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Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L.

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Abstract – The recruitment strategy of *Pistacia lentiscus*, an evergreen sclerophyllous shrub inhabiting the Mediterranean region, was studied in order to identify the key factors controlling seedling establishment and survival. The capacity to develop a seed bank, the loss of seed viability with time, the presence of dormancy mechanisms, the conditions to promote seed germination and the seedling dynamics were investigated. The results show that *P. lentiscus* has a transient seed bank with rapid seed germination occurring within the year. Dormancy was not present as seeds germinated successfully without light or temperature pretreatments. Only pulp removal and a long and abundant rain event (≥ 7 days; ≥ 100 L·m^{-2}) appeared to be necessary for germination. Seed viability decreased drastically after 1 year. More seedlings emerged under shrub canopy than in open sites, as expected by the seed dispersal pattern and canopy effects on plant establishment. The high mortality observed in the few weeks after establishment indicates that seedling survival is a bottleneck in the recruitment process of *P. lentiscus* in dense shrublands. Some seedlings survived in a latent mode for at least 4 years. © Elsevier, Paris

***Pistacia lentiscus* / seed bank / seed germination / seed longevity / seedling dynamics**

1. INTRODUCTION

Vertebrate-dispersed plants are one of the most common dispersal modes in the Mediterranean shrublands [2, 14, 15, 18, 37]. There are many studies for the identification of seed dispersal agents [3, 5, 14, 15] and the seasonality of seed dispersal [34], to describe the seed shadows [6, 7, 10, 11, 21] and for relating these patterns to the spatial distribution and demographic structure of sapling and adult plants [7–9, 26]. However, most of these studies on the consequences of vertebrate-seed dispersal on vegetation focused on the colonization of abandoned fields, whereas research on the pattern and processes of the regeneration of vertebrate-dispersed species in shrublands is still scant, especially studies about postdispersal seed predation patterns, seed germination cues and seedling dynamics. Nevertheless, Herrera and co-workers [17] found that the spatial pattern of seed deposition of *Phillyrea latifolia* by dispersers may be subsequently distorted or obscured by factors acting later in the process, such as predation, germination or seedling survival. In addition, Hulme [19] observed microhabitat differences in propagule removal in *Daphne laureola*, caused by spatial variations and foraging behaviour of their predators.

Pistacia lentiscus L. is one of the most common vertebrate-dispersed shrubs in the Mediterranean Basin [28]. Previous information existing about reproduction biology, dispersal and ability to colonize old fields of this species [10, 11, 22, 23] induced us to select this species as a model to research this topic. Moreover, the ability of this shrub to sprout after fire and to protect soil from erosion makes it valuable for management and reforestation programmes under Mediterranean climatic conditions, which contributes to the knowledge of the colonization ecology of this species.

The aim of this paper is to make a contribution towards the postdispersal biology of *P. lentiscus* in shrubland communities. We present information about seed bank, seed dormancy, seed longevity, germination phenology and seedling dynamics, and discuss their consequences for the spatial and temporal recruitment patterns of this species.

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2. STUDY SPECIES

Pistacia lentiscus (Anacardiaceae) is an evergreen, sclerophyllous, dioecious woody shrub, up to 3 or 4 m in height (see [38] for more details about taxonomy and distribution). Females produce many one-seeded drupes in late summer and autumn. The colour of the fruits is strongly associated with seed viability: black fruits usually contain viable seeds whereas red ones contain nonviable seeds (aborted or parthenocarpic) (see [22, 23] for more details and [13] for embryology and fruit development). Seeds are relatively heavy (15.72 ± 0.44 mg) and large (3.31 ± 0.18 × 2.08 ± 0.17 mm) and they are enclosed in an indehiscent endocarp which is hard and somewhat resistant to the passage of water [4]. Vertebrate species, mostly birds, disperse the seeds, generating seed shadows around perches [11, 21]; however, seed predation rates did not differ between under and away from the perches [36]. Piotto [27] showed that neither mechanical scarification of seeds or prechilling treatments improve the amount of germination, and that only mechanical scarification can slightly increase the germination speed. Salvador and Lloret [29] reported that high temperatures similar to those registered at the soil surface at 1–2 cm depth during forest fires (70 °C for 1 h or 125 °C for 5 min), are lethal to the seeds.

