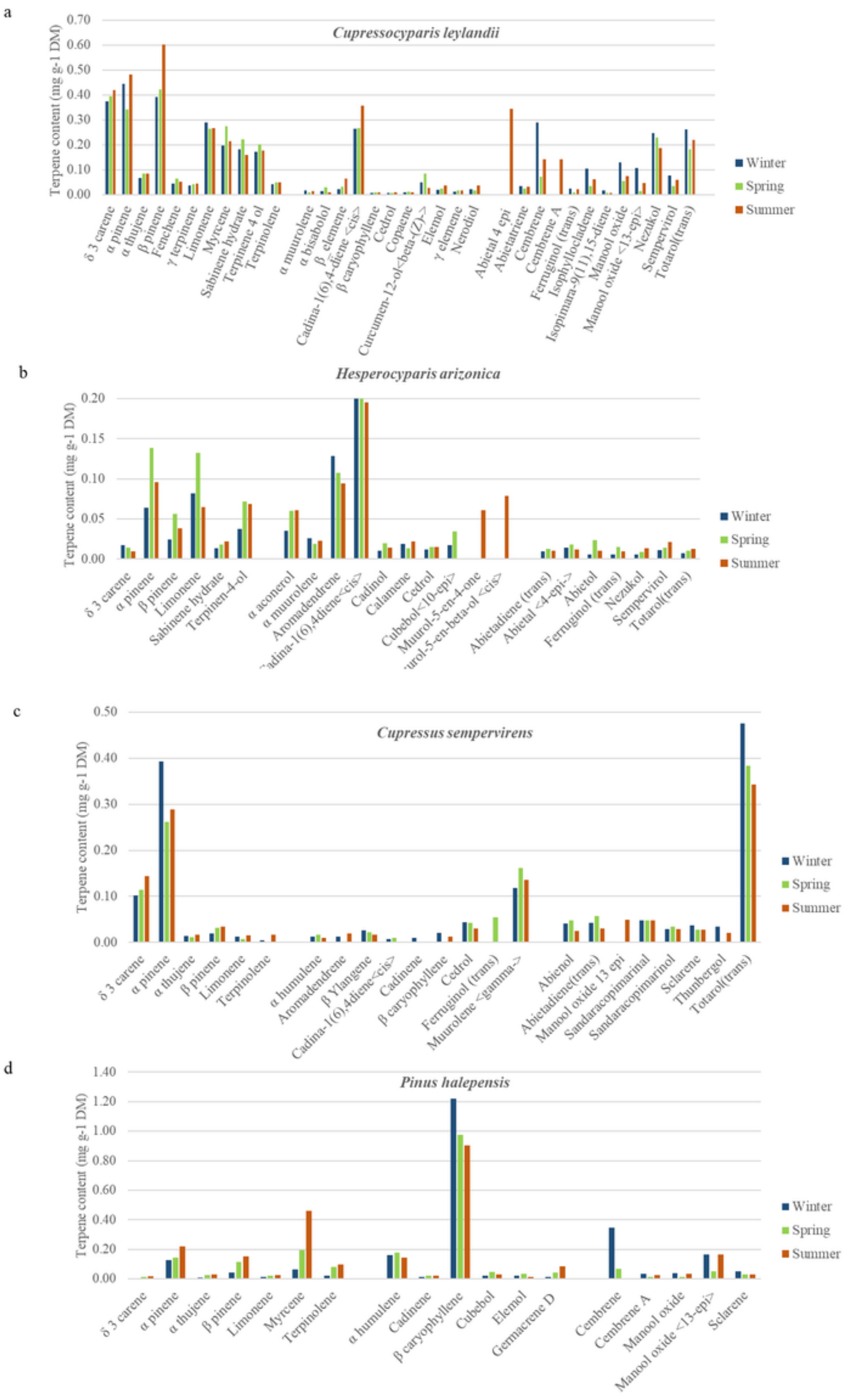

Figure 2

Seasonal variation of the single terpene content for the four species studied (Kruskal-Wallis test: **: $p < 0.01$). Bars refer to mean values for n=5. Compounds (within a terpene subgroup) are shown in alphabetical order

