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Understory fuel load and structure eight to nine years after prescribed burning in Mediterranean pine forests

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ABSTRACT

Prescribed burning is being widely used in fire-prone forests to modify stand structure, reduce risks of severe wildfire, and increase ecosystem resilience to natural disturbances. This study focuses on changes to understory cover, phytovolume, and species richness eight to nine years after underburning, by comparing the understory structure of burned and paired unburned (100 m^2) plots in eight Mediterranean pine stand locations (Catalonia, Spain). Taking into account the assumptions of the space-for-time substitution in our study design, phytovolume was significantly lower in burned plots compared to the unburned plots. These differences varied, however, across localities, ranging from negligible changes to a reduction of more than 90%. Differences attributable to management were greater in forest plots with higher overstory cover, which was assessed by hemispherical photograph analysis. This result suggests that the lack of light availability may limit the reestablishment of understory in managed dense stands. Crown Fire Initiation and Spread (CFIS) simulations indicated that these changes in understory structure would only decrease the behavior of a potential wildfire when occurring in low or moderate weather conditions. In both burned and unburned plots, woody obligate resprouters represented more than 60% of the total cover, while facultative resprouters or obligate seeders accounted for less than 20%. No differences were detected in the richness of resprouter, seeder, graminoid or legume functional groups between burned and unburned plots. Our results support the application of prescribed fires to reduce surface fuels in the studied forest types, and the hypothesis that fuel load reduction is most effective in a forest with a closed overstory.

1. Introduction

The occurrence and impact of wildfires is increasing due to environmental, climate and social changes, which are leading to longer dry periods and higher fuel loads (Piñol et al., 1998). In addition, contemporary land use trends promote biomass accumulation and landscape-level continuity of highly flammable fuel types, thus favoring large and severe fires (Vega-García and Chuvieco, 2006). To reduce wildfire intensity and severity, forest management agencies have shifted emphasis from fire suppression to the proactive treatment of forest stands. Prescribed burning (PB) is the planned use of fire under defined environmental conditions to achieve precise and clearly-defined management objectives (Wade and Lunsford, 1989), and is taught through a professional training system in Europe (Colaco and Molina, 2010). Despite the relative low importance of fuel in comparison with weather as a driving force of wildfire behavior under extreme fire danger conditions (Bessie and Johnson, 1995; Bradstock et al., 1998), understory PB aims to reduce fire hazard by decreasing fuel loads (Pyne et al., 1996), but also by disrupting the horizontal and vertical continuity of the fuel complex to modify fire behavior and potentially decrease the fire's severity (Agee and Skinner, 2005).

Reducing fuel load under a threshold level without impacting ecosystem functions is the main goal of PB as a tool for wildfire hazard reduction. Increasing the longevity of fuel treatment is a key management objective, defining the management strategy and the appropriateness of burning as a tool. As expected, understory cover and height decrease just after burning, but they may either re-establish to near pretreatment levels within a few growing seasons, or remain lower for several years (Fernandes and Botelho, 2003 and references here-in). Thus, the assessment of the recovery of fuel loads several years after burning is key to evaluate the effectiveness of the management. Considering that underburning is typically a low intensity fire and that Mediterranean plant species recover rapidly after fire, we hypothesized that

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understory fuel load eight to nine years after PB will be similar to that before management.

Disparities in the recovery timing after PB depend, among other factors, on specific management characteristics (i.e. fire intensity, season), understory composition, and the success of each individual plant to survive and compete in the new micro-environment. Understanding the responses of plant species to disturbance is relevant for the comprehension of long-term vegetation dynamics and undesired ecosystem impacts, as well as for defining appropriate management options. The plant richness of Mediterranean forest understories is high, possessing a wide range of traits that operate after different levels of perturbation to reestablish each species and better compete for the acquisition of resources. Many plant species are able to resprout after disturbance (resprouters), while others rely on the recruitment from seeds (seeders) (Keeley and Zedler, 1978; Trabaud, 1987). In addition, a third group, facultative resprouters, may persist after fire by both resprouting and seed recruitment. These different functional groups may respond differently to burning management, resulting in an increase of one group in respect to others. Resprouters' and seeders' adaptation to disturbance can lead to different resource allocation and growth. Although it has been suggested that seeders maximize their growth after disturbance in comparison with resprouters, results are not consistent (Knox and Clarke, 2005; Chew and Bonser, 2009). Resprouting species may nearly recover their pre-fire size within a few years following PB, if fire had not affected below-ground organs (Bellingham and Sparrow, 2000). The recruitment of seeder species may depend on the seed longevity within the seedbank, the effects of burning on the buried seeds and the availability of light and water after emergence (Tyler, 1995; Knox and Clarke, 2006). Since resprouting seems to be advantageous following fire because it allows for quick occupation of space in comparison with the recruitment of seeders (Bond and Midgley, 2001), we hypothesized that the relative cover of resprouting species will increase in respect to seeders after burning.

In the NE Iberian Peninsula (Catalonia, Spain), resprouters and seeders are both present in fire-prone landscapes, but resprouting constitutes the dominant mechanism of post-fire regeneration in forests (Lloret et al., 2005). Intraspecific variability in resprouting is related to the pre-disturbance state of individuals (e.g. non-structural carbohydrates and nutrient levels) and the post-fire capacity to acquire resources (Moreira et al., 2012). Although water and soil nutrients usually control primary productivity in Mediterranean ecosystems, the growth of resprouting plants may be less sensitive to these resources due to their favorable root:shoot ratio and reduced competition after fire (Midgley, 1996). In contrast, low light availability has been suggested to explain the low resprouting vigor of different shrub species individuals (Gracia and Retana, 2004; Quevedo et al., 2007) or the low understory plant cover in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) forest 30 years after PB (Scudieri et al., 2010). Therefore, we hypothesized that the reestablishment of understory fuel load will be limited by the density of overstory cover, as a proxy for the understory light availability.

Several computer models have been developed for estimating the potential for crown fires at forest stand scale, and can be used to compare potential effectiveness of fuel treatments (Scott, 1999; Finney, 2004; Alexander et al., 2006). Examining the structure and composition of vegetation after PB, together with modeling the behavior of potential wildfires may contribute to understanding the effectiveness of using PB as a management tool in reducing fuel hazard, define management timing and assess the effort required to reach the targeted objective.

Much of the current knowledge on the effects of PB on Mediterranean forest understory comes from wildfires or short-term post-fire studies. Hence, the main goal of this study was to quantify the effects of PB on the structure and composition of Mediterranean pine forests' understory, eight to nine years after management. As far as we know, long-term experimental designs specifically aimed to test the effects of burning on fuel load do not exist for our region. Hence, this study is based on comparing contemporary spatial differences between burned and paired unburned stands as a surrogate for the effects of fire treatment in the burned plots, eight to nine years after management in eight Mediterranean pine forests.

2. Material and methods

2.1. Experimental design

This study is based on the comparison of prescribed burned and paired unburned plots. The experimental design minimized the confounding effects of climate, topography or soil type between both burned and unburned stands, but is subject to the assumptions inherent to the space-for-time substitution (Picket, 1989). Hence, it assumes that the contemporary differences between burned and paired unburned plots, if they exist, are only due to the burning treatment and that other factors (e.g. abiotic characteristics, historic management and disturbances) are the same between paired plots. To minimize the effect of these assumptions on our results, stands were carefully selected to ensure burned and unburned plots were as similar as possible.

2.2. Site selection

PB in Catalonia (Spain) is carried out by the Forest Actions Support Group (GRAF) of the Autonomous Government (Generalitat de Catalunya). GRAF has compiled a database documenting all PBs that have been conducted from 1998 to date. The database includes information about fire characteristics (burn data, times of initiation and termination, ignition pattern, burned area), the assigned human resources, a burned-area perimeter map, and photographs taken in selected points. From the 233 underburn dataset performed between 1998 and 2011, we pre-selected 12 forest stands, treated with fire between the years 2003 and 2004, and not re-burned after. Site pre-selection was done after checking for potential paired unburned stands with the same slope, aspect and historic land-use as in the burned stand. Using historic series of georeferenced aerial photographs (http://www.icc.cat/vissir3/), we confirmed that selected sites have been forested since at least 1956, with no apparent differences in management or changes in land-use between burned and paired unburned stands since then. In addition, we checked for the absence of wildfires using historical wildfire database. Definitive stand selection was done after a field visit: sites showing traces of clear-cutting or mechanical management after burning were discarded.

Eight sites were finally selected (Table 1). In the managed stands, fire was ignited by hand and burned with backing fires (i.e., downhill or downwind) under fuels with moderate moisture content, from late winter to early spring between 2003 and 2004. Woody understory was not thinned before burning. Field sampling was done in 2011, at the peak of the growing season (May–July), eight or nine years after the treatment.

2.3. Study sites

The study sites are located in the NE Iberian Peninsula, at 0.7–1.7°E and 41.0–42.2°N, between 260 m and 1010 m a.s.l. (Table 1, Fig. 1). The climate is typically Mediterranean with dry summers and wet winters in three sites and Submediterranean, as defined

Table 1
Site characteristics.

