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1 **How terpene content affects fuel flammability of wildland-urban interface vegetation**

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15 Running head title: Role of terpenes on flammability

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18

19 **Abstract**

20 Among plant characteristics promoting flammability, terpenes have received far less attention,
21 especially regarding the vegetation surrounding housing. Here, mono-, sesqui-, and diterpenes
22 were screened in live and dead leaves of ornamental species found in Wildland-Urban Interfaces
23 (WUI) of southeastern France. Terpene content and composition were compared among species
24 and between fuel types. Their influence on flammability was assessed through several variables
25 and compared to that of leaf thickness and moisture content. Six of the 17 species examined
26 contained terpenes. Terpene diversity and content differed among species but not between fuel
27 types. Mono-, sesqui-, and diterpenes (especially the highly concentrated compounds) were
28 involved to varying degrees in both leaf and litter flammability. Their effects could be the opposite
29 according to the flammability variable and the fuel type considered. Leaf sesquiterpene content
30 and litter total terpene content had the strongest influence on maximum temperature; the former
31 also mainly drove leaf flaming duration. The other flammability variables were more strongly
32 associated with either moisture content or leaf thickness. Our findings underlined the idea that fire
33 management in WUI must also acknowledge the potential for ornamental species containing
34 terpenes, such as *P. halepensis*, in affecting fire behavior.

35

36

37 *Key Words* – *Pinus halepensis*; Fire prevention; Leaf traits; Fire-prone species; Ornamental
38 vegetation; Volatile Organic Compounds

39

40

41 *Short summary* - We compared terpene content and composition in leaves of species found in
42 Wildland-Urban Interfaces of southeastern France and evaluated their influence on flammability.
43 Terpene content had the strongest influence on maximum temperature and flaming duration. Other

44 flammability variables were more strongly associated with either moisture content or leaf
45 thickness.

46

47 **Introduction**

48 Mediterranean regions are characterized by climatic conditions conducive to fire and these areas
49 are often composed of highly flammable species. In some of these high fire risk areas, the human
50 population has considerably increased wildfire frequency (Syphard et al. 2007; Ganteaume and
51 Jappiot 2013), including wildland-urban interfaces (WUI) in southeastern France (Ganteaume and
52 Long-Fournel 2015).

53 Plant species found in WUI (hereafter referred as “ornamental species” or “ornamental
54 vegetation”), either native or exotic species, are important fuels during wildfires. Indeed, they can
55 allow fire propagation from wildland vegetation to structures, possibly damaging or destroying
56 buildings as highlighted during the destructive wildfires in 2016 in southeastern France
57 (Ganteaume 2018a). Consequently, to better understand the role of the ornamental vegetation as a
58 vector for the fire propagation (either due to massive firebrand showers or to the radiant heat
59 emitted by the flame front), previous studies focused on the assessment of this vegetation’s
60 flammability (Ganteaume et al. 2013a, 2013b; Ganteaume 2018b). These works targeted both live
61 leaf particles and dead surface fuels but did not consider the effect of volatile or non-volatile
62 organic compounds on the flammability of these fuels.

63 Plant flammability has been widely studied and experimentally assessed under laboratory
64 conditions as well as *in situ* during prescribed fires, for instance. Laboratory methods focus on
65 deriving the metrics of flammability, such as the three major dimensions (i.e. ignitability, heat
66 release and fire spread rate) recently highlighted in Pausas et al (2017), typically via the
67 measurement of individual species fuels (leaf, litter bed, etc.). For a given fuel scale, these
68 flammability dimensions are not necessarily correlated (Engber & Varner 2012; Magalhães &

69 Schwilk 2012; Pausas & Moreira 2012; Cornwell et al. 2015) and each of them has relevance
70 across fuel scales (Pausas & Moreira 2012). Previous works showed that these axes of
71 flammability were primarily controlled by different plant traits (Scarff & Westoby 2006; Engber
72 at al. 2012; Schwilk & Caprio 2011; Clarke et al. 2014), also called drivers of flammability. Some
73 leaf traits continue to affect fuel bed flammability, scaling up from leaf to fuel bed (Varner *et al.*
74 2015). Among these characteristics, thickness was one of the main drivers of leaf ignitability
75 (Murray et al. 2013; Grootemaat et al. 2015; Ganteaume 2018b) and can sometimes override the
76 effects of other essential drivers of leaf flammability (e.g., specific leaf area, surface area-to-volume
77 ratio, or fuel moisture content as highlighted in several works, e.g., White and Zipperer 2010;
78 Marino et al. 2011; Madrigal et al. 2013; Murray et al. 2013; Santoni et al. 2014; Grootemaat et
79 al. 2015), as found in Ganteaume (2018b).

80 Along with fuel moisture content (FMC), terpenes are among the chemical compounds
81 associated with flammability (Dimitrakopoulos 2001; Alessio et al. 2008a, 2008b). Indeed, some
82 terpenes are volatile organic compounds naturally very flammable (Barboni et al. 2011) because
83 of their high heating value, relatively low flash point, and low flammability limit (See, for instance,
84 Sigma-Aldrich Data Sheets at [https://www.sigmaaldrich.com/united-kingdom/technical-](https://www.sigmaaldrich.com/united-kingdom/technical-services/datasheets.html)
85 [services/datasheets.html](https://www.sigmaaldrich.com/united-kingdom/technical-services/datasheets.html)). Terpenes can be stored in the plant or directly emitted once synthesized,
86 depending on their molecular weight. Their production and storage in the leaf require adapted
87 structures such as resin ducts or trichomes (Martin et al. 2002), the location of these structures in
88 the leaf depending on the species. These compounds are also involved in several ecological roles;
89 for instance, coping with abiotic stresses (Paré and Tumlison 1999) such as water deficit (Peñuelas
90 and Llusà 2003), or deterring herbivory as signal molecules in the communication between plants
91 (Dicke et al. 2003) or between insects and plants (Pichersky and Gershenson 2002). Because of
92 their chemical characteristics (such as low flash point), terpenes can also affect plant flammability.
93 Even though, previous works linking terpene content and flammability are scarce as compared to

94 those dealing with the impact of FMC or of other leaf traits. Most of these works investigated
95 terpenes in live fuel, but only a few targeted both live and dead fuels such as Ormeño et al. (2009)
96 and Della Rocca et al. (2017) for instance. Moreover, the previous works predominantly took into
97 account either the total amount of terpenes without distinguishing subgroups (De Lillis et al. 2009)
98 or focused on their most abundant fraction, the monoterpenes (White et al. 1994; Alessio et al.
99 2008a, 2008b), sometimes supplemented by the sesquiterpenes (Owens et al. 1998; Ormeño et al.
100 2009; Pausas et al. 2016; Della Rocca et al. 2017). Often, results as to these relationships were not
101 conclusive or were contradictory (De Lillis et al. 2009; Alessio et al. 2008b). For instance,
102 monoterpenes were found to enhance flammability in White et al. (1994) as well as in Owens et
103 al. (1998) while sesquiterpenes positively affected flammability in Pausas et al. (2016) and in Della
104 Rocca et al. (2017). These differences could sometimes be due to different species or terpene
105 subgroups studied but not in every case (e.g., Alessio et al. 2008b and Della Rocca et al. 2017).
106 Furthermore, excluding the works of Ormeño et al. (2009) or Della Rocca et al. (2017),
107 flammability was mostly assessed through only one variable (such as time-to-ignition in Pausas et
108 al. 2016), therefore lacking results on other flammability components. The positive impact of
109 terpenes on plant flammability could be an issue in Mediterranean areas where summer drought
110 induces a water stress that forces some species to increase their terpene production, and possibly
111 their storage amount (Llusià and Peñuelas 1998; Ormeño et al. 2007; Genard-Zielinski et al. 2014)
112 if they are able to store compounds, thereby making them potentially more flammable. Moreover,
113 as large amounts of these compounds can be emitted in response to high temperatures (Centritto
114 et al. 2011), episodes of massive terpene emission can result from wildfire events.

