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Effects of fire recurrence on plant growth in three Mediterranean perennial woody species

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Abstract

Recurrent fires at short fire intervals tend to simplify vegetation structure and to reduce phytomass production in Mediterranean plant communities. Here we compared growth of three Mediterranean perennial woody species between areas affected by one fire *versus* areas affected by two fires during their recent fire history (20 years). Design consisted of 13 study sites distributed over Barcelona and Tarragona provinces in Catalonia (NE Iberian Peninsula). Each study site corresponded to *Pinus halepensis*-dominated communities, and was conformed by two areas: an area burned only once (in 1994) and an area burned twice (once between 1975-1989, and again in 1994). Selected species were the seeder subshrub *Rosmarinus officinalis*, the resprouter shrub *Pistacia lentiscus* and the resprouter tree *Quercus ilex*, which are common and widespread in the Mediterranean Basin. We measured branch elongation and basal area increment during three growing seasons, between 10 and 11 years after the last fire, which was in 1994 in all areas. Significant growth differences were found for *R. officinalis*, whose basal area increment was higher in twice-burned areas relative to once-burned ones, as reburning likely resulted in a release from competition. Contrastingly, *Q. ilex* and *P. lentiscus* showed similar basal area increments. No significant differences in branch elongation were found for any species, probably because light was not a limiting resource in these environments. These results suggest that re-burning at short fire intervals resulted in a release from competition that allowed enhanced growth of the seeder species but did not affect growth of the resprouter species, which may rely mostly on resources stored in underground organs.

Key words: Mediterranean-type ecosystems, plant growth, *Pinus halepensis* communities, *Pistacia lentiscus*, *Quercus ilex*, *Rosmarinus officinalis*, resprouters, seeders.

Introduction

In Mediterranean-type ecosystems (MTEs), plant growth rates are slow compared to other moister temperate regions (Margaris and Mooney, 1981). Two main factors limiting plant growth and primary productivity are water and nu-

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trient availability (DeBano and Conrad, 1978; Rundel, 1982), as supported by growth responses to irrigation and fertilization experiments (McMaster *et al.*, 1982; Witkowski *et al.*, 1990). Moreover, plant growth is often disrupted by fire. During a common stand-replacing wildfire, above-ground biomass and part of the soil organic layers are combusted, and a resource-rich environment is generated. Space, light, and nutrients become available for plant recruits, given that soil fertility is enhanced by ashes (Kutiel and Shaviv, 1989; Gimeno-García *et al.*, 2000).

In the Mediterranean Basin, plant species show two main post-fire regenerative strategies allowing post-fire community recovery: seeder species are killed by fire and recruit by seeds stored in canopy or soil seed banks, whereas resprouter species usually lose most of their above-ground biomass and regrow vegetatively (Pausas *et al.*, 2004). Regenerative strategies are closely tied with physiological and morphological attributes (*reproductive syndromes*, *sensu* Keeley [1998] and *functional types*, *sensu* Pausas [1999]), and thus, seeders and resprouters show different growth responses to post-fire conditions. Resprouters are thought to have a competitive advantage over seeders in the first few years after fire (around less than 5 years), since they use stored reserves to support growth (Bowen and Pate, 1993; Canadell and López-Soria, 1998) and already-developed root systems to access soil water reserves (Clemente *et al.*, 2005). However, resprouters appear to have lower growth rates than seeders in the medium-term (around more than 5 years), as a tradeoff from allocating resources to storage (Bond and Midgley, 2001; Pausas *et al.*, 2004).

A growing concern has arisen in MTEs regarding the limits of post-fire resilience of plant communities, given the observed shifts in historical patterns of fire occurrence, which include an increase of fire frequency (Moreno *et al.*, 1998; Keeley *et al.*, 1999; Pausas, 2004). Increased levels of fire recurrence at short time intervals have been observed to result in compositional changes towards less diverse communities where dominance by few species is enhanced (Zedler *et al.*, 1983; Haidinger and Keeley, 1993), in reduced phytomass production (Trabaud, 1991; Delitti *et al.*, 2005), in simplified vegetation structure (Eugenio and Lloret, 2004), and also in delayed reconstruction of soil organic layers (Ferran *et al.*, 2005; Eugenio *et al.*, 2006).

