

# POST-FIRE REGENERATION OF NATURAL *PINUS HALEPENSIS* FORESTS IN THE EAST MEDITERRANEAN BASIN

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## Introduction

*Pinus halepensis* Mill. forests are estimated to cover from  $2.5 \times 10^6$  ha (Quézel 2000) to about  $3.5 \times 10^6$  ha (Dafis 1987) in the Mediterranean basin. They extend from Morocco and Algeria in the Southwest, Portugal and Spain in the Northwest and Italy to Greece in the Northeast and to Syria, Israel and Jordan in the Southeast (Nahal 1962, Panetsos 1981, Quézel and Barbéro 1992, Barbéro *et al.* 1998, Quézel 2000). The division of the Mediterranean basin into four distinct parts reflects climatic differences in the annual average rainfall and temperatures, the duration of the drought season and the amount of summer rains, all of which are reflected in the average annual potential evapotranspiration (Blondel and Aronson 1995). The main Aleppo pine forests are in Spain, France and North Africa and grow under the line of 1250 mm annual potential evapotranspiration (Blondel and Aronson 1995, Quézel 2000). The Aleppo pine forests of Greece (which cover 371984 ha, 8.72% of the total forested area) and the Middle East (where they form mostly small and isolated stands) grow in more arid conditions than those of the west Mediterranean (Barbéro *et al.* 1998). Such a climatic difference may affect fire intensity and frequency, but mainly the post-fire regeneration process that is the focus of this chapter.

Fire incidents are very common in the Mediterranean. Between 1989-1993, it is estimated that 225,000 fire events consumed 26,000,000 ha of forests in the South of the European Union (European Commission 1996), including Greece, Italy, Spain, France and Portugal. During a 26 year period (1965-1990) almost one fifth (~21%) of the fire events in Greece, burst over *P. halepensis* forests, consuming 122,015 ha, which are approximately 17% of the total burned area. Considering that *P. halepensis* forests constitute 8.72% of the total forested area in Greece, this amount becomes increasingly important. In Israel, during a 12 year period (1980-1991) 7,528 fires consumed about 13,600 ha of natural maquis and planted pine forests (Kleiot and Keidar 1992). In the east Mediterranean region, fire regime may be connected to the long human intervention in this region (Naveh 1975). However, the first

archaeological evidence of fire occurrence in the xerophytic landscapes goes back to the end of the Middle Stone Ages (Higgs *et al.* 1967).

To study the post-fire regeneration of natural *P. halepensis* forest it is necessary to tackle the responses of individual species both at the population level and at the level of the whole plant community. Most of the short-term (1-10 y) studies of post-fire regeneration were carried out by repeated measurements (diachronic studies) of permanent plots. However, long-term changes are usually studied simultaneously in several plots that differ mainly in their age since last fire (synchronic or chronosequence studies). Because of methodological differences among the studies, comparison of data should be done with special care.

Plant nomenclature follows Flora Hellenica (Strid and Tann 1997), Med Checklist (Greuter *et al.* 1984-1989) and Flora Europaea (Tutin *et al.* 1964-1980) for Greece and Feinbrun and Danin (1991) for Israel.

### Plant Adaptive Traits

According to their post-fire mode of regeneration, plants are divided into two groups. Post-fire resprouters survive fires and resprout mainly from root crown buds. They have non-refractory seeds, that do not survive fires. Post-fire seeders are killed by fires and recruit from soil or canopy stored seed banks (Trabaud 1987, Keeley 1991).

Mature Aleppo pine forests usually have an understorey composed mainly of several small trees and shrubs (e.g., *Arbutus unedo*, *A. andrachne*, *Quercus coccifera*, *Q. calliprinos* and *Pistacia lentiscus*), some dwarf shrubs (e.g., *Cistus creticus*, *C. salvifolius* and *C. monspeliensis*), several woody lianas (e.g., *Smilax aspera*, *Clematis vitalba*), and some perennial herbs (e.g., *Brachypodium sylvaticum*, *Reichardia picroides*) as well as many annual plants.

The post-fire regeneration mode of common species in the pine forest communities of Greece and Israel is presented in *Appendix 1*. Most of the evergreen sclerophyllous trees and shrubs are obligate resprouters (Lahav 1988, Trabaud 1987, Arianoutsou 1998). *Pinus halepensis* is exceptional among all trees, as it is the only obligate seeder. Most of the post-fire regenerating perennial species in pine forests in Greece and Israel (*Appendix 1*) are facultative resprouters. Among the dwarf shrubs, members of the Cistaceae constitute the major group of obligate seeders (Thanos *et al.* 1992, Kazanis and Arianoutsou 1996), although there is evidence that some representatives may also regenerate through resprouting (e.g., *C. salvifolius*, Skourou and Arianoutsou unpublished data). Among the annual herbs, which are obviously obligate seeders, members of the Leguminosae family are a prominent group (Arianoutsou and Thanos 1996, Kazanis and Arianoutsou 1996). A relatively small group of plants regenerate both by germination and resprouting (e.g., *Rhus coriaria*, *Calicotome villosa*, *Sarcopoterium spinosum*, *Salvia fruticosa*, *Anthyllis hermanniae*, *Genista acanthoclada*, *Satureja thymbra* and some perennial herbs).

### Population Reconstruction of Key Groups

Resprouting species are not killed by fire and their post-fire populations remain almost unchanged by fire. Three key groups of seeding species will be considered in detail: the herbaceous legumes, the rockroses (*Cistus* spp.) and the Aleppo pine itself.

#### Legumes

The herbaceous legumes (Leguminosae) are an important functional key-group of the Aleppo pine forest communities of the east Mediterranean for two main reasons. Firstly, because of their large contribution to vegetation cover and biomass during the early post-fire period (Fig. 1), they protect the soil from erosion. Secondly, they contribute to the system's nitrogen replenishment. It is well known that among the essential nutrients nitrogen is the most sensitive one, as it is lost into fire's smoke (Arianoutsou and Margaris 1981a). Herbaceous legumes contribute to the N-replenishment in two ways: (1) they are able to fix nitrogen almost immediately after the establishment of their post-fire seedlings (Papavassiliou and Arianoutsou unpublished data), (2) the decomposition rate of their litter in the post-fire soil environment is relatively rapid (Arianoutsou *et al.* in preparation). Thus the subsequent nitrogen release from the decomposing plant material should also be rapid within the period of the respective decomposition process (Arianoutsou 1993).