3. MATERIALS AND METHODS

3.1. Study sites

The three populations studied, El Saler, Cabanes and Porta-Coeli, are sclerophyllous shrublands located in the Valencia province, eastern Spain. The climate is Mediterranean-type, with dry and hot summers and mild winters. Mean annual temperature ranges from 15.7 °C in the Cabanes site to 17.5 °C in the El Saler site. Mean minimum temperature (January) and mean maximum temperature (August) range from 6.5 to 7.0 °C and from 27.1 to 28.9 °C, respectively, at these sites. Mean annual precipitation is 410 mm for the Porta-Coeli site, 460 for El Saler and 540 for Cabanes.

El Saler (39°18' N, 0°19' W) is a coastal sandbar formed by the quaternary sediments carried by several rivers. Shrubland has developed on the sandbar and have fixed the dunes. Woody vegetation cover ranges from 25 to 75 %. *Pistacia lentiscus, Quercus coccifera* and *Pinus halepensis* are the dominant woody species.

Cabanes (40°10' N, 0°8' W) is located 5 km inland, at 150 m altitude. The terrain is a very rocky limestone and the vegetation consists of a secondary shrubland dominated by *Q. coccifera, P. lentiscus* and *Rosmarinus officinalis* with 25–50 % cover.

Porta-Coeli (39°40' N, 0°30' W) is 20 km inland, at 200 m altitude. The terrain is a very rocky limestone and the vegetation consists of a secondary shrubland dominated by *Stipa tenacissima, P. lentiscus, P. halepensis, Q. coccifera* and *R. officinalis*. Woody vegetation cover ranges from 25–50 %.

3.2. Methods

3.2.1. Analysis of the seed bank

Seed bank sampling was carried out in September 1992 and August 1993 at the El Saler site, before the dispersal of the next seed generation started. Soil samples, 50 cm square and 5 cm deep, were collected and sifted through a 2-mm sieve to separate the *P. lentiscus* seeds. Five centimetres depth was considered to be enough because large seeds are unlikely to be buried at greater depths. In 1992, samples were taken at 2, 4 and 8 m in each direction (N, S, E, W) from one female specimen. In 1993, samples were taken at 2, 4 and 8 m away from each of ten females in a randomly selected direction.

A complementary experiment was carried out to determine whether the seeds of *P. lentiscus* were able to maintain their germination ability over 1 entire year in outdoor conditions. Four lots of 50 seeds without pulp from Cabanes and Porta-Coeli were placed in trays with sand collected from El Saler. The trays were covered on the top with a 1 × 1 cm hardware mesh that avoided seed predation but not rain. The trays were placed in an experimental area 5 km away from the city of Valencia. Weather conditions (rainfall and temperatures) in the experimental site were similar to the El Saler study area, where natural seedling emergence was studied during the same period (see later). The experiment started in December 1992 and after 1 year, the germination ability of the seeds which had not germinated was tested in the same standard conditions as control seeds in the dormancy experiments.

3.2.2. Seed dormancy

Heat effect on *P. lentiscus* seed germination was already known (Lloret, pers. comm. in 1991, later published in 1995 [29]) and, therefore, heat experiments were not performed. After our experimental work was carried out, Piotto [27] published information about the effects of scarification and prechill treatments on seed germination. Although we also performed experiments on these topics, our results did not differ from that of Piotto, and thus we do not include here our experiments and results. Other potential factors controlling seed dormancy and germination can be fruit pulp and light regime.

An experiment was carried out to assess the existence of barriers to germination due to fruit pulp. The experiment consisted of comparing the germination success of fruits and seeds without pulp. Seeds from Cabanes were used because they proved to have the highest germination rate amongst the three populations studied (see later). The seeds were placed in a germination chamber a.s.l. and maintained in an alternate environment 12 h at 25 °C under light (52.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 12 h at 20 °C in darkness. In each Petri dish, 50 seeds were placed on two filter papers moistened with 5 mL distilled water. Four Petri dishes were used per treatment. Seeds were previously disinfected in 2 % sodium hypochloride solution for 10 min and then imbibed in distilled water during 24 h. The Petri dishes were covered with polyethylene sheets to avoid evaporation. A seed was considered to be germinated when the radicle had emerged. Dishes were checked for germinated seeds every 2 or 3 days, removing the germinated seeds. Seeds that had not germinated after 28 days were dissected and a tetrazolium test was used to check their viability and exclude nonviable seeds from the counting.

