

A germination study of herbicide-resistant field poppies in Spain

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Abstract – Field poppy, *Papaver rhoeas* L., is a very common weed in winter cereals in North-Eastern Spain. Its control is becoming difficult due to expanding herbicide resistance. To control field poppies there are alternative strategies such as non-chemical control that take into account the weed emergence period. However, there is a lack of knowledge of *P. rhoeas* emergence patterns in semi-arid conditions. Thus, here we conducted pot experiments on the emergence of *P. rhoeas*. We aimed to describe the emergence period and to quantify the emergence of a susceptible and of a herbicide-resistant *P. rhoeas* population at two locations in Catalonia, Spain, from 1998 to 2001 and until 2004 at one of them. Therefore, pots containing seeds of both populations were established at the two locations and emergence was recorded monthly. We studied the origin of the population, the sowing location, the effect of cultivation and the sowing year. First, we found that the main emergence peaks in our experiments occurred in autumn, accounting for between 65.7 and 98.5% of the annual emergence from October to December, and only little emergence was recorded in spring. This emergence pattern is different from those found in the literature corresponding to Northern European countries, where in some cases main flushes occur only in autumn, in spring and winter or only in spring. The emergence was mainly affected by cultivation, but the effect of light stimulus was observed several months later. As a consequence, cultivation should be done in early autumn, promoting emergence during the whole autumn and winter so that emerged seedlings can be controlled before sowing a spring crop. Second, most experiments showed that the emergence was significantly higher in the first autumn than in the following seasons, e.g. 4.1% emergence in the first year and only 2.1, 2.3, 0.5 and 0.6% new emergence at one of the locations for the second, third, fourth and fifth years. Thus, after having a severe *P. rhoeas* infestation causing a big seed rain, emergence should be stimulated by autumn cultivation in the following season and seedlings controlled by trying to deplete the soil seed bank as much as possible. Despite the fact that emergence will be staggered throughout several years and that there was a significant relationship between rainfall and emergence, so that dry years will cause a smaller emergence rate of the weed, these findings define a cultural management strategy to reduce *P. rhoeas* infestations and to contribute to integrated weed management strategies combining it with other tools.

emergence period / dormancy / cultivation / seed bank / *Papaver rhoeas*

1. INTRODUCTION

To achieve long-lasting effective weed management, especially when using cultural weed control methods, it is necessary to have a sound understanding of components of weed biology such as weed seed bank dynamics and weed seedling emergence (Bhowmik, 1997). Liebman and Gallandt (1997) consider that information regarding spatial and temporal patterns of weed abundance is necessary to develop weed management strategies based on submitting weeds to multiple and temporally variable stresses. In North-Eastern Spain, field poppy (*Papaver rhoeas* L.) is a weed competing with winter cereals and difficult to control, especially due to herbicide resistance. The number of populations resistant to the herbicides 2,4-D and/or sulfonylureas in North-Eastern Spain is increasing steadily since herbicide resistance appeared in the late 1990s (Cirujeda, 2001). This problem forces farmers to combine different methods, including non-chemical control such as mechanical control, and mouldboard ploughing, to manage

P. rhoeas. The survey conducted by Weber and Gut (2005) demonstrates the importance of this weed species occurring throughout Europe in all kinds of crops and which is considered to be not easy to control.

Knowing weed emergence periods is important for better timing of interventions in a weed management strategy. As emergence is highly weather-dependent it is useful to study the emergence behaviour over several years in the same area to establish a general response. Long-term studies are also valuable for the establishment of the approximate time needed to deplete the soil seed bank up to acceptable levels. Despite the fact that studies on emergence periods and population dynamics for *P. rhoeas* have been conducted in Northern European countries for a long time, e.g. in Denmark (Madsen, 1962), in Great Britain (Roberts and Feast, 1972), in Switzerland (Salzman, 1954) and in Sweden (Milberg and Andersson, 1997) data for this species under Mediterranean conditions are sparse.

Although *P. rhoeas* is one of the most important broad-leaved weeds infesting winter cereals in North-Eastern Spain (Photo 1), only a one-year experiment in one location has been

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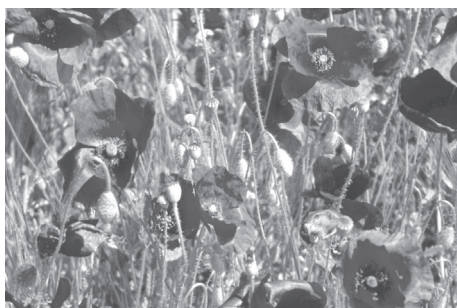


Photo 1. Field poppies (*Papaver rhoeas* L.) in a cereal field.

conducted in the semi-arid conditions of North-Eastern Spain by Izquierdo and Recasens (1992). In a survey conducted in 1990 in Catalonia, this species occurred in 39% of the surveyed fields (Riba et al., 1990).

The studies in Northern Europe indicate that *P. rhoeas* has two main periods of emergence, a minor flush in autumn (September–December) and a major flush in spring (January–May) (Roberts and Boddrell, 1984; Froud-Williams et al., 1984b; Baskin et al., 2002). In a preliminary study conducted in North-Eastern Spain, *P. rhoeas* germinated in autumn, but not in spring (Izquierdo and Recasens, 1992). There are two possible explanations for this discrepancy. Various studies have shown that light induction (Froud-Williams et al., 1984b) and soil moisture are essential for *P. rhoeas* germination. In a detailed study, Baskin et al. (2002) found that physiological dormancy of *P. rhoeas* is broken during exposure to high temperatures in summer but only when seeds are imbibed. If seeds come out of this dormancy in summer or autumn but fail to germinate in autumn, low winter temperatures cause them to enter conditional dormancy (Baskin et al., 2002). The same authors found that light is required afterwards for embryo growth, i.e. for morphological dormancy to be broken.

While springs in Northern Europe are characterised by moist soil conditions and frequent tillage operations, springs in North-Eastern Spain are typically dry, forcing farmers to shift the main period of cultivation from spring to autumn and winter. We hypothesise that either the low moisture content in the soil or the lack of a light stimulus associated with cultivation in spring, or both factors simultaneously, may be responsible for the absence of the spring germination flush in NE Spanish *P. rhoeas* populations.

Knowledge of the possible seasonal variation of seed emergence may improve strategies for either favouring *P. rhoeas* emergence previous to crop sowing or reducing *P. rhoeas* emergence during the crop-growing cycle by preparing the seed-bed in non-optimal emergence conditions for the weed. These data could also help determine whether non-tilled fallow is a possible control strategy, or what time of cultivation is most effective at reducing the *P. rhoeas* soil seed bank. As little detailed data on annual emergence are available for North-Eastern Spain (Torra et al., 2003; Cirujeda et al., 2003, 2006), a field experiment was carried out at two locations to describe the yearly emergence pattern of two *P. rhoeas* populations over three years in one location and five years in the

other. Additionally, the studies assessed natural conditions for *P. rhoeas* germination in North-Eastern Spain, where continuous moisture is not guaranteed. The effects of cultivation in autumn and early winter were also investigated, to help define possible control methods based on stimulating *P. rhoeas* germination before sowing.

