

# Lack of hard-seeded species in pre-fire and post-fire seed banks in the region of Murcia (south-eastern Spain)

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## Abstract

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Permanent seed banks are thought to be of essential importance for the reproductive success of many obligate seeder species during early post-fire succession. To evaluate the role of seed banks for post-fire regeneration in SE Spain, seed bank analyses were carried out on recently burnt sites and in long-unburnt areas in two climatically different regions of the province of Murcia, using the seedling emergence method as well as the physical separation technique. We found great variability in the number of seeds between sites and expositions. Lowest seed numbers were found in the mountains while locally very dense seed banks of > 3500 seeds/m<sup>2</sup> in the upper two cm of soil were present at the coast. Species of Poaceae, Asteraceae as well as annual species such as *Asterolinum linum-stellatum* prevailed whereas hard-seeded species known to occur frequently in post-fire Mediterranean vegetation (e.g. Cistaceae, Fabaceae or Convolvulaceae) were sparse or absent in the seed bank. We conclude that the hard-seeded species are not a self-evident compound of the species composition during post-fire succession of long-unburnt sites in south-eastern Spain.

**Keywords:** Cistaceae, "Fire seeder", Post-fire regeneration, Seed bank.

## Introduction

Persistent seed banks provide an immediate source of propagules for regeneration after disturbance (Thompson 1992). In the Mediterranean Basin such permanent seed pools are necessary for the reproductive success of many obligate seeder species during early post-fire vegetation succession – at least where long-distance dispersal is limited. Thus, the study of the seed bank of a certain region supplies comprehensive information on the potential of seeder species to regenerate on the site after a disturbance.

As in other regions of the Mediterranean Basin (Morey & Trabaud 1988, Herranz et al. 1996, Ojeda et al. 1996, Thanos et al. 1996), post-fire vegetation of south-eastern Spain is mainly composed of similar species as present before the fire (Goetzenberger et al. 2003, Buhk et al. submitted-b). Species abundance, however, is altered before vs. after the fire and, depending on the location and the age since the dis-

turbance, either resprouters like *Stipa tenacissima*, *Quercus coccifera* or *Calicotome intermedia* or obligate seeders like many Cistaceae or *Pinus halepensis* are the dominant species. Dense stands of many hard-seeded species have been frequently described to prevail immediately after fire (e.g. Cistaceae, Convolvulaceae, Fabaceae; Naveh 1975, Thanos et al. 1992). The striking occurrence of hard-seeded species directly after fire has been explained on the basis of the seed morphology. A major portion of the usually large and immobile seeds is physically dormant due to a water-impermeable seed coat, which often leads to an accumulation of large long-lived seed banks (Baskin & Baskin 2001, Fenner & Thompson 2005). During a fire, germination of the seeds in the soil is frequently stimulated by heat due to seed-coat scarification that allows the entry of water (Thanos et al. 1992, Herranz et al. 1998, Ferrandis et al. 1999, Herranz et al. 1999, Buhk & Hensen in press). In many studies carried out in the Mediterranean, high numbers of hard-coated seeds were indeed found in

the soil (Trabaud et al. 1997, Izhaki & Ne'eman 2000). However, though many Fabaceae and Cistaceae are part of the vegetation in the study area (Götzenberger et al. 2003, Buhk et al. submitted-b), massive spreading e.g. of *Cistus albidus* has been observed only locally and not immediately after fire but during mid-succession more than 5 years later (Buhk & Hensen in press, Buhk pers. observation).

To examine the role of seeds in the soil for post-fire regeneration we carried out soil seed-bank studies in different zones in recently burnt as well as long-unburnt areas in the Province of Murcia. Particularly, we addressed the following questions: Which seeds are viable in the seed banks of recently burnt sites and long-unburnt areas and how does the seed bank composition differ between sites in coastal or mountainous regions and of different exposition? Is the composition of species in the seed bank on long-unburnt sites similar to the above-ground vegetation? Are species with hard-coated seeds especially abundant in the soil as previously stated for the Mediterranean?

