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Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies

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Abstract. The flammability and combustibility of plant communities are determined by species features related to growth-form, structure and physiology. In some ecosystems, such as the Mediterranean ones, these characteristics may contribute to the existence of fire-prone species. We measured several parameters associated with the flammability and fuel loading of dominant woody species with different post-fire regenerative strategies (seeders and non-seeders) in shrublands in the western Mediterranean Basin. Overall, seeder species show lower fuel load but are more prone to burning owing to a higher dead-to-live fuel ratio, live fine-fuel proportion and dead fine-fuel proportion. Moreover, they burst into flame at lower temperatures than non-seeders. In the Mediterranean Basin, most seeder species emerged mainly during the Quaternary, under a highly fluctuating Mediterranean climate and during recurrent fires. We propose that properties related to the combustibility and flammability of seeders may be the result of selective pressures associated with both fire and climate. These results suggest that ecosystems dominated by seeder species are more susceptible to fire risk than those dominated by non-seeder species in the Mediterranean Basin. Therefore, the proportion of these types of species resulting from previous fire or management history is likely to determine the characteristics of future fire events.

Additional keywords: combustibility, fire regime, resprouting, seeder, wildfire.

Introduction

Wildfire is an important disturbance in the ecosystems of the Mediterranean Basin and can determine species composition and ecosystem functioning (Whelan 1995; Lloret and Vilà 2003; Eugenio and Lloret 2004; Rodrigo *et al.* 2004; Bond *et al.* 2005). In these communities, post-fire regeneration is determined by the different mechanisms exhibited by the species, and there is evidence that the proportions of regenerative types in plant communities may be affected by the fire regime (Bellingham and Sparrow 2000; Franklin *et al.* 2001; Pausas *et al.* 2004; Lloret *et al.* 2005*a*; Pausas and Bradstock 2007; Pausas and Lloret 2007; Vilà-Cabrera *et al.* 2008). It has also been reported that morphological and physiological features (low moisture content, abundant amount of resins, oils and volatile products, persistence of dead parts in the canopy, etc.) make many Mediterranean woody species fire-prone (Papió and Trabaud 1991; Bond and Midgley 1995; Schwilk and Ackerly 2001; De Luis *et al.* 2004; Alessio 2006; Scarff and Westoby 2006). Thus, differences in the flammability of species with different post-fire regenerative strategies can be the determinant factors in the dynamics of fire-prone communities by promoting fire–vegetation feedbacks. For instance, a positive feedback may occur if more flammable species also show more successful regenerative trends (Mutch 1970), as has been reported for grasses (Vilà and Lloret 2000; Vilà *et al.* 2001; Grigulis *et al.* 2005) and pines (Schwilk and Ackerly 2001).

In the Mediterranean Basin, some preliminary studies show that species with a particular post-fire regenerative strategy (e.g. fire-stimulated germination) consistently exhibit traits that heighten flammability (e.g. lower water content in summer) (Saura-Mas and Lloret 2007). The main post-fire regenerative strategies include that of seeders, propagule-persister species in which the population persists locally in propagule form (seed, fruit) after fire. These are species with populations that regenerate by establishing seedlings promptly after fire from a persistent seed bank (seeds that resist, or are protected, from fire) and the recruitment of new individuals is often enhanced by fire (Pausas *et al.* 2004). This category includes species that only regenerate after fire from seeds (obligate seeders; R−P+: Pausas *et al.* 2004) and species that both resprout and establish seedlings after fire (facultative seeders, R+P+). In contrast, non-seeders are species whose propagules (seed, fruit) do not

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persist after fire; consequently, the propagules owe their existence entirely to dispersal from outside the fire-affected area. Also, some non-seeders may regenerate after fire by resprouting from underground or aerial parts of the plant (obligate resprouters; R+P−). As regards woody plants, seeders are usually species with a relatively short life cycle and a high degree of recruitment after fire, whereas non-seeders are species with longer life cycles and lower rates of recruitment after fire (Pate *et al.* 1990; Verdaguer and Ojeda 2002; Pausas *et al.* 2004; Knox and Clarke 2005; Schwilk and Ackerly 2005). In the Mediterranean Basin, late successional communities are often dominated by non-seeder (R+P−) species, whereas many seeders (R−P+, R+P+) may also recruit after disturbances such as clearing.

Species in our study region with the seeder trait have evolved under the Mediterranean climate established in the Quaternary, whereas the resprouter attribute exhibited by many non-seeders is an ancestral trait found in many ancient lineages and widely distributed in many ecosystems (Lloret *et al.* 1999; Verdú 2000; Bond and Midgley 2003; Bond and Keeley 2005). In fact, it is considered that non-seeder species evolved in the Tertiary before the establishment of the Pre-Mediterranean climate (Herrera 1992; Verdú 2000; Pausas and Verdú 2005).

Various determining factors are worthy of consideration with respect to the fuel loading and flammability vegetation traits. Specifically, structural and chemical plant traits are inherent factors in the vegetation cover that determine the combustibility and flammability of the community. The term combustibility is often confused with flammability but, according to Trabaud (1976), flammability in fact includes three components: ignitability, combustibility and sustainability. Ignitability indicates how easily the fuel ignites; combustibility refers to how plants burn after they have been ignited; sustainability registers the stability of the burning rate, i.e. how well the fuel continues to burn.

Several elements affect species flammability: the amount of heat received, the distribution and size of live and dry organs (branches, leaves), the chemical composition, and the water content (Philpot 1970; Trabaud 1989; Cornelissen *et al.* 2003). Specifically, tissue moisture and organ morphology (i.e. surface-to-volume ratio) are essential as they determine the respective amount of energy needed to start the fire reaction and the contact between the reagents (fuel and the atmospheric oxygen) (Papió 1994; Massari and Leopaldi 1995; Dimitrakopoulos and Panov 2001; Nelson 2001).