Our aim in the present study was to ascertain if the occurrence of two fires during 20 years in Mediterranean communities dominated by *Pinus halepensis* Mill. (Aleppo pine) resulted in diminished growth of widespread perennial woody species relative to the occurrence of a single fire during the same time period. We worked on 13 study sites distributed over the provinces of Barcelona and Tarragona in Catalonia in order to detect common patterns of growth occurring throughout a range of climatic and geomorphic conditions. Each study site was comprised of two areas differing mainly in the number of fires that had occurred during their recent fire history: an area burned only once (in 1994) and an area burned twice (first between 1975 and 1989, and second by the same 1994 fire). Since areas were located adjacent to each other and were selected to be as similar as possible in relation to geomorphic characteristics, we specifically addressed the effects of fire recurrence level on plant growth between 10 and 11 years after the last fire, which occurred in 1994 in all areas. We selected three common and widespread species: the seeder subshrub *Rosmarinus officinalis* L., the resprouter shrub *Pistacia lentiscus* L., and the resprouter tree *Quercus ilex* L., and hypothesized that growth responses may differ between these seeder and the resprouter species.

Material and methods

Study sites

Study sites were selected by conducting spatial analysis on digital maps. Vegetation maps were used to identify *P.halepensis*-dominated communities, and fire history maps for the period 1975-1998 (Díaz-Delgado and Pons, 2001) were used to identify localities where two areas affected by a different level of fire recurrence where adjacent. As for fire history, no spatial information on fire occurrence is available before 1975 in Spain. Thus, in once-burnt areas, the fire prior to 1994 occurred at least 20 years before. A total of 13 study sites, distributed over the provinces of Barcelona and Tarragona in Catalonia (fig. 1), were finally selected. Each study site corresponded to *P.halepensis*-dominated communities, and was formed by a once-burned area (burned in 1994) and a nearby twice-burned area (burned first between 1975 and 1989, and second by the same 1994 fire, in such a way that fire intervals ranged from 5 to 16 years). Study sites were located in

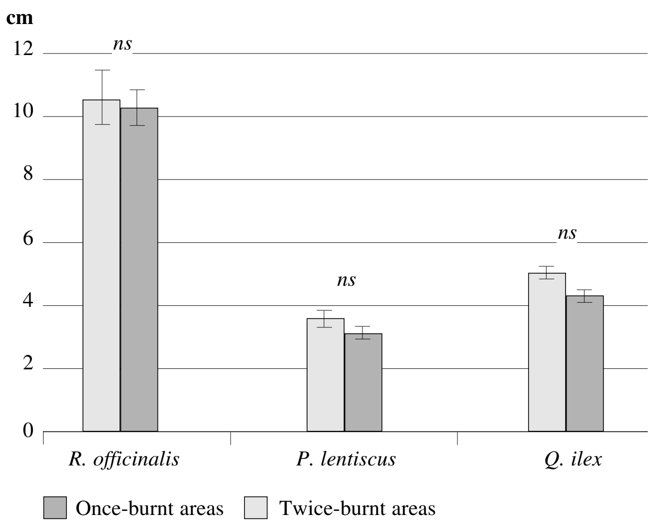

Figure 1. Absolute branch elongation (mean ± SE) of *Rosmarinus officinalis*, *Pistacia lentiscus*, and *Quercus ilex* in once —and twice— burned areas. A GLM was performed considering fire recurrence level and study site as fixed and random categorical predictors, respectively (*ns* = not significant).

the field by means of a global positioning system. One plot of ca. 1 ha was selected in each once- and twice-burned area, such that plots were as similar as possible in relation to geomorphic characteristics (table 1), and were separated by a buffer distance of 100 m, in order to avoid errors in the location of the transition.