## Materials and Methods

The research areas are located in the Province of Murcia in south-eastern Spain (figure 1). The sites of Sierra de Ricote and Moratalla, situated in the mountainous area, are part of the meso-Mediterranean zone (400 mm annual precipitation, dry period 6-8 months). The Ricote area (800 m a.s.l.) burnt in the summer of 2000 (60 ha), the Moratalla area (1000 m a.s.l.) burnt in the spring of 2001 (5 ha). The vegetation comprises *Pinus halepensis* woodlands of different density, often mixed with *Quercus coccifera* and *Stipa tenacissima*. The coastal sites of Algarrobo and La Union are characterised by a thermo-Mediterranean climate (50-100 m a.s.l., 200-300 mm annual precipitation, dry period 7-11 months) and the dominance of *Stipa tenacissima* grasslands (Carrión Vilches et al. 2003). The Algarrobo area (30 ha) burnt in the summer of 2001 as did the La Union site (7 ha). The bedrock of the research areas primarily consists of limestone and dolomite of Triassic origin at



Figure 1: Location of the 4 study areas in south-eastern Spain.

the coast and of Jurassic origin on the mountainous sites (Fontbote 1983a, 1983b).

The soil seed banks of recently burnt areas were analysed using the seedling emergence method (Auld 1996, Thompson et al. 1997). In the spring of 2001, 2 months after the fire, we collected soil from the area in Moratalla. Samples were composed of 80 randomly selected small cylindrical subsamples ( $\text{Ø}2 \times 10 \text{ cm}$ ) on each of four different sites: a terraced area, a sloped area, a steeply sloped area ( $> 40^\circ$  inclination) and, additionally, an unburnt adjacent reference site. No germination was observed at the moment of sampling. In the autumn of 2001, soil samples on sites that had burnt 3 to 15 months before (La Union, Algarrobo, Ricote and Moratalla) were composed of 70 random subsamples measuring  $3 \text{ cm} \times 3 \text{ cm} \times 5 \text{ cm}$  depth (the upper 2 and the lower 3 cm were taken separately) from different slopes and aspects including one unburnt adjacent reference site, each. On the large fire sites of Ricote and Algarrobo, three sample zones were chosen at least 50 m apart from each other. The unburnt controls were situated about 20 m away from the burnt area. The zone close to the fire site in the region of La Union was heavily disturbed and we therefore decided not to sample a reference site in the direct neighbourhood. The sites sampled in Moratalla are similar to the areas studied during the spring of 2001 except for the steep zone. All samples were well air-dried and stored in paper bags for 2-4 months. The soil was sieved ( $\text{Ø} 5 \text{ mm}$ ) to reduce the stone compartment and spread equally over 2 cm of sterile sand in plastic trays. The thickness of the soil sample layer in the trays never exceeded 1.5 cm. The conditions in the greenhouse varied between  $10\text{-}28^\circ\text{C}$  during late summer and between  $4\text{-}25^\circ\text{C}$  during autumn and winter. After 3 months, the samples were carefully turned over to encourage further germination. The samples taken in the autumn of 2001 were additionally exposed to cold temperatures of  $1\text{-}10^\circ\text{C}$  for 1 month to enhance the breaking of physiologically dormant seeds. When the direct determination of the emerging seedlings was not possible, they were transplanted and grown in separate pots until determination. However, some seedlings died before determination was possible. The experiments ended after 5 months (samples taken in spring) and 12 months (samples taken in autumn).

In order to reinsure whether the lack of hard-seeded species in the soil seed bank of the recently burnt areas was due to dormancy (Ferrandis et al. 1999), those of long-unburnt areas were sampled in the spring of 2003. We decided not to artificially stimulate hard-seed germination in the laboratory by heating the soil samples before the use of the seedling

emergence method as according to Ferrandis et al. (1999) unpredictable reactions of the species, which range from stimulation to the death of seeds, were expected. Izhaki et al. (2000), too, demonstrated only quantitative changes by comparing the germination response of heat-treated samples and unheated samples. As a consequence, the long-unburnt sites were analysed using the physical separation method (Thompson et al. 1997). The selection of the long-unburnt sites was done carefully, excluding zones where there was some indication of any kind of strong disturbance and at the same time maintaining comparability towards the burnt area in terms of inclination, direction aspect, and elevation. The distance to the burnt sites varied between 100 m and approx. 2 km. In the selected zones, the above-ground vegetation composition of  $10 \times 10 \text{ m}^2$  plots was analysed (three replicates at least 200 m apart from each other), and 20 subsamples of soil of  $1 \text{ cm} \times 2 \text{ cm} \times 3 \text{ cm}$  depth were taken on a random basis. The organic layer was removed before sampling. The soil was sieved ( $\text{Ø} 5 \text{ mm}$ ) carefully breaking up soil aggregates to avoid seed loss. The portion  $< 5 \text{ mm}$  was again sieved ( $\text{Ø} 2 \text{ }\mu\text{m}$ ) under running water to reduce the sample size and solve further aggregates. The microscope was used to search the remaining soil for seeds (Trabaud et al. 1997). We used TTC (triphenyl tetrazolium chloride; 1%) to test the viability of the seeds (Moore 1986).