Combustibility is determined by fuel load and fuel characteristics such as the proportion of live and dead material or the amount of fine and coarse materials. Standing dead branches can increase fire temperatures and heat release (Schwilk 2003) and the dead fine-fuel ratio is an effective indicator of fire danger (Bond and Van Wilgen 1996; De Luis *et al.* 2004). In fact, many fire-risk prevention and extinction programs are based on information about fuel-loading properties (Valette *et al.* 1994; Pons and Vayreda 1996; Viegas *et al.* 2001).

In this study, we investigate the relationship between flammability, fuel loading and post-fire regenerative traits according to the following hypotheses: (1) species with post-fire recruitment (seeders) may have obtained selective advantage as a result of fire occurrence, and would show more flammable traits; and (2) seeder species in the Mediterranean Basin have evolved traits associated with water-deficit tolerance (e.g. low leaf moisture) that also promote fire occurrence. We also consider some variables that influence flammability, such as leaf morphology (surface-to-volume ratio) and leaf moisture. When comparing the different types of species, we also account for the weight of the taxonomical linkage between them. We endorse these hypotheses as they are consistent with the proposition that fire acts as a selective force promoting the obligate seeder strategy, which would take advantage of the competition-free conditions found after wildfires (Zedler 1995; Bond and Van Wilgen 1996; Lloret 1998; Schwilk and Ackerly 2001; Pausas *et al.* 2004).

The main objective of this study is to explore the flammability and the fuel loading of species showing different post-fire regenerative strategies in shrublands in the Western Mediterranean Basin.

Materials and methods

Study areas and species

This study was conducted in two separate locations sharing structural and compositional features in the eastern coastal mountains of the Iberian Peninsula. This approach reinforces the consistency of common patterns and accounts for the variability of flammability traits. One site was located in the Massís del Montgrí (hereafter, Montgrí), in the north-east Iberian Peninsula (42°16′N, 3°24′W), and the second was located in the Serra de la Murta (hereafter, Murta) (39°4′N, 0°12′W), 420 km south of the Montgrí site. In both areas, vegetation was dominated by open pine woodlands and coastal shrublands. The sampling was conducted on shrublands (1–2 m high) growing on limestone that had not been affected by wildfire for over 10 years.

Both sites have cool winters and warm summers (mean annual temperature is 14.8°C in Montgrí and 17.4°C in Murta), but Murta presents lower summer precipitation and higher summer temperatures (49.3 mm of rainfall from June to August and mean temperatures of 25.7°C in the hottest month, August) than Montgrí (113 mm of rainfall from June to August and mean temperatures of 22.4°C in the hottest month, August), indicating higher water evapotranspiration and greater water demand on the southern site (Murta) (Pérez 1994; Ninyerola *et al.* 2000; Ninyerola *et al.* 2003).

We sampled the dominant woody species of the studied shrubland communities (29 species covering all the sites and experiments; Bolòs *et al.* 2005), including data on different life-forms and post-fire regenerative strategies across a broad taxonomical range (Table 1). In order to obtain comparable results between regenerative strategies, we excluded some life-forms, such as pine trees and herbs (for instance, grasses) that are also found on these shrublands but show very different structural features. Other tree species, such as *Quercus ilex* and *Olea europaea*, often remain as shrubs in these communities. Species were classified into two regenerative groups, according to their post-fire regenerative strategies: seeders and non-seeders. For this classification, we considered the published information (Cucó 1987; Papió 1988; Lloret and Vilà 1997, 2003; Verdú 2000; Alberdi and Cavero 2003; Paula *et al.* 2009), and direct field observations from a recently burnt area in Montgrí. Species that are able to both recruit seedlings and resprout after fire were

Table 1. Study species (Bolòs *et al.* 2005), families, post-fire regenerative strategies (seeder, S; non-seeder, NS) and life-form according to Raunkiaer (1934; MP, macro-phanerophyte; P, phanerophyte; NP, nano-phanerophyte; PV, phanerophyte-vine; C, chamephyte)

F and FL columns indicate whether the species was used in the experiment to determine flammability (F) and fuel loading (FL). Numbers indicate the sites where the species were sampled (1, Montgri; 2, Murta)

Study species	Family	Life-form	F	FL	Regenerative strategy
Calicotome spinosa (L.) LK	Fabaceae	NP		1–2	S
Cistus albidus L.	Cistaceae	NP	1–2	1–2	S
Cistus crispus L.	Cistaceae	NP	1–2		S
Cistus monspeliensis L.	Cistaceae	NP	1–2	1–2	S
Cistus salviifolius L.	Cistaceae	NP	1–2		S
Coronilla minima L.	Fabaceae	C	1–2	1–2	NS
Daphne gnidium L.	Thymelaeaceae	NP	1–2	1–2	NS
Dorycnium hirsutum (L.) Ser. in DC.	Fabaceae	C		1	S
Dorycnium pentaphyllum Scop.	Fabaceae	C		1	S
Fumana ericoides (Caav.) Gandg.	Cistaceae	C		1–2	S
Fumana laevipes (L.) Spach.	Cistaceae	C		1	S
Fumana thymifolia L.	Cistaceae	C		1–2	S
Globularia alypum L.	Globulariaceae	NP	1–2	1–2	S
Helichrysum stoechas (L.) Moench.	Asteraceae	C	1–2	1	S
Lavandula latifolia Med.	Lamiaceae	C	1–2		S
Lonicera implexa Aiton	Caprifoliaceae	PV	1		NS
Olea europaea L.	Oleaceae	MP	1		NS
Osyris alba L.	Santalaceae	NP		1–2	NS
Phillyrea angustifolia L.	Oleaceae	NP	1–2	1–2	NS
Pistacia lentiscus L.	Anacardiaceae	MP	1–2	1–2	NS
Quercus coccifera L.	Fagaceae	NP	1–2	1	NS
Quercus ilex L.	Fagaceae	MP	1		NS
Rhamnus alaternus L.	Rhamnaceae	P	1–2	1–2	NS
Rhamnus lycioides L.	Rhamnaceae	P		2	NS
Rosmarinus officinalis L.	Lamiaceae	NP	1–2	1–2	S
Smilax aspera L.	Liliaceae	PV	1		NS
Staehelina dubia L.	Asteraceae	C	1		S
Teucrium polium L.	Lamiaceae	C	1–2	1–2	S
Thymus vulgaris L.	Lamiaceae	C		1–2	S