Site	Characteristics					Climate[a]			Lithology
	Long.	Lat.	Altitude	Slope	Aspect	Average annual temperature	Annual precipitation	Type[b]	
	(°)	(°)	m a.s.l.	%	(°)	°C	mm		
Canet Fals	1.75	41.76	368	70	190	14	625	Med.	Marls
Frides	0.72	40.99	264	9	230	15	575	Med.	Marls
Roc Estret	1.72	41.61	493	10	350	14	625	Med.	Sandstones
Ginestar	1.40	42.03	542	20	33	13	725	Submed.	Marls
La Vileta	0.77	42.17	857	<5	243	11	775	Submed.	Sandstones
Miravé	1.45	41.95	722	15	45	12	725	Submed.	Marls
St. Joan 1	1.09	41.35	1008	25	180	13	625	Submed.	Marls
St. Joan 2	1.09	41.35	1005	22	350	13	625	Submed.	Marls

[a] Climate variables were estimated using a georeferenced model (Ninyerola et al., 2000, http://territori.gencat.cat/atles_climatic/02/).
[b] Climate regions defined following the temperature and rainfall criteria of Sánchez de Dios et al. (2009). Med. Mediterranean climate; Submed. Submediterranean climate.

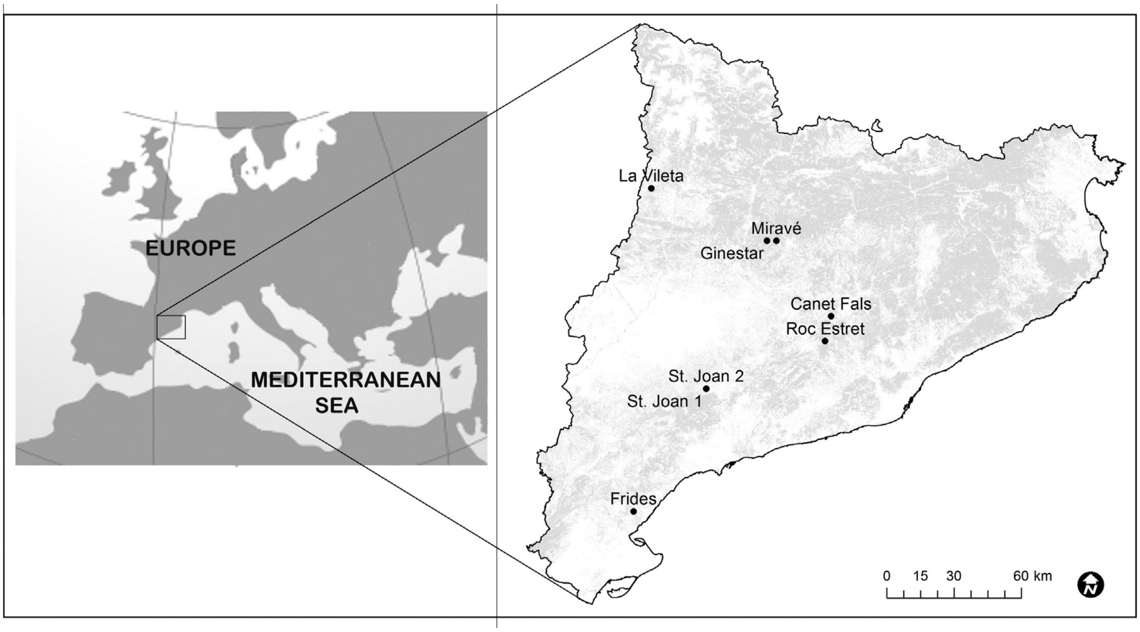

Fig. 1. Site distribution across the NE Iberian Peninsula (Catalonia, Spain).

by Ozenda (1994), with more mild temperatures in summer but lower in winter, in the five remaining sites (Table 1). Soils which have been developed over carbonate marls or sandstones are 0.5–1.0 m deep, and classified as Calcareous Inceptisols or Entisols. Forest canopy is dominated by *Pinus halepensis* Mill. or *P. nigra* ssp *salzmanii* (Dunal) Franco in Mediterranean sites and *P. n.* ssp *salzmanii* mixed with *P. sylvestris* L. and broadleaf trees (*Quercus cerrioides* Willk. et Costa, *Acer* sp.pl.) in Submediterranean ones. Common understory woody species include *Pistacia lentiscus* L., *Q. coccifera* L., *Rhamnus alaternus* L. and *Rosmarinus officinalis* L. in Mediterranean sites and *Buxus sempervirens* L., *Viburnum lantana* L., *Juniperus oxycedrus* L. and *Amelanchier ovalis* Medik. in Submediterranean ones. Woody species recorded in more than two sites are listed in Appendix A.

In this region, and similar to other Mediterranean regions, traditional forest activities were abandoned during the second half of the last century and led to an increase of forest density (Lasanta-Martinez et al., 2005; Ameztegui et al., 2010).

2.4. Plot characterization

We set up a 10 m × 10 m plot in each burned and unburned stand. The precise location of the plots in the field accounted for similar microtopography and tree density in both paired plots. As PB always involves a security perimeter strip, the plots were always located at a distance (>10 m) from the edges of the stand. In each plot, we recorded geomorphological characteristics, dasometric tree parameters and understory variables. The forest overstory cover was estimated using Gap Light Analyzer (GLA) software (Frazer et al., 1999) on hemispherical canopy photographs. These photographs were taken skyward from 0.50 m above the forest floor with a 180° hemispherical (fisheye) lens in the center of the four quadrants of each plot. For each tree (diameter at the breast height, DBH > 7.5 cm), we recorded the species name and measured the DBH and total height. In the burned plots, we measured the maximum bole char height for each tree. The bole char height average, considering all the trees in the plot, was used as a proxy of fire intensity (Storey and Merkel, 1960).

2.5. Understory vegetation characterization

To estimate understory woody phytovolume, herbaceous cover and plant species frequency, the 10 m × 10 m plot was divided into a grid of 100 contiguous 1-m^2 squares. In each square, we recorded the name of each plant species, and visually estimated herb cover (graminoids and forbs) and chamaephytes to the nearest percent (%). The cover of each individual woody plant rooted into each 1-m^2 square was estimated from the largest and orthogonal crown diameters. Bulk phytovolume was derived as an inverted cone, based on the height and cover of each individual (Etienne, 1989). For the most frequently occurring woody species, phytovolume of each individual was converted into total fuel load and 1 h-time lag fuel load using allometric equations (Appendix B) obtained either from published literature (Duguy et al., 2015) or from data on forests similar to those studied here-in (unpublished data). The remaining species without specific allometric regression were classified into biological types, and a generic equation for each type was applied (Appendix B).

Most plants, 192, were identified to species level, 15 plants to genus and four to family. Plants were grouped by growth form (Appendix C). Species nomenclature and growth form followed Bolòs et al. (2005) criteria. Herbaceous and shrub species were classified into disturbance-based functional groups using the information compiled in the BROT database (Paula et al., 2009; Paula and Pausas, 2013) and distributed into obligate seeders, obligate- or facultative-resprouters.

2.6. Wildfire simulation at stand scale

The effect on the fuel hazard-reduction of PB eight to nine years after management was estimated by simulating the potential wildfire behavior using the Crown Fire Initiation and Spread (CFIS) simulator (Alexander et al., 2006). As the interest of the analysis is to compare fire type predictions due to the changes in understory structure, we used data from either burned or unburned plots as understory fuel load inputs for each management scenario. The same overstory fuel characteristics were, however, used for each site because underburning did not affect the tree layer. Specifically, CFIS was used to estimate the probability of crown fire occurrence using the logistic model (Cruz et al., 2004) and to classify fire into surface or crown fire differentiating passive from active crown fires as defined in Van Wagner (1977).

The CFIS inputs used in the simulations include: 10 m open wind speed (WS, km h^{-1}), estimated fine fuel moisture (EFFM, %), fuel strata gap (FSG, m), surface fuel consumption (SFC, kg m^{-2}) and overstory bulk density (CBD, kg m^{-3}) (Appendix D). We tested three summer weather scenarios similar to those used by Lecina-Diaz et al. (2014) for the same region: low (WS, 10 km h^{-1} and EFFM, 13%), moderate (WS, 10 km h^{-1} and EFFM, 8%), and severe (WS, 30 km h^{-1} and EFFM, 13%) weather conditions. Both EFFM values were calculated using CFIS by selecting two contrasting relative humidity states (RH: 15–30% and 60–65%); and the constant temperature values (20.4–31.4 °C). This resulted in 8% EFFM when RH was low, and 13% when RH was high, for all sites. Simulation was carried out using a constant temperature value range (20.4–31.4 °C) and shading (<50%) for all sites, while aspect and slope corresponded to the values measured in the field, using the averaged values between paired plots for each site. The simulation was conducted in the month of July in the daytime, from 13 to 15 h, when most wildfires occur in the region.

SFC represents the amount of forest floor material, downed dead woody debris, and understory vegetation consumed by the surface fire (CFIS input options include <1.0, 1.0–2.0, or >2.0 kg m^{-2}). Woody understory fuel load was estimated according to the method described in the preceding section. The distance from the surface fuel-bed to the lower limit of the aerial fuel stratum (FSG) was calculated as the difference between canopy base height (CBH) and mean understory height. CBH was estimated for *P. halepensis* using an allometric equation developed from locally collected data ($\text{CBH} = 1.42 + 0.41 * \text{Ht}$, $R^2 = 0.54$, $n = 140$; Ht, tree height) and for *P. nigra* using the model developed by Cruz et al. (2003) for *P. ponderosa* Douglas ex. Lawson since no models exists for *P. nigra* and both species have similar tree structures. The canopy bulk density (CBD) for *P. halepensis* was estimated using the model developed by Mitsopoulos and Dimitrakopoulos (2014) which utilizes the basal area (BA) as the parameter of the model. In the case of *P. nigra*, we used the model developed by Cruz et al. (2003) for *P. ponderosa* that also uses the tree density variable. For these calculations, we used tree density and BA variables from burned plots (Table 2) for both burned and unburned scenarios. For this reason, the CBD for each pair of burned and unburned stands was the same (Appendix D).

