

Are wildfires a disaster in the Mediterranean basin? – A review

Juli G. Pausas^{A,D}, Joan Llovet^A, Anselm Rodrigo^B and Ramon Vallejo^{A,C}

^ACEAM (Centro de Estudios Ambientales del Mediterráneo), C/ Charles R. Darwin 14, Parc Tecnologic, E-46980 Paterna, Valencia, Spain.

^BCREAF (Centre de Recerca i Aplicacions Forestals), Department of Ecology, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Spain.

^CDepartment of Plant Biology, Universitat de Barcelona, E-08028 Barcelona, Spain.

^DCorresponding author. Present address: CIDE, CISC, Apartado Oficial, E-46470 Albal, Valencia, Spain.
Email: juli.g.pausas@uv.es

Abstract. Evolutionary and paleoecological studies suggest that fires are natural in the Mediterranean basin. However, the important increase in the number of fires and area burned during the 20th century has created the perception that fires are disasters. In the present paper, we review to what extent fires are generating ecological disasters in the Mediterranean basin, in view of current fire regimes and the long-term human pressure on the landscapes. Specifically, we review studies on post-fire plant regeneration and soil losses. The review suggests that although many Mediterranean ecosystems are highly resilient to fire (shrublands and oak forest), some are fire-sensitive (e.g. pine woodlands). Observed erosion rates are, in some cases, relatively high, especially in high fire severity conditions. The sensitive ecosystems (in the sense of showing strong post-fire vegetation changes and soil losses) are mostly of human origin (e.g. extensive pine plantations in old fields). Thus, although many Mediterranean basin plants have traits to cope with fire, a large number of the ecosystems currently found in this region are strongly altered, and may suffer disasters. Post-fire disasters are not the rule, but they may be important under conditions of previous human disturbances.

Additional keywords: erosion rates, Mediterranean-type ecosystems, post-fire regeneration, resilience, resprouting, soil losses.

Introduction

Fire plays an important role in structuring many communities worldwide (Bond *et al.* 2005). In the Mediterranean basin (MB), there is evidence that fires were frequent during the late Quaternary (Carrión *et al.* 2003), and they were also probably frequent much earlier, as many species have acquired adaptive mechanisms to persist and regenerate after recurrent fires (Pausas *et al.* 2004a; Pausas and Verdú 2005). Even at community level, the phylogenetic biodiversity of MB plants has been sorted out as a function of the fire regime (Verdú and Pausas 2007; Pausas and Verdú 2008), that is, MB biodiversity has been structured according to the different fire regimes. Thus, it is clear that in the MB, fires are natural, they have occurred for millennia, and plants have the capacity to cope with them. In this framework, fires should not be considered an ecological disaster but rather a part of the natural process. However, some studies suggest that current fire regimes may cause disasters in the sense of inducing abrupt community changes (Kazanis and Arianotsou 2004; Rodrigo *et al.* 2004; de Luís *et al.* 2006; Arnan *et al.* 2007) or important soil losses (Marquès and Mora 1992; de Luís *et al.* 2005). Furthermore, wildfires introduce a high risk of direct damage to humans and structures in most of the highly populated Mediterranean countries, and especially in coastal regions. Large wildfires are relatively new in the recent history of the Mediterranean basin; therefore, people see them as catastrophic events and the media amplify this perception.

To evaluate the possible role of fire in generating disasters, we first need to frame MB landscapes in their historical and cultural context. One of the most striking differences between the MB and other Mediterranean-type ecosystems is its millenary history of intensive and extensive land use. In fact, current landscapes and fire regimes in the MB cannot be understood without considering this millenary impact (Naveh 1975; Pausas 1999). Many cultures have evolved in the MB (e.g. Mesopotamian, Egyptian, Phoenician, Jewish, Greek, Arab and Roman), with many political conflicts (wars, changes in land ownership, migrations) that generated numerous socioeconomic and land-use changes. Millennia of severe pressures resulting in burning, cutting and grazing non-arable lands, and clearing (including uprooting), terracing, and cultivating arable areas have created a vast array of strongly human-modified landscapes. A large proportion of Mediterranean landscapes include terraced slopes, built for agricultural purposes long ago. Human-induced savannas (*dehesas*) and grasslands, with millenary grazing pressure by livestock, are also very important; pine plantations occur everywhere. The result of all this is that current Mediterranean landscapes are very far from being wild.

In recent decades and especially on the northern (European) rim of the Mediterranean, industrialisation and rural exodus have led to the abandonment of many fields, increasing the cover and continuity of early succession species (many of which are very flammable), and changing the landscape pattern and the fire

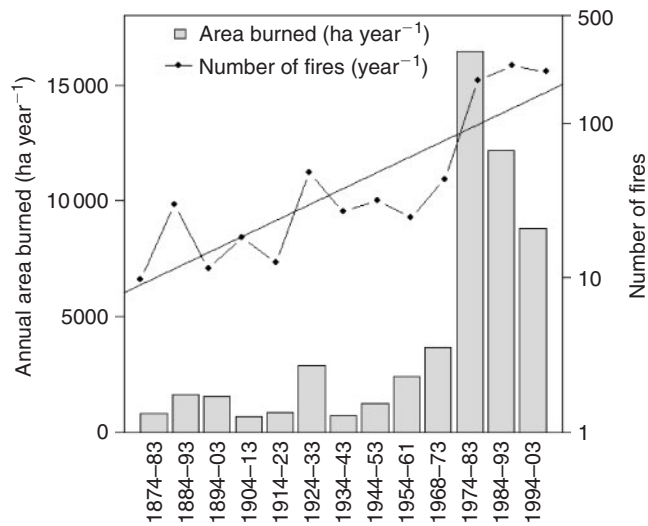


Fig. 1. Average annual area burned (bars, ha year⁻¹) and annual number of fires (dots and lines, in log scale) in the province of Valencia (eastern Spain), from 1874 to 2003 by decades (except for two periods, 1954–61 and 1968–73, in which information was not available for whole decade). Updated from Pausas (2004).

regime (Moreira *et al.* 2001; Pausas 2004). This farmland abandonment implies the buildup of large and continuous fuel beds that are prone to burn, while natural grazers are absent. Furthermore, many of these old fields have been covered by extensive pine plantations during the last decades. It is assumed that land-use change is the main driver of the increases in the number of wildfires and area burned in recent decades (Pausas 2004), although the influence of climatic changes cannot be denied (Piñol *et al.* 1998; Pausas 2004); indeed, the drier the summer, the larger the area burned that year (Pausas 2004). In addition, semi-urban populations are also increasing in rural areas, often in old fields, contributing to the risk of fire ignitions. As a consequence, both the number of ignitions and the area affected by fire increased exponentially from the 60s to the 80s (Figs 1 and 2; Moreno *et al.* 1998; Pausas and Vallejo 1999; Pausas 2004). Furthermore, another trend in fire regime changes is starting to be observed: the increase in crown fires in areas that were not traditionally subject to this type of fires, like some montane (sub-Mediterranean) areas (Fig. 3).

In the present paper, we review to what extent fires are generating ecological disasters in the MB, in view of its current fire regimes and its long human history (strongly human-modified landscapes). We only review ecosystems under Mediterranean-type climate, and we focus especially on the western part of the MB because it is the best documented area, although published examples from the east are also included. We define disaster as ecosystem degradation, such as irreversible soil losses or strong vegetation changes (e.g. losses of dominant or keystone species). Nutrient losses are not considered here as they usually have no direct short-term drastic effects on ecosystem degradation. Fauna changes due to fire are also omitted as they may require a very different approach. Nomenclature of plant species follows Tutin *et al.* (1964–1980) except for *Quercus ilex* L. ssp. *ballota* (Desf.) Samp. (= *Q. rotundifolia*) and *Q. calliprinos* Webb (often included in *Q. coccifera*).

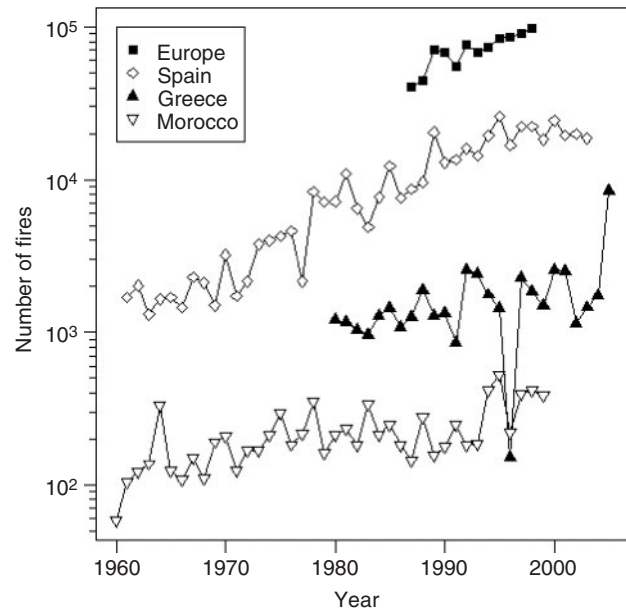


Fig. 2. Evolution of the number of fires (in log scale) during the last decades in different Mediterranean regions (Spain, eastern Spain, Morocco, Greece) and in Europe. Modified from Pausas (2004).