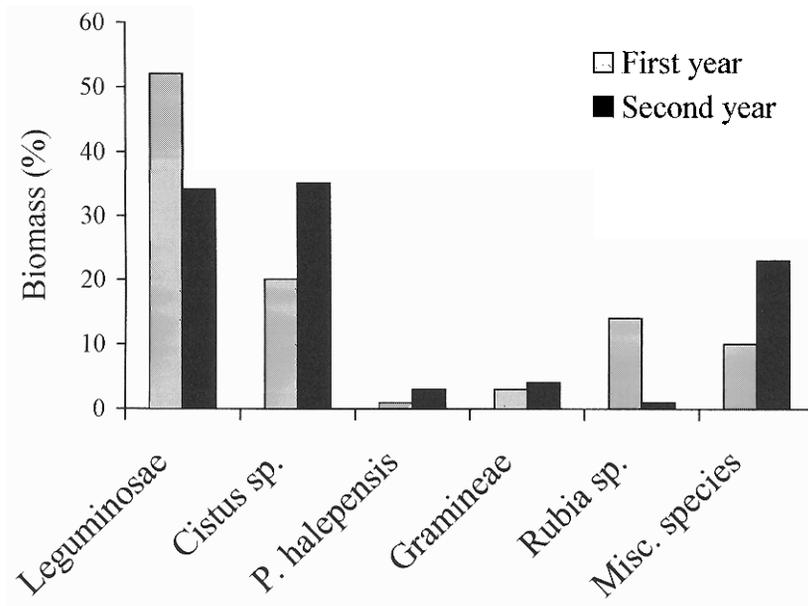


Fig. 1. Relative contribution of various taxa to the overall above ground plant biomass during the first two regeneration years after fire in an Aleppo pine forest (Kapandriti, Attica, Greece), (after Papavassiliou and Arianoutsou in: Arianoutsou 1995).

Although only a few individuals of herbaceous legumes are found in mature Aleppo pine communities, their presence and relative contribution to the plants' cover and biomass is incredibly high in the Greek post-fire regenerating forests (Papavassiliou and Arianoutsou 1993, 1997, Arianoutsou *et al.* 1996). This is due to a massive germination of their dormant hard-coated seeds in the soil seed bank, which occurs during the first three post-fire years (Fig. 2). This massive germination, during the first post-fire winter is attributed to the direct effect of heat released by fire upon their hard seed coats (Doussi and Thanos 1993, Arianoutsou 1995). Most of these taxa reach their reproductive maturity during the first post-fire year (Papavassiliou *et al.* 1994). Several of the seeds produced by the legumes germinate readily during the next two rainy seasons thus increasing legume density (Fig. 2), whereas a large proportion of the seed cohort falls on the ground, where it lies dormant forming a soil seed bank (Papavassiliou *et al.* 1994, Arianoutsou *et al.* 1996). Heat shock also increased germination of Spanish legume species (Herranz *et al.* 1998).

The herbaceous legumes remain a dominant component of the regenerating Aleppo pine forest community in Greece for about 3 years (Kazanis and Arianoutsou in preparation). After that period, only a few scattered individuals of some species (e.g., *Trifolium stellatum*, *T. campestre*, *Lathyrus digitatus*, *Coronilla scorpioides*, *Medicago minima*, *M. polymorpha*, *Onobrychis* spp., *Scorpiurus muricatus*) can be found. All other species are absent from the community but present as dormant seeds in the soil seed bank, waiting for the next fire disturbance to come.

After a wildfire in 1983 on Mt. Carmel in Israel, Lahav (1988) recorded 41 legumes out of 269 species in the burned and adjacent unburned Aleppo pine forest. Legume species were over-represented among the species with increased population size after fire (Table 1), whereas only 5 species (*Coronilla cretica*, *Lathyrus blepharicarpus*, *Medicago scutelatta*, *Onobrychis squarrosa* and *Pisum syriacum*) were present solely in the unburned forest. This indicates that fire virtually did not change the composition of legume species but did affect their abundance drastically.

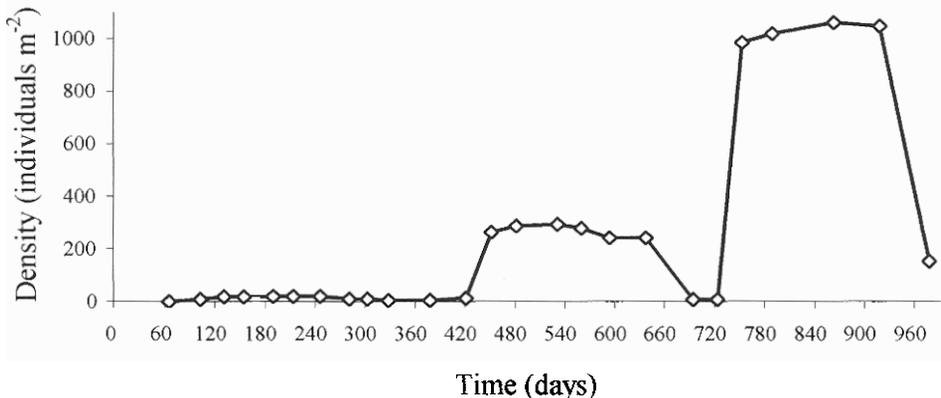


Fig. 2 Mean monthly legumes' seedling density in a burned Aleppo pine forest, Kapandriti, Attica, Greece, for 3 consecutive years after fire; time 0 is set at October 1<sup>st</sup> of the first year after fire, (after Papavassiliou and Arianoutsou in: Arianoutsou 1995)

Table 1. The number of species that their population size increased, remained unchanged, decreased or were absent from a burned pine forest on Mt. Carmel, Israel in comparison with an adjacent unburned forest (after Lahav 1988).

Abundance	Total species (#)	Legume species (#)	Legume species (%)
Increased	81	21	25.9
Unchanged	119	11	9.2
Decreased	29	4	13.8
Absent	40	5	12.5
Total	269	41	15.2 *

\* Overall average percentage.

In southern France, legumes are present after fire, but they are very scarce and do not play an important role. There, the post-fire legume species are the same as the pre-fire ones (Trabaud, personal communication). However, no specific study has investigated this issue. In SE Spain, 20% of the species recorded during four years after fire were herbaceous legumes and only 3.8% were woody legumes (Martinez-Sanchez *et al.* 1994). In another 12-years-old pine forest, no legumes were recorded in the vegetation, whereas 5 *Trifolium* species were recorded in the soil seed bank (Trabaud *et al.* 1997).

### *Cistus* species

*Cistus* is probably the most typical fire-following plant taxon in the Mediterranean basin. Many studies demonstrated that heat shock or fire induced germination in all tested *Cistus* species (e.g., Papanastasis and Romanas 1977, Arianoutsou and Margaris 1981b, Thanos and Georghiou 1988, Trabaud and Oustric 1989, Roy and Sonié 1992, Ferrandis *et al.* 1999, Ne'eman and Izhaki 1999b), as well as all other tested members of the Cistaceae family (Thanos *et al.* 1992). The hard seed coat, which is responsible for the effect of fire (Aronne and Mazzoleni 1989), was probably not selected by fire, but this does not decrease its adaptive value in case of fire (Trabaud 1987, Thanos *et al.* 1992).