The climate of the studied region is Mediterranean, characterized by mild winters and hot, dry summers, with precipitation occurring mostly in spring and autumn. In the study sites, mean annual temperature ranged from 12.6 °C to 14.9 °C, mean temperature of the hottest season (summer) from 20.5 °C to 23.3 °C, and mean temperature of the coldest season (winter) from 5.5 °C to 8.5 °C; mean annual precipitation ranged from 567 mm to 742 mm, and mean precipitation of the driest season (summer) from 111 mm to 166 mm (*Atles Climàtic Digital de Catalunya* [Pons, 1996; Ninyerola *et al.*, 2000. http://magno.uab.es/atles-climatic]).

Selected species

Pine-dominated ecosystems constitute a main landscape feature in the Mediterranean Basin, where they cover 25% of the forested surface (Barbéro *et al.*, 1998). The most abundant and widespread pine species in the western part is *P. halepensis*, which covers about 2.5 million ha (Quézel, 2000). In Catalonia, Aleppo pine is the most abundant tree species and covers a total of 239,092 ha; moreover, on 62% of this area, this species alone constitutes more than 80% of basal area (Gracia *et al.*, 2004). *P. halepensis* forms communities where it coexists with other tree species such as *Q. ilex* or *Arbutus unedo*, with dense understoreys typically consisting both of seeder species such as *R. officinalis* or *Cistus* spp. and resprouter species such as *P. lentiscus, Quercus coccifera*, or *Erica spp.* We measured growth on three characteristic perennial woody species: *Q. ilex*, *P. lentiscus* and *R. officinalis*. Since this community type shows high fuel loads and vertical and horizontal continuity of fuel beds, it is subject to recurrent fires that commonly kill all the above-ground biomass and burn part of soil organic horizons.

Q. ilex (Holm oak, Fagaceae) is a resprouter, evergreen, deep-rooted tree which is widespread across the Mediterranean Basin (Terradas, 1999; Gracia *et al.*, 1996). *P. lentiscus* (Mastic tree, Anacardiaceae) is a resprouter, evergreen shrub up to 5 m tall with root-systems over 5 m deep (Oppenheimer, 1957; Silva *et al.*, 2003), and distributed all over the Mediterranean Basin at low elevations (Quézel, 1981). *R. officinalis* (Rosemary, Labiatae) is a seeder sub-shrub up to 3 m tall with evergreen leaves, which may become semi-deciduous in the drought season (Clary *et al.*, 2004; Ain-Lhout *et al.*, 2004), and a shallow root-system —under 1 m deep (Spetch, 1988)—; it is also common in the western Mediterranean Basin (Bolòs *et al.*, 1990).

Growth measurements

Twelve individuals of each species were randomly selected in each plot among visually-estimated average-sized individuals. *R. officinalis* was present in 12

Table 1. Characteristics of the study sites. FI (fire interval years) was obtained from digital fire history maps (Díaz-Delgado and Pons 2001); elevation, slope and aspect were determined on the field; substrate categories were assigned to GPS-positioned central points of plots (*Digital Geological Data Base* 1:50,000-scale [ICC et al. 2002]).