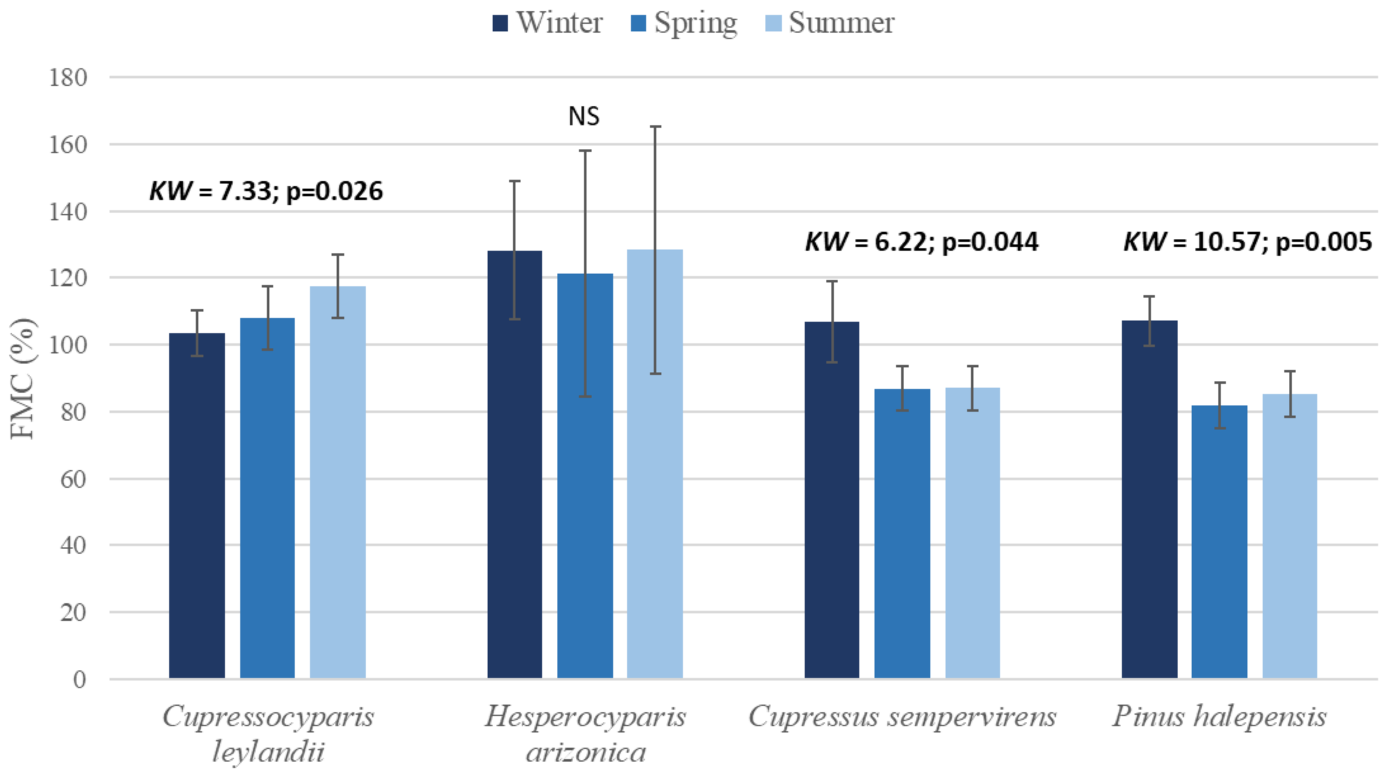

Figure 3

Seasonal variation of FMC in the leaves of the four species studied (when significant, the results of the test are shown: KW: Kruskal-Wallis test, p: probability, NS: not significant. Lowercase letters indicate significant differences among seasons with a>b. Bars represent the average for n=xxx

