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Seed dormancy pattern and germination preferences of the South African annual *Papaver aculeatum*

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SUMMARY

Seeds from two populations of *Papaver aculeatum*, collected in South Africa, were subjected to a series of experiments to investigate their dormancy and germination. Dormancy was weak: fresh seeds germinated to nearly 100% at 20/10 and 25/15°C day/night if provided with light, up to 50% at 15/5, but not at all at 30/20°C. Warm stratification increased germination, both in darkness and at 15/5°C, but did not lead to germination at 30/20°C. Cold stratification reduced germination and limited germination to the cooler temperatures. Alternating cold and warm stratifications showed that the species undergoes dormancy cycles. When subjected to three different artificial annual changing climates, with onset both in summer and autumn, most seed germinated in the first autumn. However, in cooler climates, some germination occurred during spring and the second autumn. The general dormancy pattern; reduction during a warm period and induction during a cold, was similar to that of *P. rhoeas*, a European species and a wide-spread weed. However, germination temperature preferences differed by *P. aculeatum* avoiding germination at high temperatures, having substantially weaker dormancy when fresh and having more easily reduced dormancy,

compared with *P. rhoeas*. These differences most likely result in differing temporal pattern of germination in the field.

Key words: Annual weed; bristle poppy; dormancy cycle; morphophysiological dormancy; Papaveraceae; thorny poppy.

INTRODUCTION

Papaver aculeatum Thunb. is the only *Papaver* species originating from the southern hemisphere (Kadereit 1988). It belongs within the polyphyletic *Papaver* genus, to the same clade as, for example, *P. rhoeas* but has no documented close relative (Carolan *et al.* 2006), being the only species of *P.* sect. *Horrida* (Kadereit *et al.* 1997). The annual *P. aculeatum* occurs in disturbed areas and as a weed (Bromilow 2001; Parsons and Cuthbertson 2001). It is a native of South Africa (Kadereit 1988), occurs mainly in warm temperate climate without a pronounced dry period, but is also reported from both dry winter (Kadereit 1988; Bromilow 2001) and dry summer regions (Bromilow 2001). *Papaver aculeatum* has been introduced to Australia (Kadereit 1988; Parsons and Cuthbertson 2001), but we are not aware of reports of occurrence in the northern hemisphere.

Germination ecology, including seed dormancy pattern and germination preferences, helps to explain and predict the spatial and temporal distribution of a species. *Papaver rhoeas*, which co-occurs with *P. aculeatum* in southern South Africa, is the most well studied *Papaver* regarding dormancy and germination preferences. Its degree of dormancy decreases during warm periods and increases during cool periods, resulting in dormancy cycles with germination mainly during autumns (Milberg & Andersson 1997; Baskin *et al*. 2002; Cirujeda *et al*. 2006; Karlsson & Milberg 2007).

We hypothesized that the germination ecology of *P. aculeatum* should be principally similar to its relative *P. rhoeas*, as are *P. argemone* and *P. dubium* (Karlsson & Milberg 2007), but that specific differences could occur as a result of *P. aculeatum* being adapted to its environment of origin. To study the germination preferences and possible dormancy changes over time and/or following environmental events for *P. aculeatum*, we subjected it to different pre-treatments, and combinations of pre-treatments, before testing germination in various environments. Furthermore, to evaluate the seasonal timing of germination in different climates, we subjected it to three different artificial climates for one and a half years.