## Results

Species of Poaceae (mainly *Brachypodium retusum*) prevailed in the seed bank of the freshly burnt area collected in the spring of 2001 (figure 2a). Although the number of seeds was highly variable due to inclination, the composition was fairly homogenous. The burnt terraced site and the unburnt site were most similar as regards the species composition.

In the seed bank samples collected in the autumn of 2001, coastal sites were characterised by clearly higher numbers of emerging seeds than the mountainous sites (figure 2b). The highest seed densities reached up to  $3800 \text{ seeds/m}^2$  though the variability between the samples was very high. Although the number of seeds found in 2-5 cm deep soil was clearly lower than the number of seeds in the upper 2 cm of soil (even though the amount of soil is one third less in the upper layer as compared to the layer below), the species composition hardly changed between the depth ranges. Predominant species were not found except *Asterolinum linum-stellatum* which was frequently present. *Artemisia* ssp. and *Diplotaxis* ssp. dominated locally. The seed banks of the

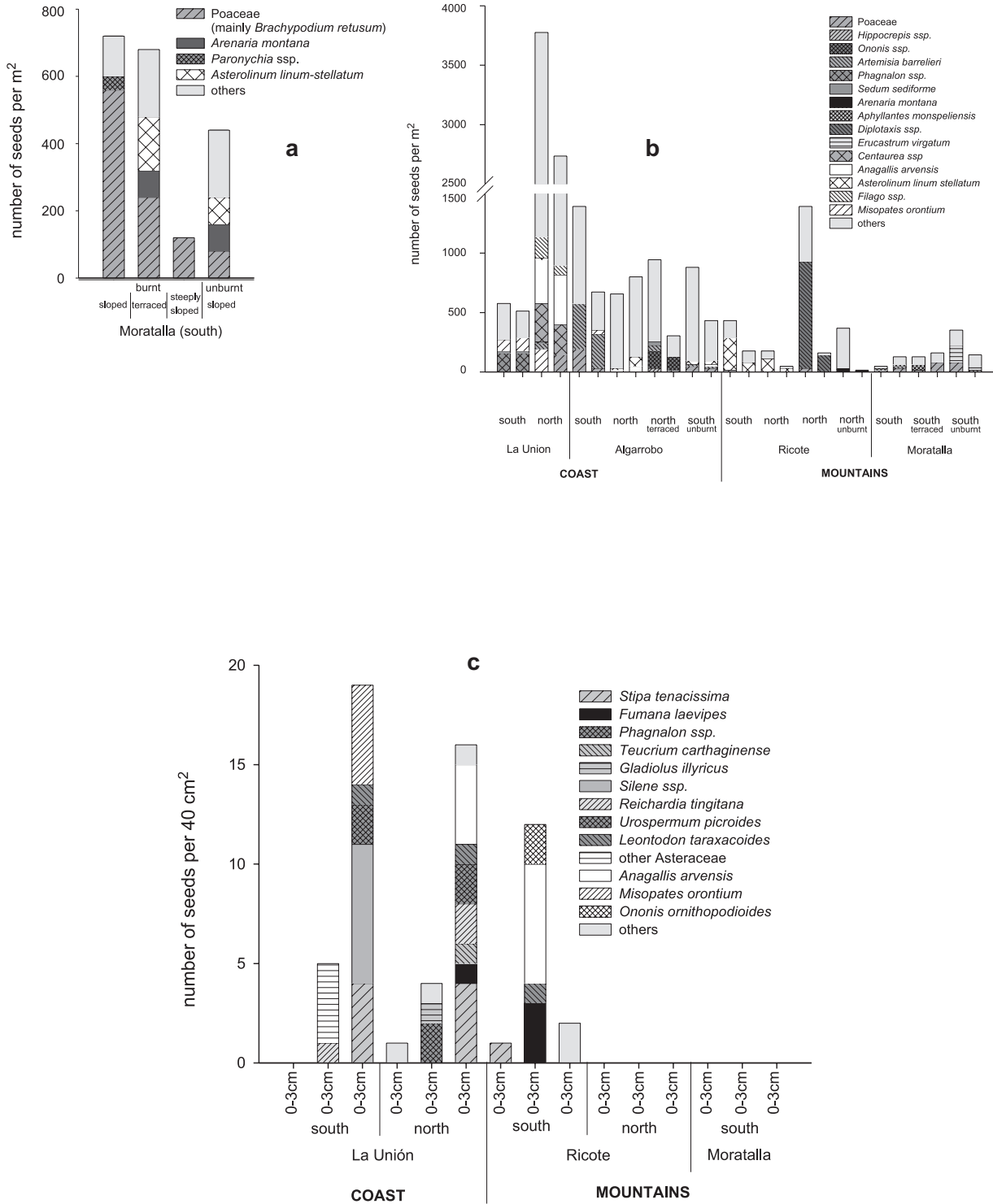


Figure 2: Number of seeds found in the different seed bank studies separated according to species / genus or family level. “Others” does not contain any hard-seeded species.  
 a) Seed banks of the samples collected in the spring of 2001, 2 months after fire. Subsamples were taken from the upper 10 cm of soil. The number of seeds refers to 1 m<sup>2</sup>.  
 b) Seed banks of the samples collected in the autumn of 2001. Subsamples were taken in two layers (0-2 cm and 2-5 cm of soil). The number of seeds refers to 1 m<sup>2</sup>.  
 c) Seed banks of the unburnt samples studied using the physical separation technique. Subsamples were taken from the upper 3 cm of soil. Notice that the number of seeds refers to 40 cm<sup>2</sup>.