115 As far as we know, except for *Pinus halepensis* and *Cupressus sempervirens*, no previous
116 studies have described in depth the live leaf and litter terpene content of ornamental species,
117 especially neglecting to take into account different terpene subgroups (e.g., the volatile
118 monoterpenes and sesquiterpenes, as well as the non-volatile diterpenes) and their influence on

119 different flammability components. Filling these gaps would provide a better understanding of the
120 live leaf and litter flammability processes regarding these chemical compounds. This is
121 particularly important as terpene content might increase in response to the predicted warmer
122 climatic conditions (Kleist et al. 2012), particularly as WUI species could be responsible for severe
123 damage to buildings during a fire.

124 To tackle these goals, we i) screened for terpenes in the live and dead leaves of a wide range of
125 common WUI species, characterizing the composition and concentration of terpenes, ii)
126 determined if they differed between both fuel types within and among species, iii) examined the
127 role of total terpene content and their constituent subgroups (e.g., monoterpenes, sesquiterpenes,
128 diterpenes) on the flammability of these fuels, testing the hypothesis that terpenes would increase
129 species' flammability, and iv) determined the relative importance of physical and chemical factors
130 on flammability. Ultimately, focusing on a test species, we checked if these metrics varied between
131 two different stages of plant maturity. This work, besides providing a better knowledge on the
132 impact of terpenes on plant flammability, will also allow the identification of WUI species that
133 could be deleterious during a fire regarding their specific terpene content.

134

135

136 **Material and Methods**

137 **Study Species and Sampling**

138 The species studied in the current work are common in the French Mediterranean WUI. They can be
139 involved in the fire propagation from the wildland vegetation to the nearby buildings, especially
140 regarding species used in ornamental hedges that provide strong horizontal fuel continuity. In total,
141 seventeen of the most common ornamental species were studied (Suppl. Mat. 1) which, except for *P.*
142 *halepensis* and *Cotinus coggygia*, have already been taken into account in the work of Ganteaume
143 (2018b) in which these species' flammability was characterized. However, for most species,

144 screening for terpenes in live and dead fuels had never been attempted. These ornamental species are
145 composed of both native (e.g., *Viburnum tinus*, *P. halepensis*, or *Cotinus coggygria*) and exotic
146 species (such as *Thuja occidentalis*). During a fire, some of them (e.g., *P. halepensis*, *Cupressus*
147 *sempervirens*) can also cause damage and ignite buildings, as often witnessed by firefighters.

148 In order to highlight a possible variation in flammability according to plant maturity (that could
149 be possibly linked to a variation in terpene content), one of the species studied, *Cupressocyparis*
150 *leylandii*, was sampled in hedges differing in maturity (a young stage and an older stage
151 corresponding to a mature plant). This species is commonly used in hedges at both stages.

152 For each species, two fuel types were targeted, live leaves (mentioned hereafter as “leaf” or
153 “leaves”) and dead leaves collected on the floor underneath the plants (mentioned hereafter as
154 “litter”). The sampling was carried out in summer (July 2016) when the climate conditions were
155 the most severe in southeastern France. Litter samples of *C. coggygria* could not be collected
156 because of the rapid decomposition of the leaves preventing sufficient litter accumulation.
157 Regarding dead fuel, we focused on dead individual leaves and not on the whole fuel bed (as done
158 in previous works, e.g., Ganteaume et al. 2013a, 2018b). The physical arrangement of leaves in
159 the litter bed (i.e. packing ratio) and the resulting air-to-fuel ratio has been shown to dominate the
160 fuel bed flammability (Grootemaat et al. 2017), adding a supplementary parameter that could mask
161 the effect of terpenes on flammability. For each species and each fuel type, a maximum of 25 g of
162 mature live leaves and of intact dead leaves were collected on or underneath (for litter only) five
163 different individuals, located at least 4 m apart. Per individual, 6 g were used for the burning
164 experiments, 5 g for FMC measurements, and 1 g for the terpene analysis. Sampling was conducted
165 at least 48 h following a precipitation event to avoid any impact of the recent rain on FMC. Litter
166 samples were air-dried for 48 h, time necessary for the stabilization of their weight; oven-drying
167 was avoided as this process could involve the degradation of terpenes. As soon as their weight
168 stabilized, the litter samples were burned. The live leaves sampled were placed in plastic bags and

169 stored in a cool box for transportation to the laboratory, minimizing changes in water content; the
170 samples were burned directly upon returning to the laboratory.

171

172 **Terpene content**

173 For the terpene analysis, leaf and litter samples were stored at -80°C in order to stop leaf metabolism.
174 For both fuel types, terpene content was analyzed for each species using 500 mg of fuel collected
175 from five different individuals and ground for extraction purposes using liquid nitrogen and put into
176 a 4 mL of extraction solution (cyclohexane and dodecane). This vial was agitated for 30 min, filtered
177 (PTFE – 0.22 µm filter), and put into a 3 mL-vial for analysis. Dodecane was used as an internal
178 standard and was not naturally present in the samples.

179 This analysis was conducted using gas chromatography (GC-MS System 7890B – Agilent
180 Technologies®). One microlitre was injected into a 30m x 0.25 mm x 0.25 µm thickness capillary
181 column (HP-5MS – Agilent J&W GC Columns), at a constant flow (1 mL min⁻¹) and in the splitless
182 mode. The injection temperature was maintained at 250°C with Helium (99.99%) as the carrier gas.
183 The initial temperature was 40°C and increased at 3°C min⁻¹ up to 300°C during analysis. A 5 min-
184 solvent delay was respected and the total run time was 90 min.

185 The identification of terpenes was made using the molecule retention time (RT) as well as their
186 mass spectrum which was compared to libraries in Adams (2007) and NIST (2011). To complete
187 this identification, retention indexes (RI) were calculated for each molecule identified and compared
188 to the libraries. We established these experimental RI from alkanes injected at each session:

$$189 \text{RI}_{(\text{mol})} = 100 \times X(\alpha) + \frac{RT(\text{mol}) - RT(\alpha)}{RT(\beta) - RT(\alpha)} \times 100$$

190 where α = alkane before the molecule, β = alkane after the molecule, X = Carbon number, and RT
191 = retention time.

192 To calculate the terpene content, several dilutions of many authentic reference compounds
193 (Aldrich, Darmstadt, Germany and Firmenich, Geneva, Switzerland) were carried out in order to

194 establish the response factor of the terpene subgroup as compared to the internal standard
195 (dodecane). Then, the integrated area of each peak was multiplied by the appropriate response
196 factor and divided by the sample volume. The sample dry mass was previously calculated to obtain
197 the mass of terpene compound per dry mass unit. In the current work, we focused on the content
198 of mono-, sesqui-, and diterpenes as well as on the total terpene content.

199

200 **Flammability Experiments**

201 Flammability experiments were carried out only on species containing terpenes in order to highlight
202 the link between flammability and terpene content. Fuel samples were burned using a 500W
203 epiradiator composed of a 10 cm radiant disk. A pilot flame was placed 4 cm above the epiradiator
204 surface; this flame did not take part in the sample combustion but allowed a better ignition of the
205 gases emitted by the plant before combustion (Hernando-Lara 2000). A thermocouple (chromel-
206 alumel, k type, 30 μm diameter) was positioned 1 cm above the disk center to measure the
207 temperature emitted by the radiant disk at a precise point ($300 \pm 30^\circ\text{C}$ that will trigger the leaf
208 burning), then the temperature emitted by the flame when the sample burned. This thermocouple was
209 linked to a data logger (ALEMO 2590 Ahlborn, Ahlborn Mess- und Regelungstechnik GmbH
210 Holzkirchen, Germany) to record the variation of temperature (one record per second) during the
211 burning. The burning device was turned on thirty minutes before the first burning test to be sure the
212 epiradiator temperature was stabilized.

