



Reproductive traits of *Pinus halepensis* in the light of fire – a critical review

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Key words: Aleppo pine, Cone serotiny, Flammability, Germination, Mediterranean, Natural selection

Abstract

Fire is known to be a major factor in shaping plants and vegetation worldwide. Many plant traits have been described as adaptations for surviving fire, or regenerating after it. However, many of the traits are also advantageous for overcoming other disturbances. The fact that fire in the Mediterranean Basin has been almost exclusively of anthropogenic origin, and thus is of short duration in an evolutionary time scale, cast doubt on the possibility that fire can act as a selective force in the Mediterranean Basin. Our aim here is to review the ecological advantages of *Pinus halepensis* traits and their possibility to be selected by fire. The non-self pruning of cones and branches, and the high resin content increase the probability of canopy fires and consequent death of *P. halepensis* trees. Post-fire regeneration of *P. halepensis* depends totally upon its canopy-stored seed bank. The seedlings grow quickly and they first reproduce at an early age. Young reproductive trees function first as females with a high percentage of serotinous cones. Thus, young *P. halepensis* trees allocate many resources to seed production, reducing their 'immaturity risk' in a case of an early successive fire. The proportion of serotinous cones is higher in post-fire naturally regenerating stands than in unburned stands, and seeds from serotinous cones germinate better under simulated post-fire conditions. The extremely high pH of the ash-bed under the burned canopies creates the post-fire regeneration niche of *P. halepensis* exactly under their parent trees. All these traits are advantageous for post-fire regeneration, but could they also be selected during the time scale of anthropogenic fires in the Mediterranean Basin? *Pinus halepensis* is a relatively short living tree with almost no recruitment under forest canopy. The longest estimated fire-return interval and generation length are about 125 years. The earliest solid evidence for the first hominid-controlled fire in the Mediterranean basin is 780,000 years ago, and thus the estimated number of post-fire generations is 6240. We suggest that such a number of generations is sufficient for the selection and radiation of fire adaptive traits in *P. halepensis*.

Introduction

Fire, mainly as a consequence of summer thunderstorms, is a natural factor in three of the five Mediterranean-type regions in the world: Australia, California and South Africa. According to FAO reports (FAO 1999), during a single decade (1989–1998), 616,037 fires in Portugal, Spain, France, Italy, Greece, Turkey and Israel consumed 48,504 km², 2% of their total land area. In the west Mediterranean basin lightning-caused fires are limited to high mountains, were only 3.3% of all fires and burned only

7.5% of the total burned areas; the rest were anthropogenic fires (Vázquez and Moreno 1998). In the east Mediterranean all fires are almost only of anthropogenic origin; during 1980–1996 no 'natural fire' was reported (Keidar 2001). It has been suggested that fire, more than other kinds of human disturbances, such as cutting and grazing, have strongly shaped the evolution of Mediterranean plants (Naveh 1974; Naveh 1990). Thus, many dominant Mediterranean species, including *P. halepensis* Miller (Aleppo pine), have

been considered 'pyrophytes' that retain key survival traits as 'fire adaptations' (Naveh 1974; Naveh 1990).

Trabaud (1987) challenged the relevance of such terms, mainly for plants of Mediterranean regions, because fire is only one of several disturbance types that can select for 'survival traits'. This argument is especially strong given the relatively short history of the fires in the Mediterranean Basin. In fact, most life history traits are advantageous for various natural and human disturbances. Resprouting, for example, is advantageous after windfall and extreme herbivore defoliation as well as after extreme grazing, logging or canopy fire. Hard seededness is also often presented as an adaptation to post-fire regeneration from soil seed bank (Bond and van Wilgen 1996). However, this characteristic is responsible for spreading of germination over time in dormant, refractory seeds, and it is common in the Cistaceae and Fabaceae, whether the species inhabit fire prone habitats or not (Thanos et al. 1992). Even serotiny, which is generally accepted as a fire-related trait (Lotan 1976; Lamont et al. 1991), has also been shown to synchronize seed release in time of optimal conditions for long-distance seed dispersal (Nathan et al. 1999). Because early succession plant species have many common traits with post-fire obligate seeders (Keeley and Zedler 1998) it is more difficult to separate adaptations to fire from adaptations to other disturbances. In contrast, the recently found widespread smoke-stimulated germination (e.g. Keeley and Fotheringham 1997) and flowering (Keeley 1993) are advantageous solely in the case of fire. It is possible, in many cases, to demonstrate the contribution of various plant life history traits to resilience to fire, or to post-fire regeneration. However, in most cases, it is difficult to determine whether fire or any other natural or anthropogenic disturbance acted as the major selective force that caused the radiation of any specific trait.