categorised as seeders. This grouping is based on previous studies that have shown that these species exhibit a water-use strategy more similar to that of seeders than to that of species that can only resprout after fire (Saura-Mas and Lloret 2007).

Fuel loading

Sampling was carried out in summer (July to August) 2006, in five non-senescent, fully developed and healthy adult individuals per species in each of the study areas. To describe fuel-loading traits, we sampled 15 species that were present on both study sites with an additional five species in Montgrí and one in Murta (Table 1). These additional species were not considered for the comparison between the sites. Sampled individuals of the same species were growing under similar conditions outside the tree canopy. Each individual was cut at the surface of the ground. Dead and live fuel fractions were separated *in situ* and weighed (fresh weight, FW). Shoots of both dead and live material, including branches and logs, were separated in the laboratory according to two diameter classifications (fine fuel, diameter $<$ 6 mm; coarse fuel, diameter $>$ 6 mm). Leaves of live material were considered as a separate fraction. Finally, the classified material was oven-dried (3 days at 60°C) to obtain its dry weight.

Flammability

We sampled 15 species that were present in both study sites, plus five and one additional species in Montgrí and Murta respectively (Table 1). Leaf samples from 5 to 10 individuals (replicates) from each species were collected on each site. In some cases, the species considered in the fuel-load measurements could not be used in the flammability test because of their very small leaf size and their consequent small total leaf biomass per plant. Some species that were not considered in the fuel load estimations were, however, included in the flammability test (see Table 1).

Leaf samples were collected in August 2006, the month of the year with the highest fire hazard in the studied areas. We homogenised the samples by basing them only on leaves, avoiding any mixtures with shoots, which show very different structural properties. Moreover, leaves tend to have a higher surface-to-volume ratio, and therefore greater flammability, and are thus a good indicator of plant flammability (Cornelissen *et al.* 2003). Leaf samples were harvested from branches exposed to direct sunlight in well-grown plants established under similar conditions. They were fully expanded leaves, free of any herbivore or pathogen damage. The number of leaves sampled from each individual plant varied according to the size and weight of the leaves from each species.

The material from each plant was enclosed in a hermetic plastic bag and stored under ice-box conditions to avoid water loss during transportation from the field and in the laboratory (Viegas *et al.* 2001), where we separated leaves from twigs. A subsample of leaves was used from each plant to estimate the leaf moisture (LM) at the time of flammability. So, we obtained the fresh mass of material (M_f) and its respective dry mass (M_d) (with a precision of 0.001 g) after oven-drying for 48 h at 70°C. Leaf moisture (%) was determined as:

$$LM = 100 \times [(M_f - M_d)/M_d]$$

Before testing flammability, we measured the thickness of 10 leaves from each plant to estimate the surface-to-volume ratio (S : V) as:

$$S : V = S/(S \times T) = 1/T$$

where S is surface, V is volume and T is thickness of the leaf. Thickness (mm) was measured with a digital slide calliper in the central part of the leaf, avoiding the raquis.

Flammability was assessed by recording the time and the temperature of the following phases (cf. Trabaud 1976; Massari and Leopaldi 1995; Alessio *et al.* 2008):

- *Appearance of smoke*, which corresponds to the moment when pyrolysis starts (smoke phase or phase I);
- *Start of combustion*, marked by the appearance of red spots and the occurrence of ignition (smouldering phase or phase II);
- *Appearance of flame*, when flame emission occurs (flaming phase or phase III).

Ten grams of fresh leaves from each plant were tested with a quartz epiradiator (Trabaud 1976; Massari and Leopaldi 1995) coupled with a digital thermometer equipped with a probe in contact with the sampled leaves. The leaves were placed on a wire mesh at a distance of 4 cm from the epiradiator source. The epiradiator releases heat and induces the first phase; afterward, the temperature progressively rises until flames appear. A digital timer was used to record the time at which the three phases appeared. We set the timer to start when the temperature reached 60°C, to ensure that all the species received the same amount of heat. All the experiments were conducted in a closed environment to avoid any influence from draughts. The test ended when the whole sample had burned and the maximum temperature had been reached.

Statistical analysis

The variables derived from the fuel fractioning were: live fine fuel, dead fine fuel, live coarse fuel, dead coarse fuel, total live fuel, and total dead fuel. Live leaves were included in the live fine fuel fraction. All these variables were considered relative to the total dry aboveground biomass of the individual (i.e. dry weight), resulting in a ratio for each variable. The total dry biomass and the dead fuel to live fuel ratio were also estimated. A two-factor ANOVA was conducted for each variable with the regenerative strategy (seeder, non-seeder) and site (Montgrí, Murta) as fixed factors. To better approximate normality, all variables were natural log-transformed. For comparisons between the two study sites, only species sampled on both study sites were considered.

