Letter

Fires enhance flammability in *Ulex parviflorus*

Introduction

Wildfires have been occurring in terrestrial ecosystems since the early evolution of plants (Bowman *et al.*, 2009; Pausas & Keeley, 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 (Belcher *et al.*, 2010; Bond & Scott, 2010; He *et al.*, 2011). Many traits enhance plant flammability (Cornelissen *et al.*, 2003), including structural traits such as high surface area to volume ratio and retention of standing dead biomass (Papió & Trabaud, 1990, 1991; van Wilgen *et al.*, 1990; Schwilk, 2003), and chemical traits, such as high cellulose : lignin ratio and high levels of volatile compounds and waxes (Philpot, 1970; Rundel, 1981; Dimitrakopoulos & Panov, 2001; Alessio *et al.*, 2008). Indeed, it has been suggested that flammability-enhancing traits have evolved to maintain fire-prone ecosystems. This hypothesis was first proposed at the community level, where it was 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 favoured in individuals if the elevated flammability resulted in increased mortality of neighbours, and thus opened up 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 have 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; Cowan & Ackerly, 2010; Saura-Mas *et al.*, 2010; He *et al.*, 2011). However, rigorous field evidence on whether fire enhances plant flammability within populations of a particular species is lacking.

If natural selection enhances flammability traits in fire-prone ecosystems through an increase in opportunities for post-fire recruitment (Bond & Midgley, 1995), the hypothesis should be better tested in obligate seeder species, that is, in species that lack resprouting ability and for whom 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 nonoverlapping generations and higher population turnover than resprouters (Verdú *et al.*, 2007), and thus 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, in particular, between regeneration strategies (e.g. Cowan & Ackerly, 2010; Saura-Mas *et al.*, 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 will be 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 regimes.

Materials and 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, giving 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 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

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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 presumably 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 *U. 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 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. By 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; indeed, 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, 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 have differed in age. HiFi plants were 10 and 16 yr old (time since last fire; Table 1); we do not know the exact age of the NoFi populations, but, most probably, they were of a similar age to, or older than, HiFi populations (but certainly not younger). Changes in fuel structure with age in *U. parviflorus* are observed mainly at the early stages of plant development; for instance, Baeza *et al.* (2006) found differences in fuel structure between 3- and 9-yr-old stands, but not between 9- and 17-yr-old stands. That is, in our sites, age is unlikely to have driven differences in whole-plant flammability; moreover, if 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 the last growing season twigs located at the tips of the branches (see the next section).

Flammability traits

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

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

Twig flammability Flammability tests were performed for each individual on 13 twigs selected in the laboratory immediately after sampling. All selected twigs were live green twigs of a similar size (ranging from 4.5 to 6.0 cm in length) 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 have been induced by environmental variability between sites during sampling, twigs were hydrated for 24 h at 5°C in dark conditions and then allowed to balance to controlled conditions for 24 h (24°C in dark conditions and 60% humidity in a growth chamber). Immediately before each test, three of the 13 twigs were weighed and then oven dried (24 h at 70°C) to obtain the dry mass and to calculate twig moisture content (%) at the time of the flammability assay. The remaining 10 twigs were individually weighed (overall mean, 0.40 g; standard deviation (SD), 0.17 g; fresh mass) and used for flammability assays. Some replicates were discarded because of methodological issues (e.g. the twig was not placed correctly in the centre of the epiradiator), and thus the final number of replicates per individual ranged from eight to ten. Flammability assays were carried out in a fume hood using an epiradiator of 500 W (Helios Italquartz, Milan, Italy) with a thermocouple connected to a data-logger (temperature range from −50 to 1100°C; time resolution of 2 s) and placed 8 cm above the heating plate. At this point, the background temperature (i.e. without any fuel) ranged between 130

Table 1 Location, altitude, average climatic conditions (P_{ann}, annual precipitation (mm); P_{sum}, summer precipitation (mm); T, mean annual temperature (°C)), fire years during the period 1978–2010 and fire regime considered (high fire recurrence area (HiFi) and unburned area (NoFi)) for the four studied populations of *Ulex parviflorus*

Location (province)	Altitude (m asl)	P_{ann} (mm)	P_{sum} (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

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and 150°C, and on the surface of the epiradiator between 640 and 660°C. The flammability tests involved placing each twig in the centre of the epiradiator and registering the time to ignition (i.e. time to initiate a flame) and time to flame extinction. The 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 (°C s g^{-1}), and the mass loss rate as the sample fresh biomass consumed divided by the flame duration (mg s^{-1}). The maximum temperature (°C) reached by the flame in each twig was also recorded. A few twigs (2%) failed to ignite; in these cases, the time to ignition was set to the maximum observed value (60 s), which is a conservative estimate.