Although the above arguments generally hold for all Mediterranean regions, selection by fire should be carefully examined for long-lived plants of the Mediterranean basin in particular. This is because the time period during which fire of anthropogenic origin became a major force in this region (Naveh 1974; Prodon et al. 1987) is perhaps too short for the selection and radiation of new traits in relatively long-living organisms such as trees. It might be sufficient, however to cause extinction of plants that entirely lack any resilience, or any post-disturbance regeneration mechanism.

Pinus halepensis is one of the most studied Mediterranean trees (Ne'eman and Trabaud 2000). It is a post-fire obligate seeder, which does not survive fires but regenerates only from seeds in the post-fire environment. Therefore, vegetative characters are less important as potential fire adaptations than reproductive traits and features that affect early recruitment (Whelan 1995; Bond and van Wilgen 1996). *Pinus halepensis* is abundant in fire-prone habitats within the Mediterranean basin (Arianoutsou and Ne'eman 2000; Trabaud 2000). It is also known however to be a common pioneer and invasive species within its natural distribution area and elsewhere, and thus it is also adapted to regeneration in unburned disturbed areas. Shade intolerant seedlings, short juvenile period, massive annual cone production, serotinous cones and low probability of surviving fires are the main traits determining the invasive ability of *P. halepensis* in the Southern Hemisphere (Higgins and Richardson 1998; Richardson 2000).

A review of the past and current research on *P. halepensis* traits in relation to fire indicates a shift from a strong emphasis on fire as the major or even the sole factor affecting regeneration and selection, to the view that the species exhibits a 'dual life history strategy' for utilizing fire as well as other disturbances (Trabaud 1987; Nathan et al. 1999; Nathan and Ne'eman 2000). This recent recognition requires a new synthesis of data accumulated in former and recent studies and re-evaluation of their ecological role and evolutionary causes and consequences. Therefore, our aim here is to examine various life history traits of *P. halepensis*, to evaluate their contribution to post-fire versus fire-free regeneration, and to assess the possibility of their direct selection by fire.

Reproductive traits of *Pinus halepensis*

Vegetative traits

The ecological role of pines in general is described as specialized for moderate to low-fertility habitats and the exploitation of open conditions imposed by limitation of growth or by disturbance, fire in particular (Keeley and Zedler 1998). The vegetative characteristics of various pine species are correlated with fire regime and their post-fire regeneration strategy. Where only ground fires occur frequently, a grass-stage with a delayed seedling development has evolved. In areas with summer rains and high fire frequency, mainly in

the southeast USA, basal resprouting of saplings and young trees has evolved. Post-fire resprouting is correlated with thick bark, which protects the cambium from fire's heat, mainly in canopy resprouting species (e.g. *Pinus canariensis*). Serotinous species are common in low productive sites with limited tree height, which increases the danger that any fire could develop into a canopy fire. Under such conditions, pine species have only a relatively thin bark that does not supply enough heat insulation to the cambium and leads to tree death after wild fire. *Pinus halepensis* belongs to the last group; its bark is 3.8 cm thick on average, whereas bark thickness of 38 examined species ranged from 1 to 7.62 cm (Keeley and Zedler 1998). Serotinous species are not self-pruning, and dead branches are not detached from the main trunk. They constitute a highly flammable material that acts to amplify fire intensity, thus increasing the chances that a local low-intensity surface fire will become a widespread high-intensity canopy fire (Keeley and Zedler 1998). *Pinus halepensis* is not self-pruning, and it also retains an extremely large number of open empty cones that are very flammable. The non-self pruning of branches and empty cones contributes to the high flammability of *P. halepensis*, but not to its invasive ability.

Cone production

Pine species vary in their age to first reproduction from 5 years in high fire frequency habitats to 50 years in timberline and desert species (Keeley and Zedler 1998). Saplings of *P. halepensis* are fast growing; their sexual reproduction begins at the very early age of 3-6 years and is estimated to encompass the entire population after 12-20 years (Thanos and Daskalidou 2000). In even-aged populations large individuals begin their reproduction earlier than small ones; this may explain the high variability in the published data.

Monoecy is common to all pine species (Mirov 1967). However, *P. halepensis* trees start reproduction as females and later turn bisexual when they start producing also male strobili. In a three-year-old post-fire stand on Mt. Carmel, Israel, 93% of the reproductive individuals were females, 6% males and 1% bisexual. When tree size is considered, reproduction begins at 1-1.5 m height with 51% reproductive individuals, 38% females and 12% bisexual; in full reproductive stands of 9 m high trees, 99% are bisexual (Shmida et al. 2000; Table 1). This temporal gender segregation pattern contrasts with the reproductive patterns in most other monoecious species. Because female suc-

cess is often limited by resource availability (Charnov 1982), young or small individuals usually are pure males and produce female units only later (Freeman et al. 1981; Willson 1983). Such a temporal gender segregation pattern is advantageous in the post-fire environment. In large burned areas, the probability that the small amount of pollen, produced by small post-fire saplings, will pollinate some distant unburned trees seems extremely low resulting in low male success. In contrast, the chances that pollen produced by distant unburned large trees will pollinate the young post-fire trees, over the same distance, seem much higher, resulting in higher female success. Moreover, 'immaturity risk', the danger of recurrent fire before the establishment of a seed bank, is a threat to the population of post-fire obligate seeders (Lamont et al. 1991). Therefore, the contribution of even the low female success to the fitness of an individual under high fire frequency regime is much higher than that of any possible male success. This gets support also from the higher percentage of serotiny in young small trees as will be described in the next section.