213 For each species, 30 one g-samples were burned; larger fuel masses increased the possibility that
214 other fuel properties, such as fuel height, would cause differences in flammability (Ormeño et al.
215 2009). Thus, samples had to be as well distributed as possible on the radiant disk. As soon as the fuel
216 was in contact with the epiradiator surface, time and temperature recordings were started. Five
217 flammability variables were measured: i) time-to-ignition (TTI, s), defined as the time necessary for
218 the fuel to ignite once laid on the radiant disk; ii) ignition temperature (T_{TTI} , $^\circ\text{C}$), defined as the

219 temperature recorded when the flame appeared; iii) ignition frequency (IF, %), calculated as the ratio
220 between successful ignitions and the total number of samples (n=30); iv) flaming duration (FD, s),
221 time elapsed between the flame occurrence and its extinction; and v) maximum temperature emitted
222 during burning (T_{MAX} , °C). Live leaves were burned first to prevent chemical compound degradation
223 and moisture content variation before the burning.

224 Just before the burning experiments, subsamples of litter and leaves of each individual were oven-
225 dried for 48 h at 60°C in order to measure their moisture content at the time of burning. FMC was
226 calculated according to the following equation:

$$227 \text{ FMC} = \frac{Mf (g) - Md (g)}{Md (g)} \times 100$$

228 where Mf represents the fresh fuel mass and Md represents the dry fuel mass.

229 Among the physical characteristics correlated with the leaf flammability of these species, leaf
230 thickness was one of the most significant parameters because of the importance of this particle
231 geometry in determining leaf combustion (Ganteaume 2018b). This parameter was chosen, along
232 with FMC (also known to greatly influence flammability; Ganteaume et al. 2009) to be compared
233 to terpene content as drivers of flammability. Immediately before burning, leaf thickness (Th_i , cm)
234 was measured at the middle of the leaf (excluding the midrib), using a 10^{-4} m accuracy micrometer.
235 A preliminary test showed that thickness did not significantly vary between live and dead leaves
236 ($t = 0.577413$; $p = 0.565$), so only live leaf thickness was used in the analyses.

237

238 **Data Analysis**

239 The statistical analyses were performed on each fuel dataset taking into account the content of the
240 three terpene subgroups as well as the total terpene content (combining the three subgroups), FMC,
241 and thickness as explanatory factors. The different flammability variables (using a single mean
242 value per individuals of each species) were used as dependent variables.

243 To compare species and stage of maturity on terpene content and flammability, we used one-
244 way ANOVA. Regarding the stage of maturity, the Kruskal-Wallis test was performed instead of
245 the Fisher test because of the lower amount of data. Comparisons between both litter and leaf
246 flammability and terpene content were performed using t-test. The normality of residual
247 distribution was checked by the Kolmogorov-Smirnov test and data were log-transformed if
248 needed. The post-hoc LSD test was used to check for significant differences between the different
249 means ($p \leq 0.05$).

250 We used simple linear regression analyses to highlight (i) if flammability was more sensitive to
251 the total terpene content or to terpene subgroups, and (ii) the significant correlations existing
252 between flammability variables and fuel characteristics. When FMC and/or thickness explained a
253 significant proportion of the variability of a given flammability variable, we used the residuals of
254 the regression as a moisture/thickness-corrected measure of this variable. This corrected variable
255 was then regressed against the terpene content in order to highlight the effect of terpenes without
256 the bias of the above-mentioned factors (see Pausas et al. 2016). Partial least squares (PLS)
257 regression analysis was performed to determine the relative importance of the physical and
258 chemical fuel characteristics on each flammability variable. The significance of components for
259 the models was determined by uncertainty tests carried out within a full cross-validation. Then, a
260 bootstrap procedure (boot size=1000) was performed on the set of variables that presented the
261 highest regression coefficients to rebuild the model, followed by a backwards elimination process
262 until all explanatory variables were significant with p-values ≤ 0.05 . In order to take into account
263 the flammability variables and fuel characteristics in a same analysis and to pinpoint the driving
264 species of the relationships possibly highlighted, co-inertia analysis (Dolédec and Chessel 1994)
265 was performed on both fuel datasets. The complete matrix of data was transferred to the statistical
266 program under R 2.5.1 (R Development Core Team, 2005), then standardized and analysed using
267 the ADE-4 package (Thioulouse *et al.* 1997). The statistical significance of each effect or

268 combination of effects was tested using a Monte-Carlo permutation test with 1000 permutations
269 using the R ‘coin’ package.

270 All tests, except the bootstrap procedure (part of the PLS regression analyses) and co-inertia
271 analyses, were performed using StatGraphics Centurion XVII – X64 software (StatPoint
272 Technologies, Inc®).

273

274

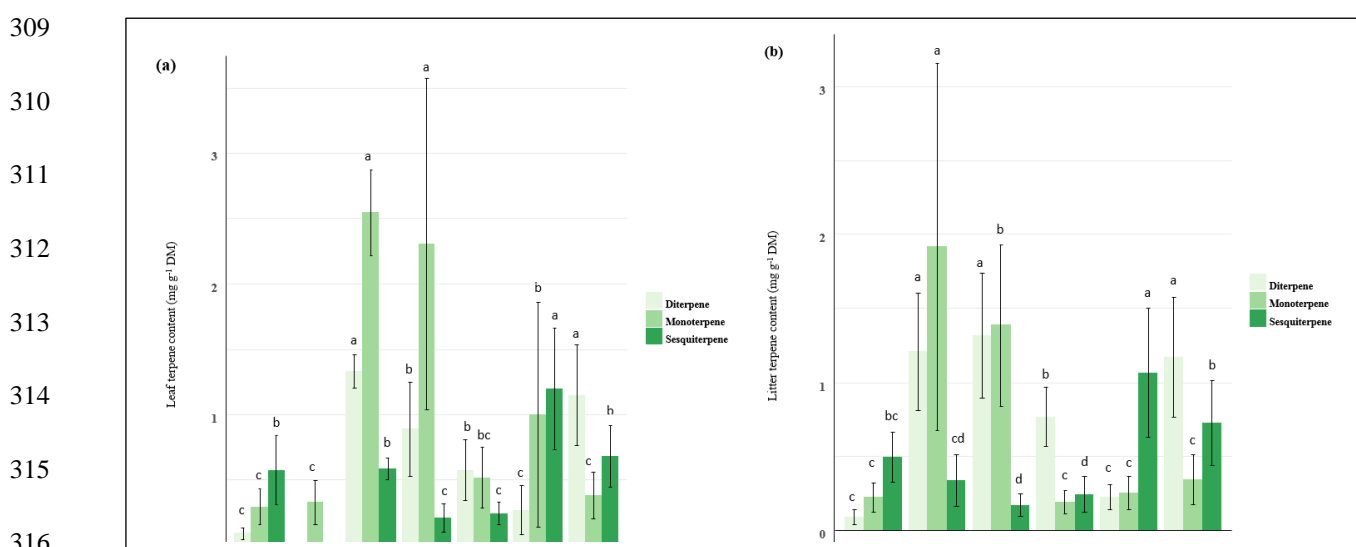
275 **Results**

276 **Terpene Diversity and Content**

277 The screening for terpenes in the different species studied revealed that only six species among the
278 seventeen studied contained terpenes, mostly conifers: *P. halepensis*, *C. sempervirens*, *T.*
279 *occidentalis*, *C. arizonica*, *C. leylandii* (in both stages of maturity), and *C. coggygria* (Suppl. Mat.
280 2). We identified 54 different compounds in the leaves and litter of these species. The subgroup of
281 sesquiterpenes was the most diverse (24 compounds, mostly in *C. leylandii* and *C. arizonica*),
282 compared to that of diterpenes (19 compounds, mainly found in *C. leylandii* and in *C. sempervirens*)
283 and monoterpenes (11 compounds, mostly in *C. leylandii*). *C. leylandii* presented the highest terpene
284 diversity with more than 30 different compounds. *C. coggygria*’s leaves contained only one
285 compound, limonene (monoterpene).