2.7. Statistical analysis

We conducted side-by-side comparisons of understory stand structure cover or phytovolume, on paired burned and unburned plots in eight different sites using a linear mixed effects model analysis with site as a random effect (block factor) and PB treatment (burned and paired unburned plots) as a fixed effect. This approach was chosen to minimize the confounding effects of climate, topography or soil characteristics between sites. To account for the effects of the fire intensity or light availability, the co-variables: forest overstory cover, stand basal area or bole char height, were included as a fixed effect in the model and tested against the model without the co-variable using the Likelihood ratio test. When the co-variable was not significant, it was removed from the subsequent analysis. To test the effect of site aspect, we included a two-level factor in the model: northern-facing sites with an aspect ranging from 270° to 45°; and southern-facing for the rest of the sites.

Normality of distribution of the residuals was verified for the final model. Unless otherwise indicated, all data are presented as mean ± standard error ($n = 8$). All analyses were performed using R software (R Development Core Team, 2014) with the “lme4” v. 1.1-7 (Bates, 2010) packages for R.

3. Results

3.1. Stand structure

The basal area of trees (DBH > 7.5 cm) in the studied plots ranged from 13.1 m^2 ha^{-1} to 46.6 m^2 ha^{-1} and the density from 600 stems ha^{-1} to 1.600 stems ha^{-1}. The overstory cover ranged from 58% to 80% (Table 2). No differences in tree density, basal area or overstory cover were found between burned and paired unburned plots (p-values = 0.304, 0.476, and 0.116, respectively; $n = 8$). In burned plots, the mean bole char height ranged from 0.10 m to 0.84 m (Table 2).

3.2. Understory cover and phytovolume

Total understory woody cover and median plant height were lower in burned plots than in paired unburned ones (Table 3). Consequently, the understory phytovolume was also lower in burned than in unburned plots, with differences between both paired plots ranging from −2.6 to 107.7 m^3 100 m^{-2}. The interaction of burning treatment with forest overstory cover was significant (Table 3, Fig. 2), but neither with the mean bole char height in the burned plot, basal area nor stem density. Understory phytovolume positively correlated with overstory cover in unburned plots ($R^2 = 0.55$, p-value = 0.035) but not in burned plots ($R^2 = 0.05$, p-value = 0.292). Woody phytovolume was higher in northern-facing sites than in those located in southern-facing slopes (treatment, p-value = 0.034; aspect, p-value = 0.033), but

Table 2
Forest characteristics in burned (*B*) and unburned (*U*) plots in each site.

Site	Pine species	Tree age[a]	Tree height[a]		Tree density[b]		Basal area[b]		Overstory cover[c]				Burn area[a]	Burn date[a]	Bole char height[a]	
					B	*U*	*B*	*U*	*B*		*U*					
		y	*m*	(SE)	No. ha^{-1}	No. ha^{-1}	m^2 ha^{-1}	m^2 ha^{-1}	%	(SE)	%	(SE)	ha		cm	(SE)
Canet Fals	*P. halepensis*	n.d.	8.0	(1.4)	600	400	14.0	13.1	58	(4.6)	59	(3.2)	4.5	February-2004	30	(25)
Frides	*P. halepensis*	n.d.	8.0	(1.4)	1100	1100	33.5	29.5	70	(0.9)	70	(0.9)	1.1	November-2004	10	(6)
Roc Estret	*P. nigra*	78	11.6	(3.6)	900	900	31.3	22.2	74	(0.8)	76	(2.1)	7.6	March-2003	32	(3)
Ginestar	*P. nigra*	93	9.1	(3.1)	800	800	30.6	28.1	76	(1.6)	76	(1.6)	2.2	March-2003	15	(7)
La Vileta	*P. nigra*	34	9.2	(1.3)	600	600	16.4	14.3	72	(1.1)	71	(1.6)	2.7	March-2003	84	(45)
Miravé	*P. nigra/P. sylvestris*	72	10.1	(2.3)	1600	1600	26.2	23.9	77	(1.2)	80	(2.0)	1.8	April-2003	76	(39)
St. Joan 1	*P. nigra*	62	12.5	(2.1)	900	900	36.9	36.6	62	(1.5)	69	(1.0)	9.2	March-2004	59	(42)
St. Joan 2	*P. nigra/P.sylvestris*	62	12.5	(2.1)	900	1000	37.7	37.7	69	(1.5)	71	(0.9)	5.2	November-2004	48	(38)

[a] Tree age and height was estimated only in burned plots (n.d., not determined); burn area, date and bole char height (mean and standard error) corresponded to burned stands.

[b] Tree density and basal area for trees greater than 7.5 cm diameter at breast height (1.35 m).

[c] Overstory cover estimated from four hemispheric inverse photographs, mean and standard error using four photographs per plot.

Table 3
Understory woody species and herb cover, phytovolume, and the relative contribution of functional groups to the cover in burned and paired unburned plots. Mean and standard error in brackets ($n = 8$). The significance of the linear mixed effects analysis of burning treatment and overstory cover co-variable and their interaction is indicated in italic and in bold, when significant ($p < 0.05$).

Variable		Treatment				Significance[a]		
		Burned		Unburned		Treatment	Overstory Cov.	Treatm. x O. Cov.
Woody understory								
Cover	m^2 100 m^{-2}	24.8	(5.5)	69.6	(8.6)	***0.001***	*0.492*	
Median height[b]	m	0.65	(0.12)	1.01	(0.17)	***0.029***	*0.258*	
Phytovolume	m^3 100 m^{-2}	10.4	(3.8)	37.0	(11.7)	***0.018***	***0.011***	***0.039***
Obligate seeders[c]	%	19.0	(7.3)	17.5	(5.6)	*0.996*	*0.388*	
Oblig. resprouters[c]	%	63.4	(9.2)	74.0	(7.0)	*0.413*	*0.157*	
Facultive respr.[c]	%	17.6	(6.6)	8.5	(2.3)	*0.184*	*0.154*	
Legumes[c]	%	4.4	(1.3)	3.4	(1.1)	*0.192*	*0.789*	
Herbaceous understory								
Cover	m^2 100 m^{-2}	53.8	(12.1)	37.9	(8.2)	*0.164*	*0.251*	
Obligate seeders[c]	%	13.0	(2.6)	12.0	(3.0)	*0.791*	***0.020***	
Oblig. resprouters[c]	%	36.0	(3.8)	35.5	(3.6)	***0.029***	*0.608*	***0.026***
Facultative respr.[c]	%	40.7	(4.9)	43.5	(4.5)	*0.616*	*0.388*	
Graminoids[c]	%	35.3	(5.4)	31.4	(5.0)	*0.799*	*0.118*	
Legumes[c]	%	5.3	(2.0)	3.3	(1.7)	***0.041***	*0.583*	

[a] The interaction was included in the model when significant.

[b] Plot understory median calculated using the maximum height in each 1-m^2. Squares without woody plants were not included in the median.

[c] Percent of functional group cover respect to the total woody or herb cover.

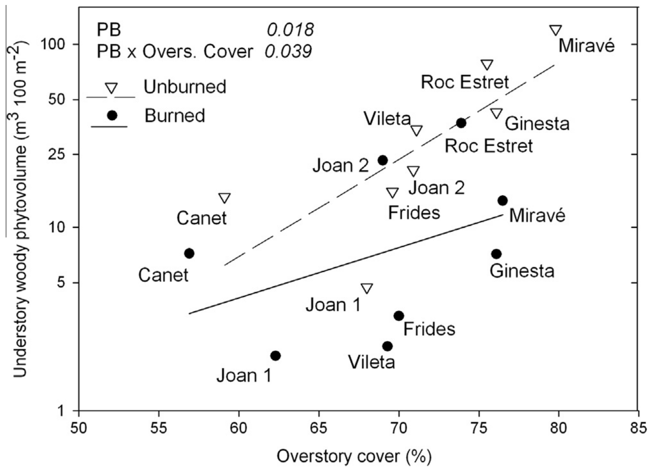

Fig. 2. Relationships between the understory woody phytovolume (log-transformed) and the forest overstory cover in burned and unburned plots. Significance of the linear mixed effect model analysis of the phytovolume with PB treatment and overstory cover as fixed effects, and site as random factor is shown. Understory phytovolume (log-transformed) correlated with overstory cover in unburned plots but not in burned ones. Lines were plotted to show the interaction between the differences in phytovolume in burned and paired unburned plots and overstory cover.

the interaction between burning treatment and aspect was not significant (p-value = 0.162). Phytovolume in burned or unburned plots did not correlate with the mean annual precipitation ($R^2 = 0.44$, p-value = 0.280, and $R^2 = -0.16$, p-value = 0.701 for unburned and burned plots, respectively).

Total woody phytovolume was lower in burned plots than in paired unburned ones in all strata, except the highest and the lowest ones (Fig. 3). No differences were found in herb cover (Table 3).