However, young age at first reproduction and the production of female cones first are also advantageous for a pioneer, invading species.

Seed dispersal and serotiny

Most of the seeds of *P. halepensis* are produced in regular cones that open regularly and release their enclosed seeds under dry weather conditions. The winged seeds are adapted for long-distance dispersal (Nathan et al. 1999). Thus, cone structure, seed morphology, and timing of seed release are major non-fire related traits determining the invasive character of *P. halepensis*.

Serotiny is the retention of mature seeds in a canopy-stored seed bank with delayed dispersal (Lamont et al. 1991). However, in many cases serotiny refers to seed release and dispersal as a result of fire (Lamont et al. 1991). The degree of serotiny in pines varies considerably among species, among populations within a species, in response to site productivity and mainly fire frequency (Keeley and Zedler 1998). The degree of serotiny in *Banksia* species was found to be dependent on resprouting ability, longevity and fire frequency (Enright et al. 1999a; Enright et al. 1999b). The high variation in serotiny percentage and its higher values in post-fire stands in North America (Lotan 1976; Gauthier et al. 1996) are explained by direct selection by fire and the simple genetic control

Table 1. The percentage of non-reproductive individuals (none), female, male and monoecious trees of *Pinus halepensis* according to average height classes (m) in the Judean Mountains (From Shmida et al. 2000).

Height (m)	n	None (%)	Female (%)	Male (%)	Monoecious (%)
1.5	203	49.3	38.0	0.4	12.3
3	147	9.2	10.3	0.7	79.8
6	95	0	2.1	0	97.9
9	38	0	0	0	100
12	75	0	0	0	100

(two alleles at one locus) of this trait (Teich 1970; Perry and Lotan 1979).

Pinus halepensis is frequently presented as serotinous pine whose cone opening and seed release are related to fire (Trabaud et al. 1985; Daskalidou and Thanos 1996; Saracino et al. 1997; Agee 1998; Doussi and Thanos 2002; Leone et al. 2000; Roittemberg and Ne'eman 1999). Serotinous cones also open, however in the absence of fire as a response to extremely dry weather and as an adaptation to favorable conditions for dispersal (Nathan et al. 1999). This demonstrates the complex situation involved in serotiny and seed dispersal in *P. halepensis*. Pyriscence, fire-induced seed release (*sensu* Lamont et al. 1991), is extensive and widespread in this species and leads to its remarkable post-fire recruitment and enlargement of its distribution area in fire-prone areas. Xeriscent, drought-induced seed release (*sensu* Nathan et al. 1999), constitutes the major portion of seeds released during a tree's lifetime, and may also result in widespread recruitment. Thus, *P. halepensis* is adapted to invading open disturbed sites generated by fire or by other factors (Nathan and Ne'eman 2000).

A compilation of four recent studies, carried out in Italy (Borghetti M., Saracino A. and Leone V. unpublished data), Greece (Thanos and Daskalidou 2000), Spain (Tapias et al. 2001) and Israel (Goubitz 2001; Goubitz et al. in press), shows that serotiny in *P. halepensis* strongly depends on the stand history in relation to fire (Figure 1). Some of the above studies present averages of several stands; therefore no means can be calculated. However, the degree of serotiny in more than 10 post-fire stands was higher than 78% and the degree of serotiny of more than 13 unburned was less than 81%. However, in the first three studies, the post-fire regenerated stands were younger than the unburned stands. This confounds

the interpretation with respect to the role of fire history, because the difference in serotiny can merely be a function of tree age/height. In fact, the percentage of serotiny in *P. halepensis* is much higher in young and small trees than in adults. In Greece, 5-12 year-old trees had 95% and 30-50 year-old trees had 48% serotinous cones (Thanos and Daskalidou 2000). In Spain, the last two crops in 3 young (18 years) and 3 adult (>40 years) stands had mean serotiny of 95% and 78%, respectively (Tapias et al. 2001). In Israel, serotiny was 90% in 3 m high stands and dropped to 20% in 8 m height stands (Figure 2). However, controlling for the age/size effect by comparing trees of similar size (up to 8 m) reveals significantly (t-test $p=0.03$) higher serotiny in 3 burned (85%) than in 4 unburned (40%) stands on Mt. Carmel, Israel. This suggests a direct and rapid selection by fire, as was also found in North American pines (Lotan 1976; Gauthier et al. 1996). The higher percentage of serotiny of young trees is also advantageous mainly in post-fire conditions. Serotinous cones contribute to the quick establishment of a canopy-stored seed bank, which is the only chance for post-fire regeneration in case of an early successive fire, thus reducing the 'immaturity risk'. Moreover, serotinous cones on small trees decrease the invasion rate in a no-fire scenario. Thus, the tendency of younger or smaller pines to produce more serotinous cones in general, and especially in post-fire scenarios, provides evidence for a specific selection by fire rather than by other disturbances.