286 Regarding the terpene content, monoterpenes presented the highest number of compounds with
287 content higher than 0.1 mg g⁻¹ dry matter (mentioned hereafter as “main compounds”), regardless
288 of species and fuel type (Suppl. Mat. 3 and 4). However, the highest values were obtained for
289 caryophyllene (sesquiterpene) in *P. halepensis*’ leaves and litter (0.905 and 0.866 mg g⁻¹,
290 respectively) and for nezukol (diterpene) in those of *T. occidentalis* (0.870 and 0.940 mg g⁻¹,
291 respectively). *C. sempervirens* and *C. arizonica* presented the lowest terpene content (<1.5 mg g⁻¹)
292 despite the high terpene diversity screened in these species (12 main compounds for both fuel types).

293 Regardless of the subgroup, terpene content differed among species (One way ANOVA: $F=25.48$
 294 and $p<0.0001$ for monoterpenes; $F=16.61$ and $p<0.0001$ for sesquiterpenes; $F=25.22$ and $p<0.0001$
 295 for diterpenes), the highest content being observed in the mature leaves of *C. leylandii* (mainly due
 296 to their high number of different compounds) and the lowest in *C. coggygia* (presenting only one
 297 compound) (Fig. 1). Regarding live leaves (Fig. 1a), *C. leylandii* and *P. halepensis* stored the largest
 298 amounts of monoterpenes ($> 2.00 \text{ mg g}^{-1}$ and 1 mg g^{-1} , respectively). It is worth noting that the
 299 amount of monoterpenes in *C. coggygia* (corresponding to limonene only) was in the same range
 300 ($\leq 0.5 \text{ mg g}^{-1}$) as in *C. arizonica* and *T. occidentalis* which presented several compounds belonging
 301 to this subgroup. *P. halepensis* presented the highest sesquiterpene content despite the small number
 302 of compounds contained in this species' leaves (around 1 mg g^{-1} , mostly due to caryophyllene;
 303 Suppl. Mat. 3). *C. leylandii* and *T. occidentalis* presented the highest diterpene content ($> 1 \text{ mg g}^{-1}$
 304 on average, mostly due to the high number of compounds in the former species and to nezukol in
 305 the latter). Regarding litter (Fig. 1 b), the three terpene subgroups differed significantly among
 306 species (One way ANOVA: $F=20.81$ and $p<0.0001$ for monoterpenes; $F=13.63$ and $p<0.0001$ for
 307 sesquiterpenes; $F=33.89$ and $p<0.0001$ for diterpenes). For litter, the different terpene subgroups
 308 were dominant in the same species as for leaves (Suppl. Mat. 4).



317 **Figure 1:** Comparison of the leaf (a) and litter (b) terpene content (means \pm SD) between species
318 according to the three terpene subgroups. Means were calculated from the total terpene content of
319 each individual. For each terpene subgroup, different letters indicate significant differences
320 between species ($p < 0.05$). No litter was sampled for *Cotinus coggygria* (Ca: *Cupressus arizonica*,
321 Cl_o and Cl_y: mature and young *Cupressocyparis leylandii*, Cc: *Cotinus coggygria*, Cs: *Cupressus*
322 *sempervirens*, Ph: *Pinus halepensis*, To: *Thuja occidentalis*). Lowercase letters indicate
323 significant differences between species for each terpene subgroup.

324

325 Comparing leaves and litter, we found that the total terpene content did not vary between fuel
326 types (all species pooled). The trend was the same when each terpene subgroup was considered
327 individually. Accordingly, regarding terpene diversity, species were characterized mostly by the
328 same compounds in both fuel types (Suppl. Mat. 3 and 4). Among monoterpenes, alpha-pinene was
329 one of the most abundant compounds in most species, regardless of the fuel type. The results were
330 mixed for the content of sesqui- and diterpenes, the most concentrated compound varying according
331 to species (sesquiterpene caryophyllene in *P. halepensis* and diterpene nezukol in *T. occidentalis*,
332 for instance), for both leaves and litter.

333

334

335 **Relationships Between Flammability and Fuel Characteristics**

336 Flammability was assessed for the six species containing terpenes (Table 1). For both fuel types, all
337 the flammability variables but leaf T_{TTI} (ranging between 319 and 376°C) and litter IF (100% for
338 all species) significantly differed among species ($p < 0.0001$). Litter flammability was significantly
339 higher than that of leaves, except for T_{TTI} (TTI: $t = 12.33$, $p < 0.0001$; FD: $t = -6.45$, $p < 0.0001$; T_{MAX}:
340 $t = -11.24$, $p < 0.0001$). *P. halepensis* had the highest leaf flammability (higher T_{MAX} and IF, longer
341 FD as well as shorter TTI and lower T_{TTI} than the other species; Table 1); the results were mixed

342 regarding litter flammability, several species (e.g., *C. leylandii*, *P. halepensis*, or *C. sempervirens*)
343 presenting characteristics of high flammability (e.g., short TTI, high T_{MAX} or IF, etc.).

344 Checking for a possible effect of other fuel characteristics (FMC and thickness) than terpene
345 content, we found that FMC significantly impacted leaf TTI (positive effect) and IF (negative
346 effect) while, for both fuel types, leaf thickness was significantly correlated with TTI (positive
347 effect) and FD (negative effect and strongest relationship: $R^2=0.75$) as well as with litter T_{TTI}
348 (positive effect). These flammability variables were thus moisture and/or thickness-corrected
349 when correlated with terpene content (Simple linear regression analyses; Table 2). Results
350 revealed that terpene content could have a different impact on flammability from one fuel type to
351 the other. Indeed, sesquiterpene content was negatively related to leaf TTI and to litter FD but
352 positively to leaf T_{MAX}. In the same manner, diterpene content was negatively related to leaf FD
353 (as was total terpene content) but positively to litter FD and T_{MAX} (as was total terpene content
354 regarding the latter variable). Leaf and litter T_{MAX} were only impacted by terpene content (leaf
355 sesquiterpenes and litter mono- and diterpenes, as well as litter total terpene content), highlighting
356 the strong influence of terpenes on this variable. Leaf ignition frequency was not impacted by
357 terpene content and there was no significant relationship between leaf T_{TTI} and any of the fuel
358 characteristics. It is worth noting that, for both fuel types, most flammability variables were
359 impacted by the content of one or several subgroups of terpenes rather than by the total terpene
360 content.