The main objectives of this study were (a) to describe the seasonal distribution of *P. rhoeas* seedling emergence in North-Eastern Spain as affected by the seed origin, by the experimental site, by the sowing year and by the influence of cultivation; (b) to determine the accumulated emergence of *P. rhoeas* after five years as affected by the same factors to acquire information on the likely speed of *P. rhoeas* seed bank depletion in the soil in North-Eastern Spain, and (c) to describe the influence of rainfall on the emergence processes. These aspects were studied with the overall aim of contributing to the design of successful weed control strategies for *P. rhoeas*.

2. MATERIALS AND METHODS

The two *P. rhoeas* populations used in this study were (1) the herbicide-susceptible population referred to as A/98 from Algayón (La Llitera region) and (2) the tribenuron-methyl and 2,4-D multiple-resistant population referred to as B/98 in Baldomar (La Noguera region). The population in Algayón was collected in a fallow field, while the one in Baldomar was harvested in a field where barley had been grown under minimum tillage for more than 10 years.

A sample of mature seeds was collected across the whole field from each of these two sites in summer 1998, 1999 and 2000 and air-dried for 7 days prior to sowing. The remaining seeds were kept in plastic pots in a warehouse at 20 °C. Initial seed viability was determined by the tetrazolium bioassay (MAPA, 1987) and ranged between 90 and 100% in all cases. Thousand-seed lots were prepared by weighing after determining the 1000-seed weight of each population separately (Tab. I). The bottom of 18-cm high and 19-cm-diameter plastic pots was cut off. The pots were filled with seed-free silt loam soil and 1000 *P. rhoeas* seeds were sown on the surface of each pot and mixed with the first 2 cm of soil in July, imitating natural seed rain, except in the year 2000 in Algayón, where the pots had to be re-sown in September because of vandalism. Seeds from Algayón were taken to Baldomar and vice versa. The pots were sunk in the soil so that the rims remained just above the surrounding soil surface, as described in other experiments carried out by Madsen (1962), Froud-Williams et al. (1984a) and Roberts and Boddrell (1984). Each year, six pots of each population were established at both sites, sowing freshly-harvested seeds. Three were designated for each tillage system, explained later. Barley was sown in the soil around the pots to shade them, imitating the crop situation.

Field soil from a 0 to 15 cm depth containing an unknown amount of differently-aged *P. rhoeas* seeds was collected at each site in July and placed in the pots which were sunk in the soil in the same manner as the sown pots at the respective sites. Six pots, three for each tillage system, were established each year in summer 1998, 1999 and 2000 with the aim of observing if similar emergence responses could be expected from a

Table I. Sequence of cultural operations on the outdoor pot experiments conducted in Algayón and in Baldomar with *Papaver rhoeas*. Due to drought, simulated cultivation was conducted more times in the first year. The 1000-seed weight is expressed in $g \pm$ standard error. The field in Algayón is located at 41.836°N, 0.383°E, the field in Baldomar at 41.918°N, 1.014°E.

	1998	1999	2000
Algayón			
1000-seed weight	0.1251 \pm 0.00094	0.0827 \pm 0.00194	0.0921 \pm 0.00222
<i>P. rhoeas</i> sowing date	27/07	16/07	19/09*
Cultivation 1	09/09	–	–
Cultivation 2	07/10	–	–
Cultivation simulation cereal sowing	27/10	21/09	10/10
Baldomar			
1000-seed weight	0.1053 \pm 0.00181	0.0881 \pm 0.00330	0.1150 \pm 0.00182
<i>P. rhoeas</i> sowing date	28/07	16/07	19/07
Cultivation 1	09/09	–	–
Cultivation 2	06/10	–	–
Cultivation simulating cereal sowing	26/10	21/09	07/09

* In Algayón seeds had to be re-sown in September 2000 due to vandalism.

mixture of differently-aged *P. rhoeas* seeds in comparison with the uniformly-aged sown seed lots.

Half of all pots with sown seeds as well as those with field soil were kept undisturbed during the testing period. In the other half, autumn cultivation was simulated at the same dates as the farmer conducted these operations in the field. The normal farming practice was seedbed preparation and a second cultivator pass combined with cereal sowing after rainfall. In the pots, cultivation was simulated with a metallic fork at 4-cm depth. In 1998, two cultivation passes were performed in the field before sowing and both were simulated in the pots, in addition to the soil disturbance associated with sowing. In 1999, seedbed preparation and sowing were conducted in dry conditions. There had not been any rainfall since April; therefore no additional soil movement was simulated. In 2000, seedbed preparation was performed in humid soil conditions and sowing was done immediately afterwards, so that only one soil disturbance was simulated in the pots. The timing of the operations is shown in Table I. In the following years in Baldomar one single soil disturbance was also conducted on the 27th October 2001, the 6th November 2002 (delayed by rainfall) and the 24th September 2003. This was not possible in Algayón because the experiment had to be concluded in May 2001 due to vandalism.

At both locations, three replicates of each treatment were established. Three seed treatments, i.e. two seed origins, one field soil and two cultivation treatments, i.e. uncultivated vs. cultivated with three replicates repeated in three successive years resulted in 54 pots at each location. Pots were placed randomly at the field edge in Baldomar and in the middle of the fallow field in Algayón. Pots from subsequent years were added to the trial following the same original spatial design.

Plant emergence of both populations was recorded at both sites at monthly intervals, and counted seedlings were subsequently removed. From the end of June until August of each year, pots were covered with a fine net to prevent seed rain

from nearby *P. rhoeas* plants. The experiment was finished in April 2001 in Algayón but continued until March 2003 in Baldomar, when the 18 cm of soil contained in the pots was collected and placed in 0.20 \times 0.15 m aluminium trays and kept in a greenhouse. Trays were periodically watered and emergence was enhanced by soil stirring, which was conducted six times until January 2006. Then, soil was watered with a solution containing 0.3 mL gibberelins (GA_3) per litre of soil, following Nievas (1998). As no new emergences were observed even after this treatment, soil samples were considered not to contain any more viable seeds.