	UTM coordinates			Elevation (m)		Slope (º)		Aspect (º)		Substrate	
Stydy site	Once burnt	Twice burnt	FI	Once burnt	Twice burnt	Once burnt	Twice burnt	Once burnt	Twice burnt	Once burnt	Twice burnt
1	0420137, 4597203	0420418, 4597133	12	259	273	15	25	230	220	clays	conglomerates
2	0408667, 4603201	0408306, 4603286	13	455	465	30	30	30	40	clays	argillites
3	0405425, 4601920	0405327, 4601913	8	275	285	40	40	180	170	argillites	limestones
4	0405857, 4603435	0405978, 4603438	8	192	239	30	25	270	280	clays	clays
5	0401825, 4585068	0401882, 4585018	5	400	412	30	30	290	300	dolomites	dolomites
6	0404905, 4582792	0405131, 4582730	9	480	470	20	15	80	80	limestones	limestones
7	0400975, 4572358	0400881, 4572294	16	239	243	10	0	120	0	gravels	gravels
8	0401135, 4572089	0401328, 4572157	12	247	251	0	0	0	0	marls	marls
9	0366493, 4592155	0366391, 4592142	13	651	628	20	15	334	340	limestones	limestones
10	0369610, 4570280	0369710, 4570335	11	317	289	20	15	40	40	limestones	limestones
11	0314713, 4546851	0314583, 4547065	9	606	637	40	40	220	220	limestones	limestones
12	0403162, 4640109	0402911, 4640061	11	469	459	15	15	210	210	marls	marls
13	0399323, 4629579	0399420, 4629254	11	419	415	25	25	70	60	marls	marls

study sites, *P. lentiscus* was present in 10 study sites, and *Q. ilex* was present in 5 study sites. The final number of surveyed individuals was 142, 119, and 57, respectively, since 2, 1, and 3 individuals, respectively, died or were injured during the survey. Eight branches per individual were arbitrarily selected among outer, adult, and visually-estimated well-developed branches, in such a way that they were distributed all over the plant, and located at medium plant height. Branches were permanently tagged and a line was painted on the branch from which it was measured up to its apical tip. All stems were permanently tagged at 20 cm above ground, where a line was painted. Diameter was measured at this point with a digital caliper. Branches or stems that were found dead or injured during the second survey were excluded from data.

A survey was conducted first in winter 2004, and later in summer 2005. Growing seasons in the Mediterranean Basin are spring and autumn, when temperatures are mild and soil water is available (Di Castri and Mooney, 1973; Dunn *et al.*, 1976). Therefore, three growing seasons —corresponding to spring-2004, autumn-2004 and spring-2005— were considered in growth measurements. We considered the absolute branch elongation, and the relative basal area increment, since relative values of basal area are less influenced by initial size (Mayor and Rodà, 1994).

Climatic data

Cumulative precipitation and mean temperature for the time period considered in growth survey (February 2004 to July 2005) were used as predictive variables. Values corresponded to the nearest climatic station of the Xarxa Agrometeorològica de Catalunya (Departament de Medi Ambient 2006. http://xarxes.meteocat.com/xac).

Actual solar radiation, which reflects local levels of incoming radiation and is a summarizing measure of latitude, altitude, and topography (Safford and Harrison, 2004) was also used as a predictive variable. Values of climate variables were assigned to GPS-positioned central points of every once- and twice-burned plot from the *Atles Climàtic Digital de Catalunya* (Pons, 1996; Ninyerola *et al.*, 2000), a collection of digital raster maps displaying climatic values for Catalonia with a 180-m resolution. Actual solar radiation values were based on 4 or more year-long series of climatic data.

Statistical analyses

To compare growth between areas burned once and areas burned twice, a set of GLMs (General Linear Models) were performed. For each species, two analyses were conducted: one in which the values of absolute branch elongation for each individual were the dependent variable, and fire recurrence level and study site were fixed and random categorical predictors, respectively, and other in which the values of relative basal area increment for each individual were the dependent variable, and fire recurrence level and study site were fixed and random categorical predictors, respectively.

To test correlation between climatic variables and absolute branch elongation and relative basal area increment, simple regression models were performed separately for once- and twice-burned areas.

To test correlation between fire interval and absolute branch elongation and relative basal area increment, simple regressions models were performed for twice-burned areas.

Results

Growth measurements

Mean absolute branch elongation of the three species was similar in areas burned once and twice (figure 1). Moreover, absolute branch elongation was significantly different among locations for the three species. In the case of *R. officinalis*, the interaction between fire recurrence and study site was also significant (table 2a).