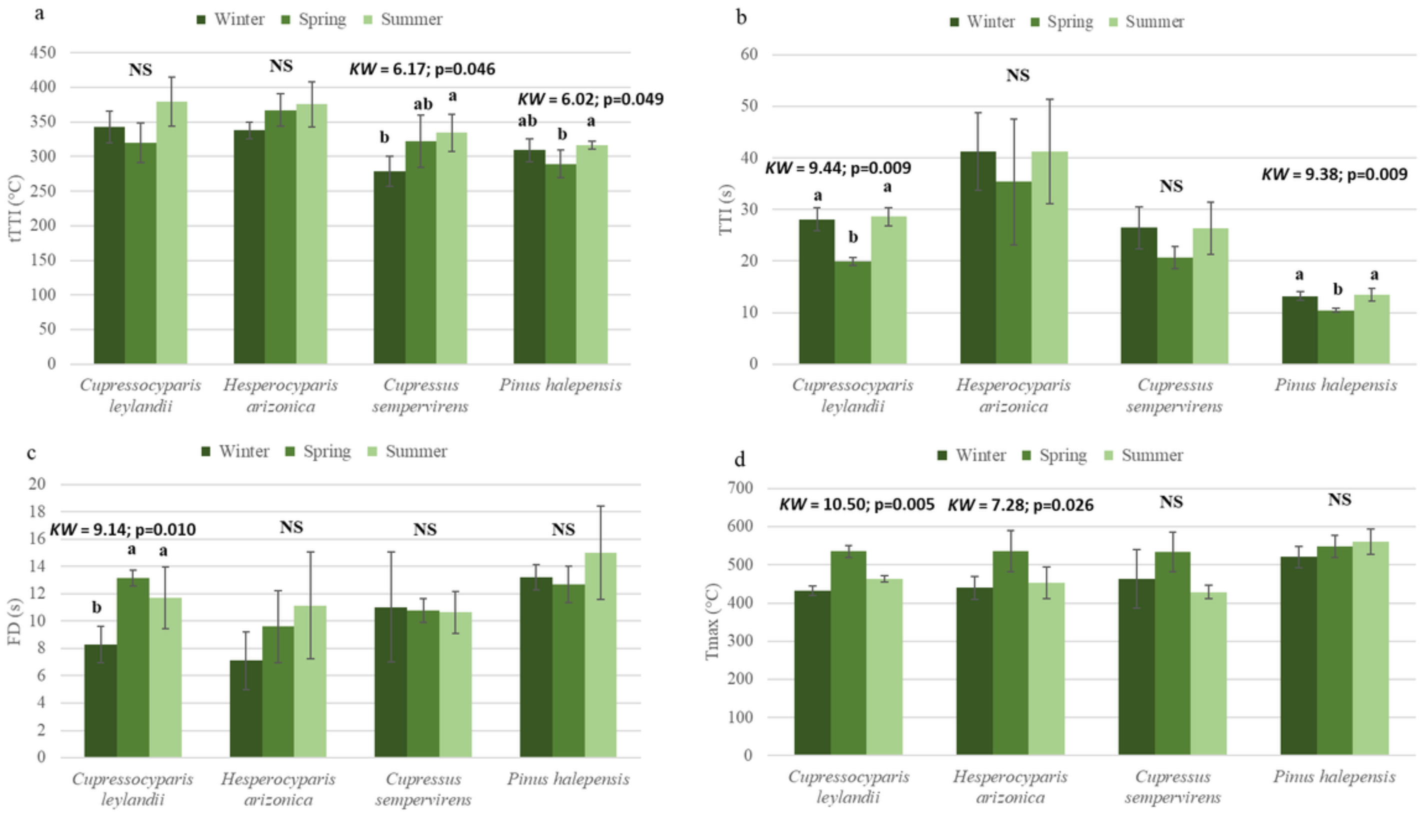

Figure 4

Seasonal variation of flammability of the four species studied (tTTI: ignition temperature, TTI: time-to-ignition, Tmax: maximum temperature, FD: flaming duration, NS: non significant, KW: Kruskal-Wallis test, p: probability. Lowercase letters indicate significant differences among seasons)