*Cistus* seeds are a major component in Mediterranean pine soil seed banks (Izhaki and Ne'eman 2000). The very high density of *Cistus* seedlings emerging during the first post-fire winter is well documented all over the Mediterranean basin (Legrand 1987, Ne'eman *et al.* 1992, Legrand 1993, Espirito-Santo *et al.* 1993, Ne'eman 1994, Santiesteban *et al.* 1993, Kazanis and Arianoutsou 1996, Ferran and Vallejo 1998, Tarrega *et al.* 1998). From all these studies it is clear that seedling recruitment of all *Cistus* species studied occurs massively during the first post-fire year, although a few seedlings may appear during the second post-fire year as well. Except in Portugal (Clemente *et al.* 1994) where reported densities are relatively low, *Cistus* species densities in all Mediterranean countries range between 35-100 seedlings m<sup>-2</sup>. Seedling mortality is high during the first post-fire summer. Thereafter, as described in the only long-term study published so far (Luis-Calabuig *et al.* 1994), the densities of *Cistus* remained the same for three more years.

Roy and Sonié (1992) studied the age structure of *C. monspeliensis* and *C. albidus* populations in France. They concluded that most recruitment occurs during the first 5 years following fire. Reproductive maturity begins 1-2 years after fire, and full reproductive capacity is reached at the stand age of 5, and natural death occurs at about 12-15 years. Troumbis (1993) studied a *C. creticus* population in Central Greece 60 years after fire with an age range of 1-11 years, and 5 and 6 year old plants constituted about 50% of the population. In Greece, *Cistus* species, generally, reach reproductive maturity in the second post-fire year, and they appear to have a relatively short life span, usually not more than 15 years (Arianoutsou 1998).

To conclude, the establishment of a dense *Cistus* population is dependent on fire. The short juvenile period until first reproduction makes it resilient in a relatively frequent fire regime. The decline of a population begins at an age of 15. However, if local conditions are not favourable for pine trees and it is not shaded, the *Cistus* population can remain for several decades. In such cases, 10-15 year old individuals dominate the population and recruitment is achieved by the small proportion of the non-dormant seeds and by older ones with eroded seed coats. If the canopy of the regenerating forest is completely closed, the *Cistus* stand will disappear from the understorey, but its soil seed bank will ensure its regeneration after the next forest fire.

### *Pinus halepensis*

Fire causes a massive seed release from the Aleppo pine cones, the opening of which is induced by the high temperatures during fire (Nathan and Ne'eman 2000). Seeds fall on the burned ground mainly during the first post-fire month, and germinate massively during the first post-fire year after the onset of the rainy season (Fig. 3). Germination of *P. halepensis* seeds is optimal at 20°C in darkness, but is inhibited by far red light, indicating that germination is under phytochrome control (Thanos and Skordilis 1987, Skordilis 1992). Therefore, the increased post-fire seed germination may be partially attributed to the more favourable light conditions after the consumption of the plant canopy by fire (Thanos and Skordilis 1987, Skordilis 1992, Thanos 2000). Pine seeds are practically absent from the soil seed bank of pine stands of all post-fire ages (Izhaki and Ne'eman 2000), therefore, almost no new seedlings are registered during the second post-fire year (Daskalakou and Thanos 1997, Kazanis and Arianoutsou in preparation).

In Attica, Central Greece, maximal density of post-fire *P. halepensis* seedlings is between 3 and 30 m<sup>-2</sup> at the end of the first germination period and falls to 2-23 seedlings m<sup>-2</sup> at the end of the second post-fire year (Daskalakou and Thanos 1997, Kazanis and Arianoutsou in preparation, respectively). Tsitsoni (1997) presents total mean regeneration indices ranging from 0.60 to 14.26 for a period of 1-8 years after fire for burned stands of Aleppo pine in Chalkidiki, North Greece. In natural Aleppo pine stands on Mt. Carmel, Israel, the average density was about 27 seedling m<sup>-2</sup> at the end of the first winter and varied between 6 and 14 seedling m<sup>-2</sup> after the first summer (Ne'eman *et al.* 1992, Izhaki and Ne'eman 1996). Seedling density in a planted Aleppo pine stand on the Judean Mountains, Israel, in the first post-fire winter ranged from 12 to 25 seedlings m<sup>-2</sup> (Eshel *et al.* 2000). Saracino and Leone (1993) and Leone *et al.* (1999) reported a mean seedling density of 1.2 m<sup>-2</sup>

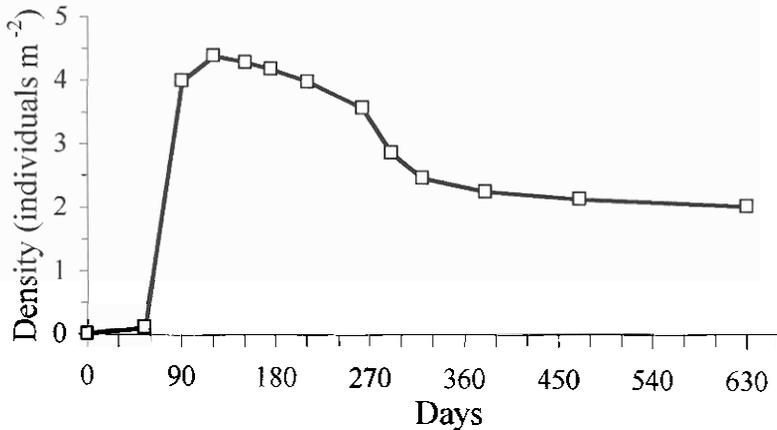


Fig. 3. Density of *P. halepensis* seedlings in a burned forest (Stamata, Attica, Greece), for 2 consecutive years after fire; time 0 is set at October 1<sup>st</sup> of the first year after fire, (after Daskalakou and Thanos 1997).

two years after fire and 0.59 m<sup>-2</sup> four years after fire in pine forests growing on sand dunes in southern Italy. The wide range of recorded densities reflects various differences among sites such as: latitude, altitude, slope and aspect that affect temperatures and precipitation, age and density of the burned trees, fire season and intensity. However, the high variability also reflects the large heterogeneity of the pine forest that is composed of gaps, shrubby area, small and large trees. The thick ash layer left after fire under large trees drastically reduces seedling density and affects the spatial pattern of post-fire seedling recruitment (Ne'eman 2000).

Mortality of the young pine saplings is highest during the first post-fire summer (Fig. 4). The percentage of surviving seedlings during the first three years after fire, in Greece, is best described by the equation  $Y = 73.145 e^{-0.154(X-9)} + 20$  (d.f. = 6,  $r = 0.978$ ,  $P < 0.001$ ), where Y is the percentage of survival, and X is time since fire, in months (Thanos 1999). The mortality in subsequent years is considerably lower than during the early establishment period and accounted for only 25% of the overall death records during the first two post-fire years (Thanos 1999). This also has been reported by Saracino *et al.* (1993) for an Aleppo pine stand in a dune habitat in southern Italy. Seedling mortality during the first and second post-fire years on Mt. Carmel, Israel, was 58% and 27% respectively (Ne'eman *et al.* 1993, 1995). Intense intraspecific competition among Aleppo pine saplings as well as interspecific competition mainly with the numerous *Cistus* seedlings were observed during the first four-year period after fire on Mt. Carmel, Israel (Lahav 1988, Katz 1993, Ne'eman *et al.* 1993, 1995). Because water is the main limiting resource during the first summer, it seems that competition should play a more important role in the eastern part of the Mediterranean than in the western part.