neighbouring unburnt areas were not clearly differentiated from those of the burnt samples. The fire sites in Moratalla sampled in autumn (figure 2b) showed lower seed numbers than the samples taken shortly after the fire (spring samples; figure 2a). Poaceae still played an important role, but the species other than the Poaceae family had changed.

The seed bank composition of the long-unburnt sites (figure 2c) revealed a pattern similar to the one found in the former experiments, which showed clearly higher numbers of seeds close to the coast than in the mountains. Again there was a high variation in seed abundance within the replications. The absence of viable seeds in many samples in the mountains, except for the south-exposed sites of Ricote, was striking. Plenty of seeds of *Rosmarinus officinalis* in particular were found dead (data not shown). The species composition above ground was much richer than the seed bank composition (appendix 1), and the

few species we found in the soil were usually absent from the above-ground vegetation.

The taxa identified in the seed bank during the study are summarised in table 1 which includes information on familiar affiliation, prevailing regeneration mechanism and life form. In the soils under study, high numbers of seeds of therophytes were found and most species are known to be obligate seeders. The importance of wind-dispersed species such as many Asteraceae is obvious. Only a few hard-seeded species were found in all analyses (table 1). Exceptions are two hard-seeded taxa (*Ononis* and *Hippocrepis*), of which only a few were found on a north-facing post-fire site in Algarrobo (figure 2b), and *Fumana laevipes* and *Ononis ornithopodioides* which were present on a long-unburnt south-facing mountainous site in Ricote. We also found a single seed of *Fumana laevipes* on a long-unburnt site in La Union (figure 2c).

Table 1: Taxa found in the seed bank (only viable seeds) during the studies (figure 2a,b and c) including information on familiar affiliation, prevailing regeneration mechanism (r: resprouter, s: obligate seeder, b: facultative resprouter, Buhk et al. 2005) and life form (Raunkiaer 1934). \* = hard-seeded species according to Baskin & Baskin (2001), Buhk & Hensen (in press).