Mean relative basal area increment of the seeder subshrub *R. officinalis* was significantly higher in twice-burned areas. No significant differences were found for the resprouter species *Q. ilex* and *P. lentiscus*, although in *Q. ilex* mean growth was higher in once than in twice-burned areas (figure 2). Moreover, relative basal area increment of *R. officinalis* was significantly influenced by study site. There was a significant interaction between fire recurrence and study site for relative basal area increment of *P. lentiscus* (table 2b).

Basal area increment of *P. lentiscus* was marginally and inversely correlated to mean temperature during the growth period in once-burnt areas (P= 0.058, R^2= 0.38), but not in twice-burnt ones (P= 0.815, R^2= 0.02). No significant correlations were found between basal area increment or branch elongation of *Q. ilex* or *R. officinalis* and either mean temperature or cumulative precipitation during the growth period.

Basal are increment of *Q. ilex* was significantly and inversely correlated to actual solar radiation in once-burnt areas (P= 0.026, R^2= 0.85), but not in twice-burnt areas (P= 0.815, R^2= 0.02). No significant correlations were found between basal area increment or branch elongation of *P. lentiscus* or *R. officinalis* and actual solar radiation.

Discussion

R. officinalis basal area increment between 10 and 11 years after fire was ca. 40% higher in areas affected by two fires compared to areas affected by a single fire during the same time period. We hypothesize that enhanced basal area growth of this species may be due to the release from competition generated through fire repetition in twice-burnt areas. Work on the same study sites revealed that between 8 and 10 years after fire, vegetation was shorter and more open in twice-burnt areas than in once-burnt ones (Eugenio and Lloret, 2004). Total plant cover as measured by the point-interception sampling procedure was significantly lower in twice-

Table 2. Results of GLMs considering fire recurrence level and study site as fixed and random categorical predictors, respectively, for (a) Absolute branch elongation, and (b) Relative basal area increment of *Rosmarinus officinalis*, *Pistacia lentiscus*, and *Quercus ilex*.

a) Absolute Branch Elongation

	R. officinalis		***P. lentiscus***		***Q. ilex***	
	F	***P***	**F**	***P***	**F**	***P***
Study site	4.73	0.008	7.54	0.003	24.20	0.005
Fire Recurrence	0.1	0.762	1.59	0.239	4.46	0.102
Interaction	1.9	0.040	1.63	0.109	0.70	0.593

b) Relative Basal Area Increment

	R. officinalis		***P. lentiscus***		***Q. ilex***	
	F	***P***	**F**	***P***	**F**	***P***
Study site	6.60	0.002	1.93	0.171	1.43	0.369
Fire Recurrence	12.86	0.004	0.83	0.387	1.86	0.244
Interaction	1.65	0.086	2.24	0.021	1.12	0.353

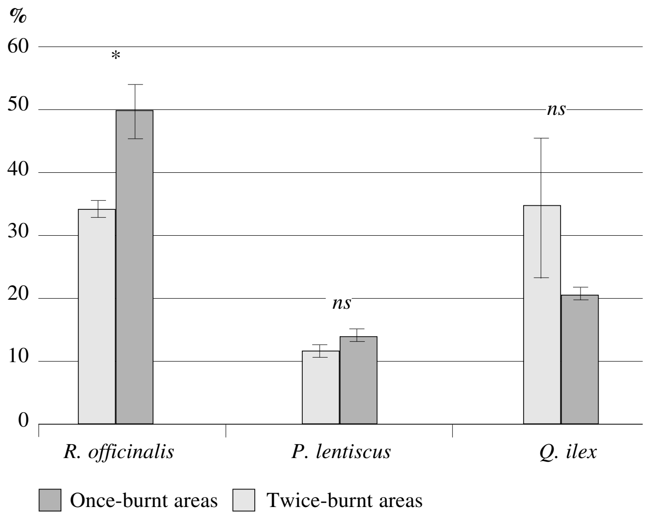

Figure 2. Relative basal area increment (mean ± SE) of *Rosmarinus officinalis*, *Pistacia lentiscus*, and *Quercus ilex* in once- and twice-burned areas. A GLM was performed considering fire recurrence level and study site as fixed and random categorical predictors, respectively (*ns*: not significant, *: $P < 0.05$).