Between the ages of about two and five and later, between 20 and 40 years, the main cause for mortality in pine plantations in Israel is the pine bast scale *Matsucoccus josephi* Bodenheimer & Hrpaz (Homoptera). The scale settles on all above ground parts and secretes a poisonous saliva during feeding that disrupts water

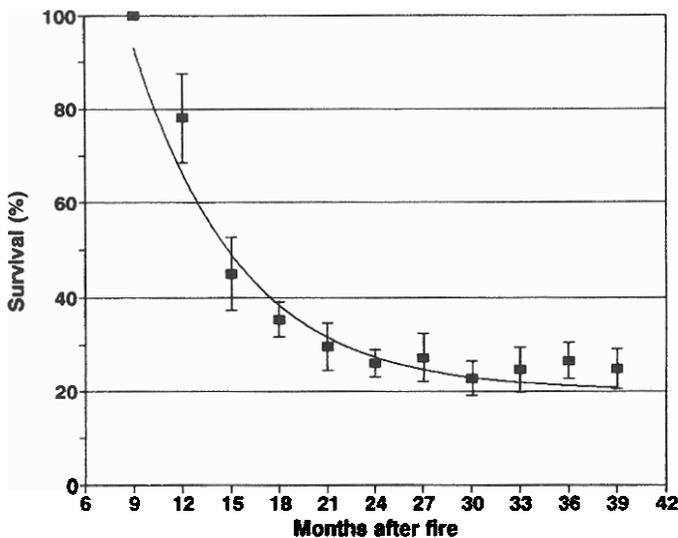


Fig. 4. Percentage of survived *P. halepensis* saplings in an Aleppo pine forest (Mt. Parnes, Attica, Greece) during the first 3 post-fire years (after Thanos 1999).

transport and results in the death of new growth or the entire plant (Mendel and Lipshchitz 1988). The scale originates from *P. brutia* and therefore damages Aleppo pine forests of the east Mediterranean region (Mendel 2000), but it also might be a threat to west Mediterranean forests in the future.

Pine trees are not preferred forage for domestic herbivores. However, heavy grazing, mainly by goats, which are more common in the eastern part of the Mediterranean basin, can damage young regenerating Aleppo pine saplings. Porcupines also may cause local but serious damage to young post-fire saplings, as was observed on Mt. Carmel, Israel (Izhaki and Ne'eman 1996).

Because of the effect of the large pine trees on post-fire seedling recruitment (Ne'eman *et al.* 1992) and the differences among microhabitats (Ne'eman and Izhaki 1999b), pine saplings growing in the microsites of their burned 'mother' trees develop faster than their siblings in the rest of the burned forest. These saplings have high probability of becoming the post-fire pine generation (Ne'eman 2000).

As a result of the above factors, that is, competition, pests and herbivores, tree density in regenerating pine forests on Mt. Carmel, Israel, is constantly decreasing from the extremely high initial post-germination density of about 270,000 seedlings ha<sup>-2</sup>, reaching the average density of 312 ha<sup>-2</sup> in unburned mature forests (Fig. 5). At this point we should clearly indicate that data for the early post-fire period are usually obtained from permanent plots in regenerating forests, whereas data for the later regeneration are gathered from various forest stands, which form a post-fire chronosequence. The results of a study that combined both methods demonstrate a constant decrease in pine density along the time scale (Fig. 5, Table 2). A similar decrease in pine density was found in Greece (Kazanis and Arianoutsou in preparation). In southern France the

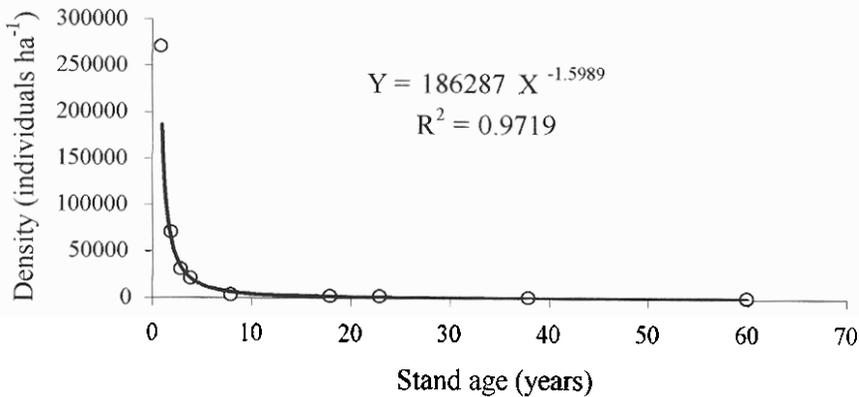


Fig. 5. Pine sapling density in various pine stands (see Table 2) (Mt. Carmel, Israel) differing in their post-fire age.

initial Aleppo pine sapling density is low, but it is followed by a temporal increase to a maximal density at 10–15 years, before a decrease to the final density occurs (Trabaud *et al.* 1985, Trabaud 2000).

*Pinus halepensis* saplings do not seem to grow very fast, although their growth follows a rather linear kinetic strategy for the first 8 years after fire (Fig. 6), as reported by Thanos (1999) for Mt. Parnes, Greece. Konstantinidis and Chatziphilipidis (1994) reported that Aleppo pine saplings in forests of Chalkidiki Peninsula, Greece, doubled their height from a mean of 8 cm in the first year post-fire to 16 cm in the second year. On Mt. Carmel, Israel, seedling heights were 15, 21 and 27 cm in the second, third and fourth year after fire (Izhaki and Ne'eman 1996). Tsitsoni (1997) states that the height of *P. halepensis* saplings is positively correlated with their position on the slope with maximal growth in the foothills. Growth of post-fire pine seedlings in the west Mediterranean during the first post-

Table 2. Aleppo pine tree densities in various stands on Mt. Carmel, Israel.

