

FIRE-RELATED TRAITS IN MEDITERRANEAN BASIN PLANTS

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ABSTRACT

Fire is a frequent and severe disturbance that affects plants on large scales, especially in Mediterranean-type ecosystems (MTE). Plants have evolved traits that confer resilience to fire and other disturbances, ensuring their persistence in fire-prone systems, but MTE floras differ in fire-related traits and their frequencies. Using available literature, we compare fire-related plant traits and syndromes of the flora of the Mediterranean Basin with those of other MTEs, discuss the differences and their possible causes, and point to knowledge gaps. Plants with lignotubers are relatively rare in the Mediterranean, as is serotiny. Many Mediterranean species have physically dormant seeds that are cued to germinate after fire by heat shock, while the effect of smoke on seed germination in the Mediterranean flora is less common than in other MTEs. The geophytes in the MB that flower massively after fire are opportunistic and not obligate fire-stimulated flowering species. Based on this literature survey, we conclude that differences in current and historic fire regimes could account for differences among MTEs in plants' fire-related traits.

Keywords: Plant adaptive traits, flammability, germination, lignotuber, re-sprouting, serotiny, smoke.

INTRODUCTION

Fire is the largest and most frequent disturbance affecting biomes on the largest scale (Bond and Keeley, 2005) and has affected plants on planet Earth since early geological eras (Pausas and Keeley, 2009; He et al., 2012). Consequently, plants have evolved traits that confer resilience to general disturbances and specifically to fire, ensuring their persistence (Pausas et al., 2004; Keeley et al., 2011). These traits are generally accepted as fire adaptations, namely, they were selected by fire during current (historical) or past (geological) fire regimes (Keeley et al., 2011; Keeley, 2012), or they are “exaptations” (Bradshaw et al., 2011), which are “features that now enhance fitness but were not built by natural selection for their current role” (Gould and Vrba, 1982).

Four out of the five Mediterranean-type ecosystems (MTEs) are known as the most

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fire-affected biomes of the world (Bond and Keeley, 2005). The floras of the MTEs are known as convergent in their adaptations to Mediterranean-type climate (e.g., Mooney and Dunn, 1970). MTEs are also rich in species exhibiting several fire-related traits, defined as “fire syndrome”, that together benefit the plant in case of fire (Pausas et al., 2004). Fire-related traits and fire syndromes present more adaptation to fire regimes than to single fire events (Keeley et al., 2011).

In spite of their similar climates and convergent vegetation types, MTEs differ in the frequency of species representing various fire-related traits and syndromes. These differences could reflect differences in current or past environmental factors among MTEs such as frequency of summer thunderstorms, soil fertility, human disturbance, and anthropogenic fires, or reflect differences in fire regimes in the geological and evolutionary past (Keeley et al., 2011; Keeley, 2012).

Recently an important database was compiled for vascular plants of the Mediterranean basin containing the most updated and comprehensive information on fire-related traits that permit regeneration after fire and persistence in time (Paula et al., 2009).

Using available literature, we review the major fire-related plant traits and their syndromes in the Mediterranean Basin flora, compare them with floras of other MTEs, propose explanatory hypotheses for the apparent differences, and identify knowledge gaps. However, a comprehensive survey of the literature is beyond the scope of this paper.

FIRE REGIME

Summer thunderstorm lightning, when the landscape is extremely dry, is the main cause for natural fires. Summer thunderstorms are not uncommon in California (Keeley, 1982), South Africa (Edwards, 1984), and Australia (Bell, 2001), and they also occur in the western MB (Soriano et al., 2005). In contrast, in the eastern MB thunderstorms are restricted to autumn and winter (Yair et al., 1998; Altaratz et al., 2003), when the vegetation is commonly wet and almost non-ignitable. At present, most fires in the entire Mediterranean basin are due to anthropogenic ignition by negligence or arson. Human- and lightning-ignited fires tend to have different geographical distributions, the former occurring mostly in the populated coastal areas and the latter in higher elevations of mountains in Spain (Vázquez and Moreno, 1998), as well as in California (Keeley, 1982).

