THE CONTRIBUTION OF LEGUMES TO POST-FIRE REGENERATION OF *QUERCUS SUBER* AND *PINUS HALEPENSIS* FORESTS IN NORTHEASTERN ALGERIA

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Résumé. — *Contribution des Légumineuses à la régénération après feu des forêts de* Quercus suber *et* Pinus halepensis *du Nord-Est Algérien*. — Le rôle des Légumineuses dans la régénération après feu a été largement étudié sur la rive nord de la Méditerranée, mais aucune donnée n'est disponible concernant la rive sud. Le but de cet article est d'analyser la dynamique des Légumineuses dans une subéraie et une pinède à Pin d'Alep du Nord-Est Algérien durant les premiers mois après un feu de faible intensité. Les aspects de la démographie des germinations des Légumineuses, leur contribution à la biomasse totale et la richesse spécifique sont considérés. Les deux communautés ne présentent pas de différences majeures. Toutes deux montrent des modèles démographiques similaires : les germinations de Légumineuses commencent à émerger très tôt (novembre) après le feu (octobre) et continuent à s'établir abondamment avec un premier pic en décembre et un deuxième en mars, avec un ralentissement significatif en janvier et février. La germination diminue à partir d'avril pour atteindre son minimum en mai et complètement s'arrêter en début juin. Ce modèle en deux pics plutôt qu'un seul, comme déjà rapporté, serait vraisemblablement dû au froid exceptionnel durant janvier et février 2005 (neige jusqu'au niveau de la mer) d'où un ralentissement de la germination et son décalage à mars. Huit mois après l'incendie (vers la fin juin, période où la végétation herbacée commence à sécher), la biomasse aérienne des Légumineuses affiche un maximum de $37,8 \pm 1,83$ g/m^2 dans la subéraie et $26,7 \pm 1,63$ g/m^2 dans la pinède. Sept mois après le feu, relativement aux autres familles de plantes, les Légumineuses sont floristiquement bien représentées avec $19,8 \pm 1,11$ % des espèces dans la subéraie et $24,3 \pm 2,05$ % dans la pinède, valeurs nettement supérieures à celles rapportées pour d'autres écosystèmes de type méditerranéen (3,8 - 13,3 %), probablement en raison de la localisation géographique (basse latitude) de notre aire d'étude et la pression de surpâturage qui favorise l'installation des Légumineuses.

Summary. — The role of legumes in post-fire forest regeneration has been extensively studied in the northern Mediterranean basin but no published data are available concerning the southern part of the area. The aim of the present paper is to analyse the dynamics of the leguminous species in a *Q. suber* and a *P. halepensis* forests in Northeastern Algeria during the first months after a wildfire of low intensity. The aspects of seedling demography of legumes, their contribution to total biomass and species richness were considered. No major differences were detected between the two communities. They presented similar demographic patterns: legume seedlings began to emerge very early (November) after the fire (October) and continued to increase massively with a peak in December and another in March, and a significant slowdown in January and February; in April, they resumed to gradually decrease again to reach their minimum in May and completely stop in early June. This pattern with two peaks rather than only one in seedling demography was likely due to the exceptional coldness of January and February 2005 (snow down to sea level) whereby the germination slowdown and its delay to March. Eight months after the fire (towards the end of June, as the herbaceous vegetation began to dry), the above-ground biomass of legumes reached a maximum of 37.8 ± 1.83 g/m^2 in the *Q. suber* forest and 26.7 ± 1.63 g/m^2 in the *P. halepensis* one. Seven months after the

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disturbance, in comparison with the other taxa, the legumes were floristically well represented with 19.8 ± 1.11 % and 24.3 ± 2.05 % of species in the Cork oak and the Allepo pine forests respectively. These richness values are far higher than those reported for other Mediterranean-type ecosystems (3.8 - 13.3 %) probably because of the geographic location (lower latitude) of our study area and the overgrazing pressure favouring installation of leguminous species.

In the Mediterranean basin and Mediterranean-type areas, vegetation is mainly shaped by the action of frequently recurring fires (Naveh, 1975; Trabaud & Lepart, 1980; Arianoutsou, 1998; Pausas *et al.*, 2008). It has been clearly demonstrated that the seed bank and the number of species are significantly reduced in the case of a long period without fire (Keeley *et al.*, 2005). That's why post-fire seed germination is to be interpreted as a strategy of adaptation to fire-prone habitats of hard-coat-seeder taxa, such as *Leguminosae* and *Cistaceae* (Arianoutsou, 1998).

Legumes and *Cistaceae* recovery is accomplished by massive seedling emergence closely confined to the first post-fire years through their soil seed bank whose dormancy is broken by the impact of fire (Auld & O'Connell, 1991; Roy & Sonié, 1992; Thanos *et al.*, 1992; Herranz *et al.*, 1998, 1999; Ferrandis *et al.,* 1999; Baeza & Vallejo, 2006). This fast and abundant germination after fire is mainly provided by the soil seed bank (Arianoutsou, 1998), the contributions by dissemination being less significant (Luzuriaga *et al.*, 2005).

While the role of *Cistaceae* is practically limited to soil protection against water erosion during the first months after fire, the leguminous species play multiple other roles represented in hampering the invasion by exogenous species and soil enrichment before an effective resumption of native woody plants (Arianoutsou & Margaris, 1981; Trabaud & Oustric, 1989; Buhk *et al.*, 2007). Input of organic N from legumes can stimulate recovery of microbial activity and N cycling which can serve to facilitate community succession and promote ecosystem resilience (Johnson *et al.*, 2004; Chambers *et al.*, 2007; Goergen & Chambers, 2009).