Both serotinous and non-serotinous cones open after fire and gradually release their seeds. In Italy, seed rain was highest immediately after a fire, but it has still been observed 4-5 months after the fire (Saracino et al. 1997). Similar temporal patterns of seed release were observed in several post-fire stands in Israel (G. Ne'eman et al., unpublished). Saracino

shock of 40 °C for 5 min and germination at pH 7) conditions. The treatments variously affected the germination of the seeds according to their cone type. Percentage and rate of germination of seeds from non-serotinous cones was higher in the no-fire simulation than in the post-fire simulation. In the post-fire simulation, seeds from serotinous cones germinated better than seeds from non-serotinous cones (Goubitz 2001; Goubitz et al. 2003). The different germination responses could not be attributed to differences in cone age, because no difference was detected in the germination of seeds from one- and four-year-old serotinous cones. These results indicate that the cone type is linked to the germination response of the seeds in *P. halepensis*, with seeds from serotinous cones being more tolerant of fire-related factors. Moreover, the results revealed that in addition to protecting the seeds during fire and dispersing them after fire, the seeds from serotinous cones germinate in the post-fire environment better than seeds from non-serotinous cones. Such a difference indicates that in the case of fire, individuals with a high percentage of serotinous cones have an advantage over individuals with a low percentage of serotinous cones. We thus conclude that fire may cause direct selection to increase the percentage of serotinous cones.

Seed-bank and regeneration niche

Post-fire seeders may regenerate from the soil seed bank or from a serotinous canopy-stored seed bank. Because of the high predation pressure of about 97%, *P. halepensis* seeds are almost completely absent from the pine forest soil seed bank (Izhaki and Ne'eman 2000). The seeds that succeed to germinate under the forest canopy produce seedlings that have no chance to grow and reproduce in the shade of the mature trees. Consequently, regeneration without fire drastically increased with distance from the adult trees. The probability of a seed surviving to a sapling (3 years) stage can increase by more than two orders of magnitude when it is just 30 m from adult pines (Nathan et al. 2000). This is presumably because more distant sites have lower predation (R. Nathan, unpublished), lower competition with both seedlings and adults, and lower interference from adult litter and needle debris.

In the absence of soil seed bank, all post-fire regeneration depends on canopy-stored seeds in serotinous and non-serotinous cones. The dispersal curve of *P. halepensis* is similar to those of other wind-dispersed species, exhibiting a rapid decline with increasing dis-

tance from the source (Nathan et al. 2000). This was also verified in a post-fire situation (Eshel et al. 2000). However, because of the inhibitory effect of the high pH value of the ash (Henig-Sever et al. 1996), which accumulates under the burned canopies of large burned pines, pine seedlings appear in high density among the trees and in sparse stands under the projection of the burned pine canopies (Eshel et al. 2000). During the early post-fire stage (2–5 years), the density of seedlings in the mineral rich ash near the burned trunks is low. Because of the reduced competition and enriched mineral nutrition, growth rate of these seedlings is high and their mortality low. Outside the effect of the burned trees, seedling density is high as is intra- and inter-specific competition; the consequent growth is slow and mortality high. At the end of the later stage (5–20 years), there are no differences in tree density, but those growing in the exact site of their mother trees are 10 times larger than trees that grew elsewhere (Ne'eman and Izhaki 1998; Ne'eman 2000). The high heat and ash accumulation under the large pine trees create the regeneration niche for the next forest generation. This is of utmost importance in light of the high competition in the post-fire environment among annual and perennial post-fire seeders.

Flammability

Running crown fires are most likely in coniferous forests with stratified fuel beds consisting of needle litter, twigs, cones and understorey shrubs below a canopy of live foliage, under hot and dry conditions (Bond and van Wilgen 1996). Such conditions are typical for pine forests in low to moderate productive sites in the Mediterranean basin resulting in high intensity fires and predictable stand replacing fires (Keeley and Zedler 1998). *Pinus halepensis* trees are more flammable than oaks (Dimitrakopoulos 1994). Pine forests are even more flammable than single trees because of the litter and the understorey shrub layer, many of which contain resins or flammable essential oils (Traubaud 2000). *Pinus halepensis* forests represent about 33% of the total burned area in the Mediterranean basin (Le Houérou 1974) and 17% of the burned area in Greece while it constitutes only 8.7% of the forested area (Arianoutsou and Ne'eman 2000). However, flammability is not necessarily a disadvantage. When flammability is entangled with other beneficial traits and less flammable neighbors have a lower survival rate, a single flammable mutant can spread and dominate a population (Bond and Midgley 1995). *Pinus*

halepensis fits this model because the resin content in pine needles contributes to its flammability and serves also as a defensive agent (Phillips and Croteau 1999) and because it has immense post-fire regeneration potential.