Site	Fire	Average age	Individuals • ha <sup>-1</sup>
Hai-bar	1989	1	270000
Hai-bar	1989	2	70000
Hai-bar	1989	3	30000
Hai-bar	1989	4	20000
Hai-bar	1989	8	2750
Beit Oren	1983	18	1500
Etzba	1973	23	1590
Arkan	1956	38	670
Oranim	unburned	50	200
Sanatorium	unburned	50	190
Etzba	unburned	50	310
Me'arot	unburned	50	550

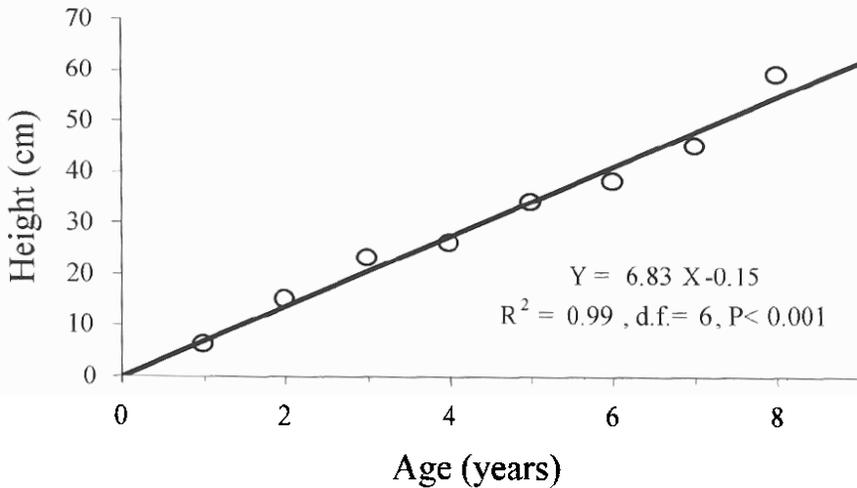


Fig. 6. Early post-fire growth of Aleppo pine saplings in a burned area (Mt. Parnes, Attica, Greece); sapling height was measured at the end of each growing season (after Thanos 1999).

fire decade is linear with an average rate of about 10 cm per year (Trabaud 2000); whereas in the east Mediterranean the annual growth is about 7 cm. Saplings growing in the microsites of the burned trees presented faster growth than their siblings (Ne'eman and Izhaki 1999a)

Evidence from a post-fire synchronic study in Attica, Greece (Kazanis and Arianoutsou in preparation) reveals that Aleppo pine saplings have gained almost 40% of their final height in 25-year-old stands. On Mt. Carmel, Israel, the average height of four unburned mature pine forests was 9.3 m (not including individuals less than 1 m high), and that of a stand 38 years old was 10.4 m. It should be noted that height is sometimes an insufficient parameter for determining tree development, especially in post-fire stands. In dense stands, trees might be taller but with lower biomass and lower reproductive capacity than shorter trees with wide canopies.

As reported by Thanos (1999), the reproductive shift in Aleppo pine occurs at an early age. In a burned Aleppo pine forest on Mt. Parnes, a few pine saplings produced female conelets at the age of 4 years after fire. However, at the population level, cone production definitely commences 6-7 years after fire both in Greece and Israel (personal observations). Two main factors could be connected with selection by relatively frequent fires. Young pine trees begin their reproduction as females rather than as males (Shmida *et al.* 2000, Thanos and Daskalaku 2000), and they produce a relatively high fraction of serotinous cones (Goubitz *et al.* unpublished data). The early production of serotinous cones enhances the establishment of a canopy stored seed bank, thus reducing the immaturity risk, namely the risk of being re-burned at a juvenile stage without post-fire recruitment ability. The reproduction of Aleppo pine is reviewed in this volume (Shmida *et al.* 2000, Thanos and Daskalaku 2000).

To conclude, depending on local conditions, it takes about 30-40 years for post-fire regenerating pine trees to gain the cover and size of mature unburned pines (Schiller *et al.* 1997).

## Pine Forest Community

Only a few studies dealing with post-fire recovery of *P. halepensis* forest communities have been conducted in the east Mediterranean region. Kazanis and Arianoutsou (1996) and Kazanis and Arianoutsou (in preparation) have extensively studied a number of sites in Attica and Euboea, Greece. These sites form a chronosequence from age 0 to over 50 years after fire, which is considered a mature Aleppo pine community. These sites also have been studied diachronically for 2-4 consecutive years. At most of the time-points, more than one site was monitored. Changes in community composition were also studied diachronically for four years after the 1983 fire on Mount Carmel, Israel (Lahav 1988) and synchronically covering up to 38 years after fire. Several mature unburned stands have also been studied for the same parameter (Schiller *et al.* 1997). Kutiel (1997, 2000) studied the effects of local parameters, such as aspect and repeated fires, on species diversity. The results of all the above-cited studies follow the same pattern as described for France (Trabaud and Lepart 1980) and for the whole west Mediterranean basin (Trabaud 2000). Species richness during the first post-fire spring is already higher than that in unburned mature pine forests. Species richness increases more during the second and third post-fire year. Thereafter, a decrease in species richness occurs, which is best described by a power function, until a constant value typical to mature unburned forests is reached (Fig. 7). A similar pattern can be observed despite the differences in the absolute values of species richness. The differences could reflect methodological differences, such as in plot area, or the use of transects instead of plots.

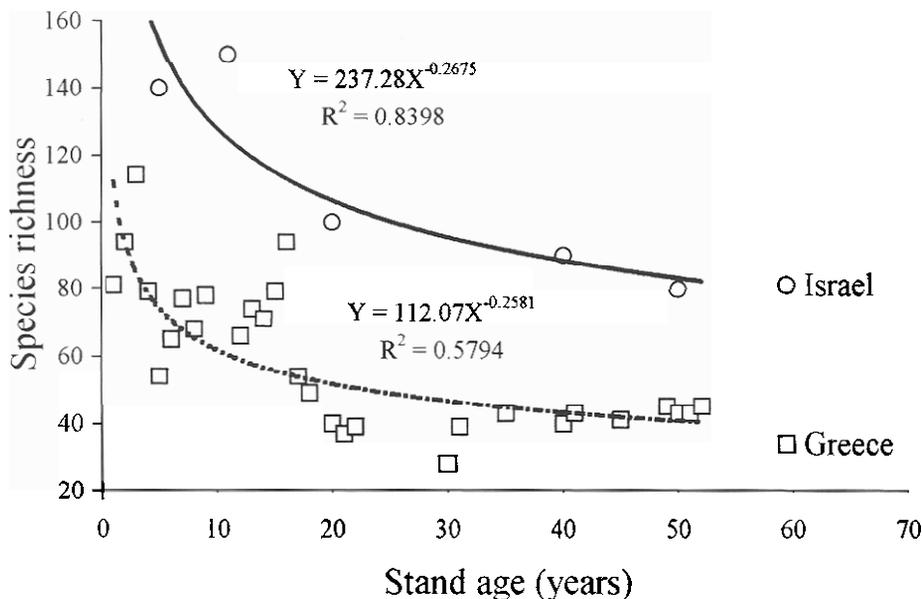


Fig. 7 Plant species richness in post-fire chronosequence of Aleppo pine forests in central Greece (after Kazanis and Arianoutsou in preparation) and on Mount Carmel, Israel (after Schiller *et al.* 1997). Forests older than 50 years represent mature unburned stands.