An experiment was also carried out to assess the existence of germination controls induced by the light regime. The experiment consisted of comparing germination in the dark with germination in a light/dark regime. Four Petri dishes per treatment, with 50 seeds each, were placed in the germination chamber with alternating temperature and light conditions as described for the pulp removal experiment. The dishes of the dark treatment were covered with foils of aluminium. Germination rates at day 28 were used for comparison. Seeds from the Cabanes population were used for this experiment.

3.2.3. Seed longevity

Seed longevity under laboratory conditions was studied using seeds without pulp that were stored for 0 months (control), 6 months, 1 year and 2 years in darkness and constant temperature (21 °C) and with a moisture content of 6 %. Seeds were collected in autumn 1992 in Cabanes, Porta-Coeli and El Saler populations. A total of 200 seeds per population and treatment were used (four replicates of 50 seeds each). A repeated-measures analysis of variance (ANOVA) was run with population as the between-subjects factor and time of storage as the within-subjects factor. As there was not enough seeds from Porta-Coeli to run the 2-year treatment, only Cabanes and El Saler data were used in the statistical analysis.

3.2.4. Seed germination phenology and seedling emergence

A series of experiments and observations were performed to know when seedling emergence occurs in the field and what climatic conditions trigger it. We sowed 182 seeds collected from the El Saler population in nine flowerpots with sand obtained from the same site. The flowerpots were placed in outdoor conditions but protected from predation by a gauze and irrigated every 2 or 3 days to maintain them at field capacity. Seedling emergence was monitored daily to obtain the number of days necessary to detect the first seedling as well as to obtain the 10, 5 and 100 % percentiles. A seedling was considered to have emerged when its cotyledons were open. The experiment ran from December 1991 to February 1992, the usual period of germination in nature.

Observation consisted of a phenological control over natural seedling emergence. It was carried out in field conditions from autumn 1991 to summer 1994 in El Saler. A 30 × 10 m plot was visited after each rain from September to May in order to record the date and number of seedlings emerging. Once a new seedling was observed, it was tagged with a numbered woody label. A total of three cohorts of seedlings were studied.

By coupling the data obtained from the experiment and the observations, and these with the meteorological data obtained from the nearest meteorological station (Valencia-Los Viveros, 8 km northward), we tried to identify the climatic traits for a rain event to trigger seedling emergence.

In addition, data was obtained about the microhabitats where the seedlings emerged at the study plot. Assuming *P. lentiscus* is mainly dispersed by small birds and that these dispersers preferentially drop seeds from perches, such as trees or shrubs [9], we considered only two microhabitat categories: i) under shrub canopy, and ii) on the open ground. They covered 70 and 30 % of the plot surface, respectively.

3.2.5. Seedling survival

We monitored the survival and possible causes of death of all the *P. lentiscus* seedlings in the 30 × 10 m plot. We considered only two causes of death: desiccation and disappearance. Seedling survival was recorded every 1 to 2 weeks at first and then more sporadically after 3 months until the end of the observations. Daily precipitation data were obtained from the Viveros meteorological station and were utilized in the interpretation of the mortality curves.

4. RESULTS

4.1. Analysis of the seed bank

No viable seeds of *P. lentiscus* were found in the soil samples taken during the 2 study years. Only eight eaten and two nonviable seeds were found in 1992, and 337 eaten and 813 nonviable seeds in 1993. Many of the nonviable seeds remained opened and rotted, containing grains of sand inside, suggesting that the germination process had been interrupted and the embryo had died (as it has also been reported for other *Pistacia* species [4]).

In outdoor conditions, most of the seeds germinated in the trays. However, none of the seeds that remained ungerminated in the tray at the end of the experiment could germinate in the germination chamber under standard conditions. The inspection of these nonviable seeds revealed that many of them were slightly open and rotten, in much the same way as the seeds found in the soil.

4.2. Seed dormancy

No germination was detected after 28 days in any of the Petri dishes with fruits (seeds with pulp), whereas the germination rate when the pulp was removed was 81.0 ± 6.8 % in the Cabanes population.

Germination in the dark reached 79.2 ± 5.9 % but did not differ from that under a 12-h photoperiod regime, which reached 81.0 ± 6.8 % ($F = 0.771$, $P > 0.1$), indicating that the light regime does not affect germination or induce secondary dormancy.