Data processing and statistical analysis

Cumulative emergence was low relative to the 1000 seeds placed in the pots so that percentage emergence was always calculated on 1000 seeds. Statistical analysis of emergence data was performed by submitting data to a standard ANOVA using the procedures PROC GLM and MIXED in SAS (SAS Institute, 1991). A completely randomised design was used for both experiments. When necessary, percent emergence data were arcsin $\{\sqrt{(x/100)}\}$ transformed. Mean values were calculated as least square means (LSM) and differences between means were analysed on the basis of ordinary *t*-tests in the case of significant interactions.

Adjustments of the model

Emergence was related to accumulated precipitation following the Weibull equation (Weibull, 1959; Calvo-Haro et al., 1994):

$$y = F(x, K, b, a) = K [1 - \exp((-bx)^a)], b < 1, a < 0$$

$$x_1 = \sqrt[a]{(a-1)/b^a}$$

where y is the percentage of emergence accumulated with one unit in cumulative precipitation x (expressed in mm), K is the maximum emergence, b is a parameter related to the speed of emergence and a is related to the inflexion point. x_1 is the value where the second derivate of the Weibull equation is zero, indicating the moment where maximum speed is reached. The adjustment to the model was done using the procedure PROC NLIN of SAS (SAS version 9; SAS Institute, Cary, NC, USA) (SAS Institute, 1991). A likelihood ratio test (Kimura, 1980) was used to compare each parameter of the model (K , b and a) and also the overall equation shape (all constants together, K , b and a), between cultivated and non-cultivated pots and between the two locations. Contrast analyses were performed with a Chi-square test between parameter estimates, with $P < 0.05$ indicating statistical significance.

3. RESULTS AND DISCUSSION

3.1. Climatic data

The main climatic parameters affecting seed emergence are temperature and rainfall. Mean monthly temperature during the seasons 1998–1999 until 2000–2001 was very similar at both locations (Fig. 1A, B; data from the nearest official meteorological stations). Main rainy periods were coincident in both locations but more rainfall and longer moist periods were observed in Baldomar than in Algayón. Quite long fog periods occurred in Baldomar during most of the winters, maintaining the humidity longer than in Algayón, where the soil dried out more frequently. Due to the higher altitude, nights were also cooler during the whole year in Baldomar and dew was very frequent in the mornings. Accumulated precipitation from August to July was variable among years within the same location, especially in Baldomar where the seasons 2000–2001 and 2002–2003 were especially moist, while 2001–2002 was drier.

3.2. Emergence periods

The emergence season of *P. rhoeas* in Algayón was found to be from October to March in 1998–1999, from September to March in 1999–2000 and from October to February in 2000–2001 (Fig. 2). The main emergence flushes occurred in December for the period 1998–1999, in October for 1999–2000 and in November for 2000–2001, accounting for 35.4, 57.3 and 69.4% of the total annual emergence, respectively. The sowing year seemed to have little or no influence on the emergence period at this location as these peaks were consistent for all three sown seed lots. The timing of the emergence peaks also seemed to be independent of seed age, of population origin and cultivation treatment. The emergence periods were in some cases longer in spring for the Baldomar than for the Algayón population. Emergence between October and December reached 74.4, 75.6 and 98.5% of the annual emergence for 1998, 1999 and 2000, respectively.

In Baldomar, the emergence season of *P. rhoeas* was found to be from November to April in the cropping season 1998–1999, from September to February in 1999–2000 and from

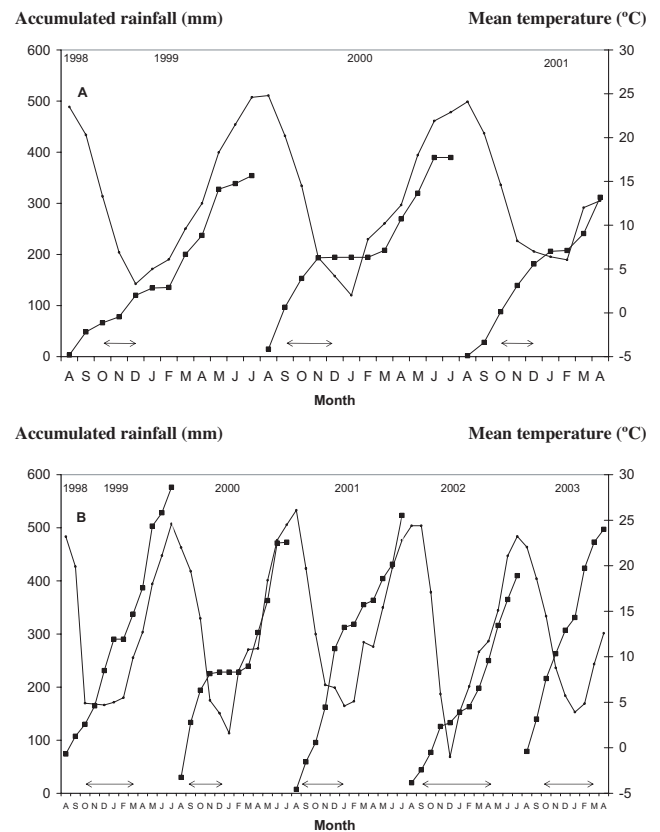


Figure 1. Climatic data (- monthly mean temperature and ■ accumulated rainfall) of the two sites during the duration of the experiments. Arrows indicate overall *P. rhoeas* emergence periods as found in the experiments. (A) In Algayón (La Llitera, Aragón). Data from the nearby climatic observatory “La Melusa” at 41.782°N, 0.378°E, 218 m altitude. (B) In Baldomar (La Noguera, Catalonia). Data from the nearby observatory in Vilanova de Meià located at 41.991°N, 1.022°E and 590 m altitude.

October to March in 2000–2001 (Fig. 3). These periods were almost coincident with those in Algayón, but one month longer in 1998–1999 and in 2000–2001. In 1998–1999, the main emergence flush was observed in October; in 1999–2000 in September or October, depending on the treatments; and in 2000–2001 between October and November, again depending on the treatments, accounting for 53.6, 63.3 and 67.0% of the total annual emergence, respectively. Also, at this location, the sowing year and the population origin did not affect the timing of the emergence peaks. Cultivation delayed the flushes on several occasions compared with the non-cultivated pots. This could be observed for seeds from Algayón on one occasion and for seeds from Baldomar on two occasions. The emergence between October and December reached 85.7, 65.7 and 96.3% of the annual emergence for 1998, 1999 and 2000, respectively.