Paleoclimatic research indicates major northern hemisphere climatic shifts in the geological record of the eastern Mediterranean and Levant over the last 25,000 years; the current climate is one of the driest periods (Robinson et al., 2006). Several small-scale dry and somewhat wet fluctuations during the Late Holocene (7,500 y ago to present) are recorded on the Israeli coast (Gvirtzman and Wieder, 2001). Therefore, there is no reason to assume that the distribution of lightning in the past was different from the present; fires in the eastern MB are mainly of anthropogenic origin and were probably so in the historic and prehistoric past as well. Archibalda et al. (2012) date the first human use of lightning fires in Africa to more than one million years ago, and the first anthropogenic domestication of fire in the eastern MB has been dated to 780,000 y BP (Goren-Inbar

et al., 2004). From that time on, fire probably escaped human control from time to time and caused wildfires. The prehistoric Mediterranean landscape was covered by denser and less fragmented forests than today. Therefore, escaped fires probably resulted in low-frequency but large-scale wildfires. Unfortunately there are no charcoal data in the eastern MB to validate this assumption. In later periods, when humans used fire as a management tool for clearing vegetation to prepare hunting grounds or grazing lands, fires probably became more frequent but smaller in size (Naveh, 1975).

Differences in current and past fire regimes could account for differences in plant fire-adaptations within and among regions, as will be discussed later.

RESPROUTING AND LIGNOTUBERS

Vegetative resprouting enables plants to persist after fire and canopy damage by wind-storms, early frost, or herbivore-induced defoliation (Trabaud, 1987). After scorching by fire, resprouting occurs from basal or epicormic stem buds, lignotubers, rhizomes, or root-buds (Gill, 1981).

Resprouting has probably evolved in both fire-prone and fire-free areas (Bond and Midgley, 2003). In the Mediterranean basin, selection for resprouting probably preceded that of propagule persistence (germination from the soil seed bank) (Verdu and Pausas, 2005). However, resprouting evolved independently in non-resprouting clades such as in the genus *Banksia* in Australia, and in northern hemisphere pines (Bond and Midgley, 2003; He et al., 2012). Resprouting variants of basically non-resprouting species have also been found in Ericaceae (Ojeda, 1998) and Fabaceae (Schutte et al., 1995) in the Cape territory in South Africa, and in *Juniperus oxycedrus* in eastern Spain (Pausas et al., 2008); accordingly, resprouting could also evolve in populations of non-resprouting species under current fire regimes.

Obligate resprouters, which do not recruit seedlings after fire, allocate more to underground storage organs than to early growth and reproduction, and live longer than non-resprouters. The fitness benefit of resprouters under high fire frequency (Pausas, 1999) depends on their growth rate, and on the age or size at which they experience fire (Bradstock and Myerscough, 1988; Bond and Van Wilgen, 1996). Resprouting of various plants depends on adequate amounts of stored carbohydrates (Jones and Laude, 1960), on their age and lignotuber size (Bradstock and Myerscough, 1988), and on their bark thickness (Lawes et al., 2011).

Most (65–78%) woody species in Mediterranean Spain are obligate resprouters that have no soil- or canopy-stored seed bank (Pausas et al., 2004); this situation is probably even more evident in the eastern Mediterranean basin, where there are only very few obligate seeders (Ne’eman, unpublished). Resprouting individuals of Mediterranean shrubs have larger leaves, that are richer in chlorophyll than unburned ones (Arianoutsou and Margaritis, 1981), representing increased plant vigor. In several cases resprouting is coupled with other fire-related traits, creating a “fire syndrome” (Pausas et al., 2004). In *Quercus coccifera*, the season of burning, pre-fire plant size, and number of stems all affect post-fire resprouting vigor (Malanson and Trabaud, 1988), while in *Q. suber*

post-fire resprouting is correlated with bark thickness (Pausas, 1997).

Based on experimental clipping of Mediterranean shrubs, Moreira et al. (2012) developed a model to explain intraspecific differences in resprouting ability. Overall, resprouting success is the outcome of variability in (1) initial resprouting ability, (2) resprouting vigour, and (3) post-resprouting survival. Depending on the species, each of the steps might limit overall resprouting success.