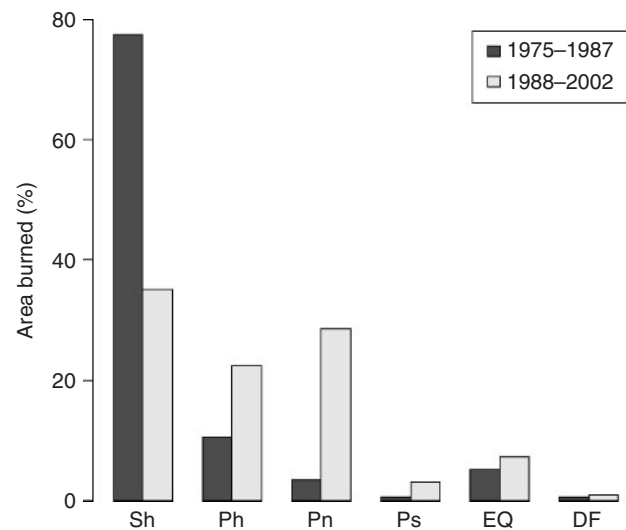


Fig. 3. Proportion of the area burned in Catalonia (NE Spain) during the period 1975–87 (dark bars) and during the period 1988–2002 (light bars) in the different vegetation types (Sh, shrublands; Ph, *Pinus halepensis* woodlands; Pn, *Pinus nigra* woodlands; Ps, *Pinus sylvestris* woodlands; EQ, evergreen *Quercus* forests; DF, deciduous forests). Data obtained by crossing the Catalonian fire history map (1975–2002; updated from Salvador *et al.* 2000) with two forest maps (one elaborated during the 70s and the other during the late 80s and early 90s; DMAH 2006).

Vegetation changes

Shrublands dominated by resprouting species

Broad-leaved evergreen shrublands dominated by resprouting species are very common in the MB. One of the most typical is the garrigue, a community dominated by the shrubby *Quercus*

coccifera (kermes oak). Traub (1991) reiteratively burned *Q. coccifera* shrublands in southern France at different frequencies (every 6, 3 and 2 years) and in different seasons for 19 years, although the burns were conducted at the beginning and end of the fire season, not during the peak fire season. In every case, *Q. coccifera* resprouted vigorously, with no clear symptom of degradation. Furthermore, Konstantinidis *et al.* (2005) did not find any differences in the resprouting of this species when comparing spring and summer burns in Greece. Delitti *et al.* (2005), in drier, more southerly regions than Traub's study, found that despite the high resprouting capacity of *Q. coccifera*, there was evidence of decreasing productivity under their highest fire frequency (three wildfires in a 16-year period); thus, depletion and reduction of the recovery capacity could be possible. However, the most recurrently burned areas with the shortest intervals presented the highest species richness. Furthermore, in these communities, soil characteristics did not show any clear trend towards fertility loss with fire frequency (Ferran *et al.* 2005), although some authors found a decrease in foliar nutrient content and concentration in *Q. coccifera* subjected to higher fire recurrence (A. Valdecantos, pers. comm.).

The main evidence of resource depletion in resprouting species is found under experimental conditions. Different researchers have tested the changes in resprouting capacity after experimental recurrent clipping. For instance, Canadell and López-Soria (1998) clipped *Arbutus unedo* and *Erica scoparia* and found evidence of nutrient and starch depletion after eight clippings over 26 months. Paula and Ojeda (2006) found evidence of reduced resprouting in three Mediterranean *Erica* species (*E. arborea*, *E. scoparia*, *E. australis*) after six recurrent clipping events (every 6 months). All these cases show the negative effect of a high disturbance frequency. These studies provide indications of the different resprouting capacities and may help to predict changes in community structure under management (e.g. in fuel breaks and prescribed fires). However, these elevated frequencies are probably unrealistic in the context of natural fire regimes, as there is not enough time between disturbances for fuels to build up. Experiments on *E. australis* suggest that although resprouting decreases after a severe experimental reduction of lignotuber carbohydrates, reserve limitation might not be critical under normal conditions (Cruz *et al.* 2003).

There are also some examples of an increase in the occurrence of some resprouting species with fire frequency. This is the case, for instance, of the tussock grass *Ampelodesmos mauritanica*, a strong resprouter that accumulates large amounts of fine and dead fuel. The seed burst that this species produces after fire permits an increase in population size (Vilà *et al.* 2001; Lloret *et al.* 2003). Similar processes are observed in other perennial grasses (Caturla *et al.* 2000).

However, the resprouting capacity of many species (mainly subshrubs or scrubs, i.e. *Chamaephytes*) has not been studied in detail, and many species considered weak resprouters may be highly sensitive to fire interval or fire severity. For instance, an ongoing database on fire traits for the MB (Pausas and Paula 2005) suggests that the resprouting capacity is unclear or ambiguous between different reference sources in ~35% of the scrub species and in ~20% of the shrubs. These figures include only the species for which some information is available; for many species, there is no information at all. Furthermore, there

are some species that seem to lose their resprouting capacity with age, such as *Cytisus striatus* (Moreno 1998) or *Calluna vulgaris* (Gingham 1972). In addition, some other species increase their resprouting capacity with size, such as *Erica arborea* and *Phyllirea angustifolia* (Moreno *et al.* 2004). There are also some regional differences in resprouting ability; for instance, in the Iberian peninsula, *Juniperus oxycedrus* is a very good resprouter in the east coast populations (López Soria and Castell 1992; Quevedo *et al.* 2007), but fails to resprout after fire in the central populations (J. M. Moreno, pers. comm.). Thus, although there is no evidence of a general reduction in the resprouting species due to fire, more work is needed to encompass the whole diversity of resprouting species. The simple dichotomy of resprouters v. non-resprouters has been a very useful concept in fire studies (Pausas *et al.* 2004a), but it may hide some nuances for understanding the details of fire ecology processes.

Shrublands dominated by non-resprouting species

Fire-prone communities may be dominated by shrubs that do not resprout after fire. In these cases, most populations survive a fire by having a seed bank that persists after fire (e.g. hard-coated seeds), thus allowing post-fire recruitment (Arianoutsou and Thanos 1996; Ferrandis *et al.* 1999; Baeza and Vallejo 2006). Consequently, most non-resprouters growing in fire-prone ecosystems are seeder species (also called post-fire recruiters). In fact, the germination of many of these species is stimulated by the heat of the fire (e.g. breaking seed dormancy) (see a review by Paula and Pausas 2008) or, in some cases, by other fire products such as smoke or charred wood (Pérez-Fernández and Rodríguez-Echeverría 2003; Crosti *et al.* 2006), and thus the population size is often increased in post-fire conditions. These species are also highly flammable and more drought-resistant than resprouting species (Paula and Pausas 2006; Saura-Mas and Lloret 2007); not only do they appear after fire, but they also colonise old fields and highly degraded ecosystems.

In general, these communities regenerate well after fire (e.g. Tárrega *et al.* 1998), although changes in species dominance have been reported (Moreno 1998; de Luís *et al.* 2006). Because their regeneration relies on the seed bank and the recruitment of new individuals, these communities are more sensitive to post-fire weather conditions (Quintana *et al.* 2004), and community age (which determines the size of the seed bank of each species).

In these communities, and because non-resprouting plants die after fire, root system recovery is much slower than in the case of resprouter communities (where root systems are almost unaffected by fire). This implies that the chances of soil (and seed) loss are higher than in communities dominated by resprouters. This fact may be important because the peak of torrential rainfalls in many MB areas occurs in autumn, just after the fire season. Extreme precipitation events do not affect seed loss and seedling emergence in non-resprouting *Ulex parviflorus* (Mediterranean gorse) shrublands; however, they often reduce seedling survival by causing seedlings to be either buried by sediments or unearthed (de Luís *et al.* 2005). Furthermore, extreme rainfall events may also reduce the grass cover, which is important for post-fire soil protection (de Luís *et al.* 2004). Thus, the combination of fire and torrential rainfall events may contribute to reducing regeneration and increasing degradation processes

in these shrublands, even if the dominant species possess traits enhancing regeneration after fire.

Shrub species that neither resprout nor recruit after fire are rare in the fire-prone ecosystems of the MB. Because of their sensitivity to fire and their slow post-fire colonisation capacity, these species are usually restricted to areas where fires are uncommon, like rocky outcrops or dunes, or they appear at high altitudes (colder or wetter conditions with lower fire frequency). This is the case of *Juniperus phoenicea*, a species with no resprouting capacity, which typically inhabits the rocky outcrops and cliffs of coastal mountains but may also be abundant in shrublands and forests that have not been burnt for a long time.

Broadleaved evergreen sclerophyllous woodlands

Mediterranean evergreen oaks resprout vigorously following severe disturbances (Pausas 1997; Debussche et al. 2001; Espelta et al. 2003). The most abundant are *Quercus ilex* (Holm oak) and *Q. suber* (cork oak) in the west of the basin, and *Q. ilex* and *Q. calliprinos* in the east of the basin. Because of the strong resprouting capacity of these species, recurrent coppicing has been used since ancient times (and continues on a diminished scale to the present) as an oak woodland management method for firewood harvesting and charcoal production. The result is the replacement of single-stemmed trees by trees with multiple trunks emerging from the base; many current oak woodlands still show these characteristic trunk clusters from recent or old coppicing. Nevertheless, this recurrent coppicing has not strongly affected the persistence of oak populations. However, we should note that it is not rare to find some old *Quercus ilex* ssp. *balota* trees that do not resprout after fire, probably due to aging (J. M. Moreno, pers. comm.).