Because of all these important roles during the first months after fire, many studies have been dedicated to legumes in Mediterranean Europe (e.g. Papavassiliou & Arianoutsou, 1993; Arianoutsou & Thanos, 1996; Herranz *et al.*, 1998; Kokkoris & Arianoutsou, 2000; Baeza *et al.*, 2006; De Luis *et al.*, 2006, 2008a, b). However, in the southern part of the area, no published data have hitherto been reported on the subject except on the effect of fire on flora and vegetation in general, without any specifications to legumes (Madoui *et al.*, 2006; Ouelmouhoub & Benhouhou, 2007; Bekdouche *et al.*, 2008).

In Algeria, the National Forest Service statistics show that, from 1963 through 2009, approximately $1.6 \ 10^6$ ha of vegetation were burnt, representing an annual average of $34 \ 10^3$ ha. *Q. suber* and *P. halepensis* forests were the most affected ecosystems especially in 1994 when about $9 \ 10^4$ ha of *Pinus* and $4 \ 10^4$ ha of *Quercus* forests were consumed by fires. To better manage the situations caused by the wildfires, every aspect of the phenomenon should be correctly understood. With the present contribution, we aim to assess the legumes dynamics during the first months (1st year) in a *Q. suber* and a *P. halepensis* forests of Northeastern Algeria after a wildfire of low intensity. The aspects analysed were (1) the seedling demography of legumes, (2) their above ground biomass and (3) the species richness. The presentation will consist on a comparison between the two communities and a confrontation of the results with those reported for other Mediterranean-type ecosystems through a review of the main relevant documentation on the topic.

MATERIALS AND METHODS

STUDY SITES

In October 2004, a wildfire devastated the *Q. suber* forest (QF) of Sidi Boudraham (36° 44' N; 5° 00' E) and the *P. halepensis* forest (PF) of Adrar Oufarnou (36° 46' N; 5° 00' E) located on the heights near the coastal city of Bejaia, *c.* 200 km east of Algiers. The previous fire in the site occurred in 2001. Given this short period of only three years,

the ecosystems would not have accumulated much fuel from which we deduce that the fire of October 2004 is to be considered of low (medium at the most) intensity. Three years old vegetation is rather young, low and loose with high rates of moisture which does not favour fire severity (Trabaud, 1980).

The dominant species are *Phillyrea latifolia, Arbutus unedo* and *Erica arborea* in QF, and *Phillyrea media* and *Erica multiflora* in PF. Average altitude of the two study sites is *c.* 380 m. According to the nearest weather station (Bejaïa), for the period 1970-2009, the average of maximum and minimum temperatures of the hottest month (August) and the coldest month (January) are 29.58 °C and 7.52 °C respectively; the annual average rainfall is 780 mm. Following Emberger (1971), the area is classified under the hot variant of the sub-humid bioclimatic stage. For the period of study (October 2004 - June 2005), the monthly precipitations and temperatures are included in Fig. 1.

EXPERIMENTAL DESIGN AND MONITORING

All the legume species were considered. To monitor the regeneration of these species, regular observations were made during the first seven months after the fire (i.e. from early November 2004 through late May 2005). For each of the two communities, counts of the different legume species seedlings were performed monthly on ten permanent 1 m^2 quadrats, regularly distributed on two equal rows. The two rows were c. 25 m apart and stretched over a 45 m long transect. Every month, the leguminous seedlings were carefully collected (destructive sampling). In both communities, the above-ground biomass was assessed on eight randomly chosen plots of 4 m^2 each. At intervals of two months (from early December 2004 through late June 2005), the above-ground biomass of a 1 m^2 quadrat was collected from each of the eight plots. The plant material was split into two categories (legumes and other non legume plant families), oven-dried at 105 °C for 24 hours and then weighed to the nearest 0.001 g. Finally, in order to determine the contribution of legumes to the richness in each forest type seven months after the fire, ten floristic relevés, made on 100 m^2 plots (Trabaud, 1980) randomly distributed over each study site, were analysed for their species composition, including all plant families (see results, Tab. I).

SPECIES IDENTIFICATION AND NOMENCLATURE

The species were identified using the Flora of Quézel & Santa (1962-1963) and their nomenclature up-dated according to Dobignard (2010). Voucher specimens are deposited in the Herbarium of the laboratory of Ecology, Department of Biology of Organisms and Populations, University of Bejaïa (Algeria).

STATISTICAL ANALYSIS

Repeated measures ANOVA and LSD tests were used for comparison between months within each community, and the Student t-test served for comparison between the two communities ($P = 0.05$). Prior to statistical analysis, data were tested for parametric assumptions with Kolmogorov-Smirnov test of normality and Levene's test of variance homogeneity. Outputs showed that there was no violation of parametric tests conditions, except for the biomass data witch had undergone a logarithmic transformation ($y = log(x+1)$) to homogenize the variances. The statistical processing was performed using SPSS 10.0 for the inferences and MicroSoft Excel 2007 for the charts. The results were presented as means ± SD or means ± 2SE.