species	family	regen. mec	life form
<i>Anagallis arvensis</i>	Primulaceae	s	T
<i>Aphyllantes monspelliensis</i>	Liliaceae	b	H
<i>Arenaria montana</i>	Caryophyllaceae	s	
<i>Artemisia barrelieri</i>	Asteraceae	s	C
<i>Asterolinum linum-stellatum</i>	Primulaceae	s	T
<i>Brachypodium retusum</i>	Poaceae	b	H
<i>Centaurea</i> ssp.	Asteraceae	s	
<i>Diplotaxis</i> ssp.	Brassicaceae	s	T
<i>Erucastrum virgatum</i>	Brassicaceae	s	T
<i>Filago</i> ssp.	Asteraceae	s	T
<i>Fumana laevipes</i> *	Cistaceae	s	C
<i>Gladiolus illyricus</i>	Iridaceae	r	G
<i>Hippocrepis</i> ssp.*	Fabaceae	s	H
<i>Leontodon taraxacoides</i>	Asteraceae	s	T
<i>Misopates orontium</i>	Scrophulariaceae	s	T
<i>Ononis</i> ssp.*	Fabaceae	s	
<i>Ononis ornithopodioides</i> *	Fabaceae	s	T
<i>Paronychia</i> ssp.	Caryophyllaceae	H	
<i>Phagnalon</i> ssp.	Asteraceae	s	C
<i>Reichardia tingitana</i>	Asteraceae	s	T
<i>Sedum sediforme</i>	Crassulaceae	s	H
<i>Silene</i> ssp.	Caryophyllaceae	s	T
<i>Stipa tenacissima</i>	Poaceae	b	H
<i>Teucrium carthaginense</i>	Lamiaceae	s	C
<i>Urospermum picroides</i>	Asteraceae	s	T



## Discussion

The results of our study show that a permanent seed bank does not play a major role during post-fire regeneration in the area of Murcia. Although large quantities of seeds were found on the coastal sites, they belonged mainly to widespread, easily dispersed species. Such species do not usually depend on seed storage and do not build up permanent seed banks (Baskin & Baskin 2001). We did not find any hard-seeded species in considerable quantities. Massive synchronised post-fire germination from the permanent seed bank directly after fire therefore seems unlikely.

The locally high abundance of many Asteraceae in the seed bank of La Union is probably due to steady disturbance in the surrounding area. Industrial plant and a waste disposal site including intense traffic of lorries lead to a large open habitat for ruderals with efficient dispersal ability. These findings also explain the high variability in seed density because prevailing wind directions and exposure strongly influence the input of seeds. The elevated species richness in the seed bank on the coastal sites as compared to the mountainous sites coincides with higher species numbers in the above-ground vegetation at the coast (Götzenberger et al. 2003) as compared to the sites in the mountains (Buhk et al. submitted-b). Accordingly, open habitats have been frequently described to contain larger seed banks than forest ecosystems (Baskin & Baskin 2001, Fenner & Thompson 2005). This also explains that especially the dense forests on north-facing sites in Ricote and at a high altitude in Moratalla were characterised by small seed banks. The high amount of seeds of *Rosmarinus officinalis* in the soil lacking viability was also recorded by Trabaud et al. (1997) in south-eastern Spain. This is in line with the fact that this species has been found to regenerate late after fire (Buhk et al. submitted-b). In the area of Moratalla, *Brachypodium retusum* was very abundant and as the seeds are not very long-lived (Buhk, unpublished data) they are probably not part of the persistent seed bank. The superficial seeds on the steeply sloped site in Moratalla are probably washed away, which might be the reason for the proportionally low seed numbers.

Studies concerning above-ground post-fire succession in the mountains underline the little importance of the seed bank; resprouters prevailed and seeders often belonged to species capable of long-distance dispersal like Asteraceae and Poaceae (Buhk et al. 2005, Buhk, unpublished data). Although the above-ground species composition in the long-unburnt plots was rich in species, the seed bank was poor in species and long-distance dispersed seeds

were overrepresented (appendix 1, table 1). Probably many large seeds of the above-ground vegetation got caught in the locally prominent organic layer. This effect can be expected especially for the mountainous forest sites where needle litter decomposes slowly.