Statistical analysis

The time to ignition (s), heat released (°C s g^{-1}), mass loss rate (mg g^{-1}), maximum temperature (°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 plants living in populations under different fire regimes (HiFi vs NoFi). Because the measured parameters related to twig flammability were significantly related to twig moisture at the time of the flammability test, 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 was obtained using a likelihood ratio test (LR; df = 1). For the traits that were significant, we also compared the variance between fire regimes (HiFi vs NoFi). To do 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 falls in the lower tail ($P < 0.05$), the variance is considered to be lower than the null expectation; if it falls 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 significantly different from the null (random) expectation.

Results

The above-ground plant biomass (dry weight) of the studied individuals varied considerably (5% quantile, 232.8 g; 95% quantile, 1877 g; mean, 855 g; SD, 535 g), 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%); however, these fractions 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, $P > 0.10$). By contrast, 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 (1–5; 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 time of the flammability tests varied greatly (mean, 56.8%; SD, 21.8%; 5% quantile, 20.9%; 95% quantile, 84.1%), but was not different between the 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 more quickly. By contrast, the moisture content was negatively related to the 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 the moister content of the samples, the lower the heat released and maximum temperature attained. Considering moisture content as a covariate, plants from HiFi populations ignited earlier (LR = 8.72, $P = 0.0032$; Fig. 2a), burned more slowly (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 those 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, whereas

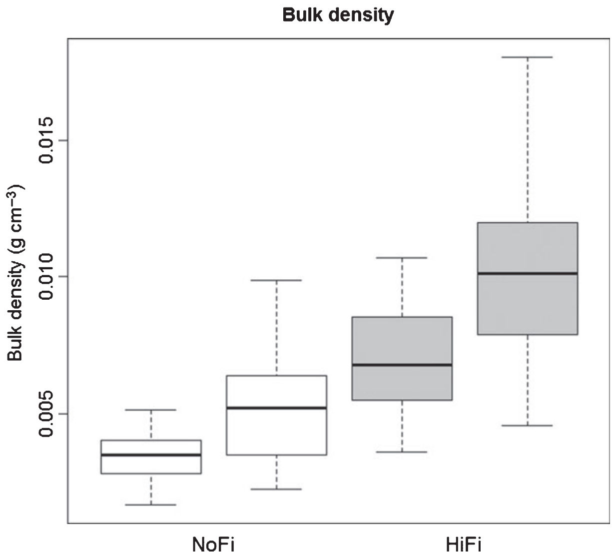

Fig. 1 Bulk density in the four studied plots located in the two fire regimes (high fire recurrence area (HiFi) and unburned area (NoFi)); differences between the fire regimes are significant (likelihood ratio (LR) = 5.5, $P = 0.019$).

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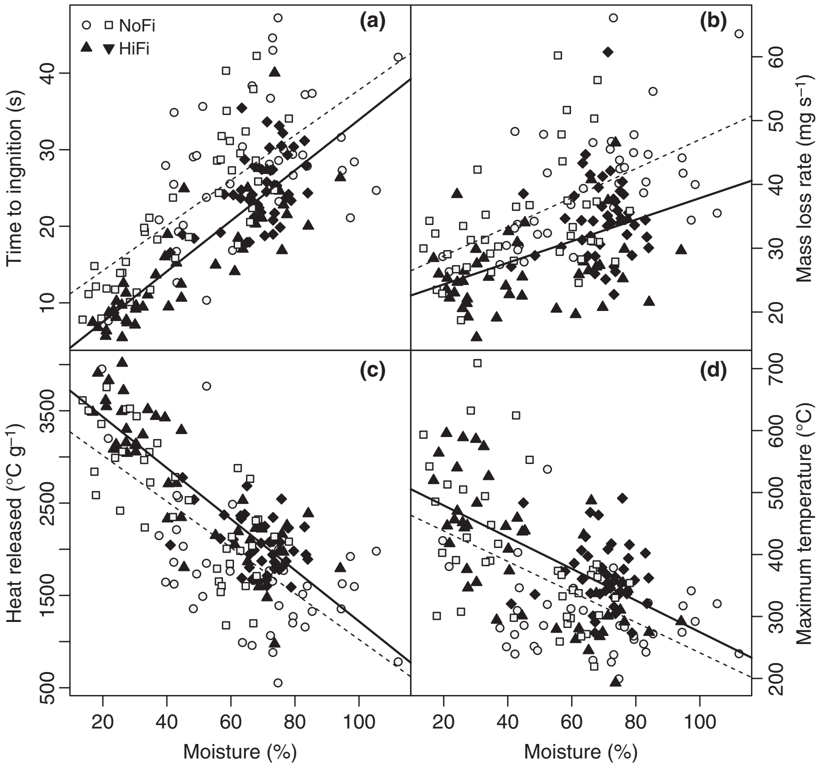