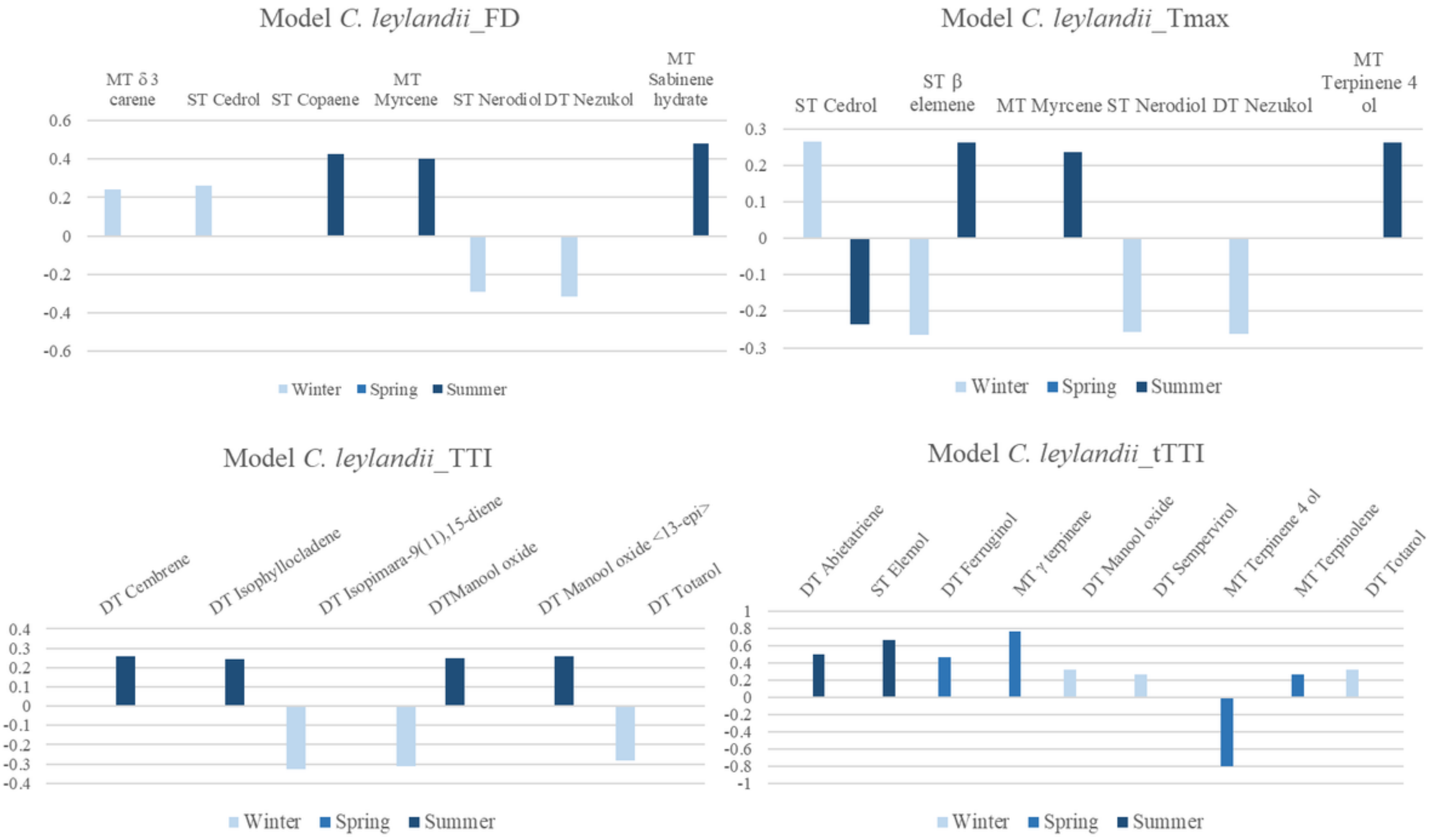

Figure 5

Scaled and centered regression coefficients of the significant (when |value|>0.2) terpene compounds (in alphabetic order) highlighted in the models for Cupressocyparis leylandii in the seasons studied (FD: flaming duration, TTI: time-to-ignition, Tmax: maximum temperature, tTTI: ignition temperature)