In the pots containing soil with differently-aged seeds, main emergence peaks were similar to those of the artificially sown seeds at both locations (data not shown). Mixtures of differently-aged seeds thus reacted similarly to the

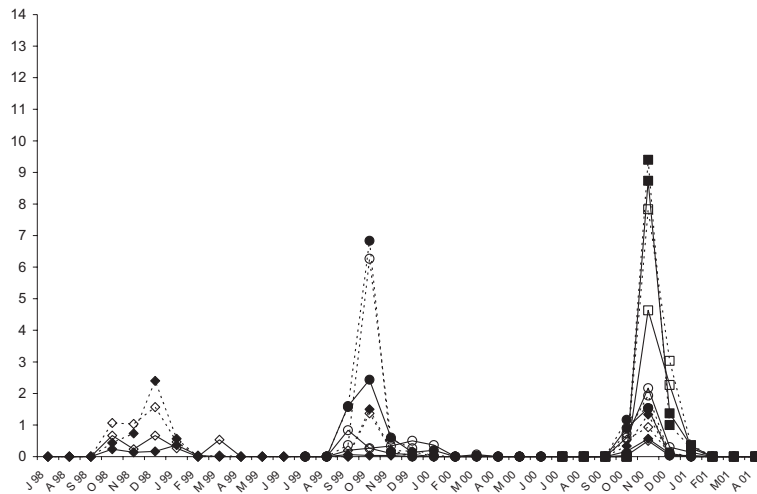
Emergence of *Papaver rhoeas* seedlings (%)

Figure 2. Emergence of two *P. rhoeas* populations from Algayón and Baldomar sown in Algayón. Mean of three replicates. Solid lines: no cultivation. Dotted lines: cultivation. ♦ Algayón 98, ● Algayón 99, ■ Algayón 00, ◇ Baldomar 98, ○ Baldomar 99, □ Baldomar 00.

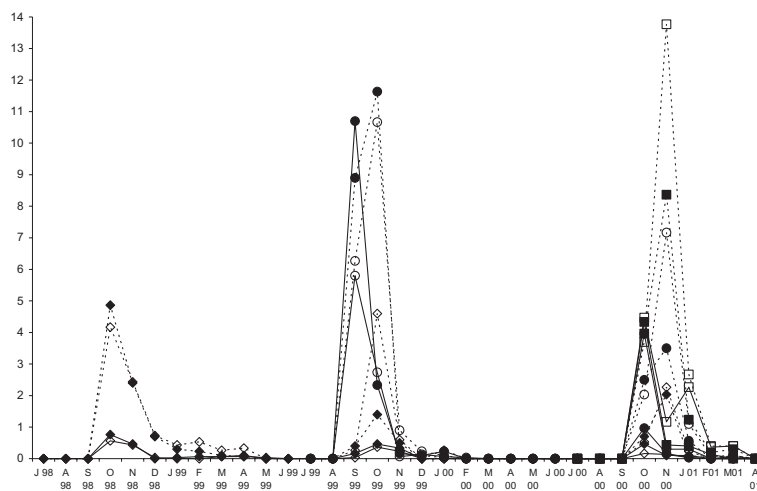
Emergence of *Papaver rhoeas* seedlings (%)

Figure 3. Emergence of two *P. rhoeas* populations from Algayón and Baldomar sown in Baldomar. Mean of three replicates. Pots were established in summer 1998, in summer 1999 and in summer 2000. Solid lines: no cultivation. Dotted lines: cultivation. ♦ Algayón 98, ● Algayón 99, ■ Algayón 00, ◇ Baldomar 98, ○ Baldomar 99, □ Baldomar 00.

environmental conditions to freshly-sown, one- and two-year old seeds.

At both sites, *P. rhoeas* had a continuous emergence during autumn, winter and part of spring. Only slight differences in the emergence periods were found depending on the origin of the population, the experimental location, the cultivation treatment and the seed age (Figs. 2, 3). Roberts (1964) also found that seed age in the seed bank did not appreciably affect annual emergence patterns. As in Baskin et al. (2002), an autumn flush was observed in our experiments, but much less emergence occurred in spring in North-Eastern Spain compared with Sweden. Contrary to the results of Baskin et al. (2002) and to our results, Milberg and Andersson (1997) described

that *P. rhoeas* germinated strictly in autumn in Swedish conditions and Froud-Williams et al. (1984a) found emergence in winter and spring, but not in autumn. Our results are also quite different from those of Roberts and Boddrell (1984), where *P. rhoeas* emergence in Britain occurred mainly in spring and only little in autumn. The lower temperatures in Britain and Sweden compared with those in Spain probably caused these differences, impeding emergence in winter and delaying it until spring. Following Baskin et al. (2002), *P. rhoeas* seeds lose physiological dormancy with high temperatures in summer if imbibed and can germinate in autumn as long as the seeds receive light and enough moisture. According to this, the most limiting factor for *P. rhoeas* emergence in our experiments

Table II. Emergence of *P. rhoeas* one year after burial (mean % of emerged seedlings) for each sowing year at both sites. Data were arcsin $\{\sqrt{(x/100)}\}$ transformed. Values in parentheses indicate the transformed means corresponding to each of the back-transformed values. Standard Error of Difference (SED) values are given on the transformed scale. D.f.: degrees of freedom.

Treatment		Emergence (%)	SED	d.f.
Site				
Algayón		5.6 (0.24)		
Baldomar		7.2 (0.27)	0.0109	48
Seed origin				
Algayón		6.2 (0.25)		
Baldomar		6.5 (0.26)	0.0109	48
Cultivation				
Without		3.6 (0.19)		
With		9.8 (0.32)	0.0109	48
Sowing year				
1998		3.4 (0.18)		
1999		6.1 (0.25)		
2000		10.5 (0.33)	0.0134	48
Site				
Cultivation	Algayón	Baldomar	SED	d.f.
Without	4.0 (0.20)	3.3 (0.18)		
With	7.4 (0.28)	12.4 (0.36)	0.0154	48

could be lack of moisture in the Mediterranean conditions during summer so that morphological dormancy could not be released. Baskin et al. (2002) found that low winter temperatures can induce conditional dormancy, possibly explaining why in our experiments few plants emerged in spring.

3.3. Cumulate emergence as affected by location, origin of population, cultivation and sowing year

The emergence for the first 14 months after sowing was mainly affected by the sowing year and by the cultivation treatment ($P < 0.01$) (Tab. II). Significantly higher emergence was recorded for the seeds sown in the year 2000 but emergence was also significantly higher for 1999 compared with 1998 ($P < 0.01$). Also, cultivation had a stimulating effect on emergence at both sites ($P < 0.01$). Generally, more emergence occurred at the cooler location Baldomar than in Algayón despite the cultivation \times site interaction showing that this was significant only under cultivated conditions (Tab. II). The seed origin had no influence on results.