We considered six variables to study flammability: temperature and time taken to reach each of the three phases. The differences in flammability between the species and the two regenerative strategies were tested by using GLMs (general linear models), including the two factors as fixed effects. LM and S : V were included as covariates (Papió 1994; Massari and Leopaldi 1995; Nelson 2001; Alessio 2006).

The differences between regenerative groups with reference to the temperatures at which the flammability phases arose were also analysed by a repeated-measures ANOVA, where regenerative strategy and site were the between-subject factors and the flammability phase the within-subject factor (with three levels: smoke, smouldering, flaming). These analyses were repeated with the inclusion of the covariates (LM and S : V). Only species that burst into flame were included in these analyses.

The differences between regenerative groups and sites for the variables LM and S : V were also analysed with two independent two-factor ANOVAs. To better approximate normality, LM was transformed to its $\ln(x + 1)$ and S : V to its $\ln(x)$. The relationships between LM and time to smoke and flaming, and between S : V and time to smoke and smouldering, were fitted by a linear regression.

In these previous analyses (except for linear regressions), we worked with the species means (i.e. one value per species and site), which was obtained from the mean of the respective sampled individuals. One difficulty in species-level analyses is the need to deal with the autocorrelation that may exist in parameters measured from species sharing a common ancestor (Blackburn and Duncan 2001; Garland *et al.* 2005; Sol *et al.* 2007). So, we also performed a GLMM (general linear mixed model) for all the fuel and combustion variables, considering a hierarchical nested design of species (as a random factor) between families to test whether there was any autocorrelation associated with the 'family' at the higher taxonomical level.

Results

Fuel loading

Although the seeder species are smaller ($F = 16.37$, $P < 0.001$, Fig. 1*a*), they produce a type of fuel loading that makes them more prone to burning (mean values per species are available in Table A1 of the Accessory publication). The dead-to-live-fuel ratio ($F = 4.04$, $P = 0.055$, Fig. 1*b*), the live fine-fuel ratio ($F = 6.83$, $P = 0.015$, Fig. 1*c*) and the dead fine-fuel proportion were higher in seeders than in non-seeders ($F = 5.99$, $P = 0.021$, Fig. 1*d*). In contrast, seeder species presented a lower proportion of live coarse fuel than non-seeders ($F = 14.25$, $P = 0.001$, Figs 1*e*, 2, Table A1 of the Accessory publication) but similar values in the dead coarse-fuel proportions ($F = 0.056$, $P = 0.810$). None of the statistical analyses showed a significant interaction between the regenerative strategy and site and no significant difference between the two study sites of Murta and Montgrí.

Flammability

Seeders presented lower smouldering and flaming temperatures and took a longer time to smoke than non-seeders, although the