Selection by fire

To examine the possibility of direct selection by fire, we first have to know how long Mediterranean plants have been exposed to fires. Because most of the fires in the Mediterranean basin are of anthropogenic origin (Vázquez and Moreno 1998; Keidar 2001) and there is a low occurrence of summer thunderstorms, it is commonly accepted that fire history in this region is tightly connected with the beginning of the control of fire by man. The first fire-controlling hominids had no motivation or possibility to extinguish run-away fires. Therefore, at least from that time on, fires have been a constant phenomenon shaping the Mediterranean landscape. We will consider the first accepted evidence of hominid controlled fire as the starting point from which Mediterranean forests were under the continuous effects of fires.

The most cited ages of anthropogenic fires in the Mediterranean basin are 50,000 years BP from Mt. Carmel, Israel (Naveh 1974), and 400,000 years BP from Terra Amata, Nice, France (Prodon et al. 1987). However, sometime in the Acheulian, the hominids already had fire, which can be traced in fire hearths, burned flints, pieces of charcoal and, rarely, burned bones. There are some disputed indications that there were signs of limited burns in Ubeidiya (Jordan Valley, Israel) at ca. 1.4 million years BP (Bar-Yosef and Goren-Inbar 1993). Recent solid evidence for the earliest hominid use of fire is at the site of Geshert Benot Ya'aqov (upper Jordan River, Israel) around OIS 19, dated about 780,000 years BP (Goren-Inbar, pers. comm.). Garrod and Bate (1937) cited the presence of hearths in the Tabun (Mt. Carmel, Israel) E layer of ca. 7 m. Later, some of the beds in this unit were dated to ca. 350,000 years BP (Mercier et al. 1995).

Because, as far as we know, there are no studies of fire scars in long-living trees in the Mediterranean forests, fire return interval, can only be estimated from the area and frequencies of fires. Such data are rare and moreover, we do not know how fire return intervals changed during pre-historical and historical times. Lloret and Mari (2001) found no difference in fire frequency between the beginning and end of the second

millennium. However, fire return intervals can also be estimated from *P. halepensis* longevity, because post-fire stands are even-aged. The estimated average fire return interval typical, for pine forests of low to moderate reproductive sites, is within the range of 10-100 years (Keeley and Zedler 1998). The estimation for the Mediterranean basin is 25–50 (Naveh 1990, Agee 1998). All these figures are within the limits of 100–150 years, which fits *P. halepensis* longevity under natural conditions (Keeley and Zedler 1998). As *P. halepensis* has no recruitment under forest canopy, fire return interval is limited by its longevity. Therefore, we have conservatively estimated the average fire return interval to be 125 years. This estimate, combined with the earliest solid evidence of hominid control of fire, 780,000 years BP, result in a conservative estimate of 6240 generations of pine forests that were subjected to selection by fire in the Mediterranean basin.

Discussion

Pinus halepensis exhibits a dual life history strategy. It is remarkably efficient in exploiting new establishment opportunities generated both by fire and by other disturbances. This dual strategy, combined with the fact that its ability to regenerate after fire is one of the main characteristics of its invasive nature, makes the evaluation of any single trait difficult. In the previous sections we have discussed various life history traits and evaluated their contribution to post-fire regeneration or invasive ability in case of no fire of *P. halepensis*. Table 2 presents a summary of the specific contribution of the 21 examined traits. The distribution of the traits according their contribution to post-fire regeneration is: 18 positive, 2 negative and 1 indifferent. The distribution of the traits according their contribution to no-fire invasion is: 7 positive, 7 negative and 7 indifferent. A clear majority of the examined traits contribute positively to post-fire regeneration. Twelve traits contribute to both or to one and are indifferent to the other. Seven traits contribute positively to post-fire regeneration and negatively to no-fire invasion and only 2 traits contribute positively to no-fire invasion and negatively to post-fire regeneration. This balance demonstrates clearly that most traits make a positive contribution to post-fire regeneration. Only xeriscence has a negative effect.

In a recent study, Schwilk (2002) tested the hypothesis of correlated selection by fire of life history

Table 2. The contribution of main life history traits of *Pinus halepensis* to its post-fire regeneration or no-fire invasive ability. + is positive value, 0 is indifferent and – is negative value, * is positive contribution to post-fire and negative to no-fire situations.