In Greece, six phases corresponding to post-fire ages can be identified (Table 3). The initial phase corresponds to the first year after fire. Either through resprouting or through seed germination, most of the species that occur in mature unburned pine stands appear in burned sites. However, the number of taxa recorded in burned sites is considerably higher than that recorded before fire. Most of the additional species are annuals that germinate from seeds, which were dormant in the pre-fire soil seed bank. Most of these taxa are legumes. The reasons for the high contribution of legumes have been discussed previously. Similar high species richness and high legume contribution were also recorded in Israel (Lahav 1988). The role of the soil seed bank in post-fire regeneration of Aleppo pine forests is discussed in detail by Izhaki and Ne'eman (2000). During the second phase (2-4 years), the flora is enriched by the addition of opportunistic, mostly annual, taxa colonising the sites from outside. Most of these taxa are wind or animal dispersed, which belong mainly to the families of Gramineae (Poaceae) and Compositae (Asteraceae). They seem to invade, germinate freely and take advantage of the open post-fire environment. Seeds of many Compositae (Doussi and Thanos 1997) as well as many other pioneer species require light for their germination. Temporal invasion by opportunistic species was also described in Israel (Lahav 1988, Schiller *et al.* 1997) and in France (Trabaud 2000). The third phase (5-7 years) is defined by the dominance of the *Cistus* species that form a rather dense cover, which seems to prevent the further establishment of seedlings of the opportunistic taxa. On the contrary, legumes seem to withstand this competition imposed by the rockroses. Although the life span of most of the *Cistus* species is estimated to be up to 15 years (Arianoutsou 1998), a gradual increase in their mortality is observed from the seventh year post-fire onwards. This results in the formation of gaps in the vegetation canopy, which subsequently allow light penetration. Several annual grasses and other ephemeral species (e.g., *Asterolinon* spp., *Filago* spp., *Bupleurum* spp.) are established then. This explains the slight increase in the flora observed in the fourth phase. Gaps persist until about 15 years after fire. During this period, the trees' canopies and those of tall shrubs expand and the understorey species face severe competition for light. The populations of certain dwarf shrubs (e.g., *Fumana* spp, *Satureja* spp. and mainly *Cistus* spp.), which are heliophilous and typical to the early post-fire stages, shrink or completely disappear from the active flora. This phase lasts until the community develops the physiognomy of the mature forest. In mature forest communities, species richness (not including soil seed bank) is related to the thickness of the overstorey, but generally it is richer than that of the previous phase. It is the only phase of the post-fire regeneration when Compositae appear to be the richest family.

Table 3. Species richness, dominant life form and family in Aleppo pine forest communities varying in their post-fire ages (after Kazanis and Arianoutsou, in preparation).

Phase	Post-fire age	Species richness	Richest life form	Richest Family
1	0-1	40-55	Therophytes	Leguminosae
2	2-4	65-85	Therophytes	Leguminosae
3	5-7	30-55	Therophytes	Leguminosae
4	8-15	35-65	Therophytes	Gramineae
5	16-Young forests	20-35	Phanerophytes	Liliaceae
6	Mature forests	35-60	Therophytes	Compositae

To conclude, in the east Mediterranean basin, as well as in its western part, post-fire regeneration does not follow the classical succession model, which is characterised by species replacement. The pine trees that comprise the highest plant growth form in the community as well as all the resprouters that form the understorey are present from the first year post-fire. The main floristic changes are due to two groups: (1) plants that are fire followers, which are a part of the soil seed bank and whose germination is regulated by fire induced cues (e.g., *Cistus* spp. and legumes) that utilise mainly the first post-fire decade or some part of it; (2) opportunistic plants that are absent from the permanent soil seed bank and are invading the burned area from its unburned surroundings. Both groups utilise the time window until the forest canopy closes again.

### Vegetation Structure

Development of plant cover after fire on Mount Camel, Israel, is rapid. Already partially by the end of the first summer post-fire and fully during the second spring, almost the soil's entire surface is covered by vegetation (Ne'eman unpublished data). In a synchronic study of 5 burned and 4 adjacent unburned Aleppo pine stands on Mount Carmel, Israel, the percentage of all perennial species was recorded along 25-m long transects. All plant growth forms were already present at the burned stands 5 years after fire with a total multi-layer cover of 150%. The cover of climbers and shrubs was almost constant along the whole chronosequence, and the main change was in the dwarf shrub and tree layers (Fig. 8). The changes in percentage cover of the two dominant species of these two growth forms, *P. halepensis* and *C. salvifolius*, are presented in Fig. 9. The pine cover increased along a logarithmic scale whereas that of *Cistus* spp. decreased along the same scale. The proportion of tree cover to dwarf shrub cover was found to be the best index to describe and predict the regeneration stage of any specific stand. This proportion increased from 0.49 for a stand 5 years after fire to 1.8 for a stand 38 years after fire, and its average was 3.2 for the unburned plots.

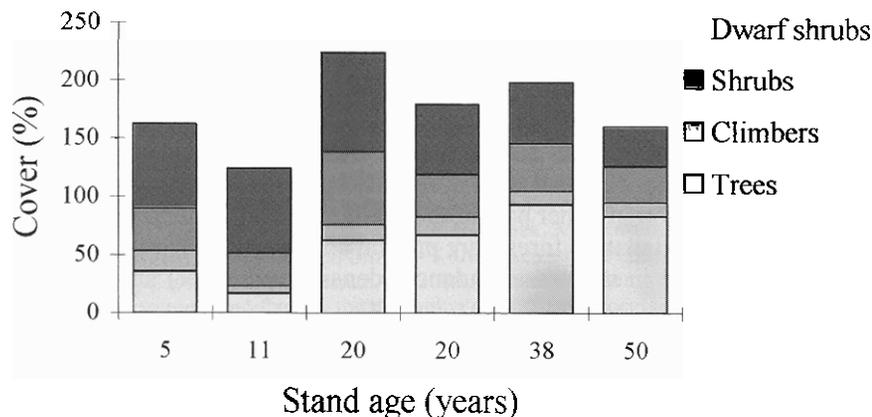


Fig 8. Cumulative percentage cover of perennial plant growth forms in a post-fire chronosequence of Aleppo pine forests on Mount Carmel, Israel. The 50-year old stand represents the average values of four mature unburned stands (after Schiller *et al.* 1997).