RESULTS

EMERGENCE OF LEGUME SEEDLINGS

In November 2004, one month after the fire, the average numbers of legume seedlings were 3.5 ± 0.45 /m^2 in QF and 1.5 ± 0.40 /m^2 in PF (Fig. 1). The two communities presented similar demographic patterns. In both forests, the leguminous seedlings began to arise very early after the fire (early November) and continued to emerge until late May; a first peak was observed in December (29.2 ± 1.16 /m^2 in QF and 30.0 ± 0.94 /m^2 in PF) and another in March (21.2 ± 1.10 /m^2 in the QF and 19.2 ± 1.14 /m^2 in PF) with a significant slowdown in January and early February; in April, the germinations resumed to gradually decrease in number again to reach their minimum in May and completely stop in early June (Fig. 1).

CHANGES IN THE ABOVE-GROUND BIOMASS OF LEGUMES

The above-ground biomass of legumes collected during the survey was very low during the first four months after the fire (Fig. 2). In April 2005, six months after the disturbance, the biomass values reached 11.17 ± 1.150 g/m^2 in QF and 8.580 ± 0.998 g/m^2 in PF. The maximal biomass was recorded in June 2005, eight months after the fire, with 37.84 ± 1.835 g/m^2 in the *Quercus* forest and 26.70 ± 1.634 g/m^2 in the *Pinus* one. The two communities presented similar biomass dynamics with values slightly higher in the *Quercus* forest, especially during the eighth month ($P < 0.05$). In late June, the herbaceous vegetation had completed its growth and began to dry.
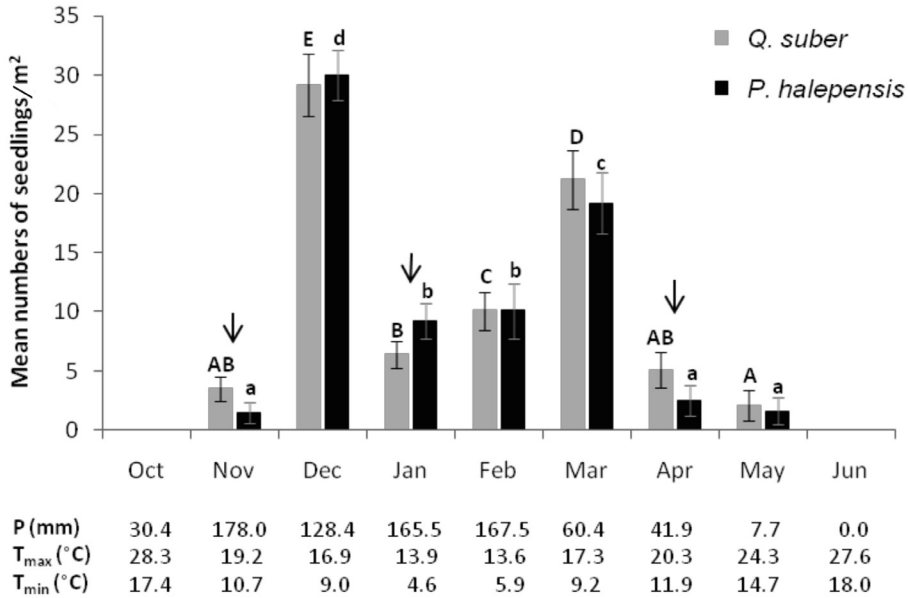
Figure 1. — Comparison of mean numbers ± 2SE of legume seedlings per m² after fire in a *Quercus suber* and a *Pinus halepensis* forests of Northeastern Algeria. Within each community, the values with different letters are significantly different (LSD test, $P < 0.05$). Between the two communities, only the values pointed at with arrows are significantly different (t-test, $P < 0.05$). The three lines facing the month axis are, respectively, mean precipitation values (mm), and maximal and minimal mean temperatures (°C) recorded from October 2004 through June 2005. Maximal and minimal mean temperatures of January and early February 2005 were the lowest ever registered. For the period 1978-2008 the second lowest maximal temperature was 14.5 °C (January 1981 and 1985) and the lowest minimal temperature was 5 °C (January 1983) (Data from The Meteorological Station of Bejaia, Algeria).
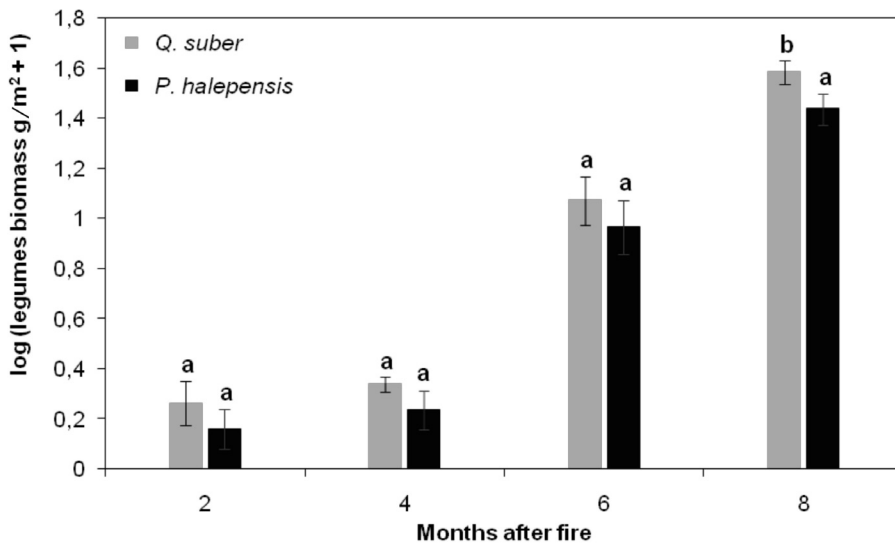

Figure 2. — After fire changes in mean ± 2SE above-ground biomass (g) of legumes in a *Quercus suber* and a *Pinus halepensis* forests of Northeastern Algeria. The two communities are significantly different at the eighth month only (t-test, $P < 0.05$).