3.3. Crown fire simulations

The differences in the CFIS simulation outputs between burned and unburned plots were greater under low and, especially, moderate weather conditions while they were minimal under the severe scenario (Fig. 4). Under low weather scenario, the simulation predicted a surface fire at all burned and unburned plots, except for the unburned plots of Miravé and Roc Estret in which active and passive crown fires, respectively, would occur (Fig. 4). Under moderate weather conditions, surface fire was predicted in all burned plots. In contrast, active or passive crown fire was likely in unburned plots except Vileta, Joan 1 and Joan 2, where surface fires will be expected. Under severe weather conditions, CFIS indicates a high probability of crown fire independent of the burning

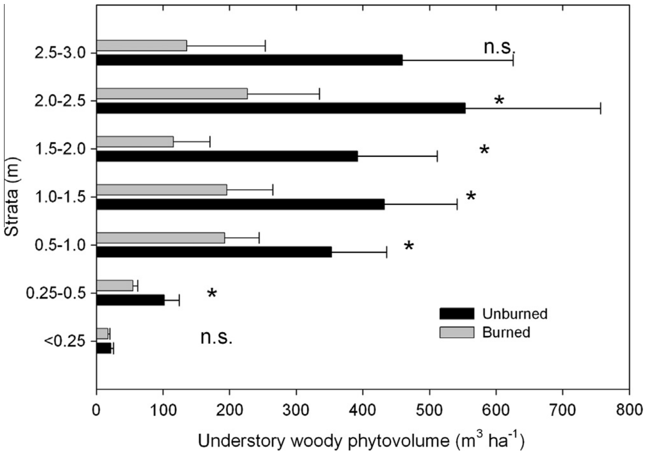

Fig. 3. Total woody phytovolume by stratum of the forest understory in burned and unburned plots (mean ± SE, $n = 8$). In each stratum, the statistical differences are indicated (*$p < 0.05$; n.s. $p > 0.05$).

treatment (Fig. 4), since active crown fire is the most common type of fire (with the exception of the *P. halepensis* stands, Canet and Frides, in which a passive crown fire would be likely occur). In terms of probability, burned plots had a lower likelihood of developing crown fire than unburned plots in all scenarios.

3.4. Functional groups cover

In both burned and unburned plots, obligate resprouter woody species represented more than 60% of the total cover while either facultative resprouter or obligate seeder species accounted for less than 20% (Table 3). In contrast, the relative cover of facultative resprouter species in the herb stratum was similar to that of obligate ones (Table 3). No differences between burned and unburned plots existed in the relative cover contribution by the different woody plant or herb functional groups; however, there was the exception of a slightly higher contribution by obligate resprouter or legume to the herbaceous cover of burned plots, in comparison with unburned plots (Table 3). Legume cover represented less than 10% of woody or herb plant cover.

3.5. Shrub and herb richness

A total of 192 vascular plants were classified to the species level in all plots (Appendix C). The richness of vascular plants ranged from 18 to 52 taxa per 100 m^2. No differences in the functional groups' richness between burned and unburned plots were detected; except for that of obligate seeder woody plants, which was slightly lower in burned than in unburned plots (Table 4). While not any species were found growing exclusively in the burned plots, three woody understory species were recorded in four or more unburned plots that were not detected on paired burned plots: the seeders *P. nigra* and *Lavandula latifolia* Medik.; and the resprouter *J. oxycedrus* L.

Table 4
Woody or herb species richness (no. 100 m^{-2}), by functional groups, in the understory of burned and paired unburned plots. Mean and standard error in brackets ($n = 8$). The significance of the linear mixed effects analysis is indicated in italic and in bold, when significant ($p < 0.05$).

	Treatment				Significance
	Burned		Unburned		
Woody species					
Obligate seeders	3.9	(1.1)	4.9	(0.8)	***0.040***
Obligate resprouters	8.4	(1.5)	10.4	(1.8)	*0.086*
Facultative resprouters	3.8	(0.5)	4.3	(0.7)	*0.430*
Legumes	2.4	(0.4)	2.0	(0.3)	*0.442*
Herbaceous species					
Obligate seeders	8.0	(1.5)	7.5	(1.2)	*0.668*
Obligate resprouters	14.0	(1.6)	15.0	(1.9)	*0.510*
Facultative resprouters	11.9	(1.4)	12.0	(1.5)	*0.857*
Graminoids	6.3	(0.6)	5.8	(0.7)	*0.316*
Legumes	2.4	(0.8)	2.0	(0.5)	*0.584*

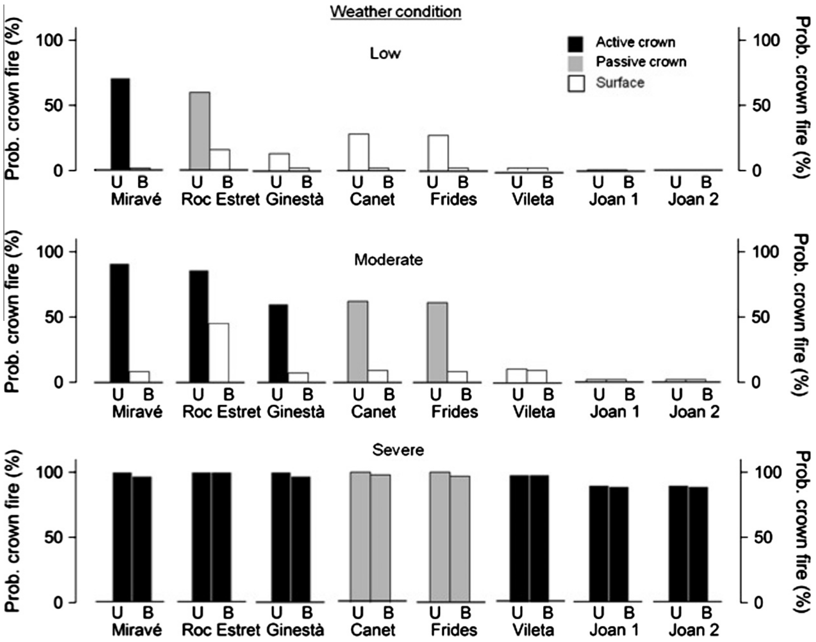

Fig. 4. Probability of crown fire (%) and type of fire under low (10 km h^{-1} wind speed and 13% of fine fuel moisture), moderate (10 km h^{-1} wind speed and 8% of fine fuel moisture) and severe (30 km h^{-1} wind speed and 13% of fine fuel moisture) weather conditions in prescribed burned (*B*) and unburned (*U*) stands in each site.

4. Discussion

4.1. Fire effects on understory phytovolume

Understory fuel treatment aims to reduce the fuel loads to be under a threshold for the spread of surface fire into the canopy as a crown fire (Molina et al., 2010; Stephens et al., 2012; Fernandes et al., 2013; Kobziar et al., 2015). Eight to nine years after PB, understory woody phytovolume in managed stands remains lower than in paired unburned ones, as a consequence of both lower cover and height. Despite the limited information available about the long-term effectiveness of PB in reducing fuel understory, some studies have found that fuel treatments can last up 10–14 years (Fernandes et al., 2004; Battaglia et al., 2008; Cheney et al., 2012). However, the longevity of PB results may be lower in more productive vegetation types (Fernandes, 2015).

The effects on fuel structure eight to nine years after burning management were different across localities; ranging from almost no differences when compared with unburned plots, to a reduction of more than 90% of the phytovolume. This differential effect of PB management was directly related to the cover of the overstory, suggesting that the reestablishment of understory after PB under a closed overstory may be limited by light availability. Other studies have also indicated that the development of plant understory after burning may be constrained by light availability in ponderosa pine stands with high basal area (Sabo et al., 2009; Scudieri et al., 2010). In contrast, no relationships were found for stand basal area or stem density with the magnitude of paired differences in understory phytovolume. The plot size used in our study (100 m^2) may not be big enough to accurately estimate these stand variables (see Section 2). Sites with lower understory phytovolume in both burned and unburned plots were located in southern-facing aspects and sites with higher understory in northern-facing aspects. However, the magnitude of the differences in understory phytovolume between burned and paired unburned plots did not interact with the aspect of the sites. Considering that the sites with a high magnitude of paired differences in phytovolume between burned and unburned plots also corresponded to those with high understory fuel load in the unburned plots, an alternative explanation is that the reinitiation of understory resprout and growth may have been retarded in high intensity burned plots. However, no relationships were found between differences in phytovolume and burned intensity, estimated as the mean plot bole char height. To some extent, the lack of concrete relationships may be related to the low magnitude of this variable in our burned plots, up to 0.84 m. This value is clearly lower than those recorded in similar forests affected by wildfires (1.6–3.1 m; Valor et al., 2013), and under 1.8 m which, together with other variables, has been indicated as an upper threshold for low intensity fires in *Pinus pungens* forests (Waldrop and Brose, 1999). Other mechanisms to explain the lower understory reestablishment after burning in dense stands may not be discarded, as for instance, below ground competition for water and nutrients with trees (Riegel et al., 1995; Devine and Harrington, 2008).