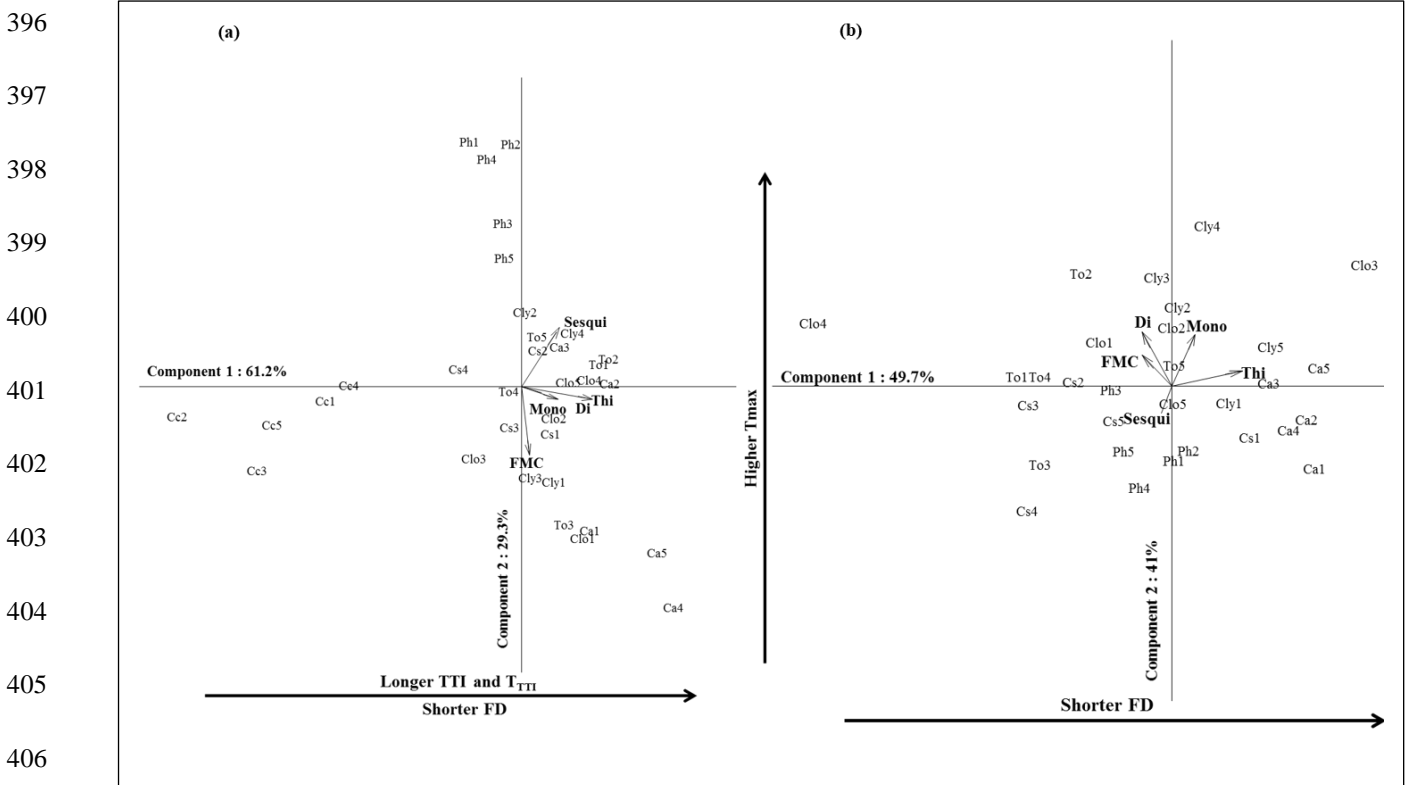
361 Determining the relative importance of the physical and chemical fuel characteristics on
362 flammability (PLS regression analyses, Table 3), we found that leaf thickness and FMC strongly
363 impacted leaf TTI ($R^2=0.73$; positive effect) as well as FD (for the former), IF and T_{MAX} (for the
364 latter) but sesquiterpene content was the main driver of T_{MAX} and FD (Table 3). Fuel characteristics
365 were not significant drivers of leaf T_{TTI}, as previously highlighted in the simple linear regression
366 analyses. When total terpene content was taken into account in the analyses instead of that of the

367 different subgroups, the results were not significant for T_{MAX} whereas the variability, explained in
368 the analysis linking FD to thickness and terpene content, strongly increased (from $R^2=0.26$ to
369 0.80), with a switch in the effect of the terpene content (negative for total terpene content instead
370 of positive for sesquiterpene content). Regarding litter (Table 4), thickness was the only significant
371 driver of litter TTI and T_{TTI} ; this fuel characteristic was also the most important driver of litter FD
372 compared to the content of the three terpene subgroups. It is worth noting that, in this relationship,
373 diterpene content negatively impacted litter FD contrary to the content of sesqui- and
374 monoterpenes. Fuel characteristics did not impact litter T_{MAX} (monoterpene content and diterpene
375 content ceased to be significant after the bootstrap procedure) but when total terpene content was
376 used in the analysis, this factor positively impacted flammability. When total terpene content was
377 taken into account, FMC did not affect litter flammability except FD, overriding total terpene
378 content, along with thickness (Table 4).

379 Most relationships between flammability variables and fuel characteristics previously
380 highlighted were confirmed performing co-inertia analyses on both fuels' datasets (Fig. 2).
381 Regarding leaf flammability (Fig. 2a), the first two axes explained 90.5% of the variance (61.2%
382 on axis 1). TTI and T_{TTI} (the latter however was not significant in the regression analyses) were
383 opposed to FD on axis 1 (highest loading on this axis) and were mainly related to thickness (highest
384 loading on this axis) and to mono- and diterpenes, at a lower extent (Suppl. Mat. 5). *C. arizonica*
385 (presenting the thickest leaves) and *C. coggygia* (presenting the thinnest leaves) also displayed
386 this opposition. T_{MAX} best characterized axis 2 and was positively related to sesquiterpene content
387 and FMC (Suppl. Mat. 5) on the positive side of this axis, confirming the results obtained in the
388 regression analyses. This axis was best characterized by *P. halepensis* which presented the lowest
389 FMC.

390 Regarding litter flammability (Fig. 2b), the two first axes explained 91% of the variance (50%
391 explained by axis 1). On the first axis, FD (and TTI as well as T_{TTI} , at a lower extent) was mainly

392 negatively related to thickness (highest loadings on this axis; Suppl. Mat. 6); *C. arizonica* and *T.*
 393 *occidentalis* best characterizing this axis. On the second axis, T_{MAX} was mainly positively related
 394 to mono- and diterpene content, *C. leylandii* (young stage) best characterizing these relationships.
 395 Litter IF was not taken into account in the analysis as this variable scored 100% for all species.



407 **Figure 2:** Biplots of co-inertia analysis illustrating relationships between leaf (a) and litter (b)
 408 flammability variables with fuel characteristics. In the litter dataset, IF was not taken into account,
 409 given it was 100% for all species and no litter was sampled for *Cotinus coggygia* (T_{MAX} :
 410 maximum temperature, FD: flaming duration, IF: ignition frequency, TTI: time to ignition, T_{TTI} :
 411 ignition temperature, Mono: monoterpene content, Sesqui: sesquiterpene content, Di: diterpene
 412 content, Thi: leaf thickness, FMC: fuel moisture content, Ca: *Cupressus arizonica*, Clo and Cly:
 413 mature and young *Cupressocyparis leylandii*, Cc: *Cotinus coggygia*, Cs: *Cupressus sempervirens*,
 414 Ph: *Pinus halepensis*, To: *Thuja occidentalis*).

415

416

417 **Variations in Terpene content and Flammability according to *Cupressocyparis leylandii*'s**
418 **Stage of Maturity**

419 *C. leylandii* presented the highest terpene diversity with 31 to 34 different compounds in the young
420 and mature stages, respectively. These two maturity stages stored the largest amounts of
421 monoterpenes (2.3 and 2.54 mg g⁻¹, respectively) in their live leaves (Fig. 1a). Accordingly, this
422 terpene subgroup was also the most abundant in litter of both mature and young plants, the content
423 being higher in the mature stage (1.77 vs 1.30 mg g⁻¹) (Fig. 1b).

424 Regarding leaf flammability, only FD differed significantly between the two stages of maturity
425 (KW=4.08, p=0.043), the mature plants presenting higher values (Tab. 2). Accordingly, FMC and
426 the content of sesqui- and diterpenes were higher in this latter stage (p ≤ 0.05). When these
427 parameters were used in the analysis, diterpene content and sesquiterpene content were the best
428 drivers of leaf FD, this relationship explaining 65% of the variability. The stage of maturity did
429 not impact litter flammability, regardless of the variable, even if FMC was lower in the mature
430 plants contrary to sesquiterpene content (the only parameters significantly varying between litter
431 of mature and young plants; p ≤ 0.05).