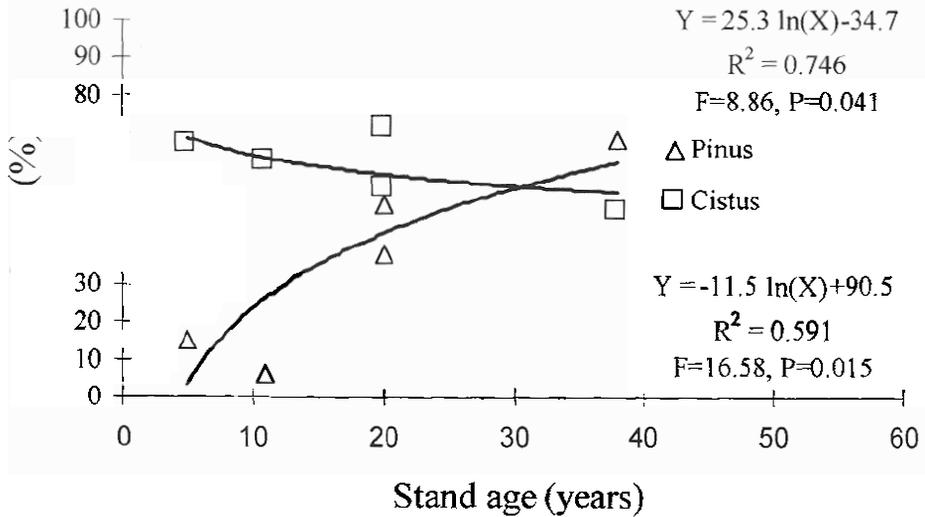


Fig. 9. Post-fire changes in the percentage cover of *P. halepensis* and *Cistus* sp. in a post-fire chronosequence of Aleppo pine forests on Mount Carmel, Israel. The 50-year old stand represents the average values of four mature unburned stands (after Schiller *et al.* 1997).

## Conclusions

The regeneration of post-fire Aleppo pine forests in the Mediterranean basin is relatively well described. A relatively high initial density of pine seedlings after fire followed by a decrease during the following 10–15 years is typical to the eastern Mediterranean basin, whereas in the western region the initial low density seems to be followed by a gradual increase. There is a large amount of published data on *Cistus* spp. regarding their contribution to the soil seed bank, the effect of heat shock on germination, post-fire changes in its population density and percentage cover as well as population age structure. Despite minor differences, all *Cistus* species belong to one ecological guild of post-fire short living perennial dwarf shrubs. Annual herbaceous plants and mainly legumes play an important role during the early post-fire stage and seem to be more prominent in the eastern than in the western Mediterranean basin. Post-fire plant species richness is reported higher in the east than in the west Mediterranean, although it follows similar patterns; an initial increase followed by a gradual decrease until the richness typical to unburned forests is reached. No classical succession, namely species replacement, occurs during post-fire regeneration in either part of the Mediterranean basin. Most of the species typical to unburned mature forests are present already in the first post-fire year. The major changes are in species abundance (density and cover) and the vertical growth of the trees.

Long-term changes are usually carried out by studying several plots that differ mainly in their age since last fire (synchronic or chronosequence studies). Therefore, conclusions and comparisons of data among studies should be done with special care. Long-term monitoring of post-fire regeneration is still needed to verify the validity of the models proposed on the basis of synchronic studies.

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Appendix 1. Growth form, Raunkiaer's life form and post-fire regeneration mode of the most common plants of the Aleppo pine forest communities in Greece (G) (Kazanis and Arianoutsou 1996, Kazanis and Arianoutsou in preparation) and in the Aleppo pine forests of Mt. Carmel, Israel (I), (after Lahav 1988).

Taxa	Growth Form	Life form	Country	Sprouting	Seeding
<i>Pinus halepensis</i>	Tree	Ph	G,I	-	+
<i>Arbutus andrachne</i>	Tall shrub	Ph	G,I	+	-
<i>A. unedo</i>	Tall shrub	Ph	G	+	-
<i>Crataegus aronia</i>	Tall shrub	Ph	I	+	-
<i>Ceratonia siliqua</i>	Tall shrub	Ph	I	+	-
<i>Cercis siliquastrum</i>	Tall shrub	Ph	I	+	-
<i>Olea europaea</i>	Tall shrub	Ph	G,I	+	-
<i>Phillyrea latifolia</i>	Tall shrub	Ph	G,I	+	-
<i>Pistacia palaestina</i>	Tall shrub	Ph	I	+	-
<i>Quercus calliprinos</i>	Tall shrub	Ph	I	+	-
<i>Q. coccifera</i>	Tall shrub	Ph	G	+	-
<i>Rhamnus palaestina</i>	Tall shrub	Ph	I	+	-
<i>Rhus coriaria</i>	Tall shrub	Ph	G,I	+	+
<i>Calicotome villosa</i>	Shrub	Ph	G,I	+	+
<i>Pistacia lentiscus</i>	Shrub	Ph	G,I	+	-
<i>Salvia fruticosa</i>	Shrub	Ph	I	+	+
<i>Asparagus aphyllus</i>	Climber	Ch	G,I	+	-
<i>Clematis cirrhosa</i>	Climber	Ph	I	+	-
<i>C. vitalba</i>	Climber	Ph	G	+	-
<i>Lonicera etrusca</i>	Climber	Ph	G,I	+	-
<i>Rubia tenuifolia</i>	Climber	Ph	I	+	-
<i>Smilax aspera</i>	Climber	Ph	G,I	+	-
<i>Anthyllis hermanniae</i>	Dwarf shrub	Ph	G	+	+
<i>Cistus creticus</i>	Dwarf shrub	Ph	G,I	-	+
<i>C. monspeliensis</i>	Dwarf shrub	Ph	G	-	+
<i>C. salvifolius</i>	Dwarf shrub	Ph	G,I	(+)	+
<i>Euphorbia hierosolemitana</i>	Dwarf shrub	Ch	I	+	+
<i>Fumana arabica</i>	Dwarf shrub	Ch	G,I	-	+
<i>F. thymifolia</i>	Dwarf shrub	Ch	G,I	-	+
<i>Genista acanthoclada</i>	Dwarf shrub	Ch	G	+	+
<i>Helianthemum syriacum</i>	Dwarf shrub	Ch	I	-	+
<i>Hypericum empetrifolium</i>	Dwarf shrub	Ch	G	+	+
<i>H. thymifolium</i>	Dwarf shrub	Ch	I	+	+
<i>Osyris alba</i>	Dwarf shrub	Ch	G,I	+	-
<i>Sarcopoterium spinosum</i>	Dwarf shrub	Ch	I	+	+
<i>Teucrium creticum</i>	Dwarf shrub	Ch	I	+	+
<i>T. divaricatum</i>	Dwarf shrub	Ch	G,I	+	+
<i>Satureja thymbra</i>	Dwarf shrub	Ch	G, I	+	+
<i>Coridothymus capitatus</i>	Sub-shrub	Ch	G,I	?	+
<i>Dorycnium hirsutum</i>	Sub-shrub	Ch	G	+	+
<i>Phagnalon graecum</i>	Sub-shrub	Ch	G	+	+
<i>Allium stamineum</i>	Perennial herb	G	I	+	
<i>Anemone coronaria</i>	Perennial herb	G	G,I	+	
<i>Asphodelus aestivus</i>	Perennial herb	G	G	+	
<i>A. ramosus</i>	Perennial herb	G	I	+	
<i>Bellevalia flexuosa</i>	Perennial herb	G	I	+	
<i>Crocus biflorus</i>	Perennial herb	G	G	+	?
<i>Cyclamen graecum</i>	Perennial herb	G	G	+	+
<i>Euphorbia apios</i>	Perennial herb	G	G,I	+	
<i>Gynandris sisyrinchium</i>	Perennial herb	G	G,I	+	