Life history traits	Post-fire regeneration	No-fire invasion
*Flammability	+	–
Thin bark	+	0
Non self pruning of branches	+	0/–
Non self pruning of empty cones	+	0/–
Early age of first reproduction	+	+
Production of female cones first	+	+
Winged seeds and long range dispersal	0	+
*Color change in post-fire dispersed deeds	+	–
Non-serotinous cones:		
Xeriscence (drought-induced cone opening)	–	+
*Pyriscence (fire-induced cone opening)	+	–
Serotinous cones:		
Xeriscence (drought-induced cone opening)	–	+
*Pyriscence (fire-induced cone opening)	+	–
*Higher percentage in young trees	+	–
*Higher percentage in post-fire stands	+	–
Germination:		
Effect of light	+	+
Effect of temperature	+	+
*Seeds from serotinous cones	+	–
Effects of ash:		
pH	+	0
ammonium	+	0
nitrate	+	0
Relative establishment success	+	0

traits in pine species. Two alternative suites were defined: fire surviving and fire embracing strategies. The fire embracing strategy, in which plants invest little to survive fire, involves traits that enhance flammability and use fire to cue seedling establishment in the post-fire environment through serotinous cones. Significant correlations were found between several traits: serotiny was positively correlated with minimal reproduction age and negatively correlated with self-pruning and needle density. Self-pruning was positively correlated with bark thickness and mature height. Fire survival traits are negatively associated with serotiny. Non-self pruning and serotiny are evolutionarily linked traits over all examined species. Dispersal shows no strong association with any other trait.

This review supports placing *P. halepensis* among species exhibiting the fire embracing strategy. The cor-

relation between flammability and life history traits may emanate from two different reasons. The fire embracing strategy may select for increased flammability to ensure canopy fire and the seed release from the serotinous cones release. Yet, the correlation may result from the opposite reason: where flammability has evolved, plants are likely to evolve regeneration traits in response to the increased probability of fire (Schwilk and Ackerly 2001). In the absence of any direct evidence to distinguish between the two alternatives, we can only speculate on the basis of currently observed characteristics. Because *P. halepensis* is only partially serotinous, it seems to better fit the second explanation that serotiny has evolved in response to increased probability of fire. Such gene interaction mediated by the environment has been termed ‘niche construction’ (Laland et al. 1996; Odling-Smee et al. 1996).

In summary, a suite of traits has evolved convergently in the serotinous pines of the USA, which are subjected to selection by natural fires, and in Mediterranean pines, which are subjected mainly to selection by human-induced fires. Yet, some fire adaptive traits, such as full serotiny, are absent in *P. halepensis*. This may result from differences in fire regimes between the two regions (Agee 1998) and the existence of many other man-induced disturbances in the Mediterranean basin. It may also reflect differences in the time available for the evolutionary process. However, our conservative estimate of 6240 generations of pine forests that were subjected to selection by fire since the beginning of hominid control of fire 780,000 years BP seems sufficient for selection of (at least) simply inherited traits such as serotiny. The high selective value of serotiny is reflected by the increase in the proportion of serotinous cones from 40% to 85% in just one fire cycle. Further evidence for selection by fire comes from other related traits, including seed germinability and non-self pruning of empty cones. Altogether, a diverse array of evidence summarized in this review clearly indicates that fire may serve as a direct selective agent that shapes plant traits in the Mediterranean basin, and in *P. halepensis* in particular.

Acknowledgements

The authors would like to thank the two guest editors of the volume for their comments and suggestion on the manuscript.