4.3. Seed longevity

Seed germinability of the seeds stored in laboratory conditions was maintained for a few months but decreased quickly in 1 or 2 years. This decrease depends on population, as indicated by the significant interaction between population and time of storage, and has both a quantitative and a qualitative effect (see *table I* and *figure 1*). So, time affected the seeds of Cabanes and Porta-Coeli sites only in their germination rate but also strongly retarded the date of first germination of the El Saler seeds. Likewise, the seeds of the Cabanes site, stored for 5 years, were unable to germinate.

4.4. Seed germination phenology and seedling emergence

The first seedlings in the flowerpot experiment were detected 23 days after the first irrigation event, whereas 10 % of the total seedling emergence was recorded 38 days after the irrigation event, 50 % after 55 days and germination was completed at day 90. Only nonviable seeds remained ungerminated after this time.

Figure 2 shows the course of precipitation, the dates when seedling emergence started and finished and the seedling number in field conditions in 1992, 1993 and 1994 (1st, 2nd and 3rd cohorts, respectively). For the 3rd cohort, the date of the first germination is lacking because it occurred before we visited the plot. Seedling density was 0.47, 0.50 and 1.42 seedlings·m^{-2} in cohorts 1, 2, and 3, respectively.

Only one cohort of seedlings was detected in each period of observation, indicating that emergence was always synchronous. The earliest seedling cohort corresponded to the 1993–1994 cohort, which emerged in December. Although the seed crop did not differ significantly across the 3 years ($F = 1.95$, $P > 0.05$; [33]), the earlier cohort was also the more numerous, probably because seeds did not remain available to predators on the soil as long.

When the dates of seedling emergence of each cohort were contrasted with those of the course of precipitation, we obtained an informative picture. There were no doubts that the rain event of 123.9 L·m^{-2} that occurred between 25 October and 4 November 1993, was the trigger for the 3rd cohort. For the 1st and 2nd cohorts, there were two rainy periods prior to the emergence of seedlings. If we consider the number of days that seedling emergence took in the flowerpot experiment, we think that the second rain event was the trigger for both cohorts. Thus, the rain event of 168.9 L·m^{-2} that occurred between 28 November and 15 December 1991, would be the trigger for seedling emergence of the 1st cohort. Similarly, the rain event

Table I. Effects of population and time of storage on *Pistacia lentiscus* seed germination.

Source of variation	SS	df	MS	*F*
Tests involving population: between-subjects effects				
Within cells	204.82	6	34.14	
Constant	133 734.99	1	1 333 734.99	3 917.60*
Population	8 112.20	1	8 112.2	237.64*
Tests involving time of storage: within-subjects effects				
Within cells	543.72	18	30.21	
Time	17 888.90	3	5 962.97	197.41*
Population × time	7 024.53	3	2 341.51	77.52*