According to Baskin et al. (2002), *P. rhoeas* seeds need temperatures higher than 15 °C in imbibed conditions in order to break morphophysiological dormancy. After this, light can stimulate emergence. The climatic conditions in Algayón were drier than in Baldomar; thus, cultivation might have not stimulated emergence due to the fact that seeds were not imbibed. In Baldomar, cultivation provided the light needed to stimulate germination, hence significantly more seeds emerged in the cultivated than in the non-cultivated pots. Roberts and Feast (1972), Milberg and Andersson (1997), Karlsson and Milberg

(2003) and Froud-Williams et al. (1984b) also observed most *P. rhoeas* emergence following disturbance or light exposure of buried seeds. In our experiment, climatic conditions in 1998 were clearly the least favourable and in 2000 the most favourable to overcome dormancy processes.

Emergence did not occur immediately after receiving the light stimulus in the cultivated pots. The main seedling emergence flush was observed some months after cultivation and some emergence still occurred in March and April even though the cultivation or sowing had been conducted 6 to 10 months earlier (Figs. 2, 3). Following Hartmann et al. (2005), a light stimulus can provoke long-lasting seedling emergence; in their experiments, up to nine months during winter. Phytochrome in the active form can remain stable for a long time, mainly with low temperatures and seeds in the dry state (Hartmann et al., 1997). From a practical point of view, this delayed response to cultivation opens the possibility of promoting emergence during the whole autumn-winter period and controlling the *P. rhoeas* seedlings afterwards, in order to enhance the chances of emergence occurring before sowing the spring crop. However, as shown in the results, complete lack of *P. rhoeas* emergence cannot be guaranteed in a spring crop.

The emergence was significantly higher in the first autumn after sowing than in the following seasons for all sowing years and at both sites, with the exception of the non-cultivated pots placed in Baldomar in 1998 and 1999, where emergence in the second year was as high as in the first year (Figs. 4, 5) (*t*-test, $P < 0.01$). Froud-Williams et al. (1984a) also found that most emergence occurred in the sowing year. This fact supports the theory of secondary dormancy acquisition. Emergence in the

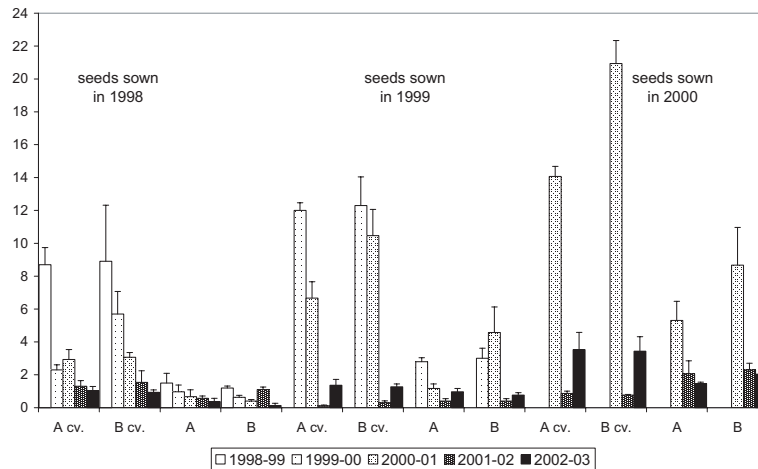
Emergence of *P. rhoeas* (%)

Figure 4. Emergence (%) of *P. rhoeas* in Baldomar in each cropping season. A: from Algayón, B: from Baldomar, cv.: cultivation. Bars indicate standard error.

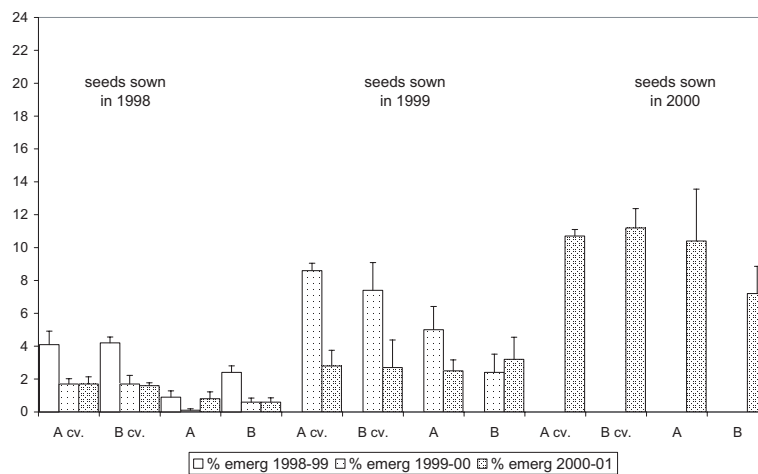


Figure 5. Emergence (%) of *P. rhoeas* in Algayón in each cropping season. A: from Algayón, B: from Baldomar, cv.: cultivation. Bars indicate standard error.

first year after seed rain seems to be mainly responsible for causing large infestations, which often occur in areas with resistant populations (Cirujeda et al., 2003) and the seed bank could be reduced if seed rain is prevented. If conditions are not very favourable in the first season, as observed for the seeds sown in 1998 at both locations (Figs. 4, 5), emergence can be much more staggered and the seed bank reduced very slowly, resulting in a certain yearly emergence. McNaughton and Harper (1964) described that *P. rhoeas* seeds showed an intermittent and long-drawn-out sequence of seedling emergence. In Great Britain, Roberts and Boddrell (1984) found that 21% of all *P. rhoeas* seeds sown emerged in the first year. In their work, only 1 to 7% of the remaining seeds emerged in each of the next three years, accounting for 38% of the seeds at the end of the four-year period. This indicates a slow depletion of the seed bank, starting with a similar emergence percentage to that found in a favourable year in our study (Figs. 4, 5). However, in an experiment conducted by Roberts and Feast

(1972) it was observed that although emergence of *P. rhoeas* was higher during the first year, there was still an appreciable emergence in the second year. In our case, this behaviour was observed in Baldomar in the pots established in 1999, which also showed considerable emergence in 2000–2001.

When analysing the emergence of the first year in Baldomar together with the cumulate emergence of the second and third years, again the sowing year and the cultivation treatment affected emergence significantly ($P < 0.01$) (Tab. IIIa). Emergence after the first year was highest for the seeds sown in 2000 (Tab. II) and was not reached by those sown in 1998 or 1999 even two years later, showing the importance of the climatic conditions of the first year after seed shedding to attain high emergence rates. The sowing year \times cultivation interaction showed that the general trend was only changed by emergence with cultivation in 2000, which was not higher than emergence with cultivation in 1999 (Tab. IIIa). Despite showing most of the emergence during the first year after sowing,

Table 3a. Cumulate emergence of two *P. rhoeas* populations of two different origins (mean % emerged seedlings of seeds sown) one, two or three years after burial in Baldomar. Data were arcsin $\{\sqrt{(x/100)}\}$ transformed. Values in parentheses indicate the transformed means corresponding to each of the back-transformed values. Standard Error of Difference (SED) values are given on the transformed scale. D.f.: degrees of freedom.