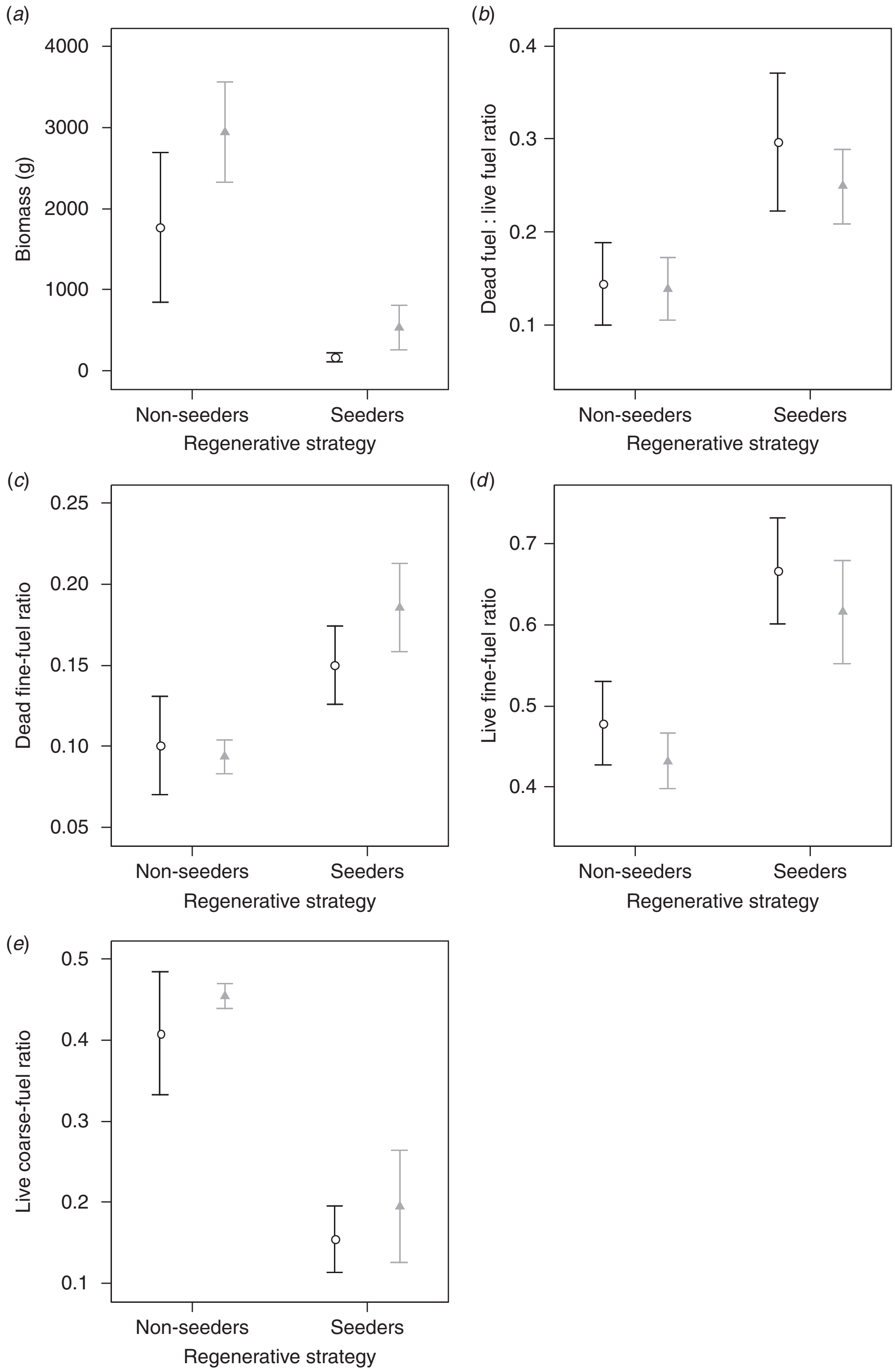

Fig. 1. Means and standard errors of total plant biomass (*a*), dead fuel–live fuel ratio (*b*), live fine-fuel ratio (*c*), dead fine-fuel ratio (*d*) and live coarse-fuel ratio (*e*) for the regenerative strategies (seeders and non-seeders) and for the two study sites (Murta and Montgrí). Montgrí values are represented by circles (○) and Murta by triangles (▲). In all cases, differences between regenerative strategies are significant ($P < 0.05$) (Fig. 1*b* presents a marginally significant difference), and those between the sites for a given strategy are not.

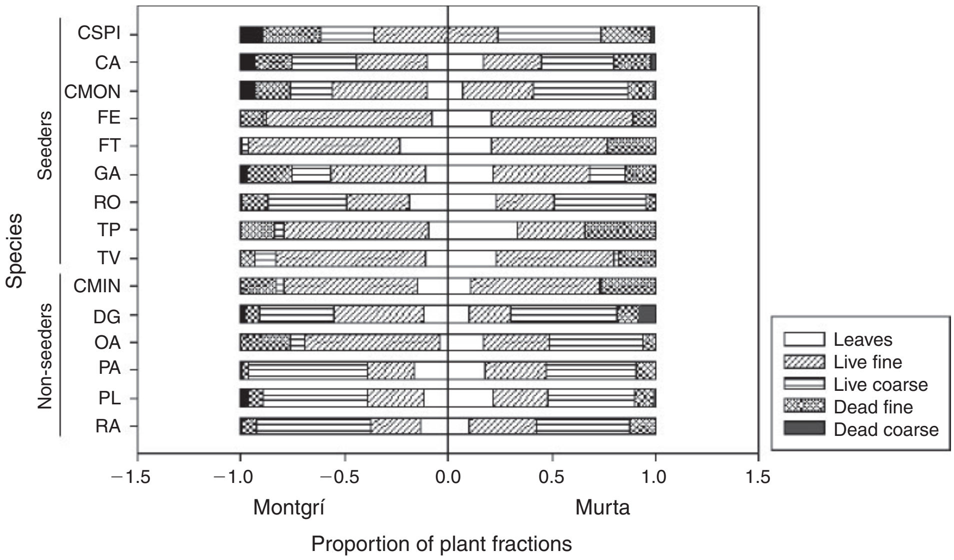

Fig. 2. Proportion of each fraction (leaves, dead, live, fine and coarse material) in relation to the total dry weight for each species in the two study sites (Montgrí and Murta). Species are first sorted according to the regenerative type and then in alphabetical order. Horizontally, the values for each species on each site (Murta and Montgrí) are represented. Species codes are: CSPI, *Calicotome spinosa*; CMON, *Cistus monspeliensis*; CA, *Cistus albidus*; FE, *Fumana ericoides*; FT, *Fumana thymifolia*; GA, *Globularia alypum*; RO, *Rosmarinus officinalis*; TP, *Teucrium poleum*; TV, *Thymus vulgaris*; CMIN, *Coronilla minima*; DG, *Daphne gnidium*; OA, *Osyris alba*; PA, *Phyllirea angustifolia*; PL, *Pistacia lentiscus*; RA, *Rhamnus alaternus*.

differences for the latter were only marginally significant (Table 2, Fig. 3). Repeated-measures ANOVA analysis testing differences in temperatures over time endorsed these results, as the main difference between seeders and non-seeders was the former's tendency to reach the flaming phase at lower temperatures (Table 3, Fig. 4). No significant differences were found between the study sites for any of the flammability variables (Tables 2 and 3).

S : V was not significantly different with respect to the regenerative strategies ($F = 0.036$, $P = 0.850$) or the sites ($F = 2.335$, $P = 0.139$); the interaction was also non-significant ($F = 1.607$, $P = 0.216$).

Leaf moisture plays a significant role in determining temperature and time to smoke and flaming. S : V significantly reduced the time and temperature before reaching the smoke phase (Table 2).

In Montgrí, leaf moisture was positively related to time to smoke and flaming (Fig. 5*a*, *b*), whereas S : V was negatively related to time to smoke and smouldering (Fig. 5*c*, *d*). The same pattern was observed in Murta, except that leaf moisture was positively related to the temperature to flaming instead of time to flaming.

No significant effect of the taxonomical affiliations was found in any of the studied variables, suggesting that taxonomical effects do not explain the variability found between regenerative strategies.

Discussion

This study shows that woody species coexisting in a Mediterranean Basin shrubland that share a similar regenerative response after fire may also show similar structural features related to their ability to enhance wildfires. Although the studied seeder species, being smaller, tend to offer less fuel load than non-seeders, they show a higher proportion of fine dead material and a lower fuel moisture content than non-seeders, thereby fomenting the spread of fire and increasing the danger of fire. The studied seeders are also species with rapid combustion, as suggested by the lower smouldering and flaming temperatures of the leaves, whereas non-seeders have more coarse fuel, promoting longer but slower fires (Andrews and Bevins 2003). This pattern concurs with previous studies that suggest that species combustibility could be highly influenced by plants' fuel structure (Schwilk 2003). The absence of differences between the two sites in this respect confirms that the observed patterns are mostly attributable to the intrinsic properties of species and not to local conditions.