Even the samples taken shortly after the fire did not show germination of fire-stimulated species. The same sites showed a very local and sparse settlement of hard-seeded species above ground during the second year of regeneration (Buhk & Hensen in press), which underlines the possible lack of stored seeds. So what could be the reason for the little quantity of hard-seeded fire-following species in the seed bank though they are reported to be very numerous in the Mediterranean Basin (Le Houerou 1973, Thanos et al. 1992, Izhaki & Ne'eman 2000)? Seed banks of hard-seeded species in *Pinus halepensis* forests were previously described to tend to vanish after low-intensity fires (Ferrandis et al. 2001) or in restricted areas with little disturbance frequency (Troumbis 1996). Species of a limited life span which are incapable of establishing within undisturbed vegetation completely depend on their permanent seed bank because the survival period of the seeds in the soil has to exceed the fire recurrence interval (Keeley & Fotheringham 2000). The fire frequency in the whole area is probably not high (Vázquez et al. 2002, Buhk et al. submitted-b). The disturbance interval may be too long in relation to the time of seed production during life span and subsequent survival until the next disturbance occurs. *Cistus albidus* is an example of a prominent hard-seeded species in the area, which establishes during a period of five years after fire, reproduces after 3 years, and whose stands begin to decline after about 15 years (Roy & Sonié 1992). The seed longevity in the soil is estimated at 20-30 years for this species (Pausas 1999, Izhaki & Ne'eman 2000). Accordingly, our data shows that seeds of *Cistus* species are not present in areas burnt more than 50 years ago (possibly much longer). In addition, further seed input from other disturbed sites is limited because the ability of hard-seeded species to disperse is usually very restricted. They are dispersed barochorously (seeds fall to the ground directly; Güemes & Mateu 1990, Auld 1996, Malo & Suárez 1996, Troumbis 1996, Bastida & Talavera 2002), e.g. 98% of the seeds of *Cistus ladanifer* and *Cistus libanotis* landed within 40 cm around the canopy of the individuals (Bastida & Talavera 2002). Even long-distance secondary movements may not be very common as e.g. seeds of the genus *Fumana* (Cistaceae) attach to the ground if moistened (Güemes & Mateu 1990). Seed movement due to erosion may be negligible according to García Fayos et al. (2000), however, the ability to move depends on the seed size

and shape (Cerdá & García Fayos 2002). Seed production is usually high (Ne'eman & Izhaki 1999, Izhaki & Ne'eman 2000, Buhk et al. submitted-a), however, seed quantities might be limited as seed predation before or after seed distribution may locally play a major role (Troumbis & Trabaud 1987, Malo & Suárez 1996, Hulme 1998, Bastida & Talavera 2002).

*Cistus* populations with plain seed banks in the pine forests studied are probably restricted to sites with steady disturbance (like footpaths) or to areas with frequent man-made fire or other disturbance events (Buhk & Hensen in press). The above-ground vegetation in the mountainous area of the reference sites did not contain many of the hard-seeded species (appendix 1) and a steady accumulation of a seed bank was therefore not possible. Further studies will be necessary to underline the theory that the re-establishment of hard-seeded species in the long-unburnt pine forests studied depends on the successful establishment of a few seeds (e.g. transported from close patches of recent disturbance by erosion or exceptionally zoochorously by ants, birds or mammals over a longer distance; Malo & Suárez 1996). This theory would contribute to the explanation of the patchy occurrence of *Cistus* populations during early post-fire regeneration in the study area (Buhk et al. submitted-b) and explains the increase in abundance of *Cistus* on many post-fire sites not before the 5<sup>th</sup> year of regeneration (Buhk & Hensen in press, Buhk pers. observation) because the population growth on the open sites is initiated not before the 3<sup>rd</sup> year when the plants start to produce a high number of seeds. At the coast, however, hard-seeded species occur quite regularly but they have not been observed to show massive germination after fire (e.g. *Fumana laevipes*, *Genista umbellata* and *Convolvulus lanuginosus*, Götzenberger et al. 2003), which is in accordance with the low seed densities of these species in the soil.