Treatment		Emergence (%)	SED	d.f.	
Seed origin					
	Algayón	8.5 (0.29)			
	Baldomar	10.9 (0.34)	0.0097	72	
Cultivation					
	Without	4.7 (0.22)			
	With	16.1 (0.41)	0.0097	72	
Sowing year					
	1998	5.9 (0.25)			
	1999	10.2 (0.33)			
	2000	13.4 (0.38)	0.0119	72	
Years after sowing					
	1	7.2 (0.27)			
	2	10.3 (0.33)			
	3	11.8 (0.35)	0.0119	72	
Sowing year					
Cultivation	1998	1999	2000	SED	d.f.
Without	1.9 (0.14)	4.7 (0.22)	8.7 (0.30)		
With	12.0 (0.35)	17.6 (0.43)	19.0 (0.45)	0.01684	72
Population					
Algayón	5.7 (0.24)	9.0 (0.31)	11.0 (0.34)		
Baldomar	6.1 (0.25)	11.5 (0.35)	16.1 (0.41)	0.01684	72

Table 3b. Cumulate emergence of two *P. rhoeas* populations of two different origins (mean % emerged seedlings of seeds sown) one to five years after burial in Baldomar. Data were arcsin $\{\sqrt{(x/100)}\}$ transformed. Values in parentheses indicate the transformed means corresponding to each of the back-transformed values. SED: Standard Error of Difference; d.f.: degrees of freedom.

Treatment		Emergence (%)	SED	d.f.
Cultivation				
	Without	2.5 (0.16)		
	With	14.1 (0.38)	0.0166	39
Population				
	Algayón	7.8 (0.28)		
	Baldomar	6.9 (0.26)	0.0166	39
Years after sowing				
	1	4.1 (0.20)		
	2	6.2 (0.25)		
	3	8.5 (0.30)		
	4	9.0 (0.30)		
	5	9.6 (0.31)	0.0259	39

new emergences in the second and third years significantly increased the total emergence ($P < 0.01$) (Tab. IIIa). Contrary to the observations after only one year (Tab. II), generally more germination was accounted for by seeds from Baldomar than from Algayón, excepting some single between-years comparisons (Tab. IIIa).

When comparing cumulate emergence for the seeds placed in 1998, the t -test showed that only emergence in the fifth year was higher than in the first and second years, so that emergence

during the third and fourth years did not significantly increase total emergence (Tab. IIIb).

3.4. Emergence related to precipitation

Different emergence rates between sites and within years were probably related to rainfall patterns. In Baldomar, seeds placed in the experiment in 2000 germinated more than those placed in 1999 or 1998 ($P < 0.001$), and also total rainfall in 2000–2001 was higher. Rain occurred more gradually and

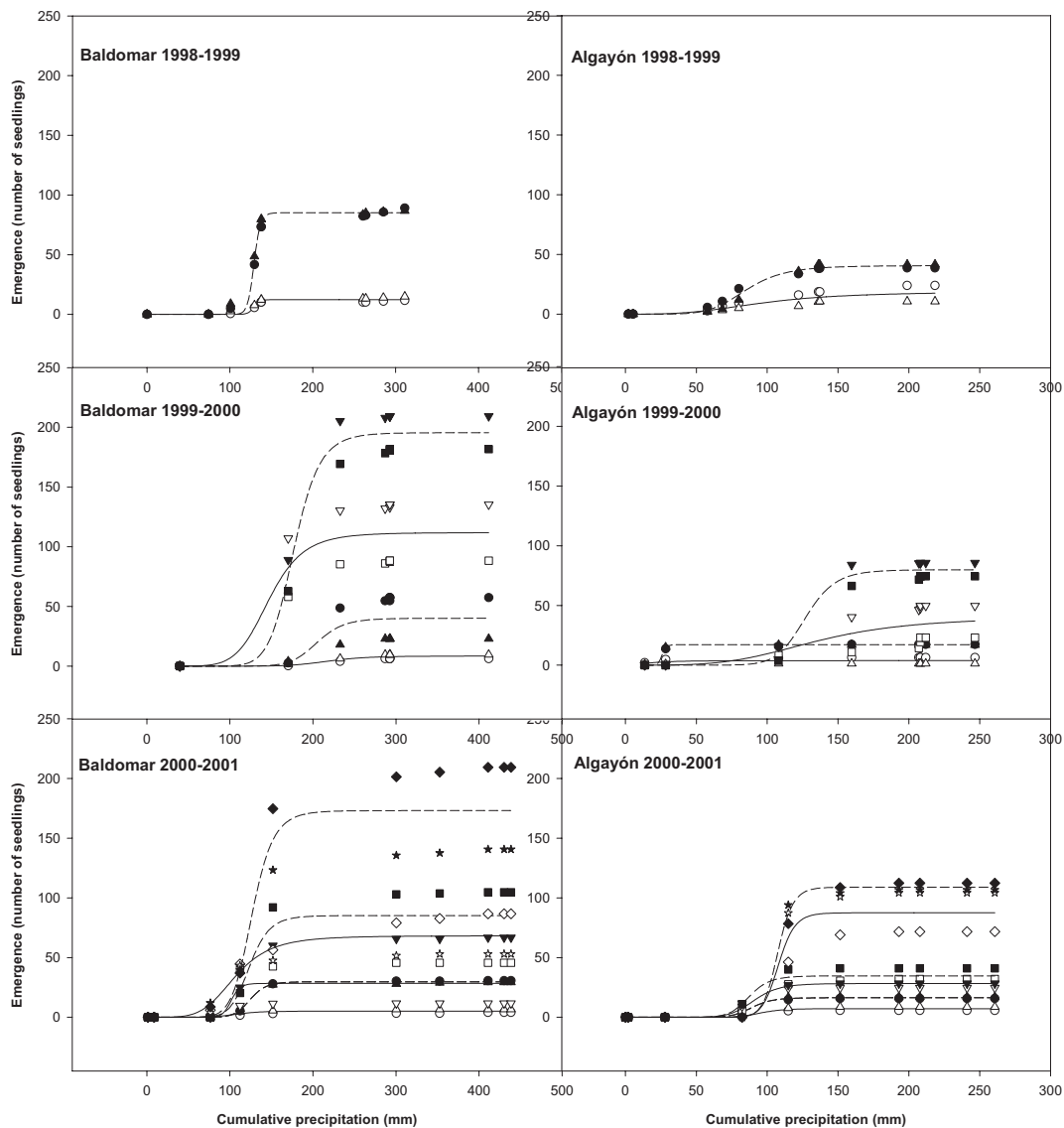


Figure 6. Cumulate *Papaver rhoeas* emergence in Baldomar (left) and Algayón (right) during three different seasons: 1998–1999, 1999–2000 and 2000–2001, related to cumulative precipitation (mean of the two seed origins). Seeds were collected and sown in both sites in July 1998, 1999 and 2000. The Weibull model was used to fit the values considering the sowing date as the starting point. Dashed line, cultivated; full line, not cultivated. Symbol legends: \circ Baldomar 1998 not cultivated; Δ Algayón 1998 not cultivated; \bullet Baldomar 1998 cultivated; \blacktriangle Algayón 1998 cultivated; \square Baldomar 1999 not cultivated; ∇ Algayón 1999 not cultivated; \blacksquare Baldomar 1999 cultivated; \blacktriangledown Algayón 1999 cultivated; \diamond Baldomar 2000 not cultivated; \star Algayón 2000 not cultivated; \blacklozenge Baldomar 2000 cultivated; \blackstar Algayón 2000 cultivated.