432

433

434 **Discussion**

435 **Variation of terpenes according to species, fuel type, and stage of maturity**

436 The screening for terpenes in the live and dead leaves of the 17 species studied revealed that only
437 six contained terpenes, all but *C. coggygia* being conifers. These species have storage structures
438 for such organic compounds, e.g., resin ducts for *C. leylandii*, *T. occidentalis*, *C. sempervirens*, *C.*
439 *arizonica*, and *P. halepensis* (Yani et al. 1993; Ormeño et al. 2008), and trichomes were found on
440 the leaf surface of *C. coggygia* (Ormeño, pers. obs.). Terpene content and composition differed
441 according to species but the main compounds (e.g., alpha-pinene, limonene, caryophyllene) found

442 in the leaf and litter of the coniferous species we studied were consistent with compounds detected
443 in previous studies (Gallis et al. 2007; Jitovetz et al. 2006; Chéraif et al. 2007). For *C. coggygia*,
444 however, the monoterpene limonene was the only compound detected whereas Novakovic et al.
445 (2007) also identified other monoterpenes (e.g., alpha-pinene and beta-pinene). Over all the
446 terpenes screened, the sesquiterpene caryophyllene and diterpene nezukol were the most
447 concentrated compounds (in *P. halepensis* and in *T. occidentalis*, respectively). The dominance of
448 caryophyllene in *P. halepensis*' leaf has been highlighted in different areas of the Mediterranean
449 Basin (Ioannou et al. 2014; Lahlou et al. 2003; Macchioni et al. 2003; Roussis et al. 1995; Tumen
450 et al. 2010; Abi-Ayad et al. 2011).

451 Another important result of this work was that leaf and litter terpene content and diversity (total
452 and by subgroup) did not differ within species nor between fuel types (54 compounds in both
453 leaves and litter). Indeed, most terpenes are retained for long periods of time, e.g., in pine
454 decomposed needles (Chomel et al. 2014); their polarity and chemical structure make them less
455 degradable and/or leachable (White 1994; and the degradability decreases with the complexity of
456 the molecule according to Kanerva et al. 2008). In both fuel types, the terpene content was higher
457 in the mature stage of *C. leylandii* (regarding sesqui- and diterpenes), agreeing with the results of
458 Peñuelas and Llusà (1997) on *Rosmarinus officinalis* and of Nowak et al. (2010).

459

460 **Impact of terpenes on flammability**

461 As expected, we found that litter was more flammable than live leaf (non-significant differences
462 for ignition temperature) which was mostly due to lower FMC, as leaf thickness and terpene
463 content did not differ from one fuel type to the other (regardless of the terpene subgroup). The
464 total terpene content had only a limited effect on flammability (negative impact on leaf flaming
465 duration but positive on litter maximum temperature) while this effect was more pronounced when
466 the different subgroups were taken into account. Indeed, sesquiterpene content was one of the main

467 driver of leaf flammability, increasing maximum temperature and flaming duration (to a lower
468 extent, sesquiterpenes were also negatively correlated to time-to-ignition), agreeing with Della
469 Rocca et al. (2017), but decreasing litter flaming duration, along with monoterpene content,
470 according to Ormeño et al. (2009). Monoterpenes primarily affected litter flaming duration but did
471 not have a predominant impact on leaf flammability. In contrast, Pausas et al. (2016) showed that
472 most compounds significantly related to *Rosmarinus officinalis*' flammability (only based on leaf
473 time-to-ignition) were monoterpenes while several works highlighted a negative impact of these
474 compounds on leaf flammability (Owen et al. 1998; Alessio et al. 2008b; Della Rocca et al. 2017).
475 Diterpene content, usually not studied in literature, impacted litter flaming duration only, but
476 positively contrary to sesqui- and monoterpene content.

477 The impact of terpenes on flammability was mostly due to the influence of the most abundant
478 compound of a subgroup (such as sesquiterpene caryophyllene in *P. halepensis* or diterpene
479 nezukol in *T. occidentalis*). Indeed, leaves of *P. halepensis* were the most flammable (especially
480 regarding both maximum temperature and flaming duration). Despite other species with high litter
481 flammability features, this pine species had already been found as one of the most flammable and
482 containing a high content of terpenes (Ormeño et al. 2009), especially caryophyllene, regardless
483 of the fuel type. Another explanation of the highest flammability of pine's needle-leaves compared
484 to the cypress' scale-leaves could be that the resin ducts, where the terpenes are stored, are located
485 deeply in the pine needles (Bernard-Degan 1988) in contrast to the cypress' sub-epidermal resin
486 glands (Castro and De Magistris 1999). This deeper location delays the vaporization of terpenes
487 whose content will be thus higher when the plant burns. In the current work, we showed that the
488 sesqui- and diterpenes stored in *P. halepensis*' live leaf and litter (high content in caryophyllene
489 and cembrene, respectively) increased flammability, especially leaf maximum temperature for the
490 former and litter flaming duration for the latter. These compounds could thus be considered as
491 functional characteristics linked to fire in the same way as serotiny, for instance. Several other

492 fire-prone species also presented high sesquiterpene content, such as some species of *Cistus* whose
493 germination is triggered by fire; for instance, *Cistus albidus* and *Cistus monspeliensis* mainly
494 synthesizing sesquiterpenes and, more precisely, caryophyllene for the latter (Llusà and Peñuelas
495 1998).

496 *C. leylandii*'s mature stage presented longer leaf flaming duration (litter flammability did not
497 differ between mature and young plants) and higher terpene content (especially cadina-1(6)4 diene
498 <cis> present only in the mature leaves) than the young plants, sesquiterpene content being the
499 only significant driver of leaf flammability.

500 Our results also showed that terpene subgroups could have opposite effects (negative for sesqui-
501 and monoterpenes and positive for diterpenes regarding litter flaming duration, for instance).
502 Moreover, a same subgroup (e.g., sesquiterpenes) could in turn enhance or mitigate a same
503 flammability variable (for instance, flaming duration) from one fuel type to the other. This could
504 be due to the higher FMC in live leaves suggesting interactions between sesquiterpenes and leaf
505 water content. Our results highlight that greater terpene content does not necessarily mean greater
506 flammability. Previous works already showed that different compounds belonging to the same
507 terpene subgroup could have opposite effects on flammability (Owens et al. 1998; Della Rocca et
508 al. 2017). We found that the terpene content did not affect some of the flammability variables (e.g.,
509 leaf ignition frequency, ignition temperature), agreeing with De Lillis et al. (2009). Sometimes this
510 effect only appeared in the simple linear regressions (as for leaf time-to-ignition or litter maximum
511 temperature), highlighting that other fuel characteristics could override the effect of terpenes on
512 flammability.

513

514 **Relative importance of the different fuel characteristics on flammability**

515 Our results showed that terpenes did not affect ignitability, regardless of the fuel type, ignition
516 frequency and time-to-ignition being primarily affected by thickness and/or FMC (but see Pausas

517 et al. 2016 or Della Rocca et al. 2017). The effect of terpenes could be hampered by FMC,
518 especially in live leaves (Alessio et al. 2008a; De Lillis et al. 2009) while this hypothesis was not
519 confirmed in the work of Della Rocca et al. (2017). The role of water as terpenes' carrier, favouring
520 or hampering their volatilization during the pyrolysis should be investigated further. Indeed,
521 terpenes could be dissolved in water, high FMC implying high terpene concentrations as suggested
522 by Ciccioli et al. (2014).

523 In our experimental conditions (fuel collected in summer), FMC was a predominant factor only
524 for leaf time-to-ignition, maximum temperature, and ignition frequency but was often overridden
525 by leaf thickness or sesquiterpene content (except for ignition frequency). Blackmarr (1972)
526 underlined the importance of exploring the effect of FMC and thickness at the same time because,
527 when a fuel is thick, more energy is required for water evaporation before ignition becomes
528 possible; that was clearly highlighted for *C. arizonica*'s live leaf and litter (longest time-to-ignition
529 as this species presented the thickest leaves and the highest FMC). Due to lower FMC in litter,
530 thickness was the predominant driver of litter flammability (except for maximum temperature)
531 whereas this factor impacted mostly leaf time-to-ignition, along with FMC. Monoterpene content
532 was among the significant drivers of litter flaming duration, along with that of sesquiterpenes and
533 diterpenes (the latter presenting an opposite effect) as well as with thickness; this result differed
534 from that of Alessio et al. (2008b) who concluded that the effect of this terpene subgroup was
535 overridden by leaf moisture content. It is worth noting that, for *C. coggygria*, the very low leaf
536 thickness (0.022 mm) compared to others species could hinder the effects of the terpene content
537 on flammability.