References

- Agee J.K. 1998. Fire and pine ecosystems. In: Richardson D.M. (ed.), *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, pp. 193–218.
- Arianoutsou M. and Ne'eman G. 2000. Post-fire regeneration of natural *Pinus halepensis* forests in the east Mediterranean. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 269–289.
- Bar-Yosef O. and Goren-Inbar N. 1993. The Lithic Assemblages of Ubeidiya. *Qedem* 34, Institute of Archaeology, Hebrew University, Jerusalem.
- Bond M.J. and van Wilgen B. 1996. *Fire and Plants*. Chapman and Hall, London.
- Bond W.J. and Midgley J.J. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73: 79–85.
- Charnov E.L. 1982. *The Theory of Sex-Allocation*. Princeton University Press, Princeton.
- Daskalakou E.N. and Thanos C.A. 1996. Aleppo pine (*Pinus halepensis*) post-fire regeneration: the role of canopy and soil seed banks. *International Journal of Wildland Fire* 6: 59–66.
- Dimitrakopoulos A.P. 1994. Methodology for measuring ignition point temperatures of plant species. In: Viegas, D.X. (ed.), *Proceedings of 2nd International Conference on Forest Fire Research*. Coimbra, Portugal, pp. 435–443.
- Doussi M.A. and Thanos C.A. 2002. The mechanism of cone opening in *Pinus halepensis* and *P. brutia* – morphology and physiology. Abstract in MEDPINE 2 International Conference 'Conservation, Regeneration and Restoration of Mediterranean Pines and their Ecosystems'. Chania, Greece, p. 20.
- Enright N.J., Marsula L., Lamont B.B. and Wissel C. 1999a. The ecological significance of canopy seed storage in fire-prone environments: a model for non-resprouting shrubs. *Journal of Ecology* 86: 946–959.
- Enright N.J., Marsula L., Lamont B.B. and Wissel C. 1999b. The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *Journal of Ecology* 86: 960–973.
- Eshel A., Henig-Sever N. and Ne'eman G. 2000. Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. *Plant Ecology* 148: 175–182.
- FAO 1999. *Forest Fire Statistics*. Timber Bulletin Vol. LII No. 4.
- Freeman D.C., Drant McArthur E., Harper K.T. and Blauer A.C. 1981. Influence of environment on the floral sex ratio of monoecious plants. *Evolution* 35: 194–197.
- Garrod D.A.E. and Bate D.M.A. 1937. *The Stone Age of Mt Carmel: Vol 1. Excavations at the Wadi El-Mughara*. Clarendon Press, Oxford.
- Gauthier S., Bergeron Y. and Simon J-P. 1996. Effects of fire regime on the serotiny level of jack pine. *Journal of Ecology* 84: 539–548.
- Goubitz S. 2001. *Reproduction Ecology of Pinus halepensis, a Monoecious, Wind-Pollinated and Partially Serotinous Mediterranean Pine Tree*. Ph.D. dissertation, Utrecht University, Utrecht.
- Goubitz S., Werger M. and Ne'eman G. In press. Canopy seed bank structure in relation to fire tree size and density. *Plant Ecology*.
- Goubitz S., Werger M. and Ne'eman G. 2003. Germination response to fire-related factors of seeds from non-serotinous and serotinous cones. *Plant Ecology* 169: 195–204.
- Habrouk A., Retana J. and Espelta J.M. 1999. The role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology* 145: 91–99.
- Henig-Sever N., Eshel A. and Ne'eman G. 1996. pH and osmotic potential of pine ash as post-fire germination inhibitors. *Physiologia Plantarum* 96: 71–76.
- Henig-Sever N., Eshel A. and Ne'eman G. 2000. Regulation of the germination of Aleppo pine (*Pinus halepensis*) by nitrate, ammonium, and gibberellin, and its role in post-fire forest regeneration. *Physiologia Plantarum* 108: 390–397.
- Higgins S.I. and Richardson D.M. 1998. Pine invasions in the southern hemisphere: modeling interactions between organisms, environment and disturbance. *Plant Ecology* 135: 79–93.
- Izhaki I. and Ne'eman G. 2000. Soil seed banks in east Mediterranean pine forests. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 167–182.
- Keeley J.E. 1993. Smoke-induced flowering in the fire-lily *Cyrtanthus ventricosus*. *South African Journal of Botany* 59: 638.