*: $P < 0.001$; ns: not significant

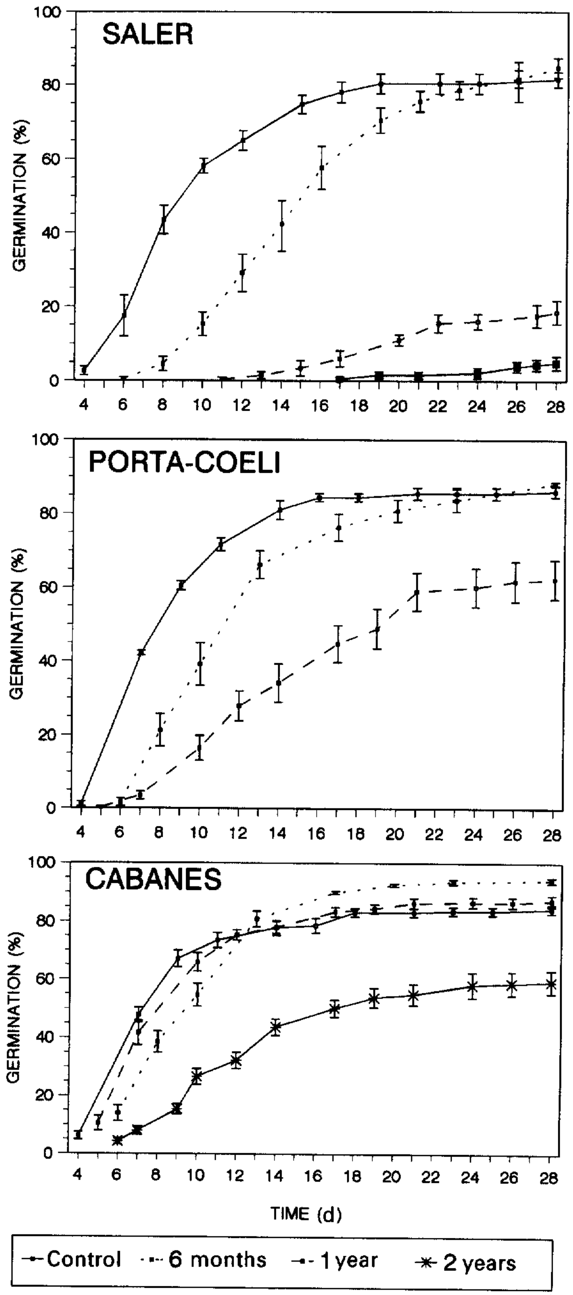

Figure 1. Variation in the percentage (means ± 1 SE) of germination of *Pistacia lentiscus* seeds in the three study sites after storage in laboratory conditions during 6 months, and 1 and 2 years.

of 102.1 L·m^{-2} that occurred between 22 and 29 December 1992, was expected to be the trigger for seedling emergence of the 2nd cohort.

All these rain events that we think triggered seedling emergence have as common features a long duration of the rainy period (7 days at least) and an important amount of water (around 100 L·m^{-2}). Indeed, the rain events that were unable to trigger seedling emergence were shorter in time and in amount (75 L·m^{-2} in 1 isolated day and 58 L·m^{-2} in 13 days, respectively).

The data suggest, furthermore, that temperature could also be an important factor in seedling phenology. Total emergence of cohorts 1 and 2 was delayed by nearly 100 days from the start of rain whereas cohort 3 was delayed by only 40 days. Range and mean temperatures of the emergence period were 2.2–18.3 and 11.1 °C, respectively, for the 1st cohort, 2.6–15.3 and 11.2 °C for the 2nd cohort and 3.6–24.0 and 13.5 °C for the 3rd cohort. A germination experiment with seeds from the Cabanes population (unpubl. data) showed that the first germination at 13 °C was delayed by more than 4 days when compared with the 20–25 °C treatment ($F = 243.00$, $P < 0.001$), whereas the time to reach 50 % of germination was delayed by more than 10 days ($F = 51.841$, $P < 0.001$).

The spatial pattern of the seedlings seems to be clearly related to the presence of a perch. In all 3 years, 90.5 % of *P. lentiscus* seedlings emerged under the canopy of shrubs (*table II*). Even if we consider the proportion each microsite reached in the plot, a significant deviation from the expected seedling emergence occurred ($\chi^2 = 351.9286$, df = 1, $P < 0.0001$; data of the three cohorts pooled).

4.5. Seedling survival

Most of the seedlings died a few weeks following germination, with less than 10 % remaining after 5 months in the three cohorts (*figure 3*). Despite the differences in initial seedling density (0.47, 0.50 and 1.43 seedlings·m^{-2} for the 1st, 2nd and 3rd cohorts, respectively) and the different shapes of mortality curves, the three cohorts resulted in a similar final seedling density (0.03, 0.05 and 0.05 seedlings·m^{-2}, respectively). The inflection of the mortality curve of the 2nd cohort in May coinciding with a rainy period suggests that climatic conditions can cause differences in the shapes of the curves of seedling mortality. This view is coherent with the evidence that desiccation was the main cause of seedling mortality (*table III*).

There were no significant differences between the number of seedlings surviving in both microsites. In April 1996, we monitored the size and morphology of the eight surviving seedlings. Three of them corresponded to the 1st cohort and five to the 3rd cohort. There were not any appreciable morphological differences between them. They had only two or three leaves each and were indistinguishable in height (6.0, 7.0 and 11.2 cm for the 4-year-old seedlings and 7.0, 7.1, 5.2, 5.0 and 4.2 cm for the 2-year-olds).