These features of the studied seeders are probably due to structural and physiological traits related to the following facts. First, seeders present a particular life history (which is characterised by a short lifespan), small size of aboveground organs, shallow roots and relatively high seedling establishment, whereas non-seeders show the opposite (high biomass and a long lifespan with high survival after fire, thanks to their resprouting capacity) (Terradas 2001). Second, seeders present, among other physiological features, high leaf-water seasonal variation, low relative water content and low leaf dry-matter content (Saura-Mas and Lloret 2007; Saura-Mas *et al.* 2009), resulting in an ability to tolerate drought conditions typical of Mediterranean environments.

Most seeder lineages diversified in the Mediterranean Basin during the Quaternary, under the Mediterranean climate (Herrera 1992; Verdú *et al.* 2003; Pausas and Verdú 2005). Therefore, their ability to germinate abundantly after disturbances may be due both to fire and to a highly fluctuating climate with harsh dry periods. Both types of environmental variability probably became more prevalent during the early

Table 2. Summary of results for general linear model (GLM) accounting for the variation in temperature and time needed to reach the phases of smoke, smouldering and flaming

Two fixed effects (regenerative strategy and site) and two covariates (leaf moisture, LM, and surface-to-volume ratio of the leaf, S : V) were considered in these analyses

	Temperature						Time					
	Smoke		Smouldering		Flaming		Smoke		Smouldering		Flaming	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
LM	5.210	0.032	1.576	0.221	5.436	0.029	14.428	0.001	0.382	0.542	7.427	0.013
S : V	7.071	0.014	1.485	0.235	0.239	0.630	13.773	0.001	3.994	0.057	0.427	0.521
Regenerative strategy	1.421	0.245	9.686	0.005	5.114	0.034	3.961	0.058	2.241	0.147	0.628	0.438
Site	4.200	0.052	1.222	0.280	0.673	0.421	1.148	0.295	0.078	0.783	1.102	0.307
Reg. strategy × site	0.767	0.390	0.316	0.579	0.971	0.335	0.038	0.847	0.005	0.946	0.323	0.576

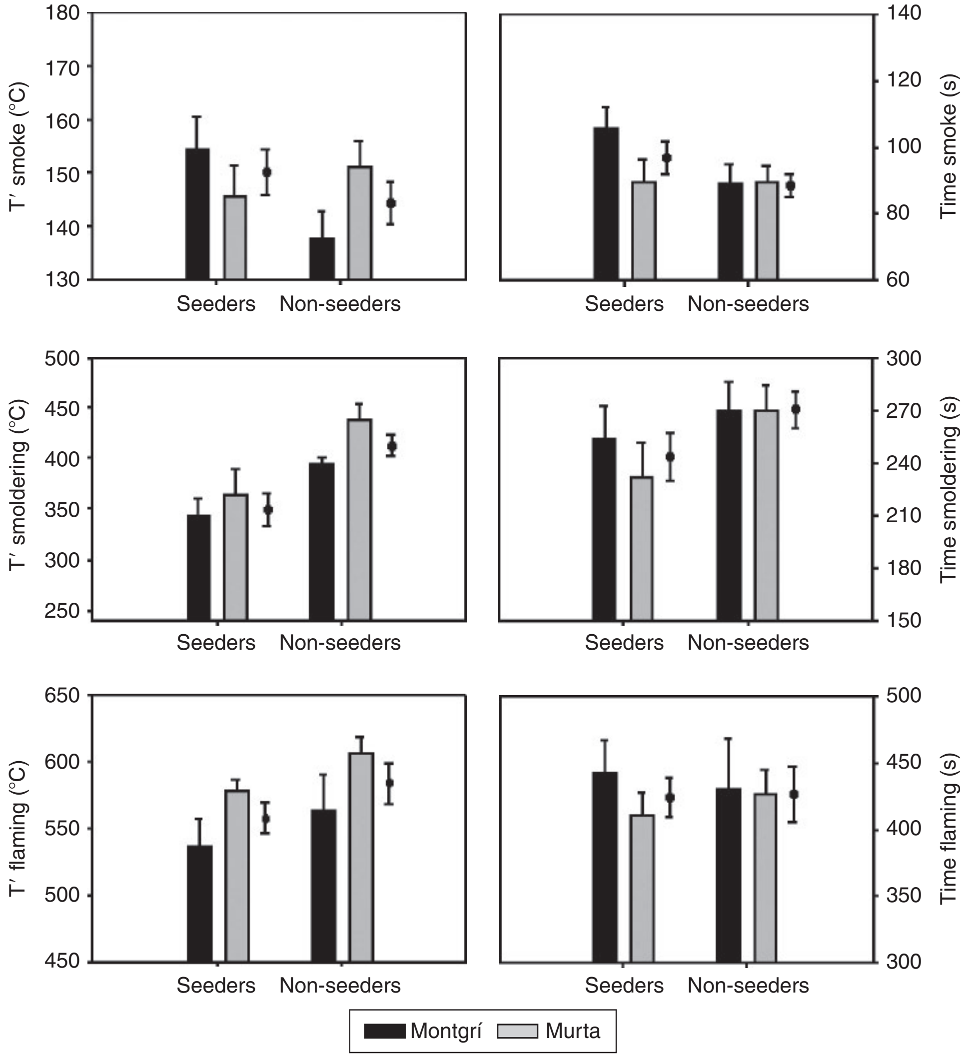

Fig. 3. Mean and standard errors of temperature and time needed to achieve the flammability phases: smoke, smouldering and flaming. The values are drawn for each regenerative strategy (seeders and non-seeders) and site (Montgrí and Murta). The mean and standard error for each regenerative strategy is drawn with a black circle after pooling the data from both sites for each species. For statistical analysis, see Table 3.