As mentioned above, another important evergreen oak occurring in the west of the basin is *Quercus suber* (cork oak; Aronson et al., in press), which has a very thick and insulating bark (the cork) that protects almost all the stem (epicormic) buds of the tree, enabling them to resprout quickly and effectively after fire (Pausas 1997). Furthermore, this species has a lignotuber (Molinas and Verdaguer 1993) that permits basal resprouting when fire kills the main stem (i.e. in the case of thin trees or individuals with a recently harvested bark). The current decline in cork oak (Tuset and Sánchez 2004) is not so much related to fire as it is to land management systems, pests and diseases, and perhaps climate change. For instance, the aging of some populations is due to the fact that the high grazing pressure by livestock is preventing seedling regeneration (Pulido and Díaz 2005). Bark harvesting also increases the susceptibility of the tree to fire by increasing the time that the trees have a thin bark (Pausas 1997).

In general, there is no evidence that fire decreases or eliminates oak tree populations. In fact, fire may provide an advantage to oaks v. pines in mixed forests, and it may also open regeneration windows for oak establishment and colonisation of new environments (e.g. pine woodlands; Pons and Pausas 2006).

Pine woodlands

None of the pines in the MB are able to resprout. For the most common lowland Mediterranean pines (*Pinus halepensis*, *P. brutia* and *P. pinaster*), post-fire regeneration relies on the canopy seed bank protected in the serotinous cones (Daskalidou and Thanos 1996; Habrouk et al. 1999; Thanos and Doussi

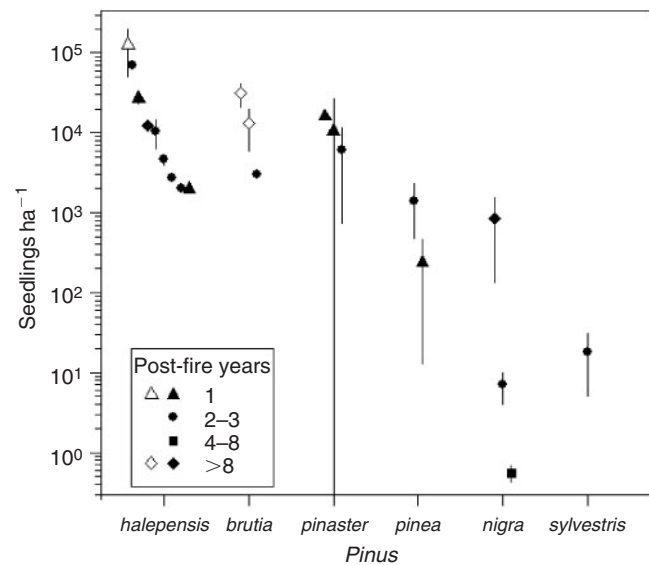


Fig. 4. Seedling density (seedling ha⁻¹; log scale) after crown fire for different *Pinus* species and different post-fire ages, in different localities of the Mediterranean basin. Symbols indicate the mean values, solid vertical lines are standard deviation, s.d. (in solid symbols), or range values (in open symbols). Sources: *P. halepensis* from Moravec (1990), Ne'eman et al. (1992), Daskalidou and Thanos (1997), Papió (1994 in Trabaud 2000), Arianoutsou and Ne'eman (2000), Pausas et al. (2003, 2004b), Rodrigo et al. (2004); *P. brutia* from Spanos et al. (2000), Thanos and Marcou (1991 in Thanos and Doussi 2000), Tsitsoni et al. (2004); *P. pinaster* from Martínez et al. (2002), Rodrigo et al. (2004), Madrigal et al. (2005); *P. nigra* from Trabaud and Campant (1991), Rodrigo et al. (2004); *P. sylvestris* and *P. pinea* from Rodrigo et al. (2004, 2007).

2000; Tapias et al. 2001), although the degree of serotiny is highly variable among individuals and populations. For instance, the percentage of serotinous cones ranges from 40 to 80% in *Pinus halepensis* and from 2 to 82% in *Pinus pinaster* among the different Iberian populations (Tapias et al. 2001), and from 6 to 94% in Near East *Pinus halepensis* stands (Goubitz et al. 2004). The degree of serotiny is related to forest structure and fire history (Goubitz et al. 2004), but the role of pine nut consumers in shaping serotiny remains to be explored in detail (Mezquida and Benkman 2004). This high variability in serotiny may explain the variability in post-fire regeneration found in some serotinous species (Fig. 4).

Pinus halepensis is the most abundant pine in the MB, covering more than 2.5 million ha. It has many characteristics that permit good regeneration after fire (Ne'eman et al. 2004). Thus, post-fire regeneration of this species is often very high (Fig. 4; Herranz et al. 1997; Arianoutsou and Ne'eman 2000; Retana et al. 2002), although it can vary widely (Pausas et al. 2004b). This high variability in post-fire regeneration has been attributed to the different fire characteristics, such as fire severity and fire size (Tsitsoni 1997; Pausas et al. 2003; Broncano and Retana 2004; Eugenio and Lloret 2004), to the different environmental and post-fire weather conditions (Daskalidou and Thanos 2004), to land uses (Pausas et al. 2004b), to the variable post-dispersal seed predation (Saracino 1997; Nathan et al. 2000; Nathan and Ne'eman 2004) and to the different degrees of serotiny in the pre-fire population (Goubitz et al. 2004).

Despite the high post-fire resilience of *Pinus halepensis*, *P. brutia* and *P. pinaster*, regeneration of these pines may fail (Kazanis and Arianotsou 2004; Eugenio *et al.* 2006) when time intervals between fires are shorter than the time required to accumulate a sufficient seed bank ('immaturity risk', as in Zedler 1995). It is considered that the time interval required to recover the canopy seed bank could be between 10 and 20 years for *P. halepensis* (Daskalakou and Thanos 1996; Verkaik and Espelta 2006). Thus, the current increase in fire recurrence (i.e. reduction in fire-free intervals) in the MB is reducing the capacity of these pines to regenerate after fire. In fact, the average age of most Spanish pine populations when they burn is below 25 years (Moreno *et al.* 1998).

Another pine occurring in coastal areas is *Pinus pinea* (stone pine). The natural distribution of this species is unknown; it has been strongly positively selected since ancient times because of its edible nuts. This species does not present serotinous cones; however, some post-fire regeneration can be observed (Fig. 4) due to the annual seed crop protected in the thick cones and the high temperature resistance of the seeds conferred by the thick seed coat (Escudero *et al.* 1999). This species has a thick bark, it has no branches in the lower portion of the tree (self-pruning), and it can survive fires that scorch more than 80% of the crown volume (Rigolot 2004; Rodrigo *et al.* 2004); thus, some individuals may persist after fire. Nevertheless, a general decline seems to be observed as a consequence of the increased fire regime in some areas. The difficulty of seedlings to establish after fire, together with the short seed dispersal distance (<20 m) and the low seedling survival in post-fire conditions would explain the low natural regeneration of *P. pinea* in burned areas (Rodrigo *et al.* 2007).

The montane pines *Pinus nigra* and *P. sylvestris* show almost nil regeneration after crown fire (Fig. 4). Neither of these pine species produces serotinous cones (Lanner 1998; Tapias *et al.* 2001), and their seeds are not able to resist the high temperatures attained during intense summer wildfires (Habrouk *et al.* 1999). Moreover, the short dispersal distance of these species, <100 m (Ordoñez *et al.* 2006), does not allow effective colonisation from unburned edges. However, *P. nigra* is a long-lived tree with a thick bark, and it can grow tall with few branches in the lower part, thus surviving surface fires. Indeed, fire scars on living old trees are frequent (Fulé *et al.* 2008), suggesting that they naturally support surface fires. Nevertheless, dense plantations and long-term fire suppression have changed the fire regime in many of these woodlands towards more frequent crown fires, making this species disappear locally after large and intense fires (Trabaud and Campant 1991; Rodrigo *et al.* 2004).

Other montane coniferous trees, such as *Juniperus communis*, *J. thurifera*, *Abies pinsapo*, and *Cedrus sp. pl.*, neither resprout nor have serotinous cones; thus, they are also sensitive to crown fire, although very little data are available on them. Currently, surface fires are rare in the MB; to what extent some of these coniferous ecosystems may have suffered frequent surface fires in the past (as in the case of *Pinus nigra*, or the North American *Pinus ponderosa*; Veblen *et al.* 2000) is unknown.

Soil losses

Soil losses are probably the best indicator of post-fire disaster, as soil recovery is notably slow. There are many cases in which fire

can lead to considerable changes in hydrological and erosion dynamics, both by changing physical, chemical and microbial soil processes, and by reducing or eliminating aboveground biomass (Neary *et al.* 1999; Shakesby and Doerr 2006). Fire promotes changes in soil organic matter, structure, hydrophobicity, infiltration capacity and other characteristics related to soil erodibility (Giovannini and Lucchesi 1997; De Bano 2000; González-Pérez *et al.* 2004; Certini 2005). Reductions in plant cover decrease interception, soil surface infiltrability and surface obstacles, facilitating erosive overland flow.

