

Fires enhance flammability in *Ulex parviflorus*

Juli G. Pausas, Giorgio A. Alessio, Bruno Moreira, Guadalupe Corcobado

CIDE-CSIC, Campus IVIA, Ctra. Nàquera Km. 4.5, 46113 Montcada, Valencia (Spain)

Correspondence: Juli G. Pausas, CIDE-CSIC, Ctra. Nàquera Km. 4.5 (IVIA), 46113 Montcada, Valencia (Spain), Email: juli.g.pausas@uv.es, Phone: (+34) 963 424124; (+34) 963 424162, Fax: (+34) 963 424160, Web: www.uv.es/jgpausas

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Introduction

Wildfires have been occurring in terrestrial ecosystems since the early evolution of plants (Pausas & Keeley 2009, Bowman et al. 2009, Bond & Scott 2010) and have shaped many species and ecosystems worldwide (Keeley et al. 2011). Plant flammability is an important driver of fire in terrestrial ecosystems and thus has a fundamental role in ecosystem dynamics and species evolution (Bond & Scott 2010, Belcher et al. 2010, He et al. 2011). Many traits enhance plant flammability (Cornelissen et al. 2003), including structural traits like high surface area to volume ratio and retention of standing dead biomass (van Wilgen et al. 1990, Papió & Trabaud 1990, 1991, Schwilk 2003), as well as chemical traits such as high cellulose:lignine ratio and high levels of volatile compounds and waxes (Philpot, 1970; Rundel, 1981; Dimitrakopoulos & Panov, 2001; Alessio et al. 2008). In fact, it has been suggested that flammability-enhancing traits would evolved to maintain fire-prone ecosystems. This hypothesis was first proposed at the community level, and stated that “fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favoured development of characteristics that make them more flammable” (Mutch 1970). However, this hypothesis was criticized, mainly for being group-selectionist and for lacking an explanation on how increased flammability of an individual would increase its fitness (Snyder, 1984, Christensen, 1985; Troumbis & Trabaud, 1989). Later, the hypothesis on the evolution of flammability was reformulated at the individual level within the framework of inclusive fitness theory (Bond & Midgley, 1995). It suggested that flammability-enhancing traits could be favored in individuals if the elevated flammability resulted in increased mortality of neighbours, and thus opening space for recruitment opportunities of the flammable individual offspring (“*kill thy neighbour*” hypothesis, Bond & Midgley 1995; also called “*born-to-burn*” hypothesis, Zedler 1995). More recent modelling studies suggested different genetic mechanisms for the evolution of flammability (Kerr et al. 1999; Schwilk & Kerr 2002). Indeed, the correlation between post-fire regeneration strategy and flammability across different species provides some evidence for the “*kill thy neighbour*” hypothesis (Keeley & Zedler 1998; Schwilk & Ackerly 2001; Saura-Mas et al. 2010; Cowan & Ackerly 2010; He et al. 2011). However rigorous field evidence on whether fire enhances plant flammability within populations of a particular species remains lacking.

If natural selection enhances flammability traits in fire-prone ecosystems through increasing opportunities for post-fire recruitment (Bond & Midgley 1995), the hypothesis should be better tested in obligate seeder species, that is, in those species that lack the resprouting ability and their post-fire regeneration relies only on germination from the seed bank (Bond & van Wilgen 1996, Pausas et al. 2004). This is because obligate seeders have shorter and non-overlapping generations and higher population turnover than resprouters (Verdú et al. 2007) and thus, they should be more sensitive to fire regime changes. Previous experimental studies on plant flammability in fire-prone

ecosystems have focused on differences between species and, particularly, between regeneration strategies (e.g., Saura-Mas et al. 2010, Cowan & Ackerly 2010) but none has studied the intraspecific variability and its relation to fire regime. In this study we predict that individuals of seeder species growing in populations subject to recurrent fires are more flammable than individuals of the same species growing in populations that rarely burn. In addition, because of this directional selection and the different population dynamics in contrasted fire regimes, we also predict that seeder species living in different fire regimes should differ in the variance structure of flammability-enhancing traits (Endler 1986). We tested these predictions in *Ulex parviflorus* (Mediterranean gorse, Fabaceae), a shrub species of the Mediterranean Basin lacking the ability to resprout and whose germination is triggered by fire. We quantified, at the individual level, flammability-enhancing traits in populations with contrasted fire regime.