Table 3. Summary of results of the repeated-measures ANOVAs considering temperature as the dependent variable and flammability phase (FP) (smoke, smouldering and flaming) as the within-subject factor

Two between-subject factors (regenerative strategy and site) and two covariates (leaf moisture, LM, and surface-to-volume ratio of the leaf, S : V) were considered in the model

	Without S : V and LM		With S : V and LM	
	F	*P*	*F*	*P*
Regenerative strategy	4.898	0.037	6.903	0.015
Site	0.367	0.550	0.045	0.833
Reg. strategy × site	0.312	0.582	0.890	0.356
FP	93.854	0.000	5.035	0.011
FP × reg. strategy	2.880	0.066	4.303	0.020
FP × site	0.099	0.906	1.346	0.271
FP × reg. strategy × site	0.057	0.945	0.895	0.416

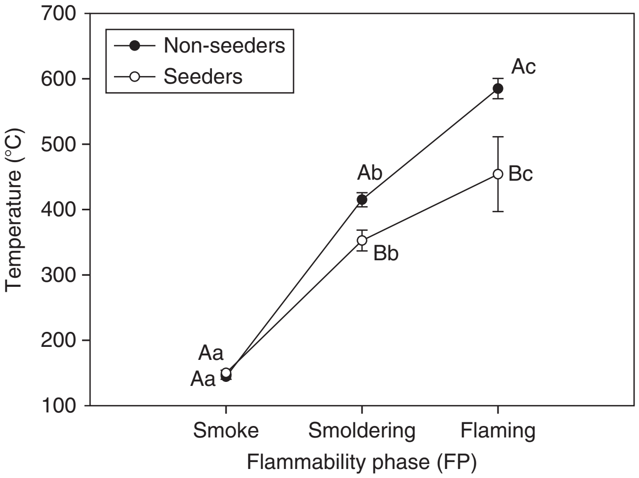

Fig. 4. Mean and standard error of temperature needed to achieve each flammability phase for the two regenerative strategies. Lower-case letters indicate differences between flammability phases for each regenerative strategy and upper-case letters indicate differences between regenerative strategies for each phase (post-hoc Fisher Least Significance Difference, after repeated-measures ANOVA including leaf moisture and leaf surface : volume as covariates). Data from the two sites have been pooled.

Quaternary (Jalut *et al.* 2000; Scott 2000; Scott 2002). In recent years, there has been intense debate about the evolution of flammability. Some authors maintain that species most suited to fire-prone habitats (i.e. those that take advantage of wildfires to recruit) may have evolved flammability to compete successfully with other species less well adapted to fire (Mutch 1970; Zedler 1995; Bond and Keeley 2005; Bond *et al.* 2005). Our study supports the hypothesis that seeders exhibit more flammable characteristics than non-seeders. However, fire may not be the only trigger for diversification in species from fire-prone Mediterranean ecosystems (Lavorel and Garnier 2002). Flammability differences between seeders and non-seeders cannot be directly attributed to differences in leaf moisture, because we obtained the same result regardless of whether or not LM was included as a covariate in the model. In fact, we did not find any differences in LM between these groups. Differences in the mineral content or volatile compounds, both of which contribute to high flammability and are very abundant in plants in the Mediterranean Basin (Owens *et al.* 1998; Alessio *et al.* 2004; Alessio 2006; Greenberg *et al.* 2006), may help explain differences in flammability between seeders and non-seeders. Certain flammability-related chemical and structural properties of plants could also be the result of physiological and morphological responses to other environmental constraints typical of Mediterranean ecosystems, with their seasonal high temperatures, low water storage and high solar radiation (Arnan *et al.* 2007; Lloret *et al.* 2007). In fact, in many communities of the western Mediterranean Basin, seedling recruitment of these species is not exclusively fire-dependent (Lloret 1998; Lloret *et al.* 2005*b*). Flammable properties may therefore enhance seeder populations after fire and these features would also help them tolerate drought periods.

Our study suggests that seeders need less energy to burst into flame, thus increasing the fire hazard. Although we did not measure the heat released by the combustion of seeders, other studies (Heim 1974; Elvira and Hernando 1989) suggest that these species may have lower specific heat capacity, promoting low to moderate temperatures. This is corroborated by the lower fuel load reported in our study. Seeders from these communities have a higher content of minerals such as calcium and phosphorus (Saura-Mas and Lloret 2009), which would result in a lower intensity of fire endothermic reactions (Philpot 1970). This moderate fire intensity would enhance seed germination but would prevent the high temperatures that deplete seed viability (Fenner 1992; Salvador and Lloret 1995; De Luis *et al.* 2005; Paula and Pausas 2008). As a result, this strategy could promote a positive feedback that allows maintaining seeder populations, as has been suggested in Mediterranean ecosystems dominated by the grass *Ampelodesmos mauritanica* (Grigulis *et al.* 2005). However, we did not undertake any direct measurements of the specific heat capacity of different species, although this would be necessary for a more comprehensive analysis of the feedbacks between vegetation and fire, which, in turn, would be determined by the relationship between post-fire regenerative strategies and fire-promoting attributes.

In general, low water content in leaves was a determining factor in the achievement of pyrolysis (smoking phase) and facilitated flame production (flaming phase). High S : V also contributed to the attainment of pyrolysis and ignition. Leaves with higher S : V reach the temperature and time needed to achieve each subsequent flammability phase earlier and at lower temperature because they have a relatively greater surface exposed to heat and oxygen. This pattern seems to indicate that ignition (the smouldering phase) depends greatly on intrinsic plant properties such as leaf morphology, while leaf water content, a variable more dependent on environmental conditions, has a greater effect on flame production.