Some resprouting species, mainly obligate ones, have large underground lignotubers that serve for storage and as a source of regeneration buds (James, 1984). Species with lignotubers are frequent in Australia, South Africa, and California but much less so in the MB, where lignotubers were documented only for *Arbutus unedo*, *Quercus suber*, *Olea europaea*, *Tetraclinis articulata*, and some *Erica* and *Phillyrea* species (Keeley et al., 2011). In contrast to optimal partitioning theory (Bloom et al., 1985), the relative size of the lignotuber of *Erica australis* in Spain develops proportionally larger lignotubers not at less fertile sites but at more fertile and less acidic ones (Cruz and Moreno, 2001).

Real lignotubers develop already at the seedling stage even in the absence of fire or any other disturbance (James, 1984), but lignotuber-like basal stem structures are common in MB trees and shrubs probably as a phenotypic response to repeated fires or cutting. The relative rarity of real lignotubers in the Mediterranean region seems to contrast with the fact that the vast majority of the perennial woody plants in this region are obligate resprouters. Most resprouters in California do not form seed banks either (Keeley, 1987), but the frequency of resprouters with lignotubers is much higher in California than in the Mediterranean. We know of no explanation for the lower frequency of species with lignotubers in the MB flora. Thus, a detailed examination of the ontogenetic development of lignotubers in various species in relation to environmental conditions and disturbance regimes, as well as a phylogenetic study of lignotubers in the MB flora, are still needed.

Simulation of the effects of fire frequency on Mediterranean forest composition in Spain (Pausas, 1999) predicted mature resprouting oak forests in areas with low fire recurrence, a mixture of non-resprouting pine and resprouting oak woodland in areas with higher fire recurrence, and mixed resprouting (*Erica*) and non-resprouting (*Cistus*) shrublands in the areas of highest fire recurrence (Pausas, 1999). Thus, resprouting species can probably prevail in low and high fire frequencies, depending on their shade tolerance, indicating the importance of complex fire syndromes (resprouting with or without shade tolerance) more than any single trait.

SEROTINY

Serotiny is defined as delayed seed dispersal from woody cones or fruits (Lamont et al., 1991), yet serotinous species do not constitute a coherent ecological and evolutionary group but are scattered unevenly among the MTEs. In Australia, where serotiny has an extremely long (geological scale) fire-driven history (He et al., 2011; Keeley et al., 2011), seed dispersal in some serotinous species (e.g. *Banksia elegans*) occurs only after heating to 500 °C (Lamont and Enright, 2000); in other species, lower temperatures are

sufficient (Enright and Lamont, 2006), while in some species spontaneous seed dispersal from old serotinous cones or fruits can occur even with no fire, e.g., *B. tricuspis* (Lamont and van Leeuwen, 1988; Midgley and Enright, 2000). North American pine species and populations also differ in degree of serotiny (Perry and Lotan, 1977; McCune, 1988). For obligate seeders producing only fully serotinous cones (e.g., *Pinus attenuata*: Vogel et al., 1977; Keeley et al., 1999) or fruits (e.g. *B. serrata*: Lamont et al., 1991), fire is the only possible agent of natural selection for their serotiny, because in the absence of fire their recruitment and fitness are zero.

Cones or fruits of many serotinous species, e.g. *Pinus* spp. and *Banksia* spp., are constructed of dead woody tissues and need extreme heat and drought to open and disperse seeds (Lamont et al., 1991; Moya et al., 2008). Other species, in several genera including *Allocasuarina*, *Eucalyptus*, *Hakea*, *Leptospermum*, *Melaleuca*, and *Leucadendron*, and other Australian Myrtaceae have living serotinous fruits (Lamont et al., 1991; Lamont and Enright, 2000; Midgley and Enright, 2000). *Cupressus* species of the northern hemisphere (Lev-Yadun, 1995) have living serotinous cones that contain photosynthetic tissues, which after the death of the plant or of a branch, even in the absence of fire, lose water, shrink, and allow seed dispersal (Lev-Yadun, 1995). Therefore, this type of serotiny may be advantageous also in other catastrophic events besides fire, which could also act as selective agent for living serotinous cones or fruits (Lev-Yadun, 1995; Ne'eman et al., 2009). However, in Californian cypress, although some cones may open without fire, their seeds do not produce successful recruitment. This can be regarded also as selection for polymorphic behavior, similar to that in species with partial serotiny and polymorphic seed banks with some individuals recruiting without fire and others being fire dependent (Keeley, pers. comm.).