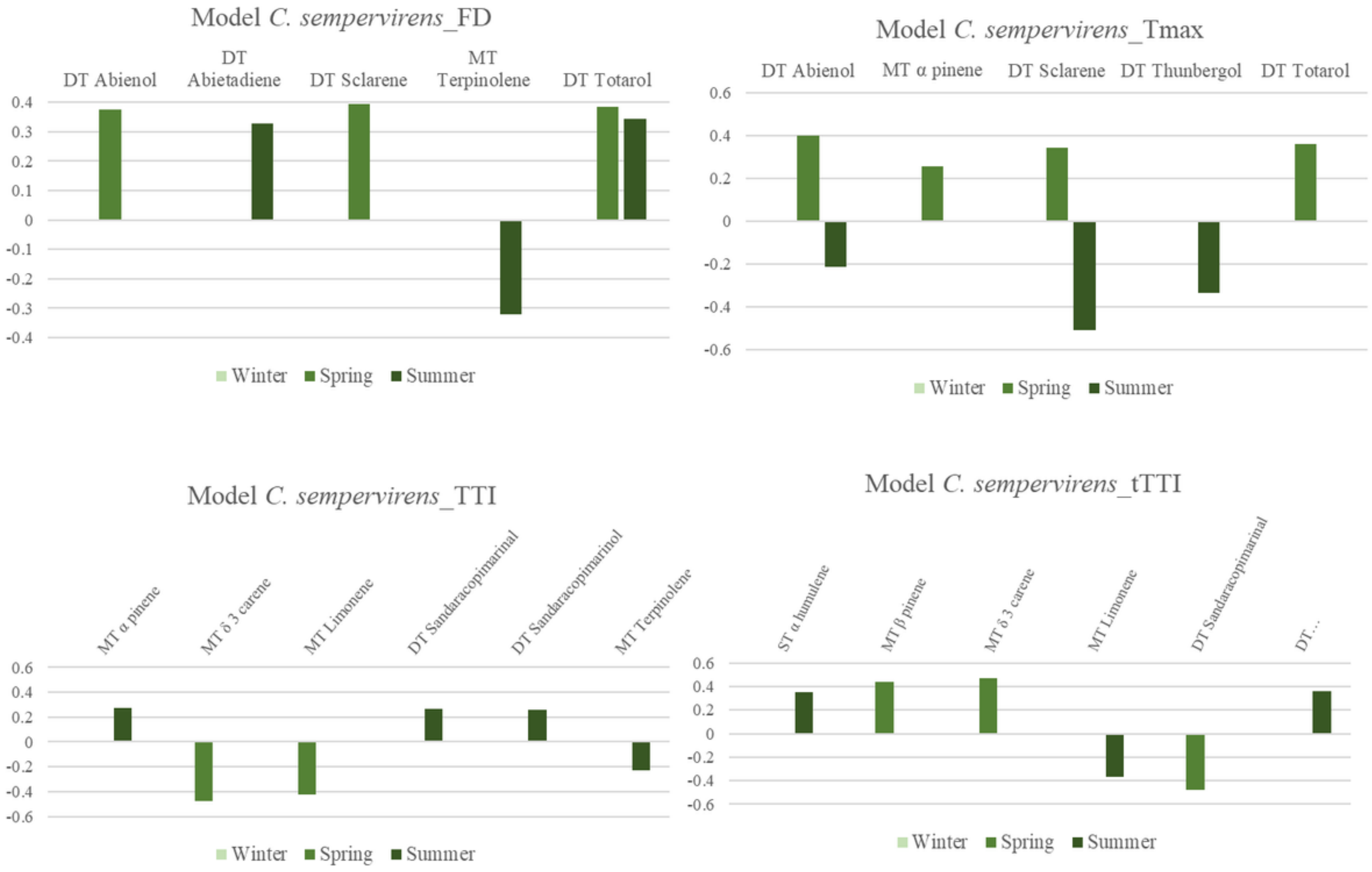

Figure 6

Scaled and centered regression coefficients of the significant (when |value|>0.2) terpene compounds (in alphabetic order) highlighted in the models for Cupressus sempervirens in the seasons studied (FD: flaming duration, TTI: time-to-ignition, Tmax: maximum temperature, tTTI: ignition temperature)