The post-fire soil losses observed in the MB are quite variable depending on vegetation and soil type, post-fire weather conditions and fire severity (Table 1, Fig. 5). For instance, the soil losses detected during the first 8 months after a fire in Eastern Spain ranged between 0.07 and 4.34 Mg ha⁻¹ in different conditions of soil type, vegetation and topography (Rubio *et al.* 1997).

Fire intensity and severity are important factors determining erosion rates (Fig. 5). After low-severity fires (i.e. low severity for trees), erosion is usually low owing to the mulching effect generated both by the charcoal and by the dead leaves falling from the partially burnt trees. In such cases, infiltration capacity can even be enhanced and soil erosion reduced, compared with unburned areas (Kutiel and Inbar 1993). As the fire severity increases, the correlation between rainfall and erosion becomes stronger (Úbeda and Sala 1996, 1998). Gimeno-García *et al.* (2000), using experimental fires in dry Mediterranean shrublands, showed that 1-year erosion rates are low (<0.1 Mg ha⁻¹ year⁻¹) in unburned conditions, become significant after a fire, and show a tendency to increase with fire severity (2.3 and 2.9 Mg ha⁻¹ year⁻¹ in moderate- and high-severity fires).

Vegetation type (and land use) is also an important factor determining soil losses. Pardini *et al.* (2004) found that post-fire erosion was five-fold in *Quercus suber* (cork oak) forest, 13-fold in 30-year-old abandoned agricultural terraces and eight-fold in 15-year-old abandoned terraces, compared with the corresponding paired unburnt plot (<0.003 Mg ha⁻¹). Although there is also evidence suggesting that post-fire soil erodibility is relatively independent of vegetation type (Giovannini *et al.* 2001), different post-fire recovery rates in different vegetation types may determine soil losses (Pausas *et al.* 1999). For instance, Marqués and Mora (1992) showed six times higher erosion rates on south-facing slopes (i.e. equator- v. pole-facing slopes) in *Pinus halepensis* woodlands (21.8 and 3.5 Mg ha⁻¹ at 16 months after fire, respectively). The high values found on south-facing slopes were due to the low plant recovery rate and rill formation; the high plant recovery rate on north slopes prevented any post-fire rill formation.

Similarly, post-fire soil losses in Eastern Spain under different land-uses but under the same climatic and soil type conditions showed contrasting results (Fig. 6, Llovet 2005). The fact that recently abandoned fields (<15 years) become covered by a continuous herbaceous layer (total plant cover = 70%) in the first year after fire determined lower soil losses than in long-abandoned fields (>35 years) with pine woodlands, where the post-fire plant response was poor (40 and 50% plant cover the first and the third year after fire, respectively). In this burned pine forest, the poor plant recovery in the ground layer led to an erosion peak 3 years after the fire, when heavy rainstorms

Table 1. Some examples of post-fire erosion rates at plot and slope scale from studies carried out in the Mediterranean basin

Fire severity (Unburned, Low, Moderate and High) was classified on the basis of the original sources. Period refers to the time since the fire (monitoring period). For describing the vegetation, the following abbreviations are used: *P* = *Pinus*, *Q* = *Quercus*, *E* = *Eucalyptus*; Pine refers to an unspecified *Pinus* species. Sources: (1) Marquès and Mora 1992; (2) Giovannini and Lucchesi 1993; (3) Kutiel and Inbar 1993; (4) Sánchez *et al.* 1994; (5) Soler *et al.* 1994; (6) Shakesby *et al.* 1996; (7) Úbeda and Sala 1996; (8) Rubio *et al.* 1997; (9) Inbar *et al.* 1998; (10) Pinaya *et al.* 1998; (11) Soto and Díaz-Fierros 1998; (12) Bautista 1999; (13) Bautista *et al.* 1996; (14) Gimeno-García *et al.* 2000; (15) Vacca *et al.* 2000; (16) Pardini *et al.* 2004; (17) Llovet 2005

Vegetation	Fire severity	Period	Erosion rate (Mg ha ⁻¹)	Notes and sources
<i>P. halepensis</i> and shrubs	High	16 months	3.52	North aspect (1)
	High	16 months	21.76	South aspect (1)
Maquis	Unburned	1 year	0.03	(2)
	Low	1 year	0.14	(2)
	High	1 year	1.47	(2)
<i>P. pinaster</i> and <i>P. brutia</i>	Unburned	4th–6th month	0.0008	(3)
	Low	4th–6th month	0.0005	(3)
<i>Stipa</i> and shrubland	Unburned	3 years	11.03	(4)
	Low	1 year	0.007	(4)
<i>Q. ilex</i> forest	Unburned	18 months	0.026	(5)
	Moderate	18 months	0.43	(5)
<i>E. globulus</i> , <i>P. pinaster</i>	Moderate	First year	0.5–2.2	(6)
	Moderate	Second year	0.9–6.6	(6)
<i>P. pinaster</i> , <i>Q. suber</i>	Unburned	18 months	0.12	Dense vegetation (7)
	Unburned	18 months	1.57	Disperse vegetation (7)
<i>P. pinaster</i> , <i>Q. suber</i>	Low	8.5 months	0.14	(7)
	Moderate	8.5 months	6.35	(7)
	High	8.5 months	30.56	(7)
Pine and <i>Q. coccifera</i>	Low	8 months	0.07	Limestone and dolomites (8)
<i>Q. suber</i> and pine	High	8 months	4.34	Sandstone (8)
<i>P. halepensis</i> and maquis	Unburned	1 year	<0.0003	(9)
	Low	1 year	0.03	(9)
	High	1 year	0.18–8.75	(9)
<i>Ulex europaeus</i>	High	20 months	<0.2	With seeding treatment (10)
	High	20 months	1.35	Without seeding treatment (10)
<i>Ulex europaeus</i>	Unburned	4 years	2.2	(11)
	Low	4 years	4.9–5.9	(11)
	High	3 years	14.7	(11)
<i>P. halepensis</i>	High	First year	0.2	(12)
	High	Fifth year	7.2	(12)
<i>P. halepensis</i>	High	18 months	0.09–0.18	With mulching treatment (13)
	High	18 months	0.18–2.92	Without mulching treatment (13)
Shrubland	Unburned	17 months	0.08	(14)
	Low	17 months	3.3	(14)
	High	17 months	4.1	(14)
Maquis	High	6 years	0.3–0.6	(15)
<i>Q. suber</i> forest	Unburned	6 months	0.0015	(16)
	Moderate	6 months	0.009	(16)
Shrubland	Unburned	6 months	0.001	(16)
	Moderate	6 months	0.016	(16)
Vineyard	Unburned	6 months	0.019	(16)
	Moderate	6 months	0.021	(16)
Dry grassland	Unburned	5 years	0.0016	(17)
Dry grassland	Low	First year	0.002	(17)
	Low	Third year	0.01	(17)
	Unburned	5 years	0.0003	(17)
<i>P. halepensis</i>	High	First year	0.17	(17)
<i>P. halepensis</i>	High	Third year	1.52	(17)

took place (Fig. 6). These temporal dynamics were also depicted at the catchment scale in the same study area (Mayor *et al.* 2007).

In conclusion, post-fire erosion rates measured in the MB are rarely higher than 10 Mg ha⁻¹ year⁻¹ and often lower than

1 Mg ha⁻¹ year⁻¹ (Table 1, Fig. 5). Although these values are low in absolute terms, they are relatively high with respect to the low available soil depth and the slow soil formation rate in the MB. Moreover, topsoil is both the most fertile and the most affected by erosion and degradation processes. In fact, soil

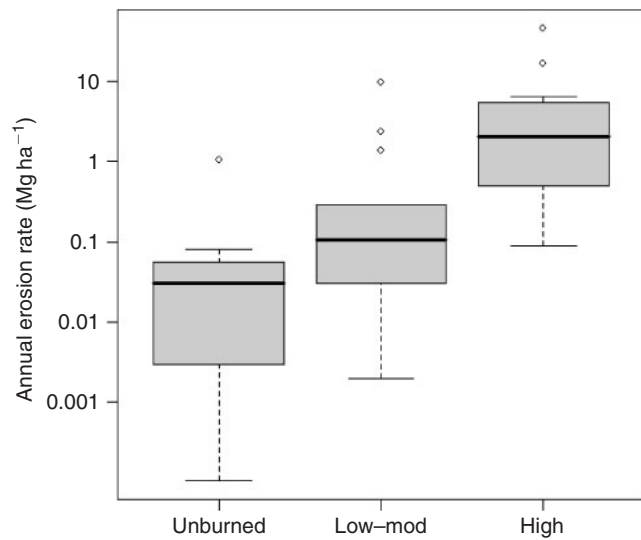


Fig. 5. Box plot statistics of annual erosion rates (Mg ha^{-1}) from different studies in the Mediterranean basin aggregated by fire severity (unburned, low-to-moderate fires, and high-severity fires). Annual erosion rates are computed from studies in Table 1 that monitored erosion for a period shorter or equal to 2 years after fire.