Serotiny is most abundant in Australia, followed by South Africa and North America (Lamont et al., 1991); it is absent from the mediterranean region of Chile because fires are extremely rare there (Keeley, 1995). The flora of the Mediterranean basin has only a few serotinous species: *Pinus halepensis*, *P. brutia*, *P. pinaster*, and *Cupressus sempervirens* (Lev-Yadun, 1995; Daskalakou and Thanos, 1996; Thanos and Dousi, 2000; Tapias et al., 2001).

In *P. contorta*, serotiny is probably a genetic trait with 1-locus, 2-allele control (Perry and Lotan, 1977). In *P. halepensis*, trees simultaneously develop serotinous and non-serotinous cones. Seeds from serotinous cones germinate better under simulated post-fire conditions than seeds from non-serotinous cones, indicating maternal or environmental effects on serotiny level and seed germination (Goubitz et al., 2004). The dramatic increase from 40% to 85% of average serotiny, at the population level, after one post-fire regeneration cycle indicates the high adaptive value and high selection rate for serotiny in this species.

Although He et al. (2012) present new evidence for the Cretaceous origin of fire adaptations in *Pinus*, one cannot exclude the possibility that anthropogenic fire affected current serotiny levels in the short-living *P. halepensis* (Goubitz et al., 2004). At present, in some regions human ignitions are probably a threat due to high fire frequency extirpating some populations. This does not exclude any other geological or phyloge-

netic explanation. Differences in the degree of serotiny between the two closely related *P. halepensis* (more serotinous) and *P. brutia* (less serotinous) (Daskalakou and Thanos, 1996; Thanos and Dousi, 2000) indicate local selection and adaptation, probably under different fire regimes.

There could be several explanations why serotiny is so rare in flora of the MB, as compared to that of South Africa and Australia. Low nutrient supply was suggested to favor seed retention in regions with poor soils (Bradshaw et al., 2011); Keeley et al. (2011) claim that geology, climate, and fire are responsible for the evolution of serotiny in Australia and South Africa. We suggest that it may also be a pre-emptive character. When many of the northern hemisphere Mediterranean plants originated from tropical floras of the Tertiary and were exposed to the Mediterranean climate, they were already adapted to fire, having epicormic buds. When a plant is a post-fire resprouter it does not need an additional mechanism to cope with this disturbance. Also, serotiny requires a fire within the lifespan of the species since once the plant dies, seed storage beyond death is very low. In California natural fires were probably infrequent, maybe on the order of once a century or perhaps much longer. Soil-stored seed banks are a much more reliable mode of storing seeds than is serotiny on this landscape (Keeley, pers. comm.).

SEED BANKS AND GERMINATION

Populations of many plant species persist through fires due to their capacity to form fire-resistant seed banks for post-fire recruitment (Keeley, 1995; Keeley and Fotheringham, 2000). Post-fire obligate seeders, which recruit after fire only by seed germination, have soil or canopy-stored seed banks. Obligate seeders that are adapted to high fire frequency are exposed to "immaturity risk" depending on their age at first reproduction and on the density of their seed bank, which must be large enough to ensure post-fire population recovery (Arianoutsou, 1998; Keeley et al., 1999; Goubitz et al., 2004).

Seeds of serotinous species (canopy-stored seed bank) are mostly non-dormant and germinate on the first convenient occasion after their dispersal (Keeley and Fotheringham, 2000). A possible exception is the MB dwarf shrub *Cistus creticus*, which, in contrast to other congeneric species, retains many seed-containing capsules for more than one year. These capsules contain exclusively hard-coated seeds that are gradually released but germinate mainly after heat shock and can be defined as non-fire-related serotiny (Arianoutsou and Margaris, 1981; Thanos and Georghiou, 1988; Skourou and Arianoutsou, 2004).