Methods

Species description

Ulex parviflorus Pourr. (Fabaceae) is a thorny perennial shrub that, in mature stages, retains a high proportion of dead biomass in the plant, conferring it a high flammability (Baeza et al. 2011). Post-fire regeneration is exclusively by seedling recruitment (i.e. it lacks the ability to resprout; Paula et al. 2009). Seeds have physical dormancy and form a persistent soil seed bank. The heat produced during a fire breaks seed dormancy and stimulates the germination in post-fire conditions (Baeza & Vallejo 2006; Paula et al. 2009, Moreira et al. 2010). However, *U. parviflorus* also recruits in the absence of fire, in open spaces such as old fields (Baeza et al. 2011), making this species an ideal model to test the consequences of living in different selective environments.

Study area

The study populations were located in the Valencia region (Spain, eastern Iberian Peninsula). Using the local government forest fire database (spatially explicit data from 1978), we selected areas with high fire recurrence (two or more fires since 1978) and areas with no fire incidences for a long time. The identification of the latter areas was based on the absence of fire records (since 1978), and the presumable much longer history without fires according to the information from local managers. After a careful field survey we selected two sites within the high fire recurrence area and two sites within the unburned area in which *Ulex parviflorus* was abundant (hereafter HiFi and NoFi populations, respectively; Table 1). The four sites were shrublands. NoFi populations grew in old-fields and the recruitment of the recent generations was independent of fire (old-field colonization); indeed, *Juniperus phoenicea*, a slow-growing fire sensitive tree, was present in the two NoFi sites, suggesting a long time since fire and agricultural abandonment. In contrast, HiFi populations were the product of recurrent fires (Table 1) and the recruitment of most individuals was assumed to have been mediated by fire (post-fire regeneration).

All four populations grew on calcareous bedrock, and the slightly different climatic conditions were not related to fire regime; in fact, the climatic conditions of HiFi populations were within the range of the conditions of NoFi populations (Table 1). The mean distance between populations was 66 km; three of the populations were between 12 and 26 km apart from each other, and the fourth (a NoFi population) was between 110 and 115 km from the other three; that is, there was no geographical segregation between HiFi and NoFi populations. The populations might differ in the plant's age. HiFi plants were 10 and 16 years old (time since last fire; Table 1); we do not know the exact age of the NoFi populations, but most probably they were of similar age or older than HiFi populations (but certainly not younger). Changes in fuel structure with age in *Ulex parviflorus* are observed mainly at earlier stages of the plant development; for instance, Baeza et al. (2006) found

differences in fuel structure between 3 and 9 years old stands, but not between 9 and 17 years old stands. That is, in our sites, age is unlikely to drive differences in whole-plant flammability, and in the case that there was an age-effect, it would be expected to be towards higher flammability in NoFi populations (i.e., against our hypothesis). In addition, flammability was tested at the twig level, in last growing season twigs located at the tip of the branches (see below).

Flammability traits

In August (summer) 2010 we selected 40-46 mature individuals in each population (a total of 170 individuals), separated by ca. 5 meters, and in each individual we measured plant structural traits (see below) and performed flammability experiments in live twigs, using an epiradiator (see below).

Plant structure: We estimated plant size in the field by measuring maximum height, and crown diameters (maximum and its perpendicular diameter). We also measured the basal stem diameter; in multiple-stemmed individuals we measured the diameter of each basal stem. We then clipped all the above-ground biomass of each individual and took it to the laboratory, where we fractioned the live and dead plant biomass in fine (< 6 mm diameter) and coarse (\geq 6 mm) portions (fuel classes). All these fractions were oven-dried at 80°C for a minimum of 48 hours and immediately weighted. From these data we estimated, for each individual, the proportion of dry biomass of the different fuel classes (%) and plant bulk density (i.e., plant dry biomass/volume, $\text{g}\cdot\text{cm}^{-3}$).