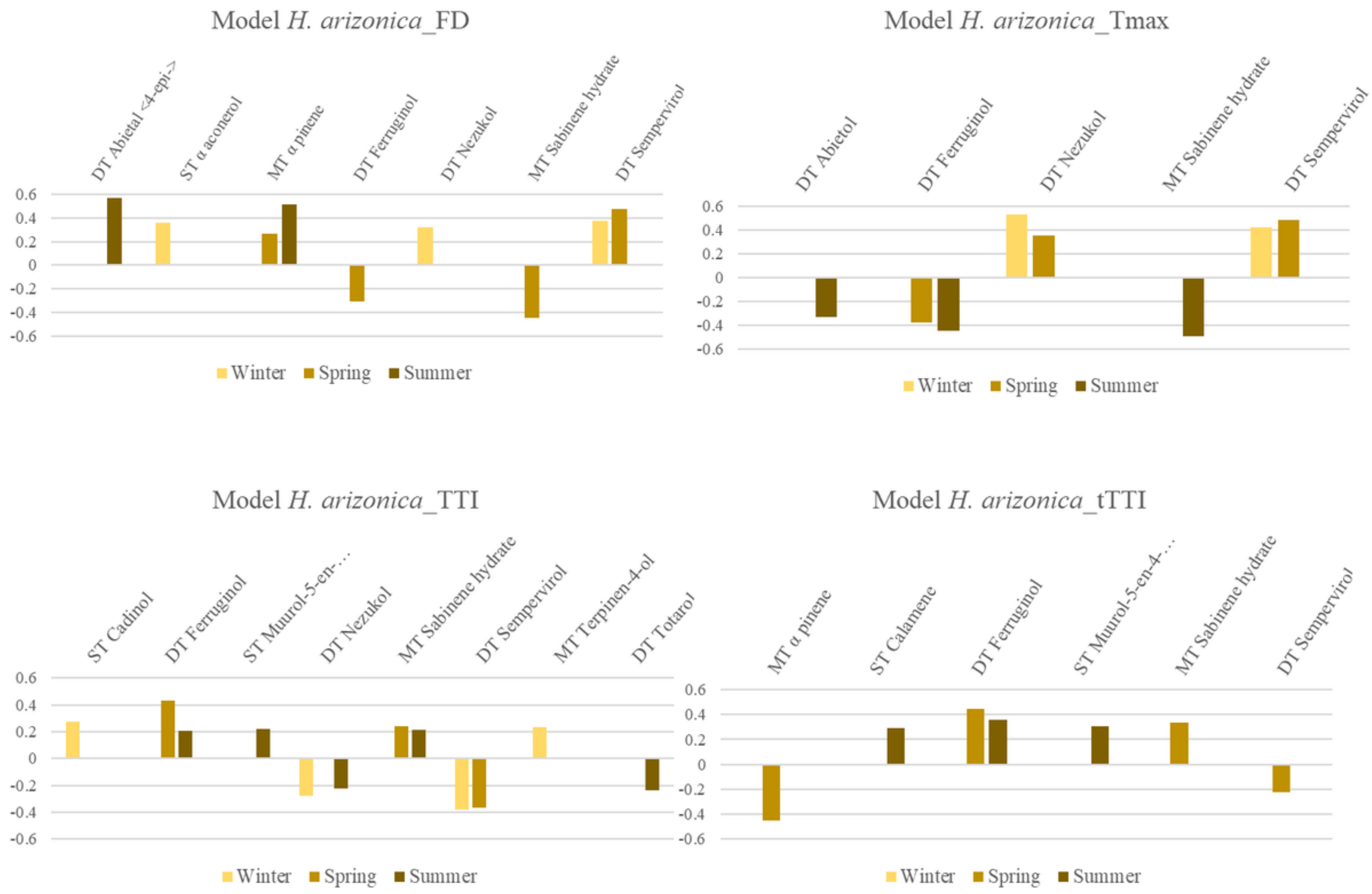

Figure 7

Scaled and centered regression coefficients of the significant (when |value|>0.2) terpene compounds (in alphabetic order) highlighted in the models for Hesperocyparis arizonica in the seasons studied (FD: flaming duration, TTI: time-to-ignition, Tmax: maximum temperature, tTTI: ignition temperature)