Higher understory phytovolume in unburned stands under high overstory cover does not follow the general pattern of negative relationships between stand basal area and understory shrub cover in Submediterranean forests, as described by Coll et al. (2011). As the characteristics of pre-closure vegetation are shown to be important in determining the understory structure (Halpern and Lutz, 2013), in our stands, the transition from open- to closed-overstory forests after the abandonment of forest activities probably resulted in an understory development parallel to overstory closure. This effect would be the reason for finding unburned stands with both high shrub density and overstory cover. Another alternative explanation of the direct relationships between phytovolume and canopy cover in unburned plots may just be an artifact of our study since north-facing sites had both higher phytovolume and canopy cover compared to sites located in a southern aspect. However, the limited number of sites prevents our study from further analyzing the mechanisms responsible for greater understory phytovolume in dense unburned plots.

The fuel load reduction and structure eight to nine years after burning treatment will likely decrease crown fire hazard, at least under low or moderate weather conditions. In these weather scenarios, the likelihood of a crown fire will be insignificant even in unburned stands in three sites: Vileta, Joan 1 and Joan 2. In these sites, the fuel loads in the unburned plots are the smallest among the studied sites and similar to their paired burned plot (Appendix D). In contrast, under severe weather conditions, the effect of PB on fuel load will have a negligible effect on wildfire behavior as in simulations conducted by Mitsopoulos and Dimitrakopoulos (2007). In two sites, Canet and Frides, the CFIS simulations predict that a wildfire would behave passively even under severe weather conditions. In comparison with the other sites, in these two the low crown bulk densities are smaller or similar to the threshold proposed by Agee (1996), 0.10 kg m^{-3}, below which an active crown fire is unlikely to occur. Even though the basal area in these two sites is similar to other studied sites, crown bulk density estimations are lower because the equation used depends on the pine species. The *P. halepensis* equation was used in these two sites while *P. ponderosa* equation as a proxy for *P. nigra* was used in the other sites (Appendix D).

4.2. Fire effects on understory composition

The obligate woody resprouter is the dominant fire-response group in the studied forests, representing more than 50% of the woody understory plant cover. This is in agreement with the results reported by Lloret et al. (2005) in the same region. In general, fire did not affect the relative abundance of seeder and resprouter species in the Mediterranean region (Eugenio and Lloret, 2006), or even contribute to maintain seeder species in moister, Mediterranean localities (Lloret et al., 2005). No changes in the relative cover of resprouters and seeders were detected between underburned and burned plots. Although our sampling design prevents us from going into detail, it may be pertinent to highlight that two woody obligate seeders (*P. nigra* and *L. latifolia*) and one obligate resprouter (*J. oxycedrus*) present in the unburned plots were not recorded in burned plots. The obligate seeder, *P. nigra* is considered a fire-sensitive species since it recruits with difficulty after wildfire (Ordóñez et al., 2006; Quevedo et al., 2007). We are not, however, aware of studies analyzing the effects of PB on the *P. nigra* seedlings' abundance. The species *J. oxycedrus* resprouts after fire in the studied region (Quevedo et al., 2007), but both resprouting and non-resprouting populations of this taxon have been described in the Iberian Peninsula (Pausas et al., 2008). The resprouting potential of this species after burning under different shade conditions requires further research.

The cover of both woody and herb legumes are very low in both burned and unburned plots. Despite the high N fixation rates of legume species in the short-term after burning (Casals et al., 2005), low legume cover likely results as a consequence of the reduced shade tolerance of the members in this family (Vitousek and Field, 1999).

Overall species richness is often enhanced by burning (Peterson and Reich, 2008). However, in our study, the number of plant species recorded in managed plots did not differ from that of unburned plots eight or nine years after burning management. Other studies have shown that low-intensity disturbances had little impact on plant composition (Keeley et al., 2003; Agee and Lolley, 2006; Eugenio and Lloret, 2006), although it is worth considering that treatment effects may vary in relation to the spatial scale considered (Dodson and Peterson, 2010). In concordance with findings by Arévalo et al. (2014), we did not expect increased plant species richness, as PB did not change the light environment of the burned understory in respect to the unburned one.

4.3. Limitations and further research needs

An accurate assessment of PB's long-term effects on fuel load dynamics, biodiversity and biogeochemical cycles is essential for understanding the efficacy of management activities and delivering appropriate recommendations in different ecosystem and management scenarios. The interpretation of patterns observed in our study was subject to the assumptions of the space-for-time substitution design (Picket, 1989). Careful selection of unburned plots may help to minimize the errors related to inferring a temporal pattern when comparing managed and paired unburned plots. In addition, the reduced number of sites in our study may not be enough to capture the response variability due to PB. For instance, the analysis of a potential interaction between the aspect and overstory cover of the sites on the understory reestablishment after PB requires a higher number of paired plots.

As stated by Picket (1989), the interest of the space-for-time substitution design relies on the potential for formulating new hypotheses to be tested in balanced long-term experiments and for identifying key management questions. Therefore, some patterns emerged from our results which may be addressed in further long-term experimental research. For instance, it may be interesting to assess the recovery of forest understory after burning under different overstory densities or to understand the mechanistic drivers of the vigor of resprouting plants under limiting light, nutrient or water conditions.

The patterns detected in our study were also constrained by the size of the plots used to estimate understory phytovolume and plant composition changes. The estimation of total plant cover, the cover of common species or functional groups seems to be quite robust when compared to different methods and sample sizes (Abrahamson et al., 2011). Hence, although we do not have any experimental evidence, the 100 m^2 plot size seems adequate for providing estimates of the understory cover and height and, therefore, deriving the understory phytovolume. In contrast, the 100 m^2 plot size is clearly insufficient to assess changes in plant species richness and our results regarding the effects of PB on colonizing plants or rare species should be considered as merely indicative. Thus, in an ongoing study where we estimated the species-area curves in five Mediterranean forests, similar to those of our study, using a 30 × 30 m P-Plot (a hybrid of a pixel nested plot and a modified Whitaker plot; e.g. Becker et al., 2013), the richness in the nested 100 m^2 subplot represented between 53.5% and 65.7% of the richness in the total plot. In the present study, species that are aggregated or occur at low abundance are therefore likely to be overlooked. Nevertheless, our results support the hypothesis that low intensity burning does not substantially change the proportion of woody functional groups to cover.

4.4. Management implications

Our study suggests that a single PB treatment results in forest stands with lower woody understory cover and height, compared to unburned stands, eight to nine years after management. This reduction in understory fuel load decreases the probability of a surface fire becoming a crown fire by reducing fire line intensity and increasing the distance between the surface and aerial layers. This simulated effectiveness in modifying wildfire effects together with the minor impact that PB has on pine growth (Valor et al., 2015) supports the application of burning to reduce fuels in Mediterranean forests. However, as stated by other authors (e.g. Fernandes and Botelho, 2003), the effectiveness of this management is unlikely to override wildfire behavior under extreme weather conditions.

Selectively cutting to address the reduction of crown density is a management option for decreasing the spread of crown fires (Agee and Skinner, 2005); but, the increase of light availability may favor the growth of woody plants depending on the understory composition and when other resources are not limiting (Knox and Clarke, 2011). Although more detailed experiments are required, our study suggests that the time-lag between understory management activities may be longer when the overstory is closed. Therefore, when management aims to reduce understory fuel load, we recommend avoiding affecting the overstory so as to retard management recurrence.

Fuel management programs need to balance the goals of wildfire hazard reduction with biodiversity and biogeochemical cycle conservation. Although our study did not find any effects of PB on plant biodiversity, it is worth highlighting that, in agreement with Agee and Skinner (2005), understory treatments could be strategically placed to optimize fire behavior reduction goals and minimize potential undesired impacts on species biodiversity or N stocks.

5. Conclusion

This study demonstrates that total woody plant height and phytovolume were lower in plots burned eight to nine years previously, compared to paired unburned plots. Higher differences between burned and unburned plots were related with greater overstory cover, suggesting that the reestablishment of woody understory after burning management may be limited by light availability in a forest with a closed overstory. Lower woody phytovolume in burned plots compared to unburned ones was predicted to reduce the probability of crown fire under moderate weather conditions, but not under severe weather conditions. No effects of prescribed burning were found in the relative cover of resprouter and seeder functional groups.

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Appendix. A

See Table A1.

Table A1
Woody species recorded in the understory of at least three sites.

	Sites							
	Canet Fals	Frides	Roc Estret	Ginesta	Vileta	Miravé	St. Joan 1	St. Joan 2
Acer monspeliensis			X	X		X	X	
Amellanchier ovalis			X	X	X	X		
Bupleurum fruticosum	X		X				X	X
Buxus sempervirens	X			X	X	X		
Crataegus monogyna			X	X	X	X		
Cytisus sessilifolius			X	X		X		
Dorycnium pentaphyllum	X	X	X		X		X	X
Genista scorpius				X	X		X	
Juniperus oxycedrus	X	X	X				X	X
Lavandula latifolia		X	X	X	X		X	X
Lithospermum fruticosus			X	X	X			
Pinus halepensis	X	X	X					
Pinus nigra			X	X	X	X	X	
P. sylvestris				X		X	X	
Pistacia lentiscus	X	X	X					
Prunus spinosa			X	X	X	X	X	X
Quercus cerrioides			X		X	X		
Q. coccifera	X		X	X		X		
Q. faginea			X	X	X			
Q. ilex		X		X	X	X	X	X
Rhamnus alaternus	X	X	X	X				
Rosa gr canina				X	X	X	X	X
Rosmarinus officinalis	X	X	X					
Rubus ulmifolius			X			X		X
Thymus vulgaris	X		X	X	X		X	X
Viburnum lantana			X	X	X	X		

Appendix. B

See Table B1.