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	COAST												MOUNTAINS											
	Portman				Alumbres				Ricote				Moratalla											
	south		north		south		north		south		north		south		north									
	v	s	v	s	v	s	v	s	v	s	v	s	v	s	v	s								
<i>Anabasis hispanica</i>																								
<i>Anagallis arvensis</i>																								
<i>Aphyllanthes monspeliensis</i>																								
<i>Arbutus unedo</i>																								
<i>Arenaria montana</i>																								
<i>Argyrolobium zanonii*</i>																								
<i>Arisarum simorrhinum</i>																								
<i>Aristolochia</i> sp.																								
<i>Asparagus acutifolius</i>																								
<i>Asparagus horridus</i>																								
<i>Asphodelus aestivus</i>																								
Asteraceae indet.																								
<i>Atrectylis humilis</i>																								
<i>Avena</i> sp.																								
<i>Ballota hirsuta</i>																								
<i>Blackstonia perfoliata</i>																								
<i>Brachypodium retusum</i>																								
<i>Bupleurum frutescens</i>																								
<i>Bupleurum rigidum</i>																								
<i>Bupleurum</i> sp.																								
<i>Calicotome intermedia*</i>																								
<i>Carex</i> sp.																								
<i>Carlina corymbosa</i>																								
<i>Carrichtera annua</i>																								
<i>Centaurea antennata</i>																								
<i>Centaurea boissieri</i>																								
<i>Centaurea melitensis</i>																								
<i>Centaurea</i> sp.																								
<i>Centaureum</i> sp.																								
<i>Chamaerops humilis</i>																								
<i>Cistus albidus*</i>																								
<i>Cistus clusii*</i>																								
<i>Cistus monspeliensis*</i>																								
<i>Convolvulus althaeoides*</i>																								
<i>Convolvulus lanuginosus*</i>																								
<i>Coronilla juncea</i>																								
<i>Dactylis glomerata</i>																								
<i>Daphne gniadium</i>																								
<i>Dipcadi serotinum</i>																								
<i>Diploxia harra</i>																								
<i>Echium humile</i>																								
<i>Erucastrum virgatum</i>																								
<i>Eryngium campestre</i>																								
<i>Fagonia cretica</i>																								
<i>Fumana ericoides*</i>																								
<i>Fumana laevipes*</i>																								
<i>Fumana thymifolia*</i>																								
<i>Genista umbellata*</i>																								
<i>Genista valentina*</i>																								
<i>Gladiolus illyricus</i>																								
<i>Globularia alypum</i>																								
<i>Helianthemum almeriense*</i>																								
<i>Helianthemum cinereum*</i>																								
<i>Helichrysum italicum</i>																								
<i>Helichrysum stoechas</i>																								
<i>Hyparrhenia</i> sp.																								
<i>Juniperus oxycedrus</i>																								
<i>Juniperus phoenicea</i>																								
<i>Launaea arborescens</i>																								
<i>Lavandula dentata</i>																								
<i>Leontodon taraxacoides</i>																								
<i>Leuzea conifera</i>																								
<i>Limonium carthaginense</i>																								
<i>Linum narbonense</i>																								
<i>Linum strictum</i>																								
<i>Lithodora fruticosa</i>																								
<i>Lonicera implexa</i>																								
<i>Lygeum spartum</i>																								
<i>Maytenus senegalensis</i>																								
<i>Melica minuta</i>																								
<i>Misopates orontium</i>																								
<i>Ononis ornithopodioides*</i>																								
<i>Opuntia maxima</i>																								
<i>Orobancha</i> sp.																								
<i>Osyris quadripartita</i>																								
<i>Pallenis spinosa</i>																								
<i>Paronychia suffruticosa</i>																								
<i>Periploca angustifolia</i>																								
<i>Phagnalon saxatile</i>																								
<i>Pinus halepensis</i>																								
<i>Pinus pinaster</i>																								
<i>Pistacia lentiscus</i>																								
<i>Pistacia terebinthus</i>																								
<i>Polygala rupestris</i>																								
<i>Quercus coccifera</i>																								
<i>Quercus rotundifolia</i>																								
<i>Reichardia tingitana</i>																								
<i>Rhamnus lycoides</i>																								
<i>Rosmarinus officinalis</i>																								
<i>Rubia peregrina</i>																								
<i>Ruta angustifolia</i>																								
<i>Salsola genistoides</i>																								
<i>Satureja obovata</i>																								
<i>Scorpiurus sulcatus*</i>																								
<i>Sedum sediforme</i>																								
<i>Serratula mucronata</i>																								
<i>Sideritis pusilla</i>																								
<i>Silene</i> sp.																								
<i>Smilax aspera</i>																								
<i>Sonchus tenerimus</i>																								
<i>Stipa parvifolia</i>																								
<i>Stipa tenacissima</i>																								
<i>Teucrium capitatum</i>																								
<i>Teucrium carthaginense</i>																								
<i>Teucrium pseudo-chamaepitys</i>																								
<i>Thymelea hirsuta</i>																								
<i>Thymus hyemalis</i>																								
<i>Thymus membranaceus</i>																								
<i>Thymus vulgaris</i>																								
<i>Ulex parviflora*</i>																								
<i>Urginea maritima</i>																								
<i>Urospermum picroides</i>																								
<i>Viola arborescens</i>																								
indet.																								

Appendix 1: Taxa found above and below ground in the long-unburnt sites (figure 2c). Species present in the epigeal vegetation (v) are marked with an x. Taxa present in the soil (s) are marked with a dot. Taxa present above and below ground are highlighted with a frame. \* = hard seeded species according to (Baskin & Baskin 2001, Buhk & Hensen in press).