538 In the framework of climate change, more severe climate conditions (especially regarding
539 drought) will involve a decrease in FMC which, according to our results, will be more easily
540 overridden by other parameters such as terpene content. Under such conditions, the terpene content
541 is expected to increase given its role in coping for water deficit, as shown in several works (increase

542 in caryophyllene for *Cistus monspeliensis* as well as in alpha-pinene and delta-3-carene for *P.*
543 *halepensis* according to Llusà and Peñuelas 1998, in monoterpenes for *Picea abies* and *Pinus*
544 *sylvestris* according to Turtola et al. 2003, and for *Salvia officinalis* according to Nowak et al.
545 2010), thereby increasing plant flammability. This role would be especially marked in the more
546 flammable fire-prone species of the Mediterranean region in summer (for *P. halepensis* or the
547 other species studied that are native to this region) or in spring in Arizona (USA) for *C. arizonica*.
548 The effect of terpene content on flammability will thus likely be more pronounced in the future.

549

550

551 **Conclusions**

552 Both terpene content and diversity varied according to species and to the stage of plant maturity
553 but the terpene content did not significantly differ between fuel types. *C. leylandii* (especially the
554 mature plants) had the most diverse spectrum and the highest total content (especially regarding
555 monoterpenes) in both leaves and litter. Terpenes and especially leaf sesquiterpenes were involved
556 to varying degrees in plant flammability, yet their effects could be the opposite according to the
557 variable and the fuel type considered. Moreover, for each subgroup, the effect on flammability
558 was mostly due to one compound, which was the most concentrated of the subgroup, showing that
559 flammability was more sensitive to a particular subgroup and, further, to a particular compound
560 than to the total terpene content. *P. halepensis*, presenting the highest leaf and litter sesquiterpene
561 content (mostly due to caryophyllene), was the most flammable species (especially regarding live
562 leaf); *C. leylandii* (mature plants) and *T. occidentalis* were the other most flammable litter.
563 However, even if the terpene content took part in plant flammability, other factors must be
564 considered, such as FMC and especially fuel thickness that could override the terpene content
565 according to the flammability variable considered. Previous studies showed a seasonal variation
566 of the leaf terpene content (along with FMC) in different species including *P. halepensis* (Owens

567 *et al.* 1998; Staudt *et al.* 2000; Alessio *et al.* 2008a). In future works, it would be pertinent to
568 highlight a possible seasonal variation of flammability according to the variation in moisture and
569 terpene content throughout the year.

570 The current work underlined once more that, given the important role of ornamental vegetation
571 in the fire propagation in WUI, the fire management in these areas must also acknowledge the
572 potential for the species containing terpenes, such as *P. halepensis*, in affecting fire behaviour.
573 Recommendations to home owners and forest managers should thus be provided accordingly.
574 Indeed, our results confirmed that *P. halepensis*, already considered as a highly flammable species
575 (Trabaud 2000; Dimitrakopoulos 2001), is a deleterious species in the case of a WUI fire and has
576 often been responsible for significant damage to structures. Likewise, in *T. occidentalis*, the
577 diterpene nezukol (which was also the terpene the most concentrated overall) played a significant
578 part in the litter flammability of this species whose litter was also one of the most flammable. This
579 highlighted once more the importance of cleaning the dead surface fuel from under the ornamental
580 hedges in WUI.

581 Given that storing terpenes could be, for fire-prone species, an adaptive strategy to fire, it could
582 be interesting to exhibit possible adaptations of species/populations to changes in fire regime
583 (intraspecific variations in terpene content among populations undergoing different fire regimes
584 or interspecific variations between two species that present different fire adaptive strategies such
585 as the fire resistant *Pinus sylvestris* and the fire resilient *P. halepensis*).

586

587

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594

595

596 **Conflict of interest statement**

597 The authors declare no conflicts of interest.

598

599

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TABLES

787 **Table 1.** Flammability variables (means \pm SD, n=30) according to species and fuel types (T_{MAX} :
 788 maximum temperature, TTI: time-to-ignition, T_{TTI} : ignition temperature; FD: flaming duration,
 789 and IF: ignition frequency; Ca: *Cupressus arizonica*, Cl_y and Cl_o : young and mature
 790 *Cupressocyparis leylandii*, Cc: *Cotinus coggygia*, Cs: *Cupressus sempervirens*, Ph: *Pinus*
 791 *halepensis*, To: *Thuja occidentalis*. *C. coggygia*'s litter was not collected).

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Species	T_{MAX} (°C)	TTI (s)	FD (s)	T_{TTI} (°C)	IF (%)
LEAF					
Ph	545 \pm 39.2	14 \pm 2.4	13.9 \pm 3.1	318.7 \pm 17	100
Cs	428.4 \pm 17.7	26.3 \pm 5.1	10.6 \pm 1.6	334.4 \pm 26.6	81
Ca	454.2 \pm 39.9	41.3 \pm 10.2	11.1 \pm 3.9	375.9 \pm 32.7	90
Cl_y	420 \pm 58.1	27.1 \pm 6.6	7.9 \pm 1.9	354.8 \pm 23.5	81
Cl_o	459.1 \pm 35.5	29.4 \pm 3.9	12.4 \pm 2.2	363.6 \pm 45.7	70
To	466 \pm 34.1	26.3 \pm 2.4	9.6 \pm 2.4	362.3 \pm 21.7	87
Cc	400.5 \pm 46.5	16.9 \pm 6.6	8.82 \pm 4.1	323.7 \pm 29.2	77
LITTER					
Ph	589.4 \pm 34.9	2.5 \pm 0.8	14.6 \pm 3.6	352.5 \pm 30.7	100
Cs	551.7 \pm 100.6	3.3 \pm 0.7	21 \pm 4.8	335.1 \pm 31.6	100
Ca	569.2 \pm 66.4	3.5 \pm 0.8	12.6 \pm 3.5	382.3 \pm 54	100
Cl_y	628.9 \pm 48.2	3.2 \pm 0.9	14.9 \pm 3.5	371.8 \pm 35.8	100
Cl_o	619.4 \pm 45.7	3.2 \pm 1.4	18.5 \pm 5.3	352.5 \pm 63.9	100
To	612.6 \pm 56.4	2.6 \pm 0.8	19.6 \pm 5.5	351.9 \pm 41.8	100
Cc	-	-	-	-	-

1
2 **Table 2:** Relationships obtained between leaf and litter flammability variables with fuel characteristics using simple linear regression analyses.
3 Litter IF was not taken into account as this variable scored 100% in all the species (in bold: significant relationships, in italic: analyses performed
4 on moisture and/or thickness-corrected flammability variable; R: correlation coefficient giving the sign of the relationship, R²: adjusted coefficient
5 of determination, and p: p-value; T_{MAX}: Maximum temperature, TTI: time-to-ignition, FD: flaming duration, T_{TTI}: ignition temperature, IF: ignition
6 frequency).