burned (mean = 77.9%, SE = 2.7) areas than in once-burned ones (mean = 87.9%, SE = 2.2) 9 years after fire (t Student = 3.69; $P < 0.01$). Moreover, reburning involved compositional shifts such as an important population decline of the dominant tree species *P. halepensis* and a significant increase in abundance of nanophanaerophytes, which would presumably have occupied the freed space and have gained access to soil resources (Eugenio and Lloret, 2006; Eugenio et al., 2006b).

Contrastingly, the increment of ca. 40% of basal area of *Q. ilex* in once-burned areas compared to twice-burned areas did not result in significant differences, likely because the statistical analysis suffered of low power due to the limited number of replicates. Basal area increment in *P. lentiscus* was very similar in once and twice-burned areas. Resprouter species show a more conservative resource-use strategy than seeder species: whereas seedlings of seeder species use the space that fire releases for establishing, resprouter individuals held their already-occupied sites through vegetative regrowth (Keeley, 1986). Moreover, resources allocated to storage might support growth of resprouters also several years after fire. Resprouters also show deeper root-systems than seeders, and thus have a higher potential for the uptake of nutrients and water, particularly during summer drought (Silva *et al.*, 2003).

As hypothesized, growth patterns differed between the studied seeder and resprouter species: whereas *R. officinalis* readily took advantage of space availability in twice-burned areas, *Q. ilex* and *P. lentiscus* showed a more conservative resource-use strategy, and grew similarly in once- and twice burned areas. However, a generalization about the behaviour of seeder and resprouter species will need a larger set of species to be compared, a complicated task due to the difficulties to obtain enough replicates in the field.

Mean absolute branch elongation was higher in once-burned areas for the three considered species, but differences were not significant. Such pattern would indicate that, a decade after fire, vegetation is not submitted to notably different levels of competition for light in areas burned once and twice. Light is not usually a limiting resource in MTEs. On the contrary, Mediterranean plants exhibit a range of morphological and physiological adaptations to cope with high light intensity together with heat and drought (Martínez-Ferri *et al.*, 2000; Ain-Lhout *et al.*, 2004). Moreover, light photosynthetic utilisation is restrained by water and nutrient availability (Lambers *et al.*, 1998). In addition, branch elongation patterns evidence a modular response rather than a whole-plant response, and are thus more variable than basal area increment patterns.

Basal area increments of the resprouter species were correlated with climatic variables in once-burnt areas, but not in twice-burnt ones, where the constraint produced by fire repetition seemed to prevail. Lower basal area increment of *P.lentiscus* in once-burnt areas was associated with higher mean temperatures during the growth period. Similarly, lower basal increments of *Q.ilex* were associated to higher actual solar radiation, i.e., drier climatic conditions. Growth of the seeder *R.officinalis* was not observed to rely on climatic variables. However, the absence of significant correlations with cumulative precipitation or mean temperature during the considered growth period may be due to the fact that data corresponded to the nearest climatic station, and thus did not specifically characterize the geographical locations considered.

Conclusions

A decade after fire, differences in growth between once- and twice-burnt areas were not present in resprouter species such as *Q. ilex* and *P. lentiscus*, whose post-disturbance growth should be favored in the first years after fire by stored resources. However, the growth of the seeder *R. officinalis* was higher in twice-burnt areas, suggesting that re-burning at short fire intervals resulted in a release from competition that remains 10-11 years after fire. Such effect was observed in basal area increment, but not in branch elongation, which is more likely determined by competition for light.

Basal area increment of the resprouter species was inversely correlated with climatic variables such as mean temperature during the growth period in once-burnt areas, but not in twice-burnt ones. Thus, fire repetition likely resulted in a stronger constraint for growth that overshadowed the effects of climatic variables.

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