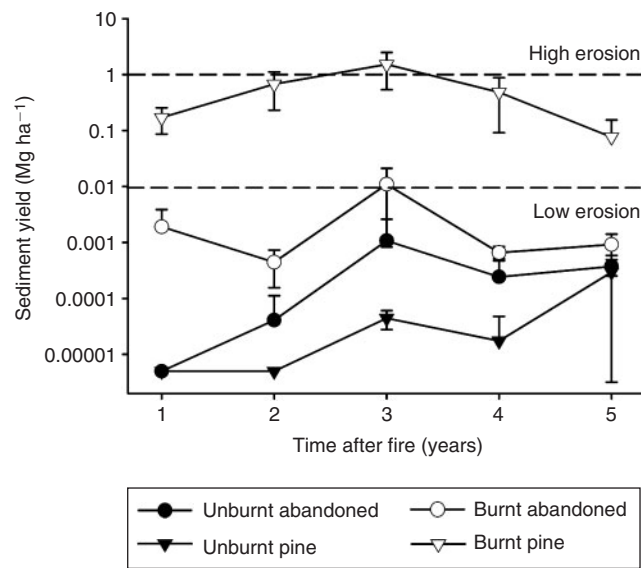


Fig. 6. Sediment yield (in Mg ha^{-1} , log scale) during a 5-year period on erosion plots located in burnt (open symbols) and unburnt (black symbols) old fields of Alicante (SE Spain; Llovet 2005). The two situations studied are recently abandoned (<15 years) old fields that are now grasslands, and long-abandoned old fields (>35 years) that are now pine woodlands.

losses higher than $1 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ($100 \text{ g m}^{-2} \text{ year}^{-1}$) have been considered unsustainable for the MB (Cerdà 2001).

Discussion and concluding remarks

Our review is obviously biased towards the more extensively studied regions of the MB, i.e. the western part of the European MB. There is a lack of information for many species and countries of the MB, and this is especially noticeable for the African

and Asian part of the Basin. Even with this bias, our review allows us to draw some conclusions that are relevant for the whole MB.

Most coastal shrublands and most oak forests are able to cope well with current and past fire regimes, and there is no evidence of strong changes in species composition and dominance. These ecosystems have suffered repeated fires for many centuries and have shown a very high resilience to them. They are certainly more susceptible to human disturbances (clearing, logging, overgrazing, urbanising) than to fire. However, there is evidence that in some Mediterranean communities, current fire regime changes are producing negative effects. Unfortunately, it is not easy to trace past fire regimes in crown fire ecosystems, and it is even more difficult in systems with long-term and intense human pressure; thus the magnitude of fire regime changes in the MB cannot be assessed in detail. In other words, it is very difficult, or impossible, to identify the fire regimes in the MB before human domination, and we only know of changes in the last few decades (Pausas 2004).

The most fire-sensitive ecosystems are the pine woodlands, especially given the crown fire regimes observed in the last few decades: that is, reduced fire intervals and crown fires occurring in montane zones that were not traditionally subject to this type of fire (Figs 1, 2 and 3). Although serotinous pines have a relatively early first reproduction (<10 years; Daskalidou and Thanos 2004; Ne’eman *et al.* 2004), some of the areas they occupied a few decades ago have been repetitively burnt with fire intervals shorter than the time these pines need to produce a large enough seed bank to replace their population (~15–20 years). Thus, many of the early pine woodlands are being taken over by shrublands (Baeza *et al.* 2007). Furthermore, in recent years, crown fires are affecting montane (sub-Mediterranean) areas where they were uncommon in the past. These ecosystems are often occupied by species lacking post-fire regeneration mechanisms (e.g. *Pinus nigra*, *Pinus sylvestris*; Fig. 3). Some of these woodlands have survived a long history of surface fires (Fulé *et al.* 2008) but current crown fires are eliminating them from extensive areas (Rodrigo *et al.* 2004). The increase of large crown fires in these sub-Mediterranean areas is not only affecting the vegetation but also other biodiversity components (Arnan *et al.* 2006; Rodrigo and Retana 2006).

Pines grow naturally in many places in the MB. However, most current MB pine woodlands are monospecific stands of anthropogenic origin, that is, they have been favoured or even planted by humans (Fig. 7). For many years, the traditional forest policy in the MB, usually based on European models, has been to plant monospecific pine woodlands (Pausas *et al.* 2004c). Some of these pine woodlands are very flammable as they consist of dense stands of pine species with branches all along the main stem (e.g. *Pinus halepensis*, *P. brutia*), and subject to few silvicultural treatments, thus facilitating large and intense crown fires. A more diverse set of species should be included in plantation and restoration plans to improve landscape resilience to current fire regimes (Pausas *et al.* 2004c; Vallejo *et al.* 2006).

Erosion studies demonstrate that relevant post-fire soil losses are observed in several ecosystems. However, these studies are biased towards erosion-prone areas as most erosion specialists work in erodible areas, and few studies have been undertaken in ecosystems with low human pressure. That is, most post-fire erosion studies are performed in strongly degraded ecosystems, and

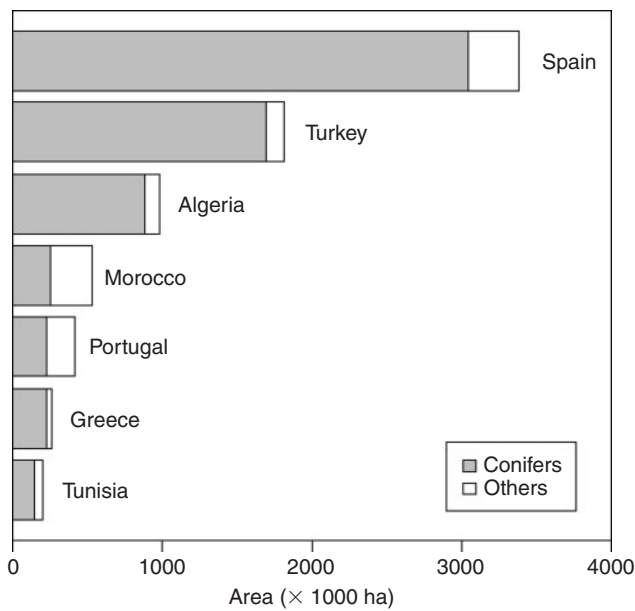


Fig. 7. Area reforested with conifer (grey) and with non-conifer (white) species in different Mediterranean countries. Data correspond to different periods: Spain (1940–84), Turkey (1920–97), Portugal (1965–95), Greece (1941–2000); periods for Tunisia, Algeria and Morocco are uncertain but they approximately refer to recent decades (before 2000). In all cases, most coniferous species are native pines, whereas others include native (e.g. *Quercus* species) and non-native (e.g. *Eucalyptus*, *Acacia*) species. Elaborated from Ortuño (1990), Lahouati (2000), FAO (2001), Directorate of Reforestation and Mountain Hydrology (Greece), S. Aslan (pers. comm., Hacettepe Üniversitesi, Ankara Turkey), M. Madeira (pers. comm., Instituto Superior de Agronomia, Lisbon, Portugal).

this degradation is not related to fire alone, but also to the long human disturbance in the area. For instance, many erosion studies are performed in old fields that were terraced in the past, then abandoned, and then planted or colonised with pines (Fig. 6). Some pine plantations were previously bulldozed for soil preparation. Furthermore, important soil losses are observed only with high-severity fires (Fig. 5); this could be due, in many cases, to the high density of unmanaged flammable pine woodlands or plantations.

Thus, although our MB biodiversity may be strongly resilient to fire, some parts of our current landscapes, which are products of a long human history with questionable land policies, are relatively sensitive to fires. In such conditions, disasters are possible.

Acknowledgements

The present work has been partially financed by the European Union project EUFireLab (EVR1-2001-00054) and the Spanish project PERSIST (CGL2006-07126/BOS). We thank A. Valdecantos and the referees for comments on the manuscript. CEAM is funded by Generalitat Valenciana, Bancaixa and the Spanish Government (GRACCIE project, Consolider-Ingenio 2010).

References

Arianoutsou M, Thanos CA (1996) Legumes in the fire-prone Mediterranean regions: an example from Greece. *International Journal of Wildland Fire* **6**, 77–82. doi:10.1071/WF9960077