The major difference between the two communities lies in their dominant species. In the *Quercus* forest, *Scorpiurus muricatus* dominated because of its extensive vegetative system. In the *Pinus* community, this role was performed by *Hedysarum coronarium*, similar to *S. muricatus* with its dense vegetative structure. Two other species, *Anthyllis tetraphylla* and *Ebenus pinnata*, showing high abundance, were associated with *Hedysarum coronarium*.

With regard to total biomass, the legumes constituted the most represented family during the first months after the fire in the two surveyed communities. Their maximal contribution to the total biomass was reached in November 2004 (66.8 ± 8.99 % in QF and 63.2 ± 2.96 % in PF) and their minimal relative biomass was recorded in January 2005 (13.7 ± 2.66 % in QF and 11.2 ± 1.34 % in PF) (Fig. 3).

The legume species, herbaceous in majority (only three out of thirty species were woody), dominated the two regenerating communities until woody shrubs of the other families recovered (Tab. I). The significant biomass of the remaining non legume species was essentially due to woody shoots. The weight of a shoot of *Arbutus unedo*, *Phillyrea media*, *Erica arborea* or *Pistacia lentiscus* can equal or even exceed numerous individuals of an herbaceous species. In addition, this woody biomass was strongly enhanced by the *Cistus* species that regenerated quickly and massively by seeds.

LEGUME SPECIES RICHNESS

The legumes were equally well represented (t-test, $P < 0.05$) in the two communities seven months after the fire, with 19.8 ± 1.11 % in the *Quercus* forest and 24.3 ± 2.05 % in the *Pinus* one. The number of legume species was 16 out of 81 in QF and 23 out of 95 in PF (Tab. I).
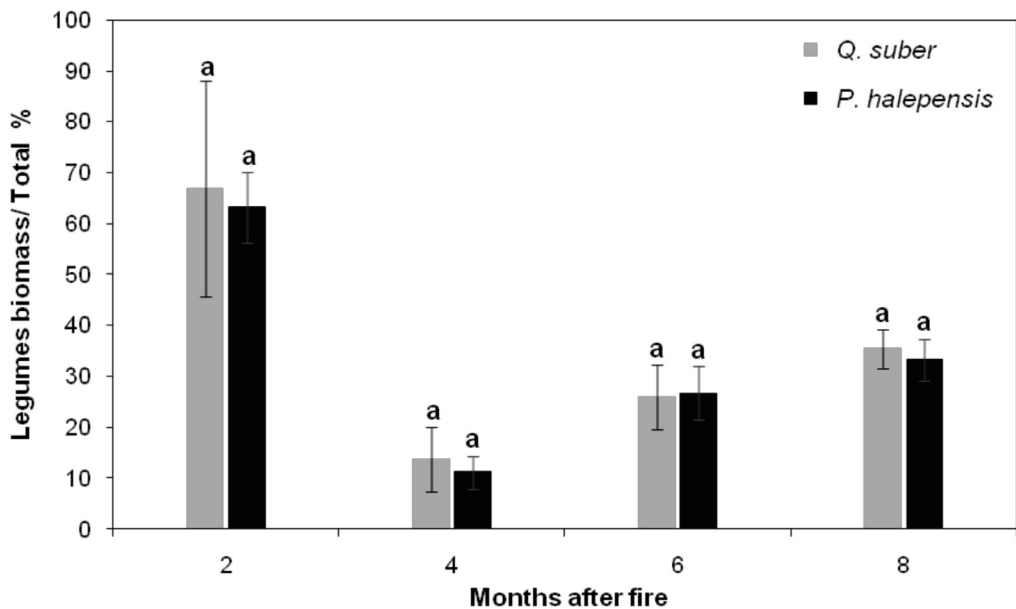

Figure 3. — Contribution of legumes to total above-ground biomass (%) over 8 months after fire (November 2004-June 2005) in a *Quercus suber* and a *Pinus halepensis* forests of Northeastern Algeria. The two communities are totally similar over the 8 months (t-test, $P < 0.05$).

TABLE I

Plant species recorded in a Quercus suber *and a* Pinus halepensis *forests of Northeastern Algeria seven months after fire.*
QF: Quercus suber *forest; PF:* Pinus halepensis *forest; +: Presence; -: Absence; Fire Reg.: Post-fire regeneration*
strategy; R = Obligate resprouter; S = Obligate seeder; SR = Seeder-resprouter; MPh: Macrophanerophyte;
NPh: Nanophanerophyte; PHl: Phanerophyte liana; Ch: Chamaephyte; H: Hemicryptophyte; G: Geophyte;
Th: Therophyte.