Table B1
Allometric equations ($y = b0 + b1\ x$) of the total and fine (1 h time lag) fuel load (y in g) and the plant phytovolume (x in dm^3) for woody species frequent in the understory of Mediterranean forests. The apparent phytovolume was calculated as an inverted conus, using the largest and normal crown diameters and the height. For each species, the number of individuals and the adjusted coefficient of determination (adj R^2, in italic) of the relations are shown. All regressions were significant ($p < 0.001$). Allometric equations for biological types resulting from grouping the different species are also indicated.

Species by biological types		Total fuel load (g)				Fine fuel load (g)				References[a]
		$b0$	$b1$	n	adj R^2	$b0$	$b1$	n	adj R^2	
Large Shrubs and juvenile trees										
	Buxus sempervirens	2.828	0.678	50	*0.859*	1.575	0.695	30	*0.808*	1, 2
	Ligustrum vulgare	0.925	0.811	30	*0.779*	1.243	0.624	27	*0.791*	1
	Phillyrea latifolia	1.262	0.769	15	*0.927*	1.134	0.752	15	*0.900*	1
	Pistacia lentiscus	2.633	0.858	17	*0.963*	2.797	0.710	17	*0.861*	3
	Quercus ilex	2.064	0.762	33	*0.849*	1.881	0.737	34	*0.883*	1
	Rosa gr. canina	1.163	0.965	20	*0.925*	1.163	0.965	20	*0.925*	2
	Viburnum lantana	1.383	0.718	30	*0.858*	1.661	0.540	29	*0.807*	1
Shrubs										
	Genista scorpius	2.189	0.913	80	*0.771*	2.189	0.913	80	*0.771*	1, 2, 3
	Quercus coccifera	2.836	0.631	39	*0.810*	2.739	0.585	39	*0.818*	1, 2, 3
	Rosmarinus officinalis	2.700	0.819	97	*0.922*	1.916	0.890	39	*0.914*	1, 3
	Ulex parviflorus	1.605	0.924	20	*0.889*	1.752	0.821	20	*0.852*	3
Scrubs										
	Cytisus sessilifolius	0.736	0.773	22	*0.878*	0.669	0.767	22	*0.903*	1
	Thymus vulgaris	3.226	0.945	21	*0.961*	3.226	0.945	21	*0.961*	2
Large Shrubs		1.751	0.794			1.636	0.718			
Scrubs		1.981	0.859			1.947	0.856			
Shrubs		2.582	0.783			2.426	0.764			

[a] References of the groups collecting the data are: (1) Pere Casals, CTFC, and Xavier Castro, Servei de Prevenció d'incendis, Generalitat de Catalunya, unpublished. (2) Lluis Coll, CTFC, unpublished. (3) Duguy et al. (2015).

Appendix. C

See Table C1.

Table C1
List of woody and herbaceous plant species recorded by Raunkiær's life form following Bolòs et al. (2005). For each species the disturbance-based functional group (FG) was indicated using compiled information from the BROT database (Paula et al., 2009; Paula and Pausas, 2013).

	Family	Species	FG[a]		Family	Species	FG[a]
Chamaephyta				Therophyta			
	Fabaceae	*Argilolobium zanonii*	S		Asteraceae	*Atractylis humilis*	S
	Ericaceae	*Arctostaphylos uva-ursi*	R		Asteraceae	*Calendula arvensis*	S
	Poaceae	*Brachypodium retusum*	R		Asteraceae	*Galactites tomentosa*	S
	Apiaceae	*Bupleurum fruticescens*	S		Asteraceae	*Lactuca serriola*	FR
	Asteraceae	*Centaurea alba*	n.a.		Asteraceae	*Sonchus oleraceus*	S
	Asteraceae	*Centaurea linifolia*	R		Asteraceae	*Urospermum picroides*	S
	Convolvulaceae	*Convolvulus lanuginosus*	n.a.		Urticaceae	*Urtica dioica*	n.a.
	Primulaceae	*Coris monspeliensis*	S	Geophyta			
	Fabaceae	*Coronilla minima sp. clusii*	S		Asparagaceae	*Asparagus acutifolius*	R
	Fabaceae	*Coronilla minima sp. minima*	FR		Liliaceae	*Asphodelus cerasiferus*	R
	Fabaceae	*Dorycnium hirsutum*	FR		Asteraceae	*Cephalanthera rubra*	R
	Fabaceae	*Dorycnium pentaphyllum*	FR		Orchidaceae	*Epipactis atrorubens*	n.a.
	Fabaceae	*Erinacea anthyllis*	FR		Apiaceae	*Eryngium campestre*	S
	Euphorbiaceae	*Euphorbia nicaeensis*	S		Liliaceae	*Lilium martagon*	n.a.
	Euphorbiaceae	*Euphorbia serrata*	S		Paeoniaceae	*Paeonia officinalis*	n.a.
	Euphorbiaceae	*Euphorbia verrucosa*	n.a.		Polypodiaceae	*Pteridium aquilinum*	R
	Cistaceae	*Fumana ericoides*	S	Hemicryptophyta			
	Cistaceae	*Fumana laevipes*	S		Fabaceae	*Astragalus monspessulanus*	S
	Rubiaceae	*Galium lucidum*	S		Rosaceae	*Agrimonia eupatoria*	
	Fabaceae	*Genista hispanica*	FR		Liliaceae	*Aphyllanthes monspeliensis*	FR
	Cistaceae	*Helianthemum hirtum*	n.a.		Poaceae	*Arrhenatherum elatius*	R
	Cistaceae	*Helianthemum oelandicum*	S		Rubiaceae	*Asperula cynanchica*	
	Ranunculaceae	*Helleborus foetidus*	R		Poaceae	*Avenula bromoides*	FR
	Lamiaceae	*Lavandula angustifolia*	FR		Poaceae	*Avenula pratensis*	R
	Lamiaceae	*Lavandula latifolia*	S		Poaceae	*Brachypodium phoenicoides*	R
	Linaceae	*Linum narbonense*	R		Poaceae	*Brachypodium sylvaticum*	R
	Linaceae	*Linum suffruticosum*	R		Poaceae	*Bromus erectus*	R
	Boraginaceae	*Lithospermum fruticosum*	FR		Apiaceae	*Bupleurum rigidum*	R
	Fabaceae	*Onobrychis saxatilis*	S		Cyperaceae	*Carex flacca*	FR
	Fabaceae	*Ononis minutisima*	S		Cyperaceae	*Carex halleriana*	n.a.
	Fabaceae	*Ononis natrix*	n.a.		Cyperaceae	*Carex humilis*	FR
	Fabaceae	*Ononis pusilla*	FR		Asteraceae	*Carlina corymbosa*	n.a.
	Fabaceae	*Ononis spinosa*	S		Asteraceae	*Centaurea montana*	n.a.
	Lamiaceae	*Origanum vulgare*	S		Asteraceae	*Centaurea paniculata*	n.a.
	Lamiaceae	*Phlomis lychnitis*	R		Asteraceae	*Crepis vesicaria*	n.a.
	Poligalaceae	*Polygala calcarea*	FR		Poaceae	*Dactylis glomerata*	R
	Poligalaceae	*Polygala rupestris*	FR		Apiaceae	*Daucus carota*	R
	Liliaceae	*Ruscus aculeatus*	R		Apiaceae	*Eryngium bourgatii*	FR
	Lamiaceae	*Salvia officinalis*	R		Euphorbiaceae	*Euphorbia cyparissias*	n.a.
	Lamiaceae	*Satureja fruticosa*	S		Euphorbiaceae	*Euphorbia segueriana*	n.a.
	Lamiaceae	*Satureja montana*	S		Poaceae	*Festuca niSrescens*	R
	Crassulaceae	*Sedum sediforme*	S		Poaceae	*Festuca ovina*	FR
	Lamiaceae	*Sideritis hirsuta*	FR		Poaceae	*Festuca rubra*	FR
	Asteraceae	*Staehelina dubia*	FR		Rubiaceae	*Galium mollugo*	FR
	Lamiaceae	*Teucrium chamaedrys*	FR		Rubiaceae	*Galium pumilum*	n.a.
	Lamiaceae	*Teucrium polium*	FR		Rubiaceae	*Galium verum*	R
	Lamiaceae	*Teucrium pyrenaicum*	R		Asteraceae	*Geum urbanum*	n.a.
	Thymelaeaceae	*Thymelaea pubescens*	n.a.		Globulariaceae	*Globularia vulgaris*	FR
	Lamiaceae	*Thymus vulgaris*	FR		Cistaceae	*Helianthemum hirsutum*	FR
	Caprifoliaceae	*Viburnum tinus*	R		Ranunculaceae	*Hepatica nobilis*	R
Phanerophyta					Asteraceae	*Hieracium glaucophyllum*	n.a.
	Pinaceae	*Pinus halepensis*	S		Asteraceae	*Hieracium murorum*	n.a.
	Sapindaceae	*Acer campestre*	R		Asteraceae	*Hieracium pilosella*	FR
	Sapindaceae	*Acer monspessulanum*	R		Clusiaceae	*Hypericum perforatum*	R
	Sapindaceae	*Acer opalus*	R		Asteraceae	*Hypochoeris maculata*	n.a.
	Rosaceae	*Amelanchier ovalis*	R		Asteraceae	*Hypochoeris radicata*	n.a.
	Ericaceae	*Arbutus unedo*	R		Dipsacaceae	*Knautia arvensis*	FR
	Buxaceae	*Buxus sempervirens*	R		Poaceae	*Koeleria pyramidata*	R
	Fabaceae	*Calicotome spinosa*	FR		Poaceae	*Koeleria splendens*	R
	Arecaceae	*Chamaerops humilis*	R		Poaceae	*Koeleria vallesiana*	R
	Cistaceae	*Cistus albidus*	S		Asteraceae	*Leontodon sp.*	S
	Cistaceae	*Cistus salviifolius*	FR		Asteraceae	*Leuzea conifera*	n.a.