By contrast, seeds of many species that germinate after fire from soil seed banks are physically or chemically dormant and germinate only after being exposed to fire-related cues, mainly heat shock, charred wood, or smoke (Keeley, 1987; Dixon et al., 1995; Keeley and Fotheringham, 1997, 2000).

Most species in the MB flora are post-fire obligate resprouters; far fewer are obligate seeders, and only very few are resprouters that also have dormant seed banks for post-fire recruitment (Pausas et al., 2004). This is in contrast to Australia and South Africa, where resprouters may have soil- or canopy-stored seed banks (Pausas et al., 2004).

Keeley et al. (2012) proposed that the resprouters, which grow fast after fire and create dense and shady vegetation, do not leave much space for the MB seeders, most of which are shrubby, light-requiring species.

HEAT

Many species from fire-prone habitats form hard-coated seed. Heat shock can trigger germination by rupturing the seed coat layer, allowing water uptake (Baskin and Baskin, 1998). Species from fire-free habitats may also have hard seed coats with physical dormancy, but their germination is cued mainly by alternating temperatures or soil moisture (Baskin, 2003). Hard seed coats have various anatomical structures typical of the phylogenetic distribution and time of origin of different plant families (Baskin et al., 2000). We argue that dormancy-breaking mechanisms by heat shock are probably not similar to those of cold stratification or alternating temperatures. A taxonomically wide comparison of seed coat anatomical structure in relation to germination physiology is needed for a better understanding of the ecology and evolution of hard seededness.

The Fabaceae and Cistaceae families are well represented in post-fire seedling communities in the MB (Arianoutsou, 1998). Many species in both families are obligatory seeders that typically have physically dormant seeds that are cued to germinate by heat shock.

A cumulative effect of the positive response of individual species was demonstrated by heating soil samples from different micro-niches in natural *P. halepensis* forests. Heated samples had higher species richness and seedling density than did untreated samples (Izhaki et al., 2000). Positive effects of heat and smoke on germination of soil seed banks were found also in Australia (Enright et al., 1997; Read et al., 2000).

SMOKE

The effects of charred wood and smoke on seed germination of fire-dependent ephemeral plants were first explored in California (Wicklow, 1977; Keeley and Fotheringham, 1997, 1998). Later, the effect of smoke on seed germination was studied in South Africa (e.g., De Lange and Boucher, 1990; Brown, 1993; Keeley and Bond, 1997), and in Australia (e.g., Dixon et al., 1995; Roche et al., 1998; Bell, 1999). Recently, a new hormone-like butanolide compound (karrikinolide) that triggers germination of many species, including plants with no apparent ecological or evolutionary connection to fire, was identified in smoke (Dixon et al., 2009). Annual plants that mostly germinate in post-fire conditions (in California and South Africa) are predominantly triggered by smoke; but a significant number of woody species in both regions are characterized by transient seed banks that apparently germinate without fire (Keeley and Bond, 1997).

A total of 92 species from the MB flora were tested by several researchers (Ne'eman and Keeley, unpublished data; Keeley and Baer-Keeley, 1999; Pérez-Fernández and Rodríguez-Echeverrías, 2003; Buhk and Hensen, 2006; Crosti et al., 2006; Rivas et al., 2006; Reyes and Trabaud, 2009; Moreira et al., 2010) (Table 1). The examined species,

Table 1 (continued)

Species	Ne'eman and Keeley unpub.	Keeley 1999	Pérez-Fernández 2003	Buhk 2006	Crosti 2006	Rivas 2006	Reyes 2009	Moreira 2010
<i>Sarcopoterium spinosum</i>		0						
<i>Scorpiurus muricatus</i>	0							
<i>Senecio jacobea</i>			+					
<i>Sideritis angustifolia</i>								0
<i>Spartium junceum</i>							—	
<i>Teucrium capitatum</i>								0
<i>Teucrium ronnigeri</i>								+
<i>Teucrium</i> sp.		0						
<i>Thymus piperella</i>								—
<i>Thymus vulgaris</i>								+
<i>Trifolium angustifolium</i>				+				
<i>Tripodium (Anthyllis) tetraphylla</i>	0							
<i>Ulex borgiae</i>								0
<i>Ulex parviflorus</i>								0
<i>Xolantha tuberaria</i>								0