## Appendix 1. Continued.

Taxa	Growth Form	Life form	Country	Sprouting	Seeding
<i>Muscari comosum</i>	Perennial herb	G	G		
<i>Anthyllis vulneraria</i>	Perennial herb	H	G		
<i>Brachypodium sylvaticum</i>	Perennial herb	H	G		
<i>Convolvulus elegantissimus</i>	Perennial herb	H	G		
<i>Crepis bulbosa</i>	Perennial herb	H	I		
<i>Ferula tingitana</i>	Perennial herb	H	I		
<i>Funeculum vulgare</i>	Perennial herb	H	I		
<i>Dittrichia (Inula) viscosa</i>	Perennial herb	H	G, I		
<i>Lotus collinus</i>	Perennial herb	H	I		
<i>Onopordum cynarocephalum</i>	Perennial herb	H	I		
<i>Poa bulbosa</i>	Perennial herb	H	G, I	+	
<i>Poligonum equisetiformis</i>	Perennial herb	H	I	-?	+
<i>Reichardia picroides</i>	Perennial herb	H	G	+	-
<i>Sanguisorba minor</i>	Perennial herb	H	G, I	-	+
<i>Scaligeria napiformis</i>	Perennial herb	H	I		+
<i>Scorzonera crocifolia</i>	Perennial herb	H	G		
<i>S. papposa</i>	Perennial herb	H	I	-?	
<i>Sedum nicaeense</i>	Perennial herb	H	I	-	
<i>Thesium bergeri</i>	Perennial herb	H	I	-	
<i>Thirincia tuberosa</i>	Perennial herb	H	I	+	
<i>Trifolium uniflorum</i>	Perennial herb	H	G	+	
<i>Aegilops geniculata</i>	Annual herb	Th	G, I		
<i>Althea hirsuta</i>	Annual herb	Th	I		
<i>Anagalis arvensis</i>	Annual herb	Th	G, I		
<i>Asterolinon linum - stellatum</i>	Annual herb	Th	G, I		
<i>Anthemis palaestina</i>	Annual herb	Th	I		
<i>Brachypodium distachion</i>	Annual herb	Th	G, I		
<i>Biscutella didyma</i>	Annual herb	Th	G, I		
<i>Briza maxima</i>	Annual herb	Th	G, I		
<i>Bromus alopecuroides</i>	Annual herb	Th	I		
<i>Catapodium rigidum</i>	Annual herb	Th	G, I		
<i>Chaetosiciadum trichospermum</i>	Annual herb	Th	I		
<i>Convolvulus altheoides</i>	Annual herb	Th	G		
<i>C. coelesyriacus</i>	Annual herb	Th	I		
<i>C. pentapetaloides</i>	Annual herb	Th	I		
<i>Coronilla scorpioides</i>	Annual herb	Th	G, I		
<i>Crepis aspera</i>	Annual herb	Th	I		
<i>Crucianella macrostachia</i>	Annual herb	Th	I		
<i>Erodium cicutarium</i>	Annual herb	Th	G, I		
<i>Euphorbia helioscopia</i>	Annual herb	Th	G, I		
<i>E. peplus</i>	Annual herb	Th	G, I		
<i>E. retusa</i>	Annual herb	Th	I		
<i>Fumaria macrocarpa</i>	Annual herb	Th	G, I		
<i>F. densifolia</i>	Annual herb	Th	G		
<i>Galium hirusalemitica</i>	Annual herb	Th	I		
<i>Geranium molle</i>	Annual herb	Th	G, I		
<i>G. purpureum</i>	Annual herb	Th			+
<i>G. rotundifolium</i>	Annual herb	Th	G, I		+
<i>Hymenocarpus circinnatus</i>	Annual herb	Th	G, I		+
<i>Hypochoeris achyrophorus</i>	Annual herb	Th	G		+
<i>Hippocrepis unisiliquosa</i>	Annual herb	Th	G, I		+
<i>Lagoecia cumminoides</i>	Annual herb	Th	G, I		+
<i>Lathyrus cicera</i>	Annual herb	Th	G		+
<i>Linum corymbulosum</i>	Annual herb	Th	I		+

## Appendix 1. Continued.

Taxa	Growth Form	Life form	Country	Sprouting	Seeding
<i>Linum nodiflorum</i>	Annual herb	Th	I	-	+
<i>L. strictum</i>	Annual herb	Th	G,I	-	+
<i>Lotus edulis</i>	Annual herb	Th	I	-	+
<i>L. peregrinus</i>	Annual herb	Th	I	-	+
<i>Medicago coronata</i>	Annual herb	Th	G,I	-	+
<i>M. orbicularis</i>	Annual herb	Th	G,I	-	+
<i>M. polymorpha</i>	Annual herb	Th	G,I	-	+
<i>M. rugosa</i>	Annual herb	Th	I	-	+
<i>M. truncatula</i>	Annual herb	Th	G,I	-	+
<i>Nigella ciliaris</i>	Annual herb	Th	I	-	+
<i>Ononis reclinata</i>	Annual herb	Th	G,I	-	+
<i>O. ornithopodoides</i>	Annual herb	Th	G,I	-	+
<i>O. pubescens</i>	Annual herb	Th	I	-	+
<i>O. viscosa</i>	Annual herb	Th	G,I	-	+
<i>Phisanthyllis tetraphylla</i>	Annual herb	Th	G,I	-	+
<i>Ragadiolus stellatus</i>	Annual herb	Th	I	-	+
<i>Scabiosa prolifera</i>	Annual herb	Th	I	-	+
<i>Scorpiurus muricatus</i>	Annual herb	Th	G,I	-	+
<i>Sedum caespitosum</i>	Annual herb	Th	I	-	+
<i>S. pallidum</i>	Annual herb	Th	I	-	+
<i>Sherardia arvensis</i>	Annual herb	Th	G,I	-	+
<i>Theligionum cynocerambe</i>	Annual herb	Th	I	-	+
<i>Trifolium campestre</i>	Annual herb	Th	G,I	-	+
<i>T. lappaceum</i>	Annual herb	Th	G,I	-	+
<i>T. scabrum</i>	Annual herb	Th	G,I	-	+
<i>Trigonella spinosa</i>	Annual herb	Th	I	-	+
<i>Urospermum picroides</i>	Annual herb	Th	I	-	+
<i>Valantia hispida</i>	Annual herb	Th	I	-	+
<i>Valerianella vesicaria</i>	Annual herb	Th	I	-	+