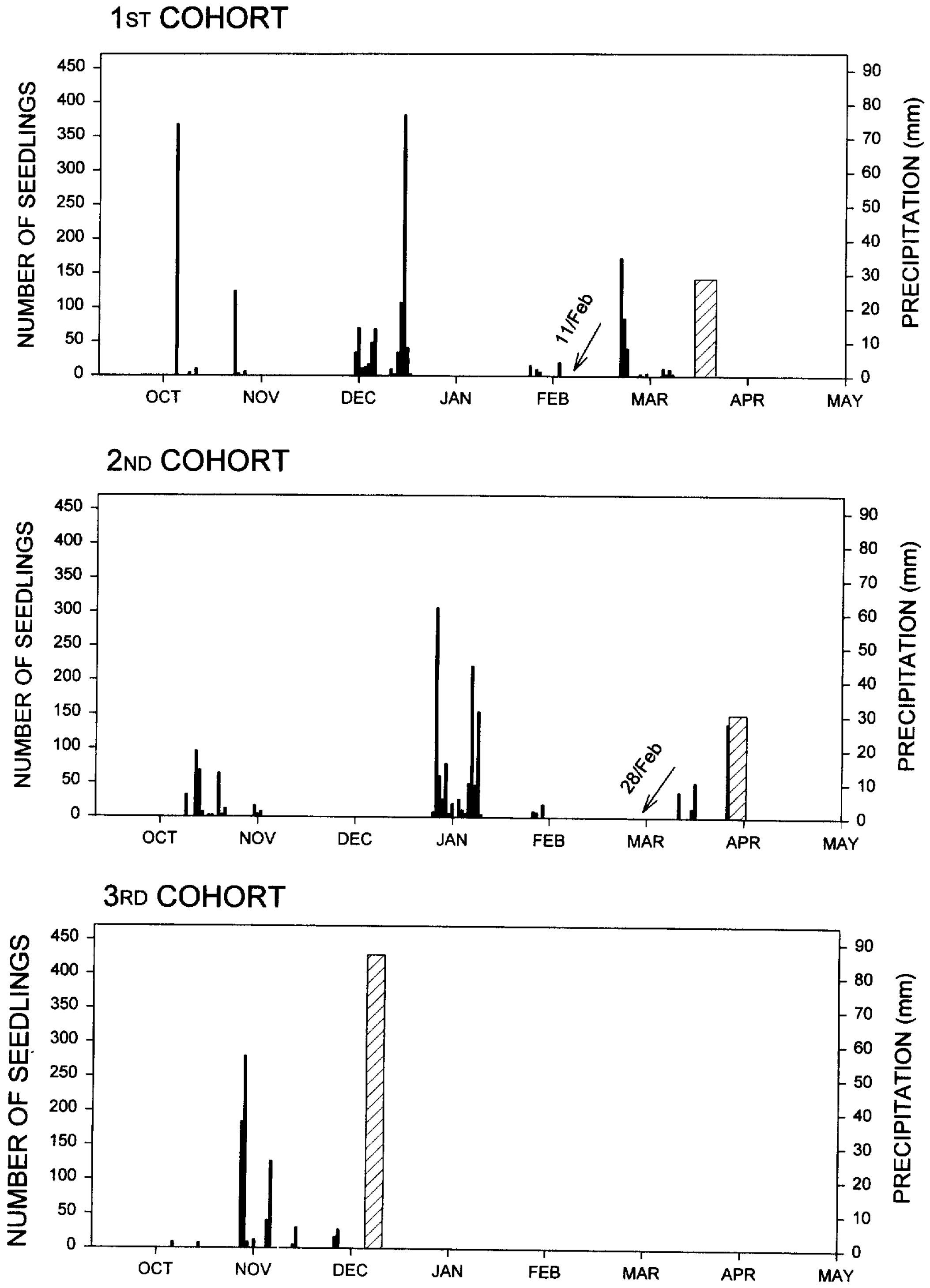

Figure 2. Record of daily rain events (black columns) from 1 October to the date when the peak of seedling emergence is observed in the 30 × 10 m plot at El Saler. The date when the first seedlings are observed and the final number of seedlings counted in the plot are also indicated (hatched columns).

Table II. Effects of microhabitat in seedling emergence and survival.

	Under perch canopy				On the open ground			
	Born		Survived		Born		Survived	
	n	(%)	*n*	(%)	*n*	(%)	*n*	(%)
Cohort 1	79	(56.0)	10	(12.7)	62	(44.0)	0	(0)
Cohort 2	145	(96.7)	16	(11)	5	(3.3)	1	(20)
Cohort 3	427	(99.8)	17	(4)	1	(0.2)	0	(0)
Total	651	(90.5)	43	(6.6)	68	(9.5)	1	(1.5)

Table III. Causes of mortality of natural seedling populations of *Pistacia lentiscus*.