Fig. 2 Time to ignition (a), mass loss rate (b), heat released (c) and maximum temperature (d) in relation to twig moisture content for plants growing in different fire regimes. Different symbols refer to different populations, and different colours refer to different fire regimes (high fire recurrence area (HiFi), black symbols and continuous lines; unburned area (NoFi), white symbols and dashed lines). In all cases, the moisture content was significant ($P < 0.001$); once accounting for the differences in moisture, the differences between fire regimes were also significant (a–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.

Table 2 Variance of the five studied flammability-enhancing traits in the two fire regime scenarios (high fire recurrence area (HiFi) and unburned area (NoFi))

	HiFi		NoFi	
Trait	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
Maximum temperature	4575.8	0.005	7747.9	0.972
Bulk density	0.000021	0.336	0.000015	0.166

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). $P < 0.05$ represents significantly lower variance than expected by chance; $P > 0.95$ represents significantly greater variance than expected by chance; otherwise ($0.05 < P < 0.95$), variance values are not significantly different from the null (random) expectation.

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 *U. 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 more quickly, burn more slowly and release more heat than NoFi plants. In addition, these plants have higher bulk density which, in *U. parviflorus* (Santana *et al.*, 2011), as well as in other shrub species (Bradstock & Auld, 1995), is associated with higher temperatures in the soil during a fire. All of these observations support the hypothesis that recurrent fires enhance plant flammability. Enhanced flammability is probably selected to ensure the elimination of neighbours, allowing the success of offspring recruited from the seed bank (Bond & Midgley, 1995; Midgley & Bond, 2011). Indeed, in this species,

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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 with 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 *U. 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 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 indicate that this trait is under selection by fire in *U. 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 also have management implications as they challenge the efficiency of recurrent prescribed burns for fuel reduction in *U. parviflorus* shrublands.

Previous studies have suggested that recurrent fires act as a community filter, precluding some species from entering 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 a result of historical effects (*in situ* post-fire regeneration vs colonization) or of 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 provide 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 may 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, populations at the highest and lowest altitudes have both been 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 regimes; indeed, one of the NoFi populations is *c.* 110–115 km from the other three populations, and the other three populations are 12–26 km apart; thus, biogeographical differences between NoFi and HiFi should be ruled out. Although 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 age can also be discarded as a driver of our results because: (1) in this species, age-related changes in flammability traits are observed at younger age classes that those considered here (Baeza *et al.*, 2006; see also the Materials and Methods section); (2) the 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 (3) flammability differences between fire regimes were observed not only at the 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 with changes in the fire regime during the Triassic–Jurassic boundary (Belcher *et al.*, 2010), with the spread of angiosperms in the Cretaceous (Bond & Scott, 2010) and with the diversification of some species (He *et al.*, 2011). All of these studies place flammability as a fundamental trait in plant evolution.

Acknowledgements

This work was financed by the VIRRA project (CGL2009-12048/BOS) from the Spanish Government. G.A.A. is supported by a Juan de la Cierva scholarship (JDC 2009-5067; Spanish Government) and B.M. by an FCT grant (SFRH/BD/41343/2007; Portuguese Government). CIDE is supported by the Spanish National Research Council (CSIC), Generalitat Valenciana and the University of Valencia. We thank R. Bossi (CEAM, GRACCIE project, CONSOLIDER-INGENIO 2010), E. Beltran, S. Paula, J. Chofre and O. González-Pelayo for their collaboration in the field and laboratory work, M. C. Castellanos for comments on an early version of the manuscript, and Fundación Caja Castellón-Bancaja for permission to work in Barranc dels Horts (Ares del Maestrat).

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Key words: evolution, fire regime, flammability traits, Mediterranean, obligate seeder, *Ulex parviflorus*.

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