typical to fire-prone habitats, included 30 dwarf shrubs, 19 annuals, 16 non-woody perennial plants, 18 shrubs, four trees, three geophytes and two climbers. There were 32 species of Fabaceae, 14 Cistaceae, eight Lamiaceae, four Ericaceae, four Poaceae, four Asteraceae, three Liliaceae, two Apiaceae, two Primulaceae, two Ranunculaceae, and one species each from 16 other families.

Smoke had no effect on the germination of 72 (out of 92) species, a positive effect on 14 species (five dwarf shrubs, four perennial non-woody plants, two shrubs, one annual, one tree, and one climbing species), and a negative effect on five species (one each of perennial grass, geophyte, dwarf shrub, shrub, tree) (Table 1). In cases where contrasting effects of smoke on seed germination were reported, and more researchers reported a certain effect more than any other effect, we classified the effect according to the majority of reports. Whenever smoke was reported by one author to have a positive effect upon seed germination of a species and the opposite effect by another author, the species was excluded from the analysis (e.g., *Rosmarinus officinalis*). Researchers used widely diverse methods, which might account for the differences they reported for *Rosmarinus officinalis*, although these could have resulted from differences among populations of a species.

These data indicate that the effect of smoke on seed germination in the MB flora is less common than in the floras of other MTEs (except Chile). Annual plants are the most

common life form affected by smoke in MTEs other than the MB, where perennial non-woody plants and dwarf shrubs seem to be affected the most, even though annuals are more frequent in the MB flora than in the other MTE floras (Shmida and Ellner, 1983). Annuals constitute the major component of soil seed banks in the MB, and the openness of the post-fire environment to direct sunlight favors them (Izhaki et al., 2000). A possible explanation is that the post-fire MB flora is rich in Fabaceae and Cistaceae, two families known for their hard and water-impermeable seed coats, and whose physical seed dormancy is broken by heat shock but not by smoke. Why the response to smoke has not evolved in annual species of other families in the MB needs still to be explored.

FIRE-STIMULATED FLOWERING

Fire-stimulated flowering is a very common phenomenon in the Australian and South African floras (Bond and Van Wilgen, 1996; Lamont and Downes, 2011) but not in California, the MB, or Chile. In their recent review, Lamont and Downes (2011) reported on 386 fire-stimulated species. Of these, 40% are obligate fire-stimulated species that flower only one or two years after fire; the rest are facultative species that continue to flower during the inter-fire period. The majority (71%) of species grow in the MTE of Australia and South Africa; 81% are monocot herbaceous plants and 59% geophytes, with orchids as the best represented family (45%).

Massive flowering of geophytes not restricted to the first two years after the fire has been reported from post-fire recovering MB ecosystems (Arianoutsou, 1979; Kazanis and Arianoutsou, personal observations). However, all these are facultative fire-stimulated flowering species.

Heat shock was experimentally proved as the proximal cause for post-fire flowering (Lamont and Downes, 2011). Smoke was proved the cue for flowering of *Crytanthus ventricosus* (Keeley, 1993), while circumstantial evidence exists for its effect also for other species (Lamont and Downes, 2011). Foliage loss and extra resources (light and nutrients) are probably the causes for fire-stimulated flowering in other species (Lamont and Downes, 2011).

FLAMMABILITY

Plant flammability is a complex trait that can be defined and measured in several ways (lowest ignition temperature, maximal temperature, fire duration, and amount of heat released) and on different scales (leaf, branch, plant, population, community, and landscape) (Whelan, 1995; Bond and Van Wilgen, 1996; Schwilk, 2003; Pausas and Moreira, 2012). In their "kill thy neighbor" hypothesis, Bond and Midgley (1995) suggested that flammability-enhancing traits could contribute to plant fitness when they increase mortality of neighbors and recruitment of the burned plant. Later models suggest different genetic mechanisms for the evolution of flammability (Schwilk and Kerr, 2002).