Twig flammability: Flammability tests were performed for each individual in 13 twigs selected in the laboratory immediately after sampling. All selected twigs were live green twigs of similar size (ranging from 4.5 to 6.0 cm long) and corresponded to the last growing season (tips of the branches). Plant moisture content is known to influence flammability (e.g., Gill et al. 1978, Alessio et al. 2008; Plucinski & Anderson 2008; Saura-Mas et al. 2010); to eliminate differences in plant moisture that could be induced by environmental variability between sites during sampling, twigs were hydrated for 24h at 5°C in dark conditions and then allowed to balance to controlled conditions for 24h (24°C in dark conditions and 60% of humidity in a growth chamber). Immediately before each test, three of the 13 twigs were weighed and then oven-dried (24h at 70°C) to obtain dry mass and calculate twig moisture content (%) at the moment of the flammability assay. The remaining 10 twigs were individually weighted (overall mean= 0.40 g, SD= 0.17; fresh mass) and used for flammability assays. Some replicates were discarded due to methodological issues (e.g. the twig was not correctly placed in the center of the epiradiator) and thus the final number of replicates per individual ranged from 8 to 10. Flammability assays were carried out in a fume hood using an epiradiator of 500W (Helios, Italquartz) with a thermocouple connected to a data-logger (temperature range from -50 to 1100°C, time resolution of 2 seconds) and placed 8 cm above the heating plate. At this point, background temperature (i.e., without any fuel) ranged between 130 and 150°C, and on the surface of the epiradiator between 640 and 660°C. The flammability tests consisted in placing each twig in the center of the epiradiator and registering the time to ignition (i.e. time to initiate a flame) and time to flame extinction. Heat released during combustion was then computed as the area under the temperature – time curve during the flame duration divided by the sample fresh biomass ($^{\circ}\text{C}\cdot\text{s}/\text{g}$), and mass loss rate as sample fresh biomass consumed divided by the flame duration (mg/s). The maximum temperature ($^{\circ}\text{C}$) reached by the flame in each twig was also recorded. Few twigs (2%) failed to ignite; in these cases, time to ignition was set to the maximum observed value (60 seconds), which is a conservative estimate.

Statistical analysis

Time to ignition (s), heat released ($^{\circ}\text{C}\cdot\text{s}\cdot\text{g}^{-1}$), mass loss rate ($\text{mg}\cdot\text{g}^{-1}$), maximum temperature ($^{\circ}\text{C}$), and moisture (%) were averaged at the individual plant level. We first compared these four twig

flammability variables, plus plant bulk density and biomass fractions, between the plants living in populations under different fire regimes (HiFi vs NoFi). Because the parameters related to twig flammability measured were significantly related to twig moisture at the moment of the flammability test (see below), this variable was included as a covariate in the model when testing the effect of fire regime. Statistical comparisons were performed with a linear mixed-effects model using population as a random factor and the significance of twig moisture content and fire regime were obtained by a Likelihood Ratio test (LR; $df=1$). For the traits that were significant, we also compared the variance between fire regimes (HiFi vs NoFi). For doing this, we compared the observed variance in each fire regime with the distribution of variances generated by resampling the data and estimating their variance 1000 times (bootstrap replications). Because twig flammability depends on twig moisture, variance values for each trait were computed from the residuals against moisture. If the observed variance fall in the lower tail ($p < 0.05$) then the variance is considered lower than the null expectation; if it fall in the upper tail ($p > 0.95$), it suggests that the variance is greater than expected; otherwise ($0.05 < p < 0.95$), variance values are not significant different from the null (random) expectation.

Results

Above-ground plant biomass (dry weight) of the studied individuals varied considerably (quantile 5%= 232.8g, and quantile 95%= 1877g, mean=855g, SD= 535g) but was not significantly different between HiFi and NoFi populations (LR= 0.26, $p=0.61$). Similarly, the area of basal stems did not differ between fire regimes (LR= 0.107, $p=0.744$). On average, individual plant biomass was quite evenly distributed in the following three fractions: coarse live (33.6%, SD= 11), fine live (29.8%, SD= 13) and fine dead (35.6%, SD= 10), although they were very variable among individuals (ranging from <15% to >60%); dead coarse biomass always represented a small fraction of the total biomass (mean <1%). None of these fractions were significantly different between fire regimes (LR < 2, $p > 0.10$). On the contrary, bulk density (g cm^{-3}) was significantly higher in HiFi than in NoFi (LR= 5.5, $p=0.019$; Fig. 1).

For most individuals all twigs tested ignited correctly; however, for 15 individuals (9%) some of the twigs (1 to 5, mean= 2) did not ignite. Most of these individuals (14 of 15) were from NoFi populations ($\chi^2= 12.25$, $p < 0.001$). The mean twig moisture of each individual at the moment of conducting the flammability tests varied greatly (mean= 56.8%, SD= 21.8%, quantile 5%= 20.9, quantile 95%= 84.1) but was not different between fire regimes (LR= 0.04, $p=0.83$). Moisture content was positively related to time to ignition (LR= 110.6, $p < 0.0001$; Fig. 2a) and mass loss rate (LR= 29.18, $p < 0.0001$; Fig. 2b); that is, samples with high moisture content took longer to dry out and ignite, and because the mass remaining was lower (a high percentage of the total weight was water), they burnt quicker. On the contrary, moisture content was negatively related to heat released (LR=118.42, $p < 0.0001$; Fig. 2c) and maximum temperature (LR= 58.82, $p < 0.0001$; Fig. 2d); that is, the higher was the moisture content of the samples, the lower were the heat released and the maximum temperature attained. Considering moisture contents as a covariate, plants from HiFi populations ignited earlier (LR= 8.72, $p=0.0032$; Fig. 2a), burned slower (LR= 7.10, $p=0.0079$; Fig. 2b) and released more heat (LR= 5.76, $p=0.0164$; Fig. 2c) than plants from NoFi populations. The maximum temperature reached during the flammability tests was marginally higher in plants from HiFi populations than in plants from NoFi populations (LR= 2.8, $p=0.09$, Fig. 2d).