LEAF	FMC	Thickness	Monoterpenes	Sesquiterpenes	Diterpenes	Total Terpenes
T _{MAX}	NS	NS	NS	F= 25.87 ; p< 0.0001 R = 0.71 ; R²= 0.48	NS	NS
TTI	F=13.28 ; p=0.001 R =-0.55 ; R²= 0.28	F= 19.57 ; p= 0.0001 R = 0.62 ; R²=0.37	NS	F= 6.67 ; p=0.016 R = -0.45 ; R²= 0.17	NS	NS
FD	NS	F= 95.95 ; p < 0.0001 rR= -0.87 ; R²= 0.75	NS	NS	F= 9.68 ; p= 0.005 R = -0.52 ; R²= 0.24	F= 5.70 ; p= 0.023 R = -0.39 ; R²= 0.13
T _{TTI}	NS	NS	NS	NS	NS	NS
IF	F=8.97 ; p=0.020 R =-0.40 ; R²=0.13	NS	NS	NS	NS	NS

LITTER	FMC	Thickness	Monoterpenes	Sesquiterpenes	Diterpenes	Total Terpenes
T _{MAX}	NS	NS	F= 6.44 ; p= 0.017	NS	F= 7.61 ; p= 0.010	F= 10.62 ; p= 0.003
			R = 0.43 ; R²= 0.16		R = 0.46 ; R²= 0.19	R = 0.52 ; R²= 0.25
TTI	NS	F= 7.11 ; p= 0.013	NS	NS	NS	NS
		R = 0.45 ; R²= 0.17				
FD	NS	F= 6.36 ; p= 0.018	NS	<i>F= 6.06 ; p= 0.020</i>	<i>F= 4.75 ; p= 0.038</i>	NS
		R = -0.43 ; R²= 0.16		<i>R = -0.42 ; R²= 0.15</i>	<i>R = 0.38 ; R²= 0.11</i>	
T _{TTI}	NS	F= 6.87 ; p= 0.014	NS	NS	NS	NS
		R = 0.44 ; R²= 0.17				

1

1 **Table 3.** Results of the partial least squares regression analyses (PLS) highlighting the significant fuel characteristics impacting leaf flammability
2 variables. A second PLS was run after the bootstrap procedure to obtain the correlation coefficients of the significant variables. Analyses were
3 separately run taking into account either the terpene content of the different subgroups or the total terpene content (in bold: significant fuel
4 characteristics, p: p value, R²: adjusted coefficient of determination, R: correlation coefficient; TTI: time-to-ignition, T_{MAX}: maximal temperature,
5 FD: flaming duration, IF : ignition frequency, T_{TTI} : ignition temperature, FMC: fuel moisture content, Thi: leaf thickness, Mono: monoterpene
6 content, Sesqui: sesquiterpene content, Di: diterpene content, Terp_tot : total terpene content; bootstrap p-value: *** : p>0.01, ** : p=0.01, * :
7 p=0.05, boot size=1000).

Flammability variable	Analyses with content of terpene subgroups			Analyses with total terpene content				
	Results of PLS1	After bootstrap	P-value	Results of PLS2	Results of PLS1	After bootstrap	P-value	Results of PLS2
TTI	p<0.0001,R ² =0.82			p<0.0001,R ² =0.73	p<0.0001, R ² =0.74			p<0.0001, R ² =0.73
	Thi: R=0.45	Thi	***	Thi: R=0.65	Thi: R=0.70	Thi	***	Thi: R=0.65
	FMC: R= 0.67	FMC	***	FMC: R= 0.58	FMC: R= 0.58	FMC	***	FMC: R= 0.58
	Mono: R= - 0.006				Terp_tot: R= - 0.13			
	Sesqui: R= - 0.16							
	Di: R= - 0.05							
Tmax	p=0.0002,R ² =0.65	FMC	***	p<0.0001,R ² =0.60	NS			
	Thi: R= 0.13	Sesqui	***	FMC: R= - 0.32				

FMC: R= - 0.43

Sesqui: R= 0.73

Mono: R= - 0.24

Sesqui: R= 0.83

Di: R= 0.27

p<0.0001,

FD

p=0.003, R²=0.29

Thi

p=0.006, R²=0.26

p<0.0001, R²=0.81

R²=0.80

Thi: R= - 0.6

Sesqui

*

Thi: R= - 0.25

Thi: R= - 0.78

Thi

Thi: R= - 0.79

FMC: R= - 0.02

Sesqui: R= 0.33

Terp_tot: R=-0.22

Terp_Tot

**

Terp_tot: R=-0.22

Mono: R= - 0.09

Sesqui: R= 0.34

Di: R= - 0.08

IF

p=0.010, R²=0.23

FMC

**

p=0.020, R²=0.16

p=0.008, R²=0.21

p=0.020, R²=0.16

Thi: R= 0.05

Di

NS

FMC: R= - 0.40

Thi: R= 0.11

FMC: R= - 0.40

FMC: R= - 0.31

FMC: R= - 0.42

FMC

Mono: R= - 0.10

Terp_tot: R= - 0.16

Sesqui: R= - 0.02

Di: R= - 0.24

T_{TI}

NS

p=0.014, R²=0.18

NS

Thi: R= 0.30

FMC: R= 0.21 FMC *

Terp_tot: R= 0.14

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2

1 **Table 4.** Results of the partial least squares regression analyses (PLS) highlighting the significant fuel characteristics impacting litter flammability
2 variables. A second PLS was run after the bootstrap procedure to obtain the correlation coefficients of the significant variables. Analyses were
3 separately run taking into account either the terpene content of the different subgroups or the total terpene content (in bold: significant fuel
4 characteristics, p: p value, R²: adjusted coefficient of determination, R: correlation coefficient; TTI: time-to-ignition, T_{MAX}: maximal temperature,
5 FD: flaming duration, T_{TTI} : ignition temperature, FMC: fuel moisture content, Thi: leaf thickness, Mono: monoterpene content, Sesqui:
6 sesquiterpene content, Di: diterpene content, Terp_tot : total terpene content; bootstrap p-value: *** : p>0.01, ** : p=0.01, * : p=0.05, boot
7 size=1000). Litter IF was not taken into account in the analysis as this variable scored 100% for all species.

Flammability variable	Analyses with content of terpene subgroups			Analyses with total terpene content				
	Results of PLS1	After bootstrap	P-value	Results of PLS2	Results of PLS1	After bootstrap	P-value	Results of PLS2
TTI	p=0.004, R ² =0.33			p=0.013, R ² =0.20	p=0.005, R ² =0.25			p=0.013, R ² =0.20
	Thi: R=0.36	Thi	*	Thi: R=0.45	Thi: R=0.52	Thi	***	Thi: R=0.45
	FMC: R= -0.17				FMC: R= -0.08			
	Mono: R= 0.20				Terp_tot: R= 0.10			
	Sesqui: R= - 0.26							
	Di: R= - 0.06							
Tmax	p=0.003, R ² =0.27	NS			p=0.001, R ² =0.31			p=0.003, R ² =0.27
	Thi: R= - 0.02				Thi: R= - 0.04			Terp_Tot:R=0.52

	FMC: R= 0.16			FMC: R= 0.24			
	Mono: R= 0.24			Terp_tot:R= 0.45	Terp_tot	***	
	Sesqui: R=- 0.002						
	Di: R= -0.25						
FD	p=0.0002, R ² =0.57	Thi	***	p<0.0001, R ² =0.56	p=0.002, R ² =0.36		p=0.003, R ² =0.35
	Thi: R= - 0.61	Mono	*	Thi: R= - 0.56	Thi: R= - 0.52	Thi	***
	FMC: R= 0.18	Sesqui	**	Mono: R= - 0.52	FMC: R= 0.44	FMC	**
	Mono: R= - 0.43	Di	***	Sesqui: R= - 0.42	Terp_tot: R= - 0.11		Thi: R= - 0.50
	Sesqui: R= - 0.42			Di : R= 0.49			
	Di: R= 0.34						
T _{TTI}	p=0.010, R ² =0.34			p=0.014, R ² =0.20	p=0.032, R ² =0.28		p=0.014, R ² =0.20
	Thi: R= 0.58	Thi	**	Thi: R= 0.44	Thi: R= 0.53	Thi	***
	FMC: R= - 0.04				FMC: R= - 0.15		
	Mono: R= 0.39				Terp_tot: R=0.29		
	Sesqui: R= 0.33						
	Di: R= - 0.04						

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3