(*continued on next page*)

Table C1 (*continued*)

Family	Species	FG[a]
Ranunculaceae	*Clematis flammula*	R
Coriariaceae	*Coriaria myrtifolia*	R
Cornaceae	*Cornus sanguinea*	R
Fabaceae	*Coronilla emerus*	FR
Rosaceae	*Crataegus monogyna*	R
Fabaceae	*Cytisus sessilifolius*	FR
Thymelaeaceae	*Daphne gnidium*	R
Thymelaeaceae	*Daphne laureola*	R
Ericaceae	*Erica multiflora*	FR
Fabaceae	*Genista scorpius*	FR
Fabaceae	*Genista tinctoria*	S
Plantaginaceae	*Globularia alypum*	FR
Araliaceae	*Hedera helix*	R
Aquifoliaceae	*Ilex aquifolium*	R
Cupressaceae	*Juniperus communis*	S
Cupressaceae	*Juniperus oxycedrus*	R
Oleaceae	*Ligustrum vulgare*	R
Caprifoliaceae	*Lonicera implexa*	R
Caprifoliaceae	*Lonicera xylosteum*	R
Oleaceae	*Olea europaea*	R
Fabaceae	*Ononis fruticosa*	FR
Oleaceae	*Phillyrea angustifolia*	R
Oleaceae	*Phillyrea latifolia*	R
Pinaceae	*Pinus nigra*	S
Pinaceae	*Pinus sylvestris*	S
Anacardiaceae	*Pistacia lentiscus*	R
Anacardiaceae	*Pistacia terebinthus*	R
Rosaceae	*Prunus spinosa*	R
Fagaceae	*Quercus cerrioides*	R
Fagaceae	*Quercus coccifera*	R
Fagaceae	*Quercus faginea*	R
Fagaceae	*Quercus ilex*	R
Fagaceae	*Quercus pubescens*	R
Rhamnaceae	*Rhamnus alaternus*	FR
Rosaceae	*Rosa canina*	R
Lamiaceae	*Rosmarinus officinalis*	S
Rubiaceae	*Rubia peregrina*	FR
Rosaceae	*Rubus ulmifolius*	FR
Smilacaceae	*Smilax aspera*	R
Rosaceae	*Sorbus aria*	R
Thymelaeaceae	*Thymelaea hirsuta*	FR
Fabaceae	*Ulex parviflorus*	S
Ericaceae	*Vaccinium myrtilus*	R
Caprifoliaceae	*Viburnum lantana*	R
Fabaceae	*Lotus corniculatus*	S
Fabaceae	*Medicago sativa*	S
Lamiaceae	*Melittis melissophyllum*	n.a.
Asteraceae	*Pallenis spinosa*	S
Asteraceae	*Picris hieracioides*	S
Apiaceae	*Pimpinella saxifraga*	n.a.
Plantaginaceae	*Plantago lanceolata*	FR
Polygalaceae	*Polygala vulgaris*	FR
Rosaceae	*Potentilla montana*	n.a.
Primulaceae	*Primula veris*	n.a.
Lamiaceae	*Prunella grandiflora*	n.a.
Lamiaceae	*Prunella laciniata*	R
Fabaceae	*Psoralea bituminosa*	FR
Asteraceae	*Reichardia picroides*	n.a.
Rosaceae	*Sanguisorba minor*	R
Dipsacaceae	*Scabiosa columbaria*	n.a.
Asteraceae	*Scorzonera angustifolia*	FR
Asteraceae	*Scorzonera laciniata*	R
Asteraceae	*Taraxacum officinale*	S
Ranunculaceae	*Thalictrum minus*	R
Santalaceae	*Thesium catalaunicum*	n.a.
Apiaceae	*Trinia glauca*	n.a.
Asteraceae	*Urospermum dalechampii*	n.a.
Violaceae	*Viola alba*	FR
Violaceae	*Viola hirta*	FR

[a] Disturbance functional group: S, Seeder; R, Obligate resprouter; FR, Facultative resprouter; n.a., not available.

Appendix. D

See Table D1.

Table D1
Inputs used in CFIS simulations in burned (*B*) and unburned (*U*) plots.

Site	Fuel strata gap (FSG) m		Surface fuel consumption (SFC) kg m^{-2}		Crown bulk density (CBD) kg m^{-3}	
	B	*U*	*B*	*U*	*B*	*U*
Canet de Fals	4.09	3.82	0.84	1.21	0.07	0.07
Frides	4.30	3.88	0.33	1.55	0.11	0.11
Roc Estret	4.88	4.46	1.06	2.42	0.30	0.30
Can Ginestar	4.69	3.97	0.37	1.38	0.28	0.28
La Vileta	4.14	4.07	0.17	0.54	0.18	0.18
Miravé	4.45	3.76	0.56	2.36	0.38	0.38
Plans St. Joan 1	6.57	6.32	0.11	0.34	0.32	0.32
Plans St. Joan 2	6.33	6.31	0.28	0.55	0.34	0.34

References

Abrahamson, I.L., Nelson, C.R., Affleck, D.L.R., 2011. Assessing the performance of sampling designs for measuring the abundance of understory plants. Ecol. Appl. 21, 452–464.

Agee, J.K., 1996. The influence of forest structure on fire behavior. In: Proceedings of the 17th Annual Forest Vegetation Management Conference, January 16–18, Redding, California, pp. 52–68.

Agee, J.K., Lolley, M.R., 2006. Thinning and prescribed fire effects on fuels and potential fire behavior in an eastern Cascades forest, Washington, USA. Fire Ecol. 2, 142–158.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96.

Alexander, M.E., Cruz, M.G., Lopes, A.M.G., 2006. CFIS: a software tool for simulating crown fire initiation and spread. In: Proceedings of the 5th International Conference on Forest Fire Research, Figueira da Foz, Portugal, November 27–30.

Ameztegui, A., Brotons, L., Coll, L., 2010. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. Global Ecol. Biogeogr. 19, 632–641.

Arévalo, J.R., Fernández-Lugo, S., Naranjo-Cigala, A., Salas, M., Ruíz, R., Ramos, R., Moreno, M., 2014. Post-fire recovery of an endemic Canarian pine forest. Int. J. Wildl. Fire 23, 403–409.

Bates, D.M., 2010. lme4: mixed-effects modeling with R. URL http://lme4.r-forge.r-project.org/book.

Battaglia, M.A., Smith, F.W., Shepperd, W.D., 2008. Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? For. Ecol. Manage. 256 (12), 2029–2038.

Becker, R.H., Zmijewski, K.A., Crail, T., 2013. Seeing the forest for the invasives: mapping buckthorn in the Oak Openings. Biol. Invasions 15 (2), 315–326.

Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 409–416.

Bessie, W.C., Johnson, E.A., 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76, 747–762.

Bolòs, O. de, Vigo, J., Masalles, R.M., Ninot, J.M., 2005. Flora Manual dels Països Catalans. Ed. Pòrtic. third ed. Barcelona. ISBN 84-7306-857-2.

Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16, 45–51.

Bradstock, R.A., Bedward, M., Cohn, J.S., 1998. Weather, ignition and fuel as determinants of fire regimes: investigation of limits to management using a simple, spatial modelling approach. In: Viegas, D.X. (Ed.), Proceedings of the 3rd International Conference on Forest Fire Research & 14th Conference on Fire and Forest Meteorology, pp. 2365–2378.

Casals, P., Romanya, J., Vallejo, V.R., 2005. Short-term nitrogen fixation by legume seedlings and resprouts after fire in Mediterranean old-fields. Biogeochemistry 76, 477–501.

Colaco, C., Molina, D.M., 2010. Learning and training on the use of prescribed burning techniques. In: Towards Integrated Fire Management – Outcomes of the European Project Fire Paradox – EFI Research Report nr. 23. "Fire Paradox", Project no. FP6-018505, European Commission, pp. 161–173. ISBN 970-952-5453-48-5.

Cheney, N.P., Gould, J.S., McCaw, W.L., Anderson, W.R., 2012. Predicting fire behaviour in dry eucalypt forest in southern Australia. For. Ecol. Manage. 280, 120–131.

Chew, S.J., Bonser, S.P., 2009. The evolution of growth rate, resource allocation and competitive ability in seeder and resprouter tree seedlings. Evolutionary Ecol. 23, 723–735.

Coll, L., González-Olabarria, J.R., Mola-Yudego, B., Pukkala, T., Messier, C., 2011. Predicting understory maximum shrubs cover using altitude and overstory basal area in different Mediterranean forests. Eur. J. For. Res. 130, 55–65.

Cruz, M., Alexander, M., Wakimoto, R., 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. For. Sci. 50, 640–658.