Flammability-enhancing traits also showed different variance structure between fire regimes. In the four twig flammability traits the variances were lower in HiFi than in NoFi populations (Table 2). Moreover, for these traits, HiFi populations showed significantly lower variance than the null expectation, while trait variances in the NoFi populations were no different or were greater than the null expectation (Table 2). Variance in bulk density did not show any trend with fire regime. The same results were obtained when using the raw data instead of the residuals against moisture (not

shown).

Discussion

Plants of *Ulex parviflorus* growing in recurrently burnt populations (HiFi) are more flammable than those growing in populations that have not suffered any fire (NoFi, i.e., populations established in old fields by colonization). Specifically, plants from HiFi populations ignite quicker, burn slower and release more heat than NoFi plants. In addition these plants have higher bulk density which, in *Ulex parviflorus* (Santana et al. 2011) as well as in other shrub species (Bradstock & Auld 1995), is associated to higher temperatures in the soil during a fire. All this supports that recurrent fires enhance plant flammability. Enhanced flammability is probably selected to ensure the elimination of neighbors for the success of the own offspring recruiting from the seed bank (Bond & Midgley 1995, Midgley & Bond 2011). Indeed, in this species, the heat released during fires breaks seed dormancy and stimulates germination (Moreira et al. 2010). These results support the hypothesis proposed by Mutch (1970) and Bond & Midgley (1995) on the evolutionary role of flammability. To what extent the variability in flammability (and fire intensity) is associated to an enhanced post-fire recruitment, as predicted by the “kill thy neighbour” hypothesis (Bond & Midgley 1995), remains to be explored. However there is evidence of higher seedling recruitment under increased fire intensity for a range of Mediterranean ecosystems, including South Africa (Bond et al. 1990), California (Moreno & Oechel, 1991, Schwilk 2003, Keeley et al. 2005), and Australia (Knox & Clarke 2006). In addition, future genetic analysis evaluating the heritability of flammability-enhancing traits would be needed to fully test the “kill thy neighbour” hypothesis.

The high proportion of dead standing biomass observed in these populations of *Ulex parviflorus* (ranging from 16% to 65% of the total biomass, mean= 36%) is within the range observed in previous studies for mature populations in this species (Baeza et al. 2006, 2011). This trait was highly variable among individuals and populations and thus, it was not significantly different between fire regimes. That is, although dead standing biomass confers high flammability to plants (Schwilk 2003), we did not find a consistent variability to support that this trait is under selection by fire in *Ulex parviflorus*. Our results suggest that the increased flammability in *U. parviflorus* populations subjected to recurrent fires is caused by changes in plant structure (e.g., plant bulk density and twig structure) or chemical composition, rather than by changes in dead standing biomass. These results have also management implications as they challenge the efficiency of recurrent prescribed burns for fuel reduction in *U. parviflorus* shrublands.

Previous studies suggested that recurrent fires act as a community filter, precluding some species to enter the community, depending on their traits (phenotypic clustering; Verdú & Pausas 2007, Pausas & Verdú 2008, Ojeda et al. 2010). Here we demonstrate that recurrent fires also act at the population level structuring intraspecific variability of flammability-enhancing traits. The lower trait variability in recurrently burned populations may be due to historical effects (in situ post-fire regeneration vs colonization) or to a directional selection (Falconer 1981, Endler 1986); with our data we cannot disentangle these two possibilities. Our results support the idea that fire is an evolutionary pressure shaping plant traits (Keeley et al. 2011) and provides field evidence suggesting that natural selection acts on flammability traits in such a way that recurrent fires enhance plant flammability.