Obligate seeders in the MB are more flammable than resprouters (Saura-Mas et al., 2010). Flammability and serotiny are correlated strategies in the evolution of pines

(Schwilk and Ackerly, 2001), which is probably true for other MTEs as well. Evidence supporting fire as the direct agent of selection for flammability comes from the MB. Plants of *Ulex parviflorus* growing in recurrently burnt populations are more flammable, ignite quicker, burn slower, and release more heat than those growing in populations that have not suffered any fire (Pausas et al., 2012). We assume the conclusions are valid for more species and other MTEs, but more research should be done in this direction.

FIRE-RELATED TRAITS IN MEDITERRANEAN-TYPE ECOSYSTEMS

Four of the five MTEs worldwide (Mediterranean basin, California, southwestern Australia, and the Cape Province in South Africa) are fire-prone (Bond and Van Wilgen, 1996). The well known similarity of plant traits in these MTEs is generally recognized as the result of evolutionary convergence driven by similar environmental conditions (Mooney and Dunn, 1970), with fires being a common environmental factor affecting plant ecology and evolution (Naveh, 1975; Whelan, 1995; Bond and Van Wilgen, 1996).

The geographical accumulation of many fire-adapted species representing many fire-related traits seems far from random, and probably reflects the ecological adaptations of these plants to the current or past high fire frequency (Keeley et al., 2011). While a plant can be benefited from single trait after non-fire disturbances, and can also be found in other biomes, MTEs display the most prominent accumulation of such fire-related beneficial traits (resprouting, serotiny, physical seed dormancy, post-fire flowering, smoke-induced germination, and flammability) representing fire-adaptation syndromes (Pausas et al., 2006). These syndromes seem to be the result of the fire-driven evolutionary history of the MTEs impelled by fire-selection, and part of the broad phenomenon of MTE-convergent evolution (Mooney and Dunn, 1970).

In some cases different fire-related traits are positively correlated, for example, (1) the effects of smoke on seed germination and on initial seedling growth (Moreira et al., 2010), and (2) the fact that serotinous pines are more flammable than non-serotinous pines (Schwilk and Ackerly, 2001). In other cases, although co-occurring, germination responses to fire-related cues (heat shock, ash, smoke, pH) were found unrelated to plants' post-fire regeneration mode (resprouting, serotiny, and soil seed banks) (Ne'eman et al., 2009). Still, the conspicuous accumulation of fire adaptations and syndromes in MTEs worldwide can best be explained by fire-selection and the long evolutionary fire history in these regions.

CONCLUSIONS

Based on the reviewed literature, we conclude:

1. Differences in current and historic fire regimes could account for differences in plant fire-adaptations between the western and eastern parts of the MB, as well as among MTEs.
2. Although the majority of the perennial woody plants of MB are obligate resprouters, taxa with lignotubers are rather rare in the region. The reason is still unknown.

3. Serotiny is an uncommon trait in the floras of the MB and California, when compared to the floras of South Africa and Australia. Differences in fire regimes and the mainly tropical origine of the northern hemisphere floras may explain this difference.
4. The Fabaceae and Cistaceae families are well represented in the post-fire environment of the MB, where many species have physically dormant seeds cued to germinate after fire by heat shock.
5. The effect of smoke on seed germination in the MB flora is less common than in other MTEs. In the MB flora, where annual plants are the commonest, perennial non-woody plants and dwarf shrubs are the main life form with smoke-cued germination, while in other MTEs annual plants are the most common life form affected by smoke.
6. Although the MB is relatively rich in geophyte species that flower massively after fire, they not obligate fire-stimulated flowering species.
7. There is recent evidence that fire acts as the driving force of selection for flammability in MB plant species, which seems to be the case also for species of other MTEs.
8. The conspicuous accumulation of fire adaptations in MTEs worldwide can best be explained by current fire selection and the long evolutionary effect of fire history in these regions.
9. The lack or rarity of some fire adaptations (lignotubers, serotiny, post-fire flowering, smoke-induced seed germination) in the MB may reflect the low frequency of natural fires and the significant role of anthropogenic fires, which is a relatively recent development in evolutionary time scales.

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