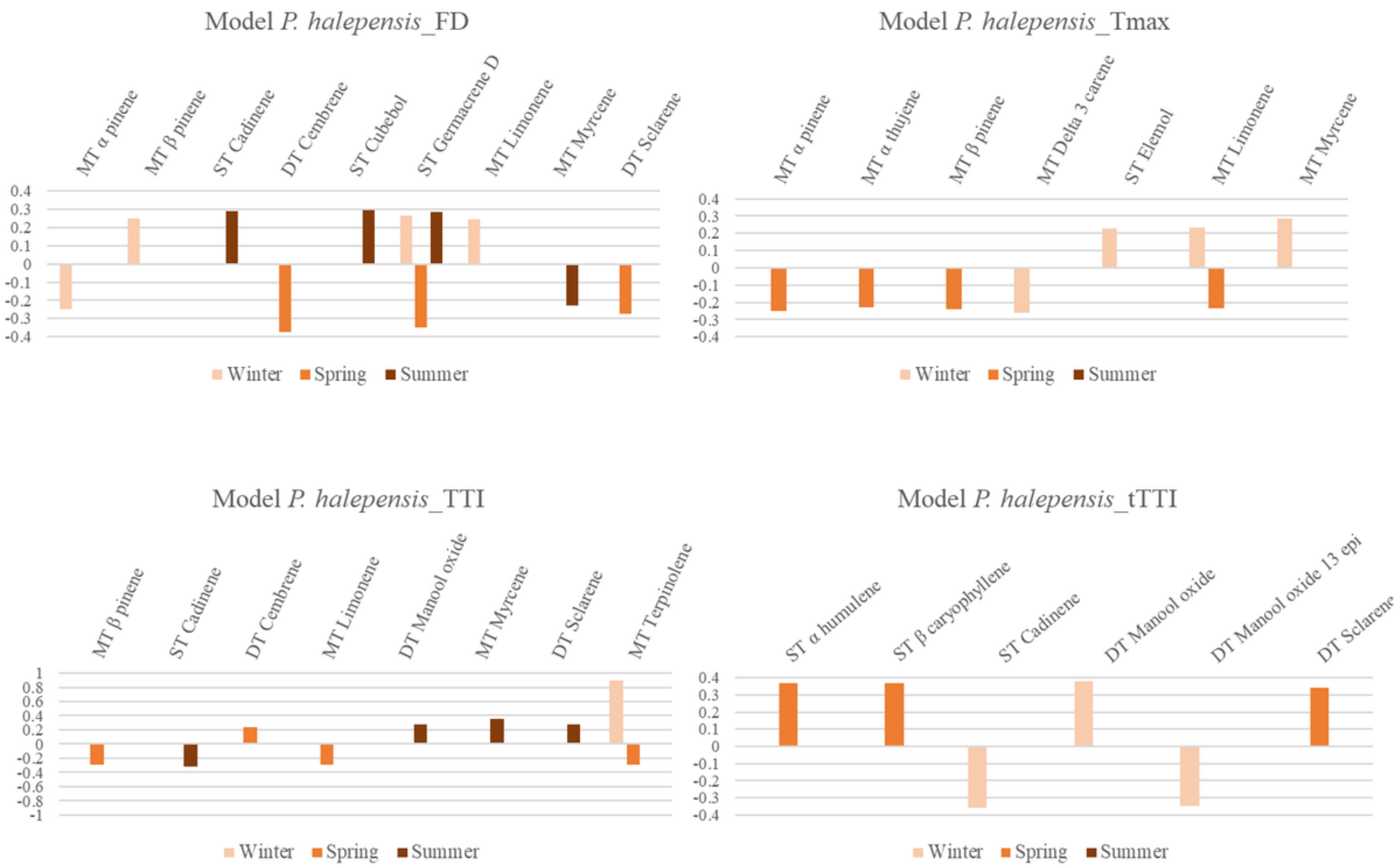

Figure 8

Scaled and centered regression coefficients of the significant (when |value|>0.2) terpene compounds (in alphabetic order) highlighted in the models for Pinus halepensis in the seasons studied (FD: flaming duration, TTI: time-to-ignition, Tmax: maximum temperature, tTTI: ignition temperature)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Suppl.Mat.1and2.docx
- Suppl.Mat.3.docx