	Dessicated		Disappeared	
	n	(%)	*n*	(%)
Cohort 1	94	(71.8)	37	(28.2)
Cohort 2	93	(69.4)	41	(30.6)
Cohort 3	256	(59.7)	173	(40.3)
Total	443	(63.8)	251	(36.2)

5. DISCUSSION

Seeds of *P. lentiscus* did not show dormancy. Neither prechilling [27], scarification [27], heat [29] nor light (present work) were necessary to germinate seeds nor enable it. Pulp removal was the only necessary condition for germination success of *P. lentiscus*, as occurred in *Rhamnus alaternus* [1]. However, in many other Mediterranean species with fleshy fruits, pulp removal only increased the rate and/or the speed of germination [1, 5, 20].

P. lentiscus seeds showed a significant and strong decrease in seed germinability over time under standard storage conditions, as well as other species of the same genus [4]. Relatively short seed longevity and lack of dormancy mechanisms would limit seed storage in soil. Furthermore, the high postdispersal predation rates suffered by seeds [36] would also limit the accumulation of a seed bank of this species. In agreement with these seed traits, we have not found any viable seed in the soil before the next dispersal season, either under field or experimental conditions. Therefore, the seed bank of *P. lentiscus* is transient (sensu Thompson [30]) because it is composed of seeds germinating within the year.

Weather conditions seem to play an important role in germination of *P. lentiscus*. Seedling emergence in field conditions, which always occurred synchronously, was observed only after a prolonged and heavy rain (≥ 7 days and ≥ 100 $\text{L}\cdot\text{m}^{-2}$). In the period studied, shorter or less heavy rainy periods did not trigger seedling emergence. To determine the frequency of these favourable conditions on a regional scale, we analyzed the meteorological record from 1950 until 1990 for a range of Mediterranean climate types where *P. lentiscus* grew in the Comunidad Valenciana (Spain). We found that these conditions occurred 85 % of the years in a Mediterranean humid climate (Pego, 1 000 $\text{L}\cdot\text{m}^{-2}$ of mean annual rainfall), 72 % in a subhumid one (Sant Jordi, 600 $\text{L}\cdot\text{m}^{-2}$) and 62 % in a semi-arid one (Valencia, 400 $\text{L}\cdot\text{m}^{-2}$). These results suggest that actual climatic conditions are not an important limitation for germination at a regional scale. Temperature also affected germination; therefore, the time needed to detect the first seedlings was longer in winter than in autumn, and these results were consistent with temperature experiments in laboratory.

More seedlings emerged under the shrub canopy than expected if seeds were distributed homogeneously on the plot. As light does not seem to affect the germination process, the spatial pattern of seedling emergence may be mainly the consequence of the preferences of seed dispersers for perches but also the consequence of microclimatic conditions affecting water balance and soil properties under theses perches [35]. However, no data exists to distinguish the importance of each of these factors.

Most of the seedlings died within a few weeks after seed germination and before the summer drought, with less than 10 % remaining after 1 year. A similar mortality pattern was reported for *Cistus villosus* and *C. salvifolius* [31] as well as for *Nerium oleander* [16]. Water deficit seems to be the principal cause of mortality, as indicated by the high contribution of seedling desiccation to mortality. Water deficit has been identified also as the main mortality cause in other Mediterranean species such as *Phillyrea latifolia* and *Nerium oleander* [16, 17]. Regardless of the initial number of seedlings, a similar final density remained after the first summer for each cohort, supporting the hypothesis that microsite limitation and not seed availability would be the main factor controlling *P. lentiscus* recruitment in closed shrublands. We found that a few seedlings survived for a long time in a near-latent mode under the canopy of established