- Keeley J.E. and Fotheringham C.J. 1997. Gas emissions in smoke-induced seed germination. *Science* 276: 1248–1251.
- Keeley J.E. and Zedler P.H. 1998. Life history evolution in pines. In: Richardson D.M. (ed.), *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, pp. 219–250.
- Keidar G. 2001. Causes and Factors in Forest Fires in Israel. Thesis submitted for MA degree, Department of Geography, University of Haifa, Haifa, Israel (In Hebrew with English abstract).
- Laland K.N., Odling-Smee F.J. and Feldman M.W. 1996. The evolutionary consequences of niche construction; a theoretical investigation using two-locus theory. *Journal of Evolutionary Biology* 9: 293–316.
- Lamont B.B., Le Maitre D.C., Cowling R.M. and Enright N.J. 1991. Seed canopy storage in woody plants. *Botanical Review* 57: 277–317.
- Le Houérou H.N. 1974. Fire and vegetation in the Mediterranean basin. Annual Tall Timber Fire Ecology Conference 13: 237–277.
- Leone V., Borghetti M. and Saracino A. 2000. Ecology of post-fire recovery in *Pinus halepensis* in southern Italy. In: Trabaud L. (ed.), *Life and Environment in Mediterranean Ecosystems*. WIT Press, Southampton, pp. 129–154.
- Lloret F. and Mari G. 2001. A comparison of the medieval and the current fire regimes in managed pine forests of Catalonia (NE Spain). *Forest Ecology and Management* 141: 155–163.
- Lotan J.E. 1976. Cone serotiny fire relationships in lodgepole pine. Annual Tall Timber Fire Ecology Conference 13: 267–278.
- Martínez-Sánchez J.J., Marin A., Herranz J.M., Ferrandis P. and de las Heras J. 1995. Effects of high temperatures on germination of *Pinus halepensis* Mill. and *P. pinaster* Aiton subsp. *pinaster* seeds in southeast Spain. *Vegetatio* 116: 69–72.
- Mercier N., Valladas H., Valladas G., Reyss J.-L., Jelinek A., Meignen L. and Joron J.-L. 1995. TL dates of burnt flint from Jelink's excavations at Tabun and their implications. *Journal of Archaeological Science* 22: 495–509.
- Mirov N.T. 1967. *The Genus Pinus*. Ronald Press, New York.
- Nathan R. and Ne'eman G. 2000. Serotiny, seed dispersal and seed predation in *Pinus halepensis*. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 105–118.
- Nathan R., Safriel U. N., Noy-Meir I. and Schiller G. 1999. Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous, wind-dispersed tree. *Journal of Ecology* 87: 659–669.
- Nathan R., Safriel U. N., Noy-Meir I. and Schiller G. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology* 81: 2156–2169.
- Naveh Z. 1974. Effects of fire in the Mediterranean region. In: Kozlowski T.T. and Ahlgren C.E. (eds), *Fire and Ecosystems*. Academic Press, New York, pp. 401–434.
- Naveh Z. 1990. Fire in the Mediterranean – a landscape ecological perspective. In: Goldammer J.G. and Jenkins M.J. (eds), *Fire ecosystem dynamics*. SPB Academic Publishing, The Hague, pp. 1–20.
- Ne'eman G. and Izhaki I. 1998. Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forest. *Ecography* 21: 535–542.
- Ne'eman G. and Trabaud L. (eds) 2000. *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden.
- Ne'eman G. 2000. The effect of burned pine trees on post-fire regeneration. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 303–320.
- Odling-Smee F.J., Laland K.N. and Feldman M.W. 1996. Niche construction. *American Naturalist* 147: 641–648.
- Perry D.A. and Lotan J.E. 1979. A model of fire selection for serotiny in lodgepole pine. *Evolution* 33: 958–968.
- Phillips M.A. and Croteau R.B. 1999. Resin based defenses in conifers. *Trends in Plant Science* 4: 184–190.
- Prodon R., Fons R. and Athias-Binche F. 1987. The impact of fire on animal communities in Mediterranean area. In: Trabaud L. (ed.), *The Role of Fire in Ecological Systems*. SPB Academic Publishers, The Hague, pp. 121–157.
- Richardson D. 2000. Mediterranean pines as invaders in the Southern Hemisphere. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 131–142.
- Roitemberg D. and Ne'eman G. 1999. Post-fire seed dispersal in *Pinus halepensis*. Abstract in MEDPINE, International Workshop on Mediterranean Pines. February 1999, Beit Oren, Israel, p. 46.
- Saracino A., Pacella R., Leone V. and Borghetti M. 1997. Seed dispersal and changing seed characteristics in *Pinus halepensis* Mill. forest after fire. *Plant Ecology* 130: 13–19.
- Schwilk D.W. and Ackerly D.D. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94: 326–336.
- Schwilk D.W. 2002. *Plant Evolution in Fire-Prone Environments*. Ph. D. dissertation Stanford University, Stanford.
- Shmida A., Lev-Yadun S., Goubitz S. and Ne'eman G. 2000. Sexual allocation and gender segregation in *Pinus halepensis*, *P. brutia* and *P. pinea*. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 91–104.
- Tapias R., Gil L., Fuentes-Utrilla P. and Pardos J.A. 2001. Canopy seed banks in Mediterranean pines of southeastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology* 89: 629–638.
- Teich A.H. 1970. Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. *Canadian Journal of Botany* 48: 1805–1809.
- Thanos C.A. 2000. Ecophysiology of seed germination in *Pinus halepensis* and *P. brutia*. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 37–50.
- Thanos C.A. and Daskalaku E.N. 2000. Reproduction in *Pinus halepensis* and *P. brutia*. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 79–90.
- Thanos C.A., Georghiou K., Kadis C. and Pantazi C. 1992. Cistaceae: a family with hard seeds. *Israel Journal of Botany* 41: 251–263.
- Trabaud L. 1987. Fire and survival traits in plants. In: Trabaud L. (ed.), *The Role of Fire in Ecological Systems*. SPB Academic Publishers The Hague, pp. 65–90.
- Trabaud L. 2000. Post-fire regeneration of *Pinus halepensis* forests in the west Mediterranean. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and P. brutia Ecosystems in the Mediterranean Basin*. Backhuys Publishers, Leiden, pp. 257–268.

- Trabaud L., Michels C. and Grosman J. 1985. Recovery of burnt *Pinus halepensis* Mill. Forests. II. Pine reconstitution after fire. *Forest Ecology and Management* 13: 167–179.
- Vázquez A. and Moreno J.M. 1998. Patterns of lightning- and people-caused fires in peninsular Spain. *International Journal of Wildland Fire* 8: 103–115.
- Whelan R.J. 1995. *The Ecology of Fire*. Cambridge University Press, Cambridge.
- Willson M.F. 1983. *Plant Reproductive Ecology*. John Wiley and Sons, New York.