moisture was maintained as the number of days with rainfall between July and August was higher: 82 days in 2000–2001 compared with 73 in 1998–1999 and 65 in 1999–2000. The same relation between emergence and rainfall could be observed in 2002–2003, when rainfall was higher than in previous years (Fig. 1) and emergence increased for seeds placed in 1999 and 2000, breaking the tendency of annual decrease (data not shown).

The data fitted very well to the sigmoidal model of Weibull at both locations (Fig. 6, Tab. IV), demonstrating the existing relationship between rainfall and emergence. The general shape of the emergence curve (described by the parameter K_{ba}

in Tab. IV) was significantly different between the cultivated and the non-cultivated seeds in all years and at both locations (Tab. IV). This was confirmed with the x_1 value (maximum speed) which tended to be lower in all cases for seeds subjected to non-cultivated conditions, so that emergence tended to start earlier in these cases. Emergence speeds characterised by the parameter b and the parameter a (inflection point) were not significantly different, but the first one tended to be higher in most of the cases in the non-cultivated pots in Baldomar (Tab. IV). As previously found, total emergence, which was described by parameter K , was higher in all cases in cultivated pots, but only statistically significant in some (Tab. IV).

Table 4. Parameter estimates and standard errors of sigmoid emergence curves of *Papaver rhoeas*. Emergence models were calculated by the Weibull equation, $y = K \cdot [1 - \exp(-bx)^c]$. Comparison of the different parameters of the equation, following the likelihood ratio test of Kimura. N.s.: non-significant differences. Significance level: * $P \leq 0.05$; (*) $P \leq 0.1$. A. Algayón.

	Parameters		No cultivation Estimate	Std error	Significance cv. vs. no cv.	Baldomar Estimate	Std error	Algayón Estimate	Std error	Significance Alg. vs. Bald.
	Cultivation Estimate	Estimate								
Sown in 00	K	173.5	68.4	7.55	*	146.1	13.95	96.2	9.67	*
	b	0.00729	0.00808	0.00028	n.s.	0.00719	0.00071	0.00781	0.00089	n.s.
	a	6.1	3.0	1.69	0.96	4.9	2.93	4.2	2.47	n.s.
	x_1	133.2	108.0			132.7		119.9		Kba: *
Sown in 99	K	34.7	28.2	1.58	*	36.4	1.23	26.5	0.46	*
	b	0.0105	0.0101	0.00085	n.s.	0.0100	0.00048	0.0108	0.00033	n.s.
	a	6.4	6.3	3.33	1.50	6.9	1.85	5.8	1.30	n.s.
	x_1	92.8	96.3			97.8		89.7		Kba: *
Sown in 98	K	16.3	7.2	0.20	*	10.7	1.25	12.8	1.05	n.s.
	b	0.0103	0.0097	0.00021	n.s.	0.0102	0.00176	0.0100	0.00122	n.s.
	a	7.0	8.3	0.84	3.39	6.6	6.42	7.8	5.34	n.s.
	x_1	95.0	101.9			95.6		98.3		Kba: n.s.
Sown in 99	K	79.8	37.1	1.63	n.s.	47.6	6.54	67.2	4.62	n.s.
	b	0.0072	0.0067	0.00026	n.s.	0.0068	0.00122	0.0074	0.00088	n.s.
	a	7.9	2.9	1.51	2.41	6.5	8.44	5.8	3.36	n.s.
	x_1	137.5	129.5			143.7		131.2		Kba: *
Sown in 98	K	17.1	3.8	0.10	n.s.	11.7	1.30	9.2	1.88	n.s.
	b	0.0370	0.0431	0.01300	0.03040	0.0393	0.01100	0.0402	0.02720	n.s.
	a	11.9	1.6	81.92	2.88	3.9	5.71	5.5	23.57	n.s.
	x_1	26.8	12.1			23.5		24.0		Kba: n.s.
Sown in 98	K	40.3	17.5	0.94	(*)	31.2	2.92	26.4	4.82	n.s.
	b	0.0102	0.0090	0.00035	n.s.	0.0100	0.00127	0.0096	0.00217	n.s.
	a	3.9	2.4	0.41	0.98	2.8	0.94	4.1	2.90	n.s.
	x_1	90.8	89.2			85.5		97.0		Kba: n.s.

Table 4. B. Baldomar.