It could be argued that the phenotypic differences observed between populations might be related to environmental conditions, plasticity, or biogeographical patterns. However this is quite improbable because differences in environmental conditions do not follow the observed differences in flammability (Table 1). For instance, the populations at the highest and at the lowest altitude had both regenerated by old field colonization (NoFi; Table 1) and are the populations with the lowest flammability. Furthermore, the four populations do not exhibit geographical aggregation following the different fire regime, in fact one of the NoFi populations is about 110-115 km from the other

three populations, while these three populations are 12 to 26 km apart each other; thus biogeographical differences between NoFi and HiFi should be ruled out. While some flammability parameters are expected to be correlated (e.g., maximum temperature and heat released), most of the studied flammability-enhancing traits are not directly linked to each other (e.g., time to ignition, heat released, bulk density), and thus we found different and independent lines of evidence towards more flammability in HiFi populations. Plant's age can also be discarded as a driver of our results because: a) in this species, age-related changes in flammability traits are observed at younger age classes than those considered here (Baeza et al. 2006; see also Methods section); b) basal area is probably a good indicator of plant age, at least in species that do not resprout, and we found no differences in basal area among our populations; and c) flammability differences between fire regimes were observed not only at whole plant scale (bulk density), but also at the scale of the twigs (last growing season twigs). Therefore, the most parsimonious explanation for the higher flammability and lower trait variability in HiFi populations is the origin of the populations (post-fire vs colonization) and the associated fire history. Flammability-enhancing traits have also been linked to different fire regimes in *Pinus* species (Keeley & Zedler 1998). Recent studies have demonstrated that changes in flammability are associated to changes in fire regime during the Triassic/Jurassic boundary (Belcher et al. 2010), to the spread of angiosperms in the Cretaceous (Bond & Scott 2010), and to the diversification of some species (He et al. 2010). All these studies are placing flammability as a fundamental trait in plant evolution.

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References

- Alessio GA, Peñuelas J, Llusà J, Ogaya R, Estiarte M, De Lillis M. 2008. Influence of water and terpenes on flammability in some dominant Mediterranean species. *International Journal of Wildland Fire* **17**: 274-286.
- Baeza MJ, Vallejo VR. 2006. Ecological mechanisms involved in dormancy breakage in *Ulex parviflorus* seeds. *Plant Ecology* **183**: 191-205.
- Baeza MJ, Raventós J, Escarré A, Vallejo VR. 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. *Plant Ecology* **187**: 189-201.
- Baeza J, Santana VM, Pausas JG, Vallejo R. 2011. Successional trends in standing dead biomass in Mediterranean basin species. *Journal of Vegetation Science* **22**: 467-474.
- Belcher CM, Mander L, Rein G, Jervis FX, Haworth M, Hesselbo SP, Glasspool IJ, McElwain JC. 2010. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. *Nature Geoscience* **3**: 426-429.
- Bond WJ, Midgley JJ. 1995. Kill thy neighbour: An individualistic argument for the evolution of flammability. *Oikos* **73**: 79-85.
- Bond WJ, Roux D, Erntzen R. 1990. Fire intensity and regeneration of myrmecochorous Proteaceae. *South African Journal of Botany* **56**: 326-330.

- Bond WJ, Scott AC. 2010.** Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* **188**: 1137-1150.
- Bond WJ, Van Wilgen BW. 1996.** *Fire and plants*. London: Chapman & Hall.
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Marston JB, Moritz MA, Prentice IC, Roos CI, Scott AC, Swetnam TW, van der Werf GR, Pyne SJ. 2009.** Fire in the earth system. *Science* **324**: 481-484.
- Bradstock RA, Auld TD. 1995.** Soil temperature during experimental bushfire in relation to fire intensity: Consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* **32**: 76-84.
- Christensen NL 1985.** Shrubland fire regimes and evolutionary consequences. In: S. T. A. Pickett, P. S. White eds. *The ecology of natural disturbance and patch dynamics*. Orlando: Academic Press, Inc., 85-100.
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H. 2003.** Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335-380.
- Cowan P, Ackerly D. 2010.** Post-fire regeneration strategies and flammability traits of California chaparral shrubs. *International Journal of Wildland Fire* **19**: 984-989.
- Dimitrakopoulos AP, Panov PI. 2001.** Pyric properties of some dominant Mediterranean vegetation species. *International Journal of Wildland Fire* **10**: 23-27.
- Endler JA. 1986.** *Natural selection in the wild*. Princeton, New Jersey: Princeton University Press.
- Falconer DS. 1981.** *Introduction to quantitative genetics*: Longman.
- Gill AM, Trollope WSW, MacArthur DA. 1978.** Role of moisture in the flammability of natural fuels in the laboratory. *Australian Forest Research* **9**: 199-208.
- He T, Lamont BB, Downes KS. 2011.** *Banksia* born to burn. *New Phytologist* **191**: 184-196.
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011.** Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406-411.
- Keeley JE, Pfaff AH, Safford HD. 2005.** Fire suppression impacts on postfire recovery of Sierra Nevada chaparral shrublands. *International Journal of Wildland Fire* **14**: 255-265.
- Keeley JE, Zedler PH 1998.** Evolution of life histories in *Pinus*. In: D. M. Richardson ed. *Ecology and biogeography of Pinus*. Cambridge (UK): Cambridge University Press, 219-250.
- Kerr B, Schwilk DW, Bergman A, Feldman MW. 1999.** Rekindling an old flame: A haploid model for the evolution and impact of flammability in resprouting plants. *Evolutionary Ecology Research* **1**: 807-833.
- Knox KJE, Clarke PJ. 2006.** Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands. *Oecologia* **149**: 730-739.
- Midgley J, Bond W. 2011.** Pushing back in time: The role of fire in plant evolution. *New Phytologist* **191**: 5-7.
- Moreira B, Tormo J, Estrelles E, Pausas JG. 2010.** Disentangling the role of heat and smoke as germination cues in Mediterranean basin flora. *Annals of Botany* **105**: 627-635.
- Moreno JM, Oechel WC. 1991.** Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* **7**: 1993-2004.
- Mutch RW. 1970.** Wildland fires and ecosystems - a hypothesis. *Ecology* **51**: 1046-1051.
- Ojeda F, Pausas JG, Verdú M. 2010.** Soil shapes community structure through fire. *Oecologia* **163**: 729-735.
- Papió C, Trabaud L. 1990.** Structural characteristics of fuel components of five Mediterranean shrubs. *Forest Ecology and Management* **35**: 249-259.
- Papió C, Trabaud L. 1991.** Comparative study of the aerial structure of five shrubs of Mediterranean shrublands. *Forest Science* **37**: 146-159.
- Paula S, Arianoutsou M, Kazanis D, Tavsanoğlu Ç, Lloret F, Buhk C, Ojeda F, Luna B,**

- Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, Pausas JG. 2009.** Fire-related traits for plant species of the Mediterranean basin. *Ecology* **90**: 1420-1420.
- Pausas JG, Bradstock RA, Keith DA, Keeley JE, GCTE_Fire_Network. 2004b.** Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**: 1085-1100.
- Pausas JG, Keeley JE. 2009.** A burning story: The role of fire in the history of life. *Bioscience* **59**: 593-601.
- Pausas JG, Verdú M. 2008.** Fire reduces morphospace occupation in plant communities. *Ecology* **89**: 2181-2186.
- Philpot CW. 1970.** Influence of mineral content on the pyrolysis of plant materials. *Forest Science* **16**: 461-471.
- Plucinski MP, Anderson WR. 2008.** Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire* **17**: 628-637.
- Rundel P 1981.** Structural and chemical components of flammability. *Fire regimes and ecosystem properties*. Washington DC: US Forest Service General Technical Report WO-26, 183-207
- Santana VM, Baeza MJ, Vallejo VR. 2011.** Fuel structural traits modulating soil temperatures in different species patches of Mediterranean Basin shrublands. *International Journal of Wildland Fire* **20**: 668-677.
- Saura-Mas S, Paula S, Pausas JG, Lloret F. 2010.** Fuel loading and flammability in the Mediterranean basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire* **19**: 783-794.
- Schwilk DW. 2003.** Flammability is a niche-construction trait: Canopy architecture affects fire intensity. *American Naturalist* **162**: 725-733.
- Schwilk DW, Ackerly DD. 2001.** Flammability and serotiny as strategies: Correlated evolution in pines. *Oikos* **94**: 326-336.
- Schwilk DW, Kerr B. 2002.** Genetic niche-hiking: An alternative explanation for the evolution of flammability. *Oikos* **99**: 431-442.
- Snyder JR. 1984.** The role of fire: Mutch ado about nothing? *Oikos* **43**: 404-405.
- Troumbis AY, Trabaud L. 1989.** Some questions about flammability in fire ecology. *Acta Oecologica* **10**: 167-175.
- van Wilgen BW, Higgins KB, Bellstedt DU. 1990.** The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* **78**: 210-222.
- Verdú M, Pausas JG. 2007.** Fire drives phylogenetic clustering in Mediterranean basin woody plant communities. *Journal of Ecology* **95**: 1316-1323.
- Verdú M, Pausas JG, Segarra-Moragues JG, Ojeda F. 2007.** Burning phylogenies: Fire, molecular evolutionary rates, and diversification. *Evolution* **61**: 2195-2204.
- Zedler PH. 1995.** Are some plants born to burn? *Trends in Ecology and Evolution* **10**: 393-395.