- Arianoutsou M, Ne'eman G (2000) Postfire regeneration of natural *Pinus halepensis* forests in the east Mediterranean Basin. In 'Ecology, Biogeography and Management of *Pinus halepensis* and *P. brutia* Forest Ecosystems in the Mediterranean Basin'. (Eds G Neeman, L Trabaud) pp. 269–290. (Backhuys Publishers: Leiden, the Netherlands)
- Arnan X, Rodrigo A, Retana J (2006) Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. *Journal of Biogeography* **33**, 1246–1258. doi:10.1111/J.1365-2699.2006.01506.X
- Arnan X, Rodrigo A, Retana J (2007) Vegetation type and dryness drive the post-fire regeneration of Mediterranean plant communities at a regional scale. *Journal of Vegetation Science* **18**, 111–122. doi:10.1658/1100-9233(2007)18[111:PROMPC]2.0.CO;2
- Aronson J, Pereira JS, Pausas JG (Eds) 'Cork Oak Woodlands on the Edge. Conservation, Adaptive Management, and Restoration.' (Island Press: Washington, DC), in press.
- Baeza MJ, Vallejo VR (2006) Ecological mechanisms involved in dormancy breakage in *Ulex parviflorus* seeds. *Plant Ecology* **183**, 191–205. doi:10.1007/S11258-005-9016-0
- Baeza J, Valdecantos A, Alloza JA, Vallejo R (2007) Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. *Journal of Vegetation Science* **18**, 243–252. doi:10.1658/1100-9233(2007)18[243:HDAEFA]2.0.CO;2
- Bautista S (1999) Regeneración post-incendio de un pinar (*Pinus halepensis* Miller) en ambiente semiárido. Erosión del suelo y medidas de conservación a corto plazo. PhD thesis, University of Alacant.
- Bautista S, Bellot J, Vallejo VR (1996) Mulching treatment for post-fire soil conservation in a semi-arid ecosystem. *Arid Soil Research and Rehabilitation* **10**, 235–242.
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *The New Phytologist* **165**, 525–538. doi:10.1111/J.1469-8137.2004.01252.X
- Broncano MJ, Retana J (2004) Topography and forest composition affecting the variability in fire severity and post-fire regeneration occurring after a large fire in the Mediterranean basin. *International Journal of Wildland Fire* **13**, 209–216. doi:10.1071/WF03036
- Canadell J, López-Soria L (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology* **12**, 31–38. doi:10.1046/J.1365-2435.1998.00154.X
- Carrion JS, Sanchez-Gomez P, Mota JF, Yll R, Chain C (2003) Holocene vegetation dynamics, fire and grazing in the Sierra de Gador, southern Spain. *The Holocene* **13**, 839–849. doi:10.1191/0959683603HL662RP
- Caturla RN, Raventos J, Guàrdia R, Vallejo VR (2000) Early post-fire regeneration dynamics of *Brachypodium retusum* Pers. (Beauv.) in old fields of the Valencia region (eastern Spain). *Acta Oecologica* **21**, 1–12. doi:10.1016/S1146-609X(00)00114-4
- Cerdà A (2001) 'Erosión Hídrica del Suelo en Territorio Valenciano. El Estado de la Cuestión a través de la Revisión Bibliográfica.' (Geoforma Ediciones: Logroño, Spain)
- Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia* **143**, 1–10. doi:10.1007/S00442-004-1788-8
- Crosti R, Ladd PG, Dixon KW, Piotta B (2006) Post-fire germination: the effect of smoke on seeds of selected species from the central Mediterranean basin. *Forest Ecology and Management* **221**, 306–312.
- Cruz A, Pérez B, Moreno JM (2003) Resprouting of the Mediterranean-type shrub *Erica australis* with modified lignotuber carbohydrate content. *Journal of Ecology* **91**, 348–356. doi:10.1046/J.1365-2745.2003.00770.X
- Daskalaku EN, Thanos CA (1996) Aleppo pine (*Pinus halepensis*) post-fire regeneration: the role of canopy and soil seed banks. *International Journal of Wildland Fire* **6**, 59–66. doi:10.1071/WF9960059
- Daskalaku EN, Thanos CA (1997) Post-fire establishment and survival of Aleppo pine seedlings. In 'Forest Fire Risk and Management'. (Eds P Balabanis, G Eftichidis, R Fantechi) pp. 357–368. (European Commission: Brussels)

- Daskalidou EN, Thanos CA (2004) Post-fire regeneration of Aleppo pine – the temporal pattern of seedling recruitment. *Plant Ecology* **171**, 81–89. doi:10.1023/B:VEGE.0000029375.93419.F9
- de Luís M, Raventós J, Cortina J, González-Hidalgo JC, Sánchez JR (2004) Fire and torrential rainfall: effects on the perennial grass *Brachypodium retusum*. *Plant Ecology* **173**, 225–232. doi:10.1023/B:VEGE.0000029321.92655.A6
- de Luís M, Raventós J, González-Hidalgo JC (2005) Fire and torrential rainfall: effects on seedling establishment in Mediterranean gorse shrublands. *International Journal of Wildland Fire* **14**, 413–422. doi:10.1071/WF05037
- de Luís M, Raventós J, Gonzalez-Hidalgo JC (2006) Post-fire vegetation succession in Mediterranean gorse shrublands. *Acta Oecologica* **30**, 54–61. doi:10.1016/J.ACTAO.2006.01.005
- DeBano LF (2000) The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* **231–232**, 195–206. doi:10.1016/S0022-1694(00)00194-3
- Debussche M, Debussche G, Lepart J (2001) Changes in the vegetation of *Quercus pubescens* woodland after cessation of coppicing and grazing. *Journal of Vegetation Science* **12**, 81–92. doi:10.2307/3236676
- Delitti WBC, Ferran A, Vallejo R, Trabaud L (2005) Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia region (Spain): I. Plant composition and productivity. *Plant Ecology* **177**, 57–70. doi:10.1007/S11258-005-2140-Z
- DMAH (2006) Departament de medi ambient i habitatge. Generalitat de Catalunya. http://mediambient.gencat.net/cat/el_medi/natura/sistema_informacio/inici.jsp [Verified October 2006]
- Escudero A, Sanz MV, Pita JM, Pérez-García F (1999) Probability of germination after heat treatment of native Spanish pines. *Annals of Forest Science* **56**, 511–520. doi:10.1051/FOREST:19990608
- Espelta JM, Retana J, Habrouk A (2003) Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. *Forest Ecology and Management* **179**, 401–414. doi:10.1016/S0378-1127(02)00541-8
- Eugenio M, Lloret F (2004) Fire recurrence effects on the structure and composition of Mediterranean *Pinus halepensis* communities in Catalonia (north-east Iberian Peninsula). *Ecoscience* **11**, 446–454.
- Eugenio M, Verkaik I, Lloret F, Espelta JM (2006) Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). *Forest Ecology and Management* **231**, 47–54. doi:10.1016/J.FORECO.2006.05.007
- FAO (2001) Global forest resources assessment 2000. Food and Agriculture Organization of the United Nations forestry paper 140. (Rome)
- Ferran A, Delitti W, Vallejo VR (2005) Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia region (Spain): II. Plant and soil nutrients. *Plant Ecology* **177**, 71–83. doi:10.1007/S11258-005-2141-Y
- Ferrandis P, Herranz JM, Martínez-Sánchez JJ (1999) Effect of fire on hard-coated Cistaceae seed banks and its influence on techniques for quantifying seed banks. *Plant Ecology* **144**, 103–114. doi:10.1023/A:1009816309061
- Fulé PZ, Ribas M, Gutiérrez E, Vallejo R, Kaye MW (2008) Forest structure and fire history in an old *Pinus nigra* forest, eastern Spain. *Forest Ecology and Management* **255**, 1234–1242. doi:10.1016/J.FORECO.2007.10.046
- Gimeno-García E, Andreu V, Rubio JL (2000) Changes in organic matter, nitrogen, phosphorus and cations in soil as a result of fire and water erosion in a Mediterranean landscape. *European Journal of Soil Science* **51**, 201–210. doi:10.1046/J.1365-2389.2000.00310.X
- Gimingham C (1972) 'Ecology of Heathlands.' (Chapman & Hall: London)
- Giovannini G, Lucchesi S (1997) Modifications induced in soil physico-chemical parameters by experimental fires at different intensities. *Soil Science* **162**, 479–486. doi:10.1097/00010694-199707000-00003
- Giovannini G, Vallejo VR, Lucchesi S, Bautista S, Ciompi S, Llovet J (2001) Effects of land use and eventual fire on soil erodibility in dry Mediterranean conditions. *Forest Ecology and Management* **147**, 15–23. doi:10.1016/S0378-1127(00)00437-0
- González-Pérez JA, González-Vila FJ, Almedros G, Knicker H (2004) The effect of fire on soil organic matter – a review. *Environment International* **30**, 855–870. doi:10.1016/J.ENVINT.2004.02.003
- Goubitz S, Nathan R, Roitenberg R, Ne'eman G, Shmida A (2004) Canopy seed bank structure in relation to: fire, tree size and density. *Plant Ecology* **173**, 191–201. doi:10.1023/B:VEGE.0000029324.40801.74
- Habrouk A, Retana J, Espelta JM (1999) Role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology* **145**, 91–99. doi:10.1023/A:1009851614885
- Herranz JM, Martínez-Sánchez JJ, Marín A, Ferrandis P (1997) Post-fire regeneration of *Pinus halepensis* Miller in a semi-arid area in Albacete province (south-eastern Spain). *Ecoscience* **4**, 86–90.
- Inbar M, Tamir M, Wittenberg L (1998) Runoff and erosion processes after a forest fire in Mount Carmel, a Mediterranean area. *Geomorphology* **24**, 17–33. doi:10.1016/S0169-555X(97)00098-6
- Kazanis D, Arianotsou M (2004) Factors determining low Mediterranean ecosystems resilience to fire: the case of *Pinus halepensis* forests. In 'Proceedings of the 10th MEDECOS Conference', 25 April–1 May 2004, Rhodes, Greece. (Eds M Arianotsou, VP Papanatasis) (Millpress: Rotterdam, the Netherlands)
- Konstantinidis P, Tsiourlis G, Galatsidas S (2005) Effects of wildfire season on the resprouting of kermes oak (*Quercus coccifera* L.). *Forest Ecology and Management* **208**, 15–27. doi:10.1016/J.FORECO.2004.09.021
- Kutiél P, Inbar M (1993) Fire impacts on soil nutrients and soil erosion in a Mediterranean pine forest plantation. *Catena* **20**, 129–139. doi:10.1016/0341-8162(93)90033-L
- Lahouati R (2000) Expérience des Plantations en Climat Aride. Cas de la Ceinture Verte en Algérie. Direction Générale des forêts, Ministère de l'Agriculture. (Alger, Algeria)
- Lanner RM (1998) Seed dispersal in *Pinus*. In 'Ecology and Biogeography of *Pinus*'. (Ed. DM Richardson) (Cambridge University Press: Cambridge)
- Lloret F, Pausas JG, Vilà M (2003) Response of Mediterranean plant species to different fire regimes in Garraf Natural Park (Catalonia, Spain): field observations and modelling predictions. *Plant Ecology* **167**, 223–235. doi:10.1023/A:1023911031155
- Llovet J (2005) Degradación del suelo posterior al fuego en condiciones mediterráneas. Identificación de factores de riesgo. PhD thesis, University of Alacant.
- López Soria L, Castell C (1992) Comparative genet survival after fire in woody Mediterranean species. *Oecologia* **91**, 493–499. doi:10.1007/BF00650321
- Madrigal J, Guijarro M, Martínez E, Díez C, Hernando C (2005) Regeneración post-incendio de *Pinus pinaster* Ait. en la Sierra de Guadarama (Sistema Central, España): modelos descriptivos de los factores influyentes en la densidad inicial y la supervivencia. *Investigación Agraria. Sistemas y recursos forestales* **14**, 36–51.
- Marquès MA, Mora E (1992) The influence of aspect on runoff and soil loss in a Mediterranean burnt forest (Spain). *Catena* **19**, 333–344. doi:10.1016/0341-8162(92)90007-X
- Martínez E, Madrigal J, Hernando C, Guijarro M, Vega JA, Pérez-Gorostiaga P, Fonturbel MT, Cuiñas P, Alonso M, Beloso MC (2002) Effect of fire intensity on seed dispersal and early regeneration in a *Pinus pinaster* forest. In 'Forest Fire Research and Wildland Fire Safety: Proceedings of IV International Conference on Forest Fire Research 2002 Wildland Fire Safety Summit', 18–23 November 2002, Luso, Coimbra, Portugal. (Millpress: Rotterdam, the Netherlands)
- Mayor AG, Bautista S, Llovet J, Bellot J (2007) Post-fire hydrological and erosional responses of a Mediterranean landscape: seven years of catchment-scale dynamics. *Catena* **71**, 68–75. doi:10.1016/J.CATENA.2006.10.006
- Mezquida ET, Benkman CW (2004) The geographic selection mosaic for squirrels, crossbills and Aleppo pine. *Journal of Evolutionary Biology* **18**, 348–357. doi:10.1111/J.1420-9101.2004.00846.X