Species	Family	QF	PF	Fire reg.	Life form
Tripodion tetraphyllum (L.) Fourr.	Fabaceae	-	+	S	Th
Anthyllis vulneraria L.	Fabaceae	-	+	S	Th (H)
Astragalus hamosus L.	Fabaceae	-	+	S	Th
Astragalus monspessulanus L.	Fabaceae	-	+	S	H
Biserrula pelecinus L.	Fabaceae	+	-	S	Th
Calicotome spinosa (L.) Link	Fabaceae	+	+	R S	NPh
Ceratonia siliqua L.	Fabaceae	-	+	R	Ph
Coronilla juncea L.	Fabaceae	-	+	S	Ch
Ebenus pinnata Aiton	Fabaceae	-	+	S	Ch
Genista tricuspidata Desf.	Fabaceae	+	+	R S	NPh
Hedysarum coronarium L.	Fabaceae	-	+	S	Th
Hippocrepis multisiliquosa L.	Fabaceae	-	+	S	Th
Lotus corniculatus L.	Fabaceae	+	-	S	H
Lotus creticus L.	Fabaceae	-	+	S	Ch
Lotus edulis L.	Fabaceae	+	+	S	Th
Lotus ornithopodioides L.	Fabaceae	+	+	S	Th
Medicago orbicularis (L.) Bartal.	Fabaceae	+	-	S	Th
Onobrychis caput-galli (L.) Lam.	Fabaceae	-	+	S	Th
Ononis natrix L.	Fabaceae	+	+	S	Th
Ononis reclinata L.	Fabaceae	-	+	S	Th
Ononis sicula Guss.	Fabaceae	-	+	S	Th
Scorpiurus muricatus L.	Fabaceae	+	+	S	Th
Trifolium angustifolium L.	Fabaceae	+	-	S	Th
Trifolium bocconei Savi.	Fabaceae	+	-	S	Th
Trifolium campestre Schreb.	Fabaceae	+	+	S	Th
Trifolium glomeratum L.	Fabaceae	+	+	S	Th
Trifolium retusum L.	Fabaceae	+	+	S	Th
Trifolium stellatum L.	Fabaceae	-	+	S	Th
Trifolium tomentosum L.	Fabaceae	+	-	S	Th (H)
Vicia lutea L.	Fabaceae	+	-	S	Th
Anacyclus clavatus (Desf.) Pers.	Compositae	-	+	S	Th
Andryala integrifolia L.	Compositae	+	+	S	H
Bellis annua L.	Compositae	+	+	S	Th
Rhaponticoides africana (Lam.) M.V.Agab. & Gr.	Compositae	+	-	SR	H
Chrysanthemum coronarium L.	Compositae	+	+	S	Th
Filago pygmaea L.	Compositae	+	+	S	Th
Galactites elegans (All.) Soldano	Compositae	+	+	S	Th
Hypochaeris radicata subsp. *radicata*	Compositae	+	+	SR	H
Hypochaeris alliatae (Biv.) Gal	Compositae	-	+	S	Th
Phagnalon saxatile (L.) Cass.	Compositae	-	+	SR	Ch
Pulicaria odora (L.) Rchb.	Compositae	+	+	SR	H
Scolymus hispanicus L.	Compositae	-	+	SR	H
Sonchus oleraceus L.	Compositae	+	+	S	Th
Aira cupaniana Guss.	Poaceae	+	-	S	Th

Ampelodesmos mauritanicus (Poir.) Durand & Sch.	Poaceae	+	+	SR	H
Avena sterilis L.	Poaceae	+	-	S	Th
Brachypodium sylvaticum (Huds.) P. Beauv.	Poaceae	+	+	SR	H
Briza maxima L.	Poaceae	+	-	S	Th
Bromus hordeaceus L.	Poaceae	+	+	S	Th
Cynosurus elegans Desf.	Poaceae	+	+	S	Th
Dactylis glomerata L.	Poaceae	+	+	SR	H
Festuca paniculata (L.) Schinz & Thell.	Poaceae	+	+	SR	H
Hyparrhenia hirta (L.) Stapf	Poaceae	-	+	SR	H
Melica minuta L.	Poaceae	+	-	SR	H
Catapodium rigidum (L.) C.E.Hubb.	Poaceae	-	+	S	Th
Clinopodium vulgare L.	Lamiaceae	-	+	SR	H
Lavandula stoechas L.	Lamiaceae	+	+	S	Ch
Stachys ocymastrum (L.) Briq.	Lamiaceae	+	+	S	Th
Teucrium flavum L.	Lamiaceae	-	+	SR	Ch
Teucrium fruticans L.	Lamiaceae	-	+	SR	Ch
Thymus algeriensis Boiss. & Reut.	Lamiaceae	+	-	SR	Ch
Arbutus unedo L.	Ericaceae	+	-	R	NPh
Erica arborea L.	Ericaceae	+	+	SR	NPh
Erica multiflora L.	Ericaceae	-	+	SR	NPh
Erica scoparia L.	Ericaceae	+	+	SR	Ch
Galium lucidum All.	Rubiaceae	+	+	S	H
Galium scabrum L.	Rubiaceae	+	+	S	Th
Rubia peregrina L.	Rubiaceae	+	+	SR	NPh
Sherardia arvensis L.	Rubiaceae	+	-	S	Th
Bupleurum plantagineum Desf.	Umbelliferae	-	+	SR	NPh
Daucus carota L.	Umbelliferae	+	+	SR	Th (H)
Eryngium tricuspidatum L.	Umbelliferae	+	+	SR	H (G)
Torilis arvensis (Huds.) Link	Umbelliferae	-	+	S	Th
Cistus salviifolius L.	Cistaceae	+	+	SR	NPh
Cistus monspeliensis L.	Cistaceae	+	+	S	NPh
Fumana thymifolia (L.) Webb	Cistaceae	-	+	S	Ch
Gladiolus italicus Mill.	Iridaceae	+	+	SR	G
Moraea sisyrinchium (L.) Ker Gawl.	Iridaceae	+	-	SR	G
Iris juncea Poir.	Iridaceae	+	+	SR	G
Allium roseum L.	Alliaceae	-	+	SR	G
Allium nigrum L.	Alliaceae	+	+	SR	G
Cerastium glomeratum Thuill.	Caryophyllaceae	+	-	S	Th
Silene secundiflora Otth	Caryophyllaceae	+	+	S	Th
Convolvulus althaeoides L.	Convolvulaceae	-	+	R	H
Convolvulus tricolor L.	Convolvulaceae	-	+	S	Th
Borago officinalis L.	Boraginaceae	-	+	S	Th
Echium asperrimum Lam.	Boraginaceae	-	+	S	H
Biscutella didyma L.	Cruciferae	+	-	S	Th
Sinapis arvensis L.	Cruciferae	+	+	S	Th
Carex distachya Desf.	Cyperaceae	+	-	R	H
Carex halleriana Asso	Cyperaceae	+	+	R	H
Quercus suber L.	Fagaceae	+	-	R	MPh
Quercus coccifera L.	Fagaceae	+	+	R	NPh
Linum corymbiferum ssp. *corymbiferum*	Linaceae	+	+	S	Ch
Linum bienne Mill.	Linaceae	+	+	S	Ch