Tables

Table 1. Location, altitude (m.a.s.l.), average climatic conditions (P: annual precipitation, mm; Psu: summer precipitation, mm; T: mean annual temperature, °C), fire years during the period 1978-2010 and fire regime considered (HiFi or NoFi) for the four studied populations of *Ulex parviflorus*.

Location (Province)	Altitude (m.a.s.l.)	P (mm)	Psu (mm)	T (°C)	Fire years	Fire regime
Ares del Maestrat (Castelló)	820	760	116	14.4	none	NoFi
Cheste (Valencia)	170	422	65	17.7	none	NoFi
Sot de Chera (Valencia)	775	600	78	14.2	1978, 1986, 1994	HiFi
Chiva (Valencia)	800	553	60	15	1990, 1994, 2000	HiFi

Table 2. Variance of the five studied flammability-enhancing traits in the two fire regime scenarios (HiFi and NoFi). For the twig traits (i.e., time to ignition, mass loss rate, heat release and maximum temperature) the values represent the variance of the residuals in the regression against moisture (Fig. 2). P values < 0.05 represent significant lower variance than expected by chance; p values > 0.95 represent significant greater variance than expected by chance; otherwise (0.05 < p < 0.95), are variance values not significant different from the null (random) expectation.

Trait	HiFi		NoFi	
	Variance	p	Variance	p
Time to ignition	19.26	<0.001	50.09	0.969
Mass loss rate	44.37	0.024	62.85	0.469
Heat released	127048	<0.001	306330	0.996
Max temperature	4575.8	0.005	7747.9	0.972
Bulk density	0.000021	0.336	0.000015	0.166

Figures

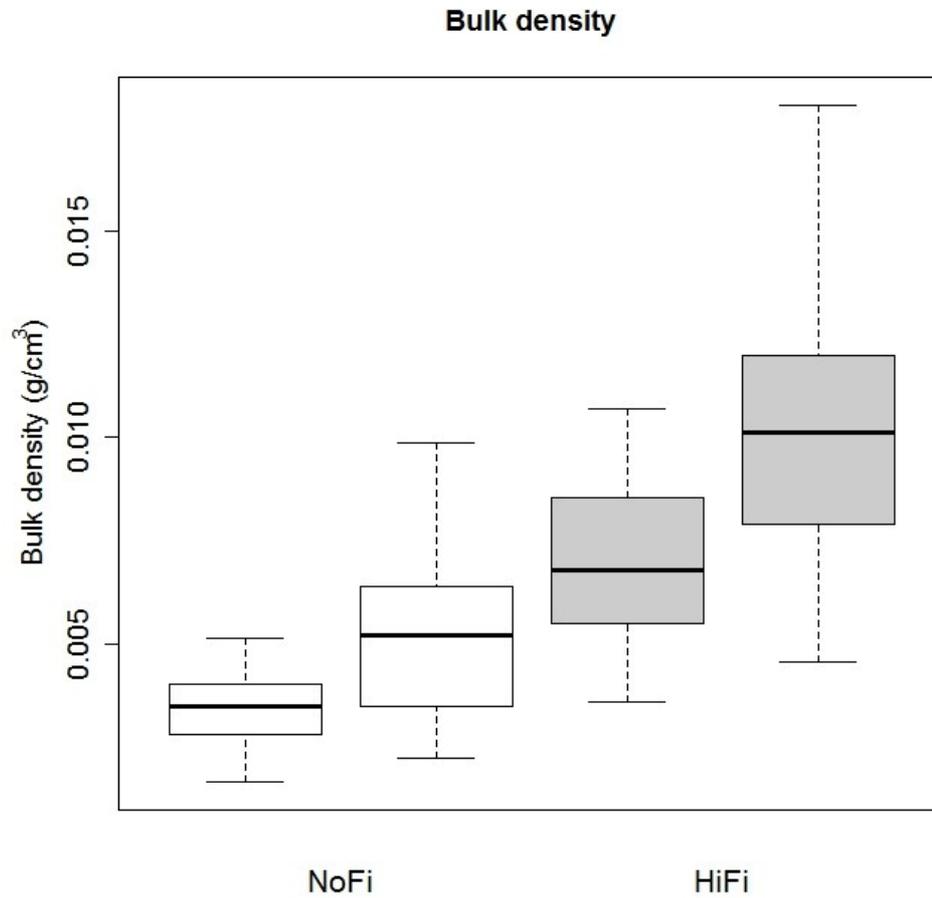


Figure 1. Bulk density (g/cm^3) in the four studied plots located in the two fire regimes (NoFi and HiFi); differences between fire regimes are significant (LR = 5.5, $p=0.019$).