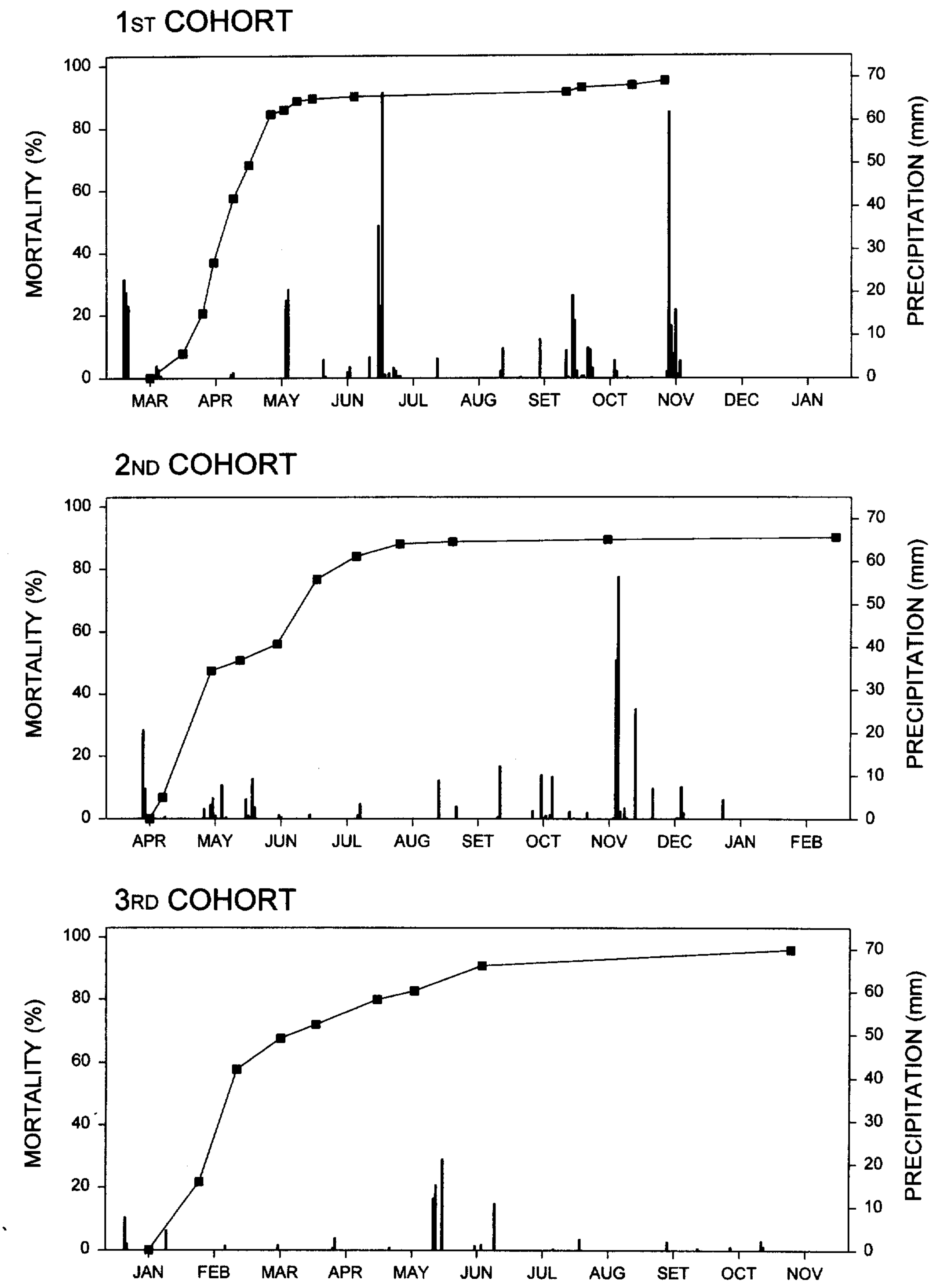

Figure 3. Mortality curves for cohorts of *Pistacia lentiscus* seedlings in 3 years. Daily rain events are also shown.

plants, suggesting that a seedling bank strategy, instead of a seed bank one, is followed by this species. A similar behaviour was reported for *Quercus ilex* and for tropical trees, whose seedlings and saplings survived under the canopies of mother plants in a latent mode, developing only when a perturbation or a gap opened the canopy [12, 32].

In conclusion, seed predation [36], seed longevity, germination features and seedling survival do not seem to modify the spatial pattern of seed shadow generated by dispersal of *P. lentiscus*. Seed predation, seed longevity and weather conditions to trigger seed germination would be limiting factors in some places and years in a regional scale at least. Nevertheless, seedling survival seems to be a true bottleneck in the recruitment of *P. lentiscus* in shrublands. All 3 years resulted in a similar low seedling density in spite of the initial density, which agrees with the view that homogeneous and dense shrublands, or woodlands under Mediterranean climates, have very few seedlings [8, 24, 25].

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