Olea europaea subsp. *europaea*	Oleaceae		+	R	MPh
Phillyrea latifolia L.	Oleaceae	+	+	R	NPh
Fumaria capreolata L.	Papaveraceae	+	+	S	Th
Papaver somniferum ssp. *setigerum* (DC.) Arcang.	Papaveraceae	-	+	S	Th
Anagallis arvensis L.	Primulaceae	+	+	S	Th
Cyclamen africanum Boiss. & Reut.	Primulaceae	+	+	R	G
Clematis flammula L.	Ranunculaceae	+	+	SR	Phl
Ranunculus macrophyllus Desf.	Ranunculaceae	+	-	SR	H
Crataegus monogyna Jacq.	Rosaceae	-	+	R	NPh
Rosa sempervirens L.	Rosaceae	+	+	R	Ph
Pistacia lentiscus L.	Anacardiaceae	+	+	R	NPh
Arisarum vulgare Targ. Tozz	Araceae	+	+	R	G
Asparagus acutifolius L.	Asparagaceae	+	+	SR	Phl
Simethis mattiazzii (Vand.) G. L.	Asphodelaceae	+	-	R	G
Campanula dichotoma L.	Campanulaceae	+	-	S	Th
Lonicera implexa Aiton	Caprifoliaceae	+	-	R	Phl
Euphorbia pterococca Brot.	Euphorbiaceae	+	+	S	Th
Geranium robertianum ssp. *purpureum* (Vil.) Nym.	Geraniaceae	+	-	SR	Th (H)
Lavatera arborea L.	Malvaceae	-	+	R	NPh
Myrtus communis L.	Myrtaceae	+	+	R	NPh
Pinus halepensis Mill.	Pinaceae	-	+	S	MPh
Rhamnus alaternus ssp. *alaternus*	Rhamnaceae	-	+	R	NPh
Smilax aspera L.	Smilacaceae	+	+	R	PHl
Solanum nigrum ssp. *nigrum*	Solanaceae	-	+	S	Th
Daphne gnidium L.	Thymelaeaceae	+	+	SR	NPh

DISCUSSION

LEGUMES SEED GERMINATION AFTER FIRE

Many of the dominant species in Mediterranean ecosystems after fire are resprouters (Lloret, 1998). Other species have no ability to survive severe damage to the adult and rely entirely on seed germination for regeneration (Ferrandis *et al*., 1999). Seed germination is the major mechanism adopted by legumes for their post-fire regeneration (Papavassiliou & Arianoutsou, 1993). Similarly, 90 % of the legumes inventoried during the present survey regenerated exclusively by seeds (Tab. I), resprouting was observed only for *Calicotome spinosa, Ceratonia siliqua* and *Genista tricuspidata*. Despite their perennial habit, herbaceous species such as *Anthyllis vulneraria, Astragalus monspessulanus, Coronilla juncea, Lotus creticus, Lotus corniculatus* and *Ononis natrix* regenerated only by seeds. Why one or the other strategy of post-fire regeneration is favoured is not yet clear (Férnandez-Santos *et al*., 2004). The germination of legumes of the burnt areas is induced by heat shock (Auld & O'Connell, 1991; Keeley & Bond, 1997; Hanley & Fenner, 1998; Herranz *et al*., 1998) or strong insolation of the stripped areas (Bazzaz, 1998). In the Sydney region, Auld & Denham (2006) have estimated that about 15 % of the fire-prone flora has dormancy broken by heat shock. Generally, temperatures ranging between 60-150 °C affect germination positively (De Luis *et al*., 2005b). For some tropical legumes, temperatures of 80-100 °C significantly increase seed germination (Williams *et al*., 2004). For some species, this germination is stimulated by the smoke generated during the combustion of vegetation (Crosti *et al*., 2006; Dayamba *et al*., 2008)). The effect of thermal shock and smoke on seed germination of some taxa of fire-prone vegetation have been shown to be additive and generate a lifting of dormancy of the soil seed bank (Roy & Sonié, 1992; Thanos *et al*., 1992; Doussi & Thanos, 1994; Pérez-Fernandez & Rodriguez-Echeverria, 2003; Thomas *et al*., 2003; Crosti *et al*., 2006; Scott *et al*., 2010). In the Sydney