Information about the flammability and fuel characteristics of the species dominating plant communities may be of great importance to the management of fire prevention and extinction, particularly in regions such as the western Mediterranean Basin, where the frequency, extent and intensity of wildfires have increased in recent decades (Moreno and Oechel 1995;

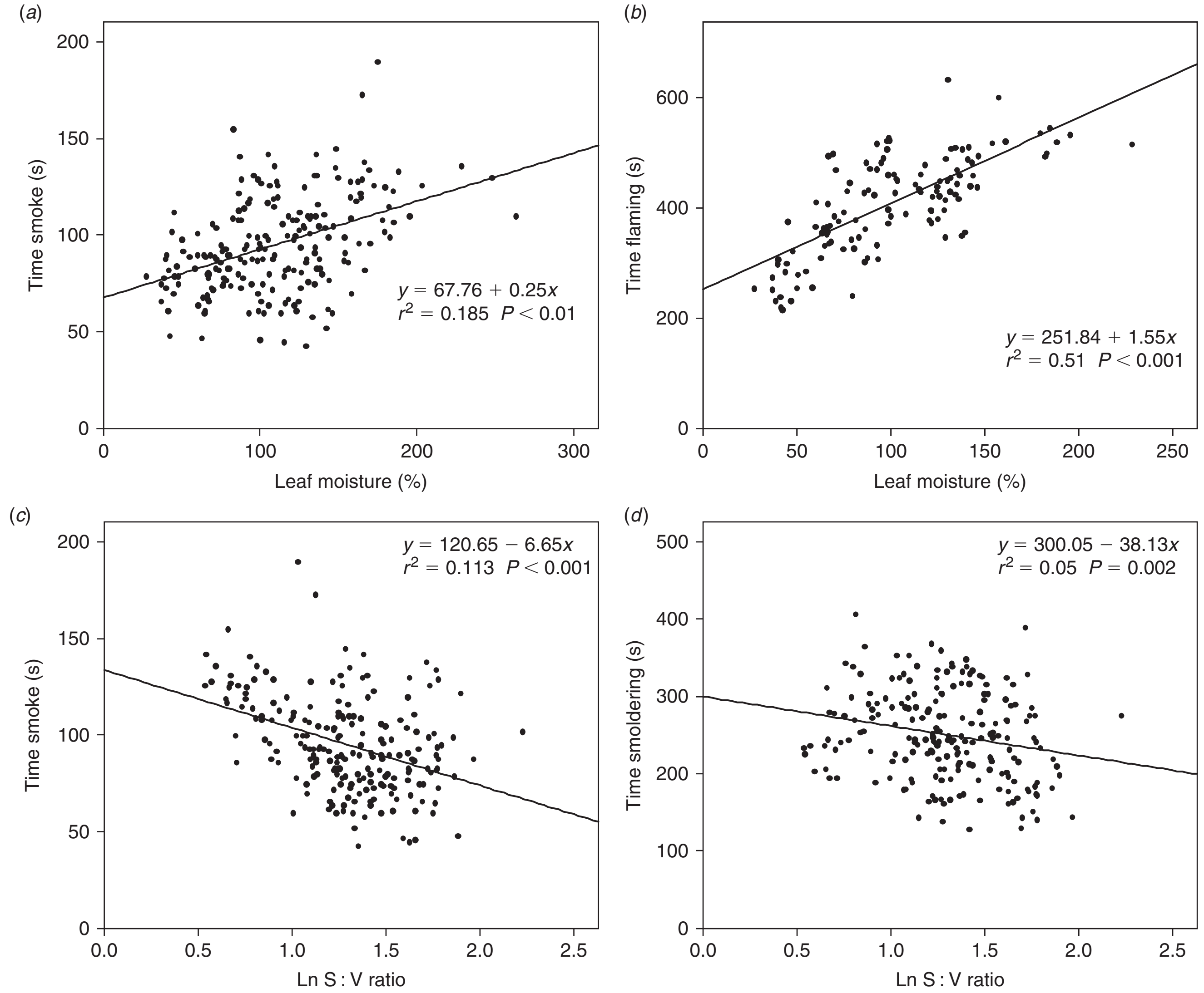

Fig. 5. Relationship between time to achieve smoke phase (*a*) and flaming phase (*b*) and leaf moisture; and relationship between time to achieve smoke phase (*c*) and smouldering phase (*d*) and S : V ratio (surface-to-volume ratio of the leaf), following a linear regression for species from Montgrí site. S : V ratio was transformed to its ln(*x*) to better approximate normality. Similar results were found for species from Murta (data not shown).

Piñol *et al.* 1998; Pausas 2004). Our study reveals that the studied seeders are more flammable than non-seeders, as they need lower temperatures to produce flames and display rapid combustion (not to mention their high percentage of fine and dead fuel). As a result, ecosystems dominated by seeder species will be more prone to fire than those dominated by non-seeder species. Seeder species also present a lower fuel load, which is likely to result in less intense fires that can be fought more easily. In contrast, non-seeders need higher temperatures to start combustion and their high amounts of fuel load may produce wildfires that are not easily extinguishable. If we consider that fire regime influences vegetation dynamics and composition, in accordance with plants' fire-regenerative traits (Zedler *et al.* 1983; Lloret *et al.* 2003; Bond *et al.* 2005), our study affirms the existence of a link between the post-fire regenerative traits and flammability traits on the studied shrubland. We thus provide empirical elements to support the notion of a positive feedback in which the risk of fire is probably influenced, in its turn, by a community's component species.

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