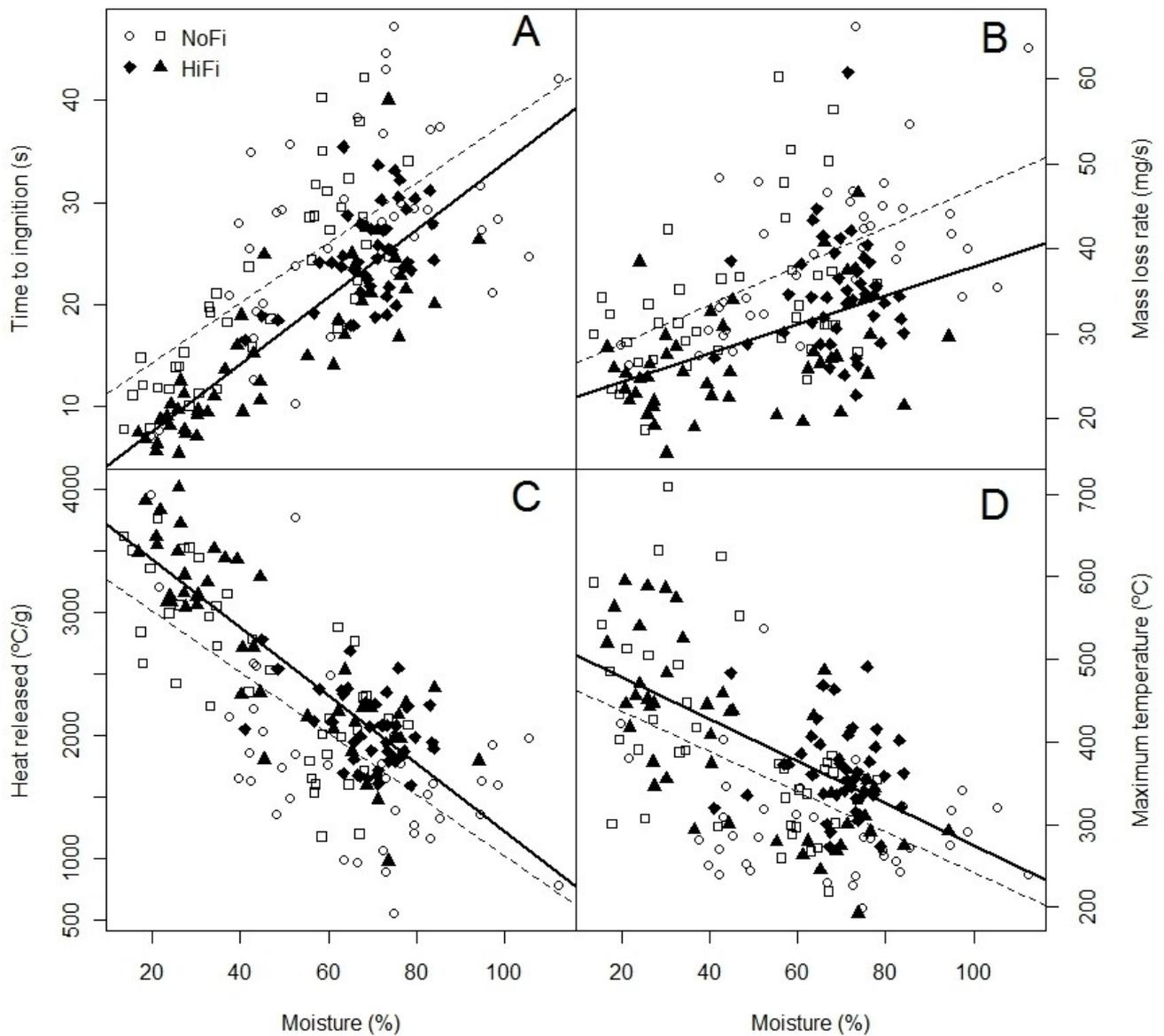


Figure 2. Time-to-ignition (seconds; A), mass loss rate (mg/s; B), heat released ($^{\circ}\text{C}/\text{g}$; C) and maximum temperature ($^{\circ}\text{C}$; D) in relation to twig moisture content (%), for plants growing in different fire regimes. Different type of symbols refer to different populations, while different color refers to different fire regimes (HiFi: black symbols and continuous line; NoFi: white symbols and dashed lines). In all cases moisture content was significant ($p < 0.001$); once accounting for the differences in moisture, the differences between fire regimes were also significant (from A to C: $p = 0.0032$, $p = 0.0079$, $p = 0.0164$) or marginally significant (D, $p = 0.09$); interactions were not significant in any of the cases).