region, approximately half of the fire-prone flora has seed dormancy broken by the interaction of heat and smoke (Auld & Denham, 2006). Smoke promotes germination increase up to a maximum and then a decrease is observed because high concentrations or duration of smoking become germination inhibitory (Light *et al*., 2002) or seed lethal (Keeley & Fotheringham, 1998). In the same way, heat intensity or duration stimulate seed germination increasingly until an optimum and then a decrease is observed because excessive thermal shocks cause seed mortality (Auld & O'Connell, 1991; Baeza & Vallejo, 2006). High temperatures affect seed viability and consequently germination rates (Lloret, 1998). In general, the responses to heat and smoke are variable. Keeley & Bond (1997) have noted that, in some cases, seed germination behaviour is phylogenetically inherited as in legume species where heat will commonly enhance germination. Crosti *et al*. (2006), in a comparison of several studies from different regions with Mediterranean-type vegetation, have concluded that there are both phylogenetic and biogeographical patterns in post-fire regeneration behaviour.

In our case, germination of legumes from the soil seed banks of the two investigated forests (QF and PF) began very early after the disturbance. The first germinations were observed after the first rains in November 2004 (Fig. 1). The seedling demography showed a bimodal pattern with a major peak in December and a second smaller one in March. This pattern with two peaks rather than only one as it has been already observed during the first season after fire (Arianoutsou, 1998; De Luis *et al*., 2008a, b) was likely due to the exceptional meteorological conditions (Fig. 1); January and February 2005 in our study area were colder than usual (snow down to sea level for a prolonged period), so germination was slowed down and delayed to March, hence the two peaks.

In a *Ulex parviflorus* dominated gorse shrubland of Eastern Spain observed over two consecutive years after a fire experimentally set in October 1996, De Luis *et al*. (2008a) recorded that seedling demography of *Leguminosae* and *Cistaceae* shows a monomodal pattern in each year with a first peak in the autumn just after the fire (1st year) and a second the following autumn (2nd year), without any peak in spring; but the *Cistaceae* dominated during the first year and the *Leguminosae* during the second year. These observations differ from ours not only by the absence of the spring peak explained above but also by the domination of *Cistaceae* before *Leguminosae* during the first year after fire.

Legume species dominated in our communities during the first year after fire because most of them are annual herbs (see Tab. I), thus they could quickly reconstruct their seed bank. Contrarily, the *Cistus* species are woody plants reaching maturity after two or three years (Roy & Sonié, 1992; Tavşanoğlu & Gurkan, 2005; Duguy & Vallejo, 2008), so, they could not sufficiently reconstitute their seed bank since the previous fire of 2001 (Three years time). Survival of *Cistus* species which reproduce only by seed may be seriously threatened by fires occurring before they have produced and accumulated seeds (Trabaud, 1980). Duguy & Vallejo (2008) have also suggested that frequent fire recurrences with repeated short intervals between fires might cause a reduction of woody species cover, probably due to a decrease of the seed bank replenishment, and increase of the presence of herbaceous species.

Furthermore, a low severity of fires stimulates mainly germination of seeds near the soil surface (De Luis *et al*., 2008a), but the depth of burial depends essentially on the seed size (Bond *et al*., 1999). The *Cistus* seeds being lighter than those of the woody legumes of the gorse shrubland studied by De Luis *et al*. (2008a) would occur at the superficial level, while those of the woody legumes would burrow deep in the soil. Our results seem to agree with this pattern too, because the seeds of herbaceous legumes, lighter than those of *Cistus* species (personal observation), would likely remain nearer to the soil surface which would favour their massive germination after a low intensity fire. As a rule, to accurately evaluate the effect of any factor on post-disturbance vegetation, the whole set of interacting factors must be considered, including pre-disturbance vegetation (determined by past disturbance regime), disturbance characteristics, spatial factors and post-disturbance conditions (Duguy & Vallejo, 2008).

LEGUMES BIOMASS AND SPECIES RICHNESS

Despite their relatively low contribution to the species richness (20-24 % in May 2005), the leguminous species participated with a significant proportion to the total biomass of the two

communities (up to 67 % in November 2004) in comparison with the whole of the other flora (especially *Cistaceae*, *Poaceae* and woody sprouts of *Erica arborea*, *E. multiflora*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Myrtus communis* and *Arbutus unedo*; tree seedlings contributing very little to biomass). The relatively low number of legume species was compensated by their remarkable abundance and dominance.

Seven months after the disturbance, the number of legume species was significant for both communities (Tab. I), resulting from seed germination stimulated by the fire. This enhancement in legumes germination densities is likely due to a heat-induced rupture of the hard coat of their seeds (Doussi & Thanos, 1994). Similar observations have been made for *Cistaceae* species (Arianoutsou & Margaris, 1981; Trabaud & Oustric, 1989; Roy & Sonié, 1992; Ferrandis *et al.*, 1999). The Mediterranean-type ecosystems throughout the globe show that legume richness after fire ranges from 3.8 % in the Chilean matorral (Rundel, 1981) to 13.3 % for the sclerophyll forests of South Australia (Specht, 1972). In a *Pinus halepensis* forest of Greece, legumes representing approximately 9 % of the flora of a mature stand have more than doubled immediately after a fire (Kazanis & Arianoutsou, 1996). Our results revealed that the legumes proportions were 19.8 ± 1.11 % and 24.3 ± 2.05 % of species in QF and PF respectively. These relatively higher richness values were probably due to the fact that our floristic samples were done during the earlier stages after the fire in the two communities shaped by the overgrazing pressure (Arianoutsou & Thanos, 1996) and situated in a climatic region (lower latitude) favouring the establishment of legumes (Garcillán *et al.*, 2003). Legumes are very present in Mediterranean-type ecosystems because of their morphological and physiological adaptations and their various dispersal modes (endozoochory, autochory, etc.) (Arianoutsou & Thanos, 1996). Their adaptive mechanisms are related to nitrogen fixation through development of nitrogen fixing root nodules in soils with limited nitrogen availability and formation of mycorrhizal associations that enhance phosphorus uptake (Goergen & Chambers, 2009). One of the particularities of the Mediterranean region is the high human pressure particularly through overgrazing which favour herbaceous legumes characterized by their potential adaptation to increase their seed germination after fire (Arianoutsou & Thanos, 1996).