- Molinas ML, Verdaguer D (1993) Lignotuber ontogeny in the cork-oak (*Quercus suber*; Fagaceae). I. Late embryo. *American Journal of Botany* **80**, 172–181. doi:10.2307/2445037
- Moravec J (1990) Regeneration of NW African *Pinus halepensis* forests following fire. *Vegetatio* **87**, 29–36. doi:10.1007/BF00045652
- Moreira F, Rego FC, Ferreira PG (2001) Temporal (1958–1995) pattern of change in a cultural landscape of north-western Portugal: implications for fire occurrence. *Landscape Ecology* **16**, 557–567. doi:10.1023/A:1013130528470
- Moreno A (1998) Gravedad del fuego y patrones espaciales y temporales postincendio de las plantas de un escobonal de la Sierra de Gredos. PhD thesis, Universidad Complutense de Madrid.
- Moreno JM, Vázquez A, Vélez R (1998) Recent history of forest fires in Spain. In 'Large Fires'. (Ed. JM Moreno) pp. 159–185. (Backhuys Publishers: Leiden, the Netherlands)
- Moreno JM, Cruz A, Fernández F, Luna B, Pérez B, Quintana JR, Zuazua E (2004) Ecología del monte mediterráneo en relación con el fuego: el jaral-brezal de Quintos de Mora (Toledo). In 'Avances en el Estudio de la Gestión del Monte Mediterráneo'. (Eds VR Vallejo, JA Alloza) pp. 17–45. (Fundación CEAM: Valencia, Spain)
- Nathan R, Ne'eman G (2004) Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Miller). *Plant Ecology* **171**, 123–137. doi:10.1023/B:VEGE.0000029379.32705.0F
- Nathan R, Safriel UN, Noy-Meir I, Schiller G (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology* **81**, 2161–2169.
- Naveh Z (1975) The evolutionary significance of fire in the Mediterranean region. *Vegetatio* **29**, 199–208. doi:10.1007/BF02390011
- Ne'eman G, Lahav H, Izhaki I (1992) Spatial pattern of seedlings 1 year after fire in a Mediterranean pine forest. *Oecologia* **91**, 365–370. doi:10.1007/BF00317625
- Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire – a critical review. *Plant Ecology* **171**, 69–79. doi:10.1023/B:VEGE.0000029380.04821.99
- Neary DG, Klopatek CC, de Bano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* **122**, 51–71. doi:10.1016/S0378-1127(99)00032-8
- Ordoñez JL, Molowny-Horas R, Retana J (2006) A model of the recruitment of *Pinus nigra* from unburned edges after large wildfires. *Ecological Modelling* **197**(3–4), 405–417. doi:10.1016/J.ECOLMODEL.2006.03.027
- Ortuño F (1990) El Plan para la repoblación forestal de España del año 1939. Análisis y comentarios. *Ecología (Fuera de Serie)* **1**, 373–392.
- Papió C (1994) Ecología del foc i regeneració en garrigues i pinedes mediterrànies. Institut d'Estudis Catalans. (Barcelona, Spain)
- Pardini G, Gispert M, Dunjó G (2004) Relative influence of wildfire on soil properties and erosion processes in different Mediterranean environments in NE Spain. *The Science of the Total Environment* **328**, 237–246. doi:10.1016/J.SCITOTENV.2004.01.026
- Paula S, Ojeda F (2006) Resistance of three co-occurring resprouter Erica species to highly frequent disturbance. *Plant Ecology* **183**, 329–336. doi:10.1007/S11258-005-9043-X
- Paula S, Pausas JG (2006) Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* **20**, 941–947. doi:10.1111/J.1365-2435.2006.01185.X
- Paula S, Pausas JG (2008) Burning seeds: germinative response to heat treatments in relation to resprouting ability. *Journal of Ecology* **96**, 543–552. doi:10.1111/J.1365-2745.2008.01359.X
- Pausas JG (1997) Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science* **8**, 703–706. doi:10.2307/3237375
- Pausas JG (1999) Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecology* **140**, 27–39. doi:10.1023/A:1009752403216
- Pausas JG (2004) Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change* **63**, 337–350. doi:10.1023/B:CLIM.0000018508.94901.9C
- Pausas JG, Paula S (2005) Plant functional traits database for Euro-Mediterranean ecosystems. EUFireLab deliverable D-04–06. Available at www.eufirelab.org [Verified November 2008]
- Pausas JG, Vallejo VR (1999) The role of fire in European Mediterranean ecosystems. In 'Remote Sensing of Large Wildfires in the European Mediterranean Basin'. (Ed. E Chuvieco) pp. 3–16. (Springer: Berlin)
- Pausas JG, Verdú M (2005) Plant persistence traits in fire-prone ecosystems of the Mediterranean Basin: a phylogenetic approach. *Oikos* **109**, 196–202. doi:10.1111/J.0030-1299.2005.13596.X
- Pausas JG, Verdú M (2008) Fire reduces morphospace occupation in plant communities. *Ecology* **89**, 2181–2186. doi:10.1890/07-1737.1
- Pausas JG, Carbó E, Caturla RN, Gil JM, Vallejo VR (1999) Post-fire regeneration patterns in the Eastern Iberian Peninsula. *Acta Oecologica* **20**, 499–508. doi:10.1016/S1146-609X(00)86617-5
- Pausas JG, Ouadah N, Ferran A, Gimeno T, Vallejo R (2003) Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant Ecology* **169**, 205–213. doi:10.1023/A:1026019528443
- Pausas JG, Bradstock RA, Keith DA, Keeley JE, GCTE Fire Network (2004a) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**, 1085–1100. doi:10.1890/02-4094
- Pausas JG, Ribeiro E, Vallejo R (2004b) Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *Forest Ecology and Management* **203**, 251–259. doi:10.1016/J.FORECO.2004.07.061
- Pausas JG, Bladé C, Valdecantos A, Seva JP, Fuentes D, Alloza JA, Vilagros A, Bautista S, Cortina J, Vallejo R (2004c) Pines and oaks in the restoration of Mediterranean landscapes in Spain: new perspectives for an old practice – a review. *Plant Ecology* **171**, 209–220. doi:10.1023/B:VEGE.0000029381.63336.20
- Pérez-Fernández MA, Rodríguez-Echeverría S (2003) Effect of smoke, charred wood, and nitrogenous compounds on seed germination of ten species from woodland in central-western Spain. *Journal of Chemical Ecology* **29**, 237–251. doi:10.1023/A:1021997118146
- Pinaya I, Soto B, Arias M, Fierros FD (1998) Erosion due to runoff from burnt hillslope plots left untreated or seeded with native species or a *Lolium multiflorum* mix. In 'III International Conference on Forest Fire Research', 16–20 November 1998, Luso, Portugal. (Ed. DX Viegas) pp. 1653–1662. (Associação para o Desenvolvimento da Aerodinâmica Industrial: Coimbra, Portugal)
- Piñol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change* **38**, 345–357. doi:10.1023/A:1005316632105
- Pons J, Pausas JG (2006) Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. *Forest Ecology and Management* **231**, 196–204. doi:10.1016/J.FORECO.2006.05.049
- Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. *Ecoscience* **12**, 92–102. doi:10.2980/11195-6860-12-1-92.1
- Quevedo L, Rodrigo A, Espelta JM (2007) Post-fire resprouting ability of 15 non-dominant shrub and tree species in Mediterranean areas of NE Spain. *Annals of Forest Science* **64**, 883–890. doi:10.1051/FOREST:2007070
- Quintana JR, Cruz A, Fernandez-Gonzalez F, Moreno JM (2004) Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. *Journal of Biogeography* **31**, 241–249. doi:10.1111/J.1365-2699.2004.00955.X
- Retana J, Espelta JM, Habrouk A, Ordoñez JL, Solà-Morales F (2002) Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in north-eastern Spain. *Ecoscience* **9**, 89–97.
- Rigolot E (2004) Predicting post-fire mortality of *Pinus halepensis* Mill. and *Pinus pinea* L. *Plant Ecology* **171**, 139–151. doi:10.1023/B:VEGE.0000029382.59284.71