	Parameters	Cultivation			No cultivation Estimate	Std error	Significance cv. vs. no cv.	Baldomar			Significance Alg. vs. Bald.
		Estimate	Std error	Estimate				Estimate	Std error	Estimate	
2000–2001	K	173.4	8.21	68.4	3.89	n.s.	146.0	15.13	96.1	10.52	*
	Sown in 00	0.0073	0.00039	0.0081	0.00083	n.s.	0.0072	0.00093	0.0079	0.00126	n.s.
	a	6.6	2.31	3.1	1.29	n.s.	5.1	4.02	4.4	3.68	n.s.
	x_1	134.0		108.9		<i>Kba</i> :*	133.5		120.1		<i>Kba</i> : n.s.
	K	85.3	4.22	28.0	3.69	*	74.9	6.52	39.0	6.21	*
	b	0.0074	0.00032	0.0098	0.00118	n.s.	0.0077	0.00066	0.0079	0.00126	n.s.
1999–2000	a	6.3	1.97	8.9	10.4	n.s.	5.0	2.70	5.1	4.85	n.s.
	x_1	130.9		100.3		<i>Kba</i> :*	124.2		121.6		<i>Kba</i> :*
	K	29.8	0.21	5.10	0.36	*	17.2	3.29	17.8	2.76	n.s.
	b	0.0074	0.00007	0.0089	0.00041	n.s.	0.0074	0.00164	0.0077	0.00161	n.s.
	a	8.1	0.44	11.9	50.24	n.s.	7.7	11.06	6.44	8.13	n.s.
	x_1	132.4		111.7		<i>Kba</i> :*	133.6		126.8		<i>Kba</i> : n.s.
1998–1999	K	195.1	3.77	111.1	6.11	*	134.4	11.37	171.8	9.21	n.s.
	Sown in 99	0.0052	0.00017	0.0064	0.00117	n.s.	0.0053	0.00073	0.0057	0.00049	n.s.
	a	6.0	1.44	3.4	5.00	n.s.	5.1	5.24	4.8	5.59	n.s.
	x_1	185.9		141.0		<i>Kba</i> :*	180.5		167.9		<i>Kba</i> :*
	K	39.8	4.08	8.1	0.50	n.s.	31.5	6.08	16.4	1.74	n.s.
	b	0.0046	0.00048	0.0043	0.00025	n.s.	0.0045	0.00093	0.0045	0.00052	n.s.
1999–2000	a	9.7	11.24	6.7	3.66	n.s.	11.6	35.66	6.3	6.32	n.s.
	x_1	216.4		212.2		<i>Kba</i> :*	219.0		215.8		<i>Kba</i> : n.s.
	K	85.8	1.01	12.6	0.47	*	48.4	9.85	50.0	9.83	n.s.
	b	0.0076	0.00003	0.0076	0.00009	n.s.	0.0076	0.00045	0.0077	0.00053	n.s.
	a	16.8	1.73	16.3	5.40	n.s.	17.3	28.91	16.1	29.89	n.s.
	x_1	131.1		130.9		<i>Kba</i> :*	132.0		130.2		<i>Kba</i> : n.s.

Table 5. Total % seedling emergence of two *P. rhoeas* populations of two different origins in Baldomar including emergence in the greenhouse after finishing the trial in the field, corresponding to 102, 90 and 78 months after burial. SED: Standard error of difference; d.f.: degrees of freedom.

Treatment	Total emergence (% of the seeds sown)		SED	d.f.
Seed origin				
Algayón	14.4			24
Baldomar	19.4		1.304	24
Cultivation				
Without	10.8			24
With	23.0		1.304	24
Sowing year				
1998	12.5			24
1999	16.8			24
2000	21.4		1.597	24
Cultivation				
Population	Without	With	SED	d.f.
Algayón	9.8	18.9		
Baldomar	11.8	27.0	1.844	24
Sowing year				
1998	5.6	19.3		
1999	9.0	24.6		
2000	17.9	24.9	2.258	24

In contrast, fewer differences were found in population origin, since they only occurred in 2000–2001. In the other years, seeds from both sites reacted very similarly to precipitation.

3.5. Total emergence

Total emergence was calculated by adding the cumulate emergence in the field to emergence in the greenhouse after finishing the field observations. Cultivation \times seed origin and cultivation \times sowing year interactions were significant ($P < 0.05$), so that generally more total emergence was observed for the cultivated samples, but only for the seeds from Baldomar. Also, more emergence was recorded for the cultivated samples, but only in Algayón (Tab. V). In general, more emergence occurred for the seeds harvested in 2000 than for those harvested in 1999 and more emergence occurred in 1999 than in 1998 but some exceptions occurred, taking into account the cultivation treatments.

In our experiments, seeds were probably not exposed for enough time to either adequate soil moisture or temperature to overcome physiological dormancy or, if they overcame it, they did not find the proper conditions to germinate and entered into a secondary dormancy status (Baskin et al., 2002). This would explain why only a small part of the seeds sown emerged. Predation of *P. rhoeas* seeds should not be too high as insects prefer seeds of grass or legume species (Westerman, pers. comm., Spafford et al., 2006). Moreover, most seed predation occurs on the surface and seeds were buried in our ex-

periment (Westerman et al., 2006). Fatal germination occurring in the soil preventing seedlings from reaching the soil surface (Roberts and Boddrell, 1984) could have also been an important mortality factor in our study.

At the experiment conducted in Baldomar, total emergence in March 2003 was low, ranging from a minimum of 2.2% (after 44 months of burial for seeds from Baldomar, without cultivation and sown in 1998) up to a maximum of 22.8% (after 56 months of burial for seeds from Baldomar, with cultivation and sown in 1999). The emergence 34 months later after enhancing germination by stirring the soil in the greenhouse and adding gibberelline was increased only by up to 3.5% for the first case and up to 24.2% for the second case and reached the maximum value of 25.1% for seeds from Baldomar, without cultivation and sown in 2000. In our study, emergence percentages are lower than those found by other authors: Roberts and Feast (1972) in Britain found from 37 to 64% cumulate emergence after five years in cultivated conditions and 7 to 20% emergence in non-disturbed soil. Roberts and Boddrell (1984) found 34% cumulate emergence after three years in cultivated conditions; Froud-Williams et al. (1984a) recorded 15.7% emergence after 24 months of burial for the most favourable treatment, which was 5-cm seeding depth plus cultivation.

Concerning seed survival, it is commonly accepted that viability of *P. rhoeas* seeds in undisturbed soil is high (Madsen, 1962; Salzman, 1954; Lutman et al., 2002; Cirujeda et al., 2006). Therefore, it could be suggested that lack of emergence

is not mainly caused by seed death. However, despite low emergence, especially in undisturbed conditions, Roberts and Feast (1972) recorded low seed survival over the five years of their experiment. They recovered 4 or 2% of the initially buried *P. rhoeas* seeds in the cultivated samples and 8 or 14% in the undisturbed samples. Compared with other weed species, the authors found these values of recovered seeds for *P. rhoeas* very low. Provided that the initial viability in that experiment was high, the losses could be due to rotting or pathogen attack on the seeds or to unsuccessful emergence. In the conditions of our pot experiment, these causes could explain the reduction in emergence of the seeds during the second and following years. The soil was irrigated for many months during the final phase of the experiment in the greenhouse and rotting could be enhanced, explaining the low total emergence.

4. CONCLUSION

Our results show that *P. rhoeas* emergence in semi-arid Mediterranean conditions occurred mainly in autumn and winter but continued until spring, i.e. from September to April, with emergence peaks between October and December, adapted to the winter cereal cycles. Despite the fact that emergence was clearly related to precipitation both in cultivated and in non-cultivated conditions, for both seed origins and at both sites, soil disturbance before rainfall can contribute to decreasing the soil seed bank, as maximum emergence was higher for the cultivated situation. Taking into account that the highest emergence was recorded in the first year after sowing, emergence could be stimulated by cultivation and/or delaying the sowing date after high seed return into the soil. This cultural method should be combined with other effective methods to establish an integrated weed management strategy and to use herbicides in a sustainable way.

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