Soon after the fire, the legumes achieved a high density and a rapid increase in biomass (Figs. 1 & 2). Because of these demographic strategies, they present great affinities with the initial stages of post-fire successions (Arianoutsou & Margaris, 1981).

Perturbations such as agricultural activity or fire provide space, nutrients and light for early successional species (mostly therophytes) which are low in the competitive hierarchy but have a strong colonization capacity in open spaces (Duguy & Vallejo, 2008). The legume species, with their massive germinations as a result of the conditions created by fire, lead the way to species of mature stages of the succession by improving the soil fertility which may favour ecosystem richness.

ROLES OF LEGUMES IN PLANT FORMATIONS DYNAMICS

Legumes play multiple roles in the dynamics of plant formations. Above all, they protect soil against water erosion during the first months after fire because the woody species in burnt communities recover more slowly by resprouting. With wildfire occurrence and strong rainfall, changes in soil properties have been reported as a major reason for accelerated erosion (Pardini *et al.*, 2004; De Luis *et al.*, 2005a). The loss of topsoil and decreased regeneration of vegetation may inhibit the formation of soil organic matter and the establishment of plant species, thereby favouring the intensification of the erosive processes (Andreu *et al.*, 1996). The legumes share the function as soil protectors against water erosion with the *Cistus* species (Trabaud & Oustric, 1989).

The herbaceous species play a more important role in protecting soil against soil erosion because of their rapid establishment soon after fire through germination or resprouting (Beyers, 2009). This is why these species are preferred in burnt landscapes rehabilitation programmes. Perennial resprouter grasses are usually used because of their faster growth and higher rate of survival; they usually dominate the first stages of post-fire recovery in Mediterranean ecosystems (De Luis *et al.*, 2005a). However, successful establishment of seeded grasses displaces native

herbaceous vegetation, particularly annuals, and can reduce the survival rates of tree seedlings (Beyers, 2004). Seeding with herbaceous native species can provide additional benefits such as preventing invasion by undesirable plants. Several studies suggest that relatively high cover of perennial herbaceous species can increase the ecosystems resilience after fire and increase resistance to invasion by exotic species (Chambers *et al.*, 2007). The rapid and massive recovery of herbaceous legume species may better favour the installation of tree seedlings because they are not as competitive as the aggressive non-native perennial grass species (*Bromus inermis, Dactylis glomerata, Festuca ovina*) generally used in post-fire rehabilitation (Beyers, 2009).

The legumes are the only plants replacing quickly the nitrogen lost via volatilization during fires by inputs from nitrogen fixers after fire (Arianoutsou & Thanos, 1996; Boring *et al.*, 2004; Johnson *et al.*, 2004; Goergen & Chambers, 2009). Johnson *et al.* (2005) have estimated that post-fire nitrogen gain equals or even exceeds total nitrogen losses due to fire and salvage logging in a Sierran forest.

After fire, legumes are able to replace N lost due to fire and facilitate community succession (seedling establishment and plant growth) and stability over time. Furthermore, input of organic N from legumes can stimulate recovery of microbial activity and N cycling, this can serve to promote resilience of native ecosystems, but also may create an avenue for invasion (Goergen & Chambers, 2009). In addition, the legumes contribute to the enrichment of soil with organic matter after their senescence because they represent a significant proportion of the biomass. From this perspective, the dominant leguminous species *Hedysarum coronarium* and *Scorpiurus muricatus* may play an effective role in landscape rehabilitation after fire because of their density and spreading vegetative systems for soil protection against erosion and their high biomass and numerous nodules for soil enrichment.

CONCLUSION

The present results constitute the first data on the role of legumes in the regeneration of plant communities after wildfire in the southern part of the Mediterranean basin. No major differences were observed between the two studied communities except that numbers of seedlings and biomass values were slightly higher in the *Q. suber* forest (dominated by *Scorpiurus muricatus*) but richness more important in the *P. halepensis* one (dominated by *Hedysarum coronarium*). In both ecosystems, seedling demography showed two peaks, a major one in December, two months after the fire of low intensity, and a second smaller one in March. This pattern with two peaks rather than only one in seedling demography was likely due to the meteorological conditions during January and February 2005 that were colder than usual whereby germination was slowed down and delayed to March. The legumes richness (19.8 and 24.3 % of species in the *Q. suber* and the *P. halepensis* forests respectively) was far higher than reported for other Mediterranean-type ecosystems (3.8-13.3 %) probably because of the geographic location (lower latitude) of our study area and the overgrazing pressure favouring installation of leguminous species.

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