Cruz, M., Alexander, M., Wakimoto, R., 2003. Assessing canopy fuel stratum characteristics in crown fire prone fuel types of western North America. Int. J. Wildl. Fire 21, 168–179.

Devine, W.D., Harrington, T.B., 2008. Belowground competition influences growth of natural regeneration in thinned Douglas-fir stands. Can. J. For. Res. 38, 3085–3097.

Dodson, E.K., Peterson, D.W., 2010. Dry coniferous forest restoration and understory plant diversity: the importance of community heterogeneity and the scale of observation. For. Ecol. Manage. 260, 1702–1707.

Duguy, B., Godoy, J., Fuentes, L., 2015. Developing allometric volume-biomass equations to support fuel characterization in North-Eastern Spain. Ecol. Mediterr. (In press)

Eugenio, M., Lloret, F., 2006. Effects of repeated burning on Mediterranean communities of the northeastern Iberian Peninsula. Veg. Sci. 17, 755–764.

Etienne, M., 1989. Non-destructive methods for evaluating shrub biomass: a review. Acta Oecologica 10, 115–128.

Fernandes, P.M., 2015. Empirical support for the use of prescribed burning as a fuel treatment. Curr. Forestry Rep. 1, 118–127.

Fernandes, P.M., Botelho, H.S., 2003. A review of prescribed burning effectiveness in fire hazard reduction. Int. J. Wildl. Fire 12, 117–128.

Fernandes, P., Loureiro, C., Botelho, H., 2004. Fire behaviour and severity in a maritime pine stand under differing fuel conditions. Ann. For. Sci. 61, 537–544.

Fernandes, P.M., Davies, G.M., Ascoli, D., Fernández, C., Moreira, F., Rigolot, E., Stoof, C.R., Vega, J.A., Molina, D., 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Front. Ecol. Environ. 11, e4–e14.

Finney, M.A., 2004. FARSITE: Fire Area Simulator–model development and evaluation. Research Paper RMRS-RP-4 Revised. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices From True-colour Fisheye Photographs, Users Manual and Program Documentation. University Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gracia, M., Retana, J., 2004. Effect of site quality and shading on sprouting patterns of holm oak coppices. For. Ecol. Manage. 188, 39–49.

Halpern, C.B., Lutz, J., 2013. Canopy closure exerts weak unburneds on understory dynamics: a 30-year study of overstory-understory interactions. Ecol. Monogr. 83, 221–237.

Keeley, J.E., Zedler, P.H., 1978. Reproduction of chaparral shrubs after fire. A comparison of sprouting and seeding strategies. Am. Midl. Nat. 99, 142–161.

Keeley, J.E., Lubin, D., Fotheringham, C.J., 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. Ecol. Appl. 13, 1355–1374.

Knox, K.J.E., Clarke, P.J., 2005. Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. Funct. Ecol. 19, 690–698.

Knox, K.J.E., Clarke, P.J., 2006. Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands. Oecologia 149, 730–739.

Knox, K.J.E., Clarke, P.J., 2011. Fire severity and nutrient availability do not constrain resprouting in forest shrubs. Plant Ecol. 212, 1967–1978.

Kobziar, L.N., Godwin, D., Taylor, L., Watts, A.C., 2015. Perspectives on trends, effectiveness, and impediments to prescribed burning in the Southern US. Forests 6, 561–580.

Lasanta-Martinez, T., Vicente-Serrano, S.M., Cuadrat-Prats, J.M., 2005. Mountain Mediterranean landscape evolution caused by the abandonment of traditional primary activities: a study of the Spanish Central Pyrenees. Appl. Geography 25, 47–65.

Lecina-Diaz, J., Alvarez, A., Retana, J., 2014. Extreme fire severity patterns in topographic, convective and wind-driven historical wildfires of Mediterranean pine forests. PLoS One 9, 85–127.

Lloret, F., Estevan, H., Vayreda, J., Terradas, J., 2005. Fire regenerative syndromes of forest woody species across fire and climatic gradients. Oecologia 146, 461–468.

Midgley, J.J., 1996. Why the world's vegetation is not totally dominated by resprouting plants: because resprouters are shorter than reseeders. Ecography 19, 92–95.

Mitsopoulos, I.D., Dimitrakopoulos, A.P., 2007. Canopy fuel characteristics and potential crown fire behavior in Aleppo pine (*Pinus halepensis* Mill.) forests. Ann. For. Sci. 64, 287–299.

Mitsopoulos, I., Dimitrakopoulos, A., 2014. Estimation of canopy fuel characteristics of Aleppo pine (Pinus halepensis Mill.) forests in Greece based on common stand parameters. Eur. J. For. Res. 133, 73–79.

Molina, D.M., Castellnou, M., García, D., Salgueiro, A., 2010. Improving fire management success through fire behavior specialists. In: Towards Integrated Fire Management – Outcomes of the European Project Fire Paradox – EFI Research Report nr. 23. "Fire Paradox", Project no. FP6-018505, European Commission, pp. 105–119. ISBN 970-952-5453-48-5.

Moreira, B., Tormo, J., Pausas, J.G., 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos 121, 1577–1584.

Ninyerola, M., Pons, X., Roure, J.M., 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. Int. J. Climatol. 20, 1823–1841.

Ordóñez, J.L., Molowny-Heras, R., Retana, J., 2006. A model of the recruitment of *Pinus nigra* from unburned edges after large wildfires. Ecol. Model. 197, 405–417.

Ozenda, P., 1994. Végétation du continent européen. Delachaux et Niestlé, Lausanne, Swizerland.

Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., Ojeda, F., Luna, F., Moreno, J.M., Rodrigo, A., Espelta, J.M., Palacio, S., Fernández-Santos, B., Fernandes, P.M., Pausas, J.G., 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90, 1420.

Paula, S., Pausas, J.G., 2013. BROT: a plant trait database for Mediterranean Basin species. Version 2013.06. URL: http://www.uv.es/jgpausas/brot.htm.

Pausas, J., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? – a review. Int. J. Wildl. Fire 17, 713–723.

Peterson, D.W., Reich, P.B., 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecol. 194, 5–16.

Picket, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), Long-term Studies in Ecology: Approaches and Alternatives. Springer, New York, pp. 110–135.

Piñol, J., Terradas, J., Lloret, F., 1998. Climate warming, wildfire hazard and wildfire occurrence in coastal Eastern Spain. Climatic Change 38, 345357.

Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. Introduction to Wildland Fire, second ed. John Wiley, New York.

Quevedo, L., Rodrigo, A., Espelta, J.M., 2007. Post-fire resprouting ability of 15 non-dominant shrub and tree species in Mediterranean areas of NE Spain. Ann. For. Sci. 64, 883–890.

R Development Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Riegel, G.M., Miller, R.F., Krueger, W.C., 1995. The effects of aboveground and belowground competition on understory species composition in a *Pinus ponderosa* forest. For. Sci. 41, 864–889.

Sabo, K.E., Sieg, C.H., Hart, S.C., Bailey, J.D., 2009. The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. For. Ecol. Manage. 257, 1656–1662.

Sánchez de Dios, R., Benito-Garzón, M., Sainz-Ollero, H., 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. Plant Ecol. 204, 189–205.

Scott, J.H., 1999. NEXUS: a system for assessing crown fire hazard. Fire Manage. Notes 2, 20–24.

Scudieri, C.A., Sieg, C.H., Haase, S.M., Thode, A.E., Sackett, S.S., 2010. Understory vegetation response after 30 years of interval prescribed burning in two ponderosa pine sites in northern Arizona, USA. For. Ecol. Manage. 260, 2134–2142.

Stephens, S.L., McIver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., Schwilk, D.W., 2012. The effects of forest fuel-reduction treatments in the United States. BioScience 62, 549–560.

Storey, T.G., Merkel, E.P., 1960. Mortality in along leaf pine stand following a Winter wildfire. J. For. 58, 206–210.

Trabaud, L., 1987. Fire and survival traits of plants. In: Trabaud, L. (Ed.), The Role of Fire in Ecological Systems. SPB Academic Publishing, The Hague, The Netherlands, pp. 65–91.

Tyler, C.M., 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. J. Ecol. 83, 1009–1020.

Valor, T., Gonzalez-Olabarria, J.R., Pique, M., 2015. Assessing the impact of prescribed burning on the growth of European pines. For. Ecol. Manage. 70, 503–513.

Valor, T., Pique, M., Lopez, B.C., Gonzalez-Olabarria, J.R., 2013. Influence of tree size, reduced competition, and climate on the growth response of *Pinus nigra* Arn. *salzmannii* after fire. Ann. For. Sci. 70, 503–513.

Van Wagner, C.E., 1977. Conditions for the start and spread of crown fire. Can. J. For. Res. 7, 23–34.

Vega-García, C., Chuvieco, E., 2006. Applying local measures of spatial heterogeneity to Landsat-TM images for predicting wildfire occurrence in Mediterranean landscapes. Landscape Ecol. 21, 595–605.

Vitousek, P.M., Field, C.B., 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. Biogeochemistry 46, 179–202.

Wade, D.D., Lunsford, J.D., 1989. A guide for prescribed fire in southern forests. USDA For. Serv. Tech. Pub. R8-TP 11, Southern region, Atlanta.

Waldrop, T.A., Brose, P.H., 1999. A comparison of fire intensity levels for stand replacement of table mountain pine (*Pinus pungens* Lamb.). For. Ecol. Manage. 113, 155–166.