- Rodrigo A, Retana J (2006) Post-fire recovery of ant communities in sub-Mediterranean *Pinus nigra* forests. *Ecography* **29**, 231–239. doi:10.1111/J.2006.0906-7590.04272.X
- Rodrigo A, Retana J, Picó X (2004) Direct regeneration is not the only response of Mediterranean forests to large fires. *Ecology* **85**, 716–729. doi:10.1890/02-0492
- Rodrigo A, Quintana V, Retana J (2007) Fire reduces *Pinus pinea* distribution in the north-eastern Iberian Peninsula. *Ecoscience* **14**, 23–30. doi:10.2980/1195-6860(2007)14[23:FRPPDI]2.0.CO;2
- Rubio JL, Forteza J, Andreu V, Cerni R (1997) Soil profile characteristics influencing runoff and soil erosion after forest fire: a case study (Valencia, Spain). *Soil Technology* **11**, 67–78. doi:10.1016/S0933-3630(96)00116-X
- Salvador R, Valeriano J, Pons X, Díaz-Delgado R (2000) A semi-automatic methodology to detect fire scars in shrubs and evergreen forests with Landsat MSS time series. *International Journal of Remote Sensing* **21**, 655–671. doi:10.1080/014311600210498
- Sánchez JR, Mangas VJ, Ortiz C, Bellot J (1994) Forest fire effect on soil chemical properties and runoff. In 'Soil Erosion and Degradation as a Consequence of Forest Fires'. (Eds M Sala, JL Rubio) pp. 53–65. (Geoforma Ediciones: Logroño, Spain)
- Saracino A (1997) Seed dispersal and changing seed characteristics in a *Pinus halepensis* forest after fire. *Plant Ecology* **130**, 13–19. doi:10.1023/A:1009765129920
- Saura-Mas S, Lloret F (2007) Leaf and shoot water content and leaf dry matter content of Mediterranean woody species with different post-fire regenerative strategies. *Annals of Botany* **99**, 545–554. doi:10.1093/AOB/MCL284
- Shakesby RA, Doerr SH (2006) Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews* **74**, 269–307. doi:10.1016/J.EARSCIREV.2005.10.006
- Shakesby RA, Boakes DJ, Coelho COA, Gonçalves AJB, Walsh RPD (1996) Limiting the soil degradational impacts of wildfire in pine and eucalyptus forests in Portugal. A comparison of alternative post-fire management practices. *Applied Geography* **16**, 337–355. doi:10.1016/0143-6228(96)00022-7
- Soler M, Sala M, Gallart F (1994) Post-fire evolution of runoff and erosion during an eighteen-month period. In 'Soil Erosion and Degradation as a Consequence of Forest Fires'. (Eds M Sala, JL Rubio) pp. 149–161. (Geoforma Ediciones: Logroño, Spain)
- Soto B, Díaz-Fierros F (1998) Runoff and soil erosion from areas of burnt scrub: comparison of experimental results with those predicted by the WEPP model. *Catena* **31**, 257–270. doi:10.1016/S0341-8162(97)00047-7
- Spanos IA, Daskalaku EN, Thanos CA (2000) Post-fire, natural regeneration of *Pinus brutia* forests in Thasos island, Greece. *Acta Oecologica* **21**, 13–20. doi:10.1016/S1146-609X(00)00107-7
- Tapias R, Gil L, Fuestes-Utrilla P, Pardos JA (2001) Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology* **89**, 629–638. doi:10.1046/J.1365-2745.2001.00575.X
- Tárrega R, Luis-Calabuig E, Valbuena L (1998) A comparative study of recovery in two *Cistus* communities subjected to experimental burning in León province (Spain). In 'Fire Management and Landscape Ecology'. (Ed. L Trabaud) pp. 147–154. (International Association of Wildland Fire: Washington, DC)
- Thanos CA, Marcou S (1991) Post-fire regeneration in *Pinus brutia* forest ecosystems of Samos island (Greece): 6 years after. *Acta Oecologica* **12**, 633–642.
- Thanos CA, Doussi MA (2000) Post-fire regeneration of *Pinus brutia* forests. In 'Ecology, Biogeography and Management of *Pinus halepensis* and *P. brutia* Forest Ecosystems in the Mediterranean Basin'. (Eds G Ne'eman, L Trabaud) pp. 291–301. (Backhuys Publishers: Leiden, the Netherlands)
- Trabaud L (1991) Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. *Journal of Vegetation Science* **2**, 307–314. doi:10.2307/3235921
- Trabaud L (2000) Post-fire regeneration of *Pinus halepensis* forest in the west Mediterranean. In 'Ecology, Biogeography and Management of *Pinus halepensis* and *P. brutia* Forest Ecosystems in the Mediterranean Basin'. (Eds G Ne'eman, L Trabaud) pp. 257–268. (Backhuys Publishers: Leiden, the Netherlands)
- Trabaud L, Campant C (1991) Difficulté de recolonisation naturelle du pin de Salzmann *Pinus nigra* Arn. spp. *salzmanii* (Dunal) Franco après incendie. *Biological Conservation* **58**, 329–343. doi:10.1016/0006-3207(91)90099-U
- Tsitsoni T (1997) Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece). *Forest Ecology and Management* **92**, 199–208. doi:10.1016/S0378-1127(96)03909-6
- Tsitsoni T, Ganatsas P, Zagas T, Tsakaldimi M (2004) Dynamics of post-fire regeneration of *Pinus brutia* Ten. in an artificial forest ecosystem of northern Greece. *Plant Ecology* **171**, 165–174. doi:10.1023/B:VEGE.0000029385.60590.FC
- Tuset JJ, Sánchez G (2004) 'La seca: el decaimiento de encinas, alcornoques y otros *Quercus* en España.' (Ministerio de Medio Ambiente: Madrid, Spain)
- Tutin T, Heywood V, Burges A, Valentine D (Eds) (1964–1980) 'Flora Europaea.' (Cambridge University Press: Cambridge, UK)
- Úbeda X, Sala M (1996) Cambios en la física del suelo e incremento de la escorrentía y la erosión tras un incendio forestal. *Cadernos do Laboratorio Xeolóxico de Laxe* **21**, 559–576.
- Úbeda X, Sala M (1998) Variations in runoff and erosion in three areas with different fire intensities. *Geoökodynamik* **XIX**, 179–188.
- Vacca A, Loddo S, Ollesch G, Puddu R, Serra G, Tomasi D, Aru A (2000) Measurement of runoff and soil erosion in three areas under different land use in Sardinia (Italy). *Catena* **40**, 69–92. doi:10.1016/S0341-8162(00)00088-6
- Vallejo R, Aronson J, Pausas JG, Cortina J (2006) Mediterranean Woodlands. In 'Restoration Ecology: the New Frontier'. (Eds J van Andel, J Aronson) pp. 193–207. (Blackwell Science: Oxford, UK)
- Veblen TT, Kitzberber T, Donnegan J (2000) Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* **10**, 1178–1195. doi:10.1890/1051-0761(2000)010[1178:CAHIOF]2.0.CO;2
- Verdú M, Pausas JG (2007) Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology* **95**, 1316–1323. doi:10.1111/J.1365-2745.2007.01300.X
- Verkaik I, Espelta JM (2006) Post-fire regeneration thinning, cone production, serotiny and regeneration age in *Pinus halepensis*. *Forest Ecology and Management* **231**, 155–163. doi:10.1016/J.FORECO.2006.05.041
- Vilà M, Lloret F, Oggeri E, Terradas J (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management* **147**, 3–14. doi:10.1016/S0378-1127(00)00435-7
- Zedler PH (1995) Are some plants born to burn? *Trends in Ecology & Evolution* **10**, 393–395. doi:10.1016/S0169-5347(00)89153-3

Manuscript received 15 October 2007, accepted 19 February 2008