METHODS

Two seed batches were collected in South Africa in 2003. The sites used were Roundvlei (34°S 23°E, *ca* 100 m a.s.l., halfway between Cape Town and Port Elisabeth), and Fouriesbourg (29°S 28°E, *ca* 2000 m a.s.l., close to the northern part of Lesotho). Both sites have a warm temperate climate without pronounced dry periods, but Fouriesbourg has colder winters and wetter summers than Roundvlei. Collection was done on the 6th and 13th of November, 2003, for Roundvlei and Fouriesbourg, respectively. The seeds were kept dry at room temperature (*ca* 20°C) until the experiments commenced on the 1st of December, 2003. About 150 to 200 seeds, distributed over two 5 cm diameter petri dishes, were used for each treatment, as described below. Seeds that germinated during stratification or apparently dead seeds were excluded from calculations of germinated fractions. The substrate was 10 mL quartz sand (0.35 mm grain size, Baskarpsand 35, AB Baskarpsand, Habo, Sweden) and 3.8 mL deionized water. The incubators used were equipped with light during daytime

("light") and for the darkness treatment dishes were wrapped in aluminium foil. The incubation time for germination tests was four weeks.

Fresh seeds were tested for germination at 15/5, 20/10, 25/15 or 30/20°C day/night with a two-hour linear transference between the maximum and minimum temperatures (Rubarth Apparatebau, Laatzen, Germany). Germination was tested in both light and continuous darkness. The dishes in light were kept until all seeds germinated or to the end of the study, *i.e*. 1.5 years, and an extra set of dishes in darkness was also incubated for 1.5 years.

Seeds were subjected to different pre-treatments before germination tests for four weeks as above: cold (5°C) or warm (30/20°C day/night) stratification in darkness for 1, 3 or 6 months, and the Roundvlei batch also for 2 or 9 months, dry storage (*ca* 20°C, *ca* 35% RH) for 3, 6 or 9 months, and the Roundvlei seed batch to combinations of cold and warm stratification in darkness (Table 1).

Table 1. Combinations of warm and cold stratification in darkness that seeds of *Papaver aculeatum*, collected in Roundvlei, South Africa, were subjected to before germination tests.

First and second stratification conditions	
First, time (months)	Second, time (months)
Warm, 3	-
Warm, 6	-
Warm, 3	Cold, 3
Warm, 3	Cold, 6
Warm, 6	Cold, 3
Cold, 3	-
Cold, 6	-
Cold, 3	Warm, 3
Cold, 3	Warm, 6
Cold, 6	Warm, 3

Possible embryo elongation during stratification was investigated by excising seeds and measuring embryo length under a dissecting microscope equipped with a micrometer. About 20 seeds of each seed batch were used each time. Embryo lengths

were also measured for remaining un-germinated seeds after 1.5 years of incubation in continuous environments.

Responses to annual changes were investigated by subjecting seeds to three different artificial annual temperature cycles, representing three different climates (cold, intermediate or warm (Table 2)) and two different moments for dispersal: summer or autumn. Seven temperature environments were used: three constant temperature ones (-12°C (LabRum AB, Sweden), 0°C (Gram, Denmark) or 5°C (ADU 200, Styrprojektering AB, Sweden)), and the four daily alternating 15/5, 20/10, 25/15 or 30/20°C described above. All treatments included light during 12 h d^{-1}. The experiment continued for 540 days, thereby including a second autumn in annual cycles.

Table 2. Seasonal temperatures in annual cycles representing three different artificial climates: cold, intermediate and warm.

Season	Time (days)	Temperature (day/night °C) Cold	Intermediate	Warm
Summer	90	20/10	25/15	30/20
Early autumn	30	15/5	20/10	25/15
Middle of autumn	30	5/5	15/5	20/10
Late autumn	30	0/0	5/5	15/5
Winter	90	-12/-12	0/0	5/5
Early spring	30	0/0	5/5	15/5
Middle of spring	30	5/5	15/5	20/10
Late spring	30	15/5	20/10	25/15

Possible germination response to gibberellic acid solution (GA_3, 1000 mg L^{-1}, BDH Electran®, VWR International Ltd, England) was tested by incubating fresh seeds in light at 15/5, 20/10, 25/15 or 30/20°C for ten weeks. Dishes were prepared as above, but with GA_3-solution instead of de-ionized water. The dishes at 30/20°C were kept to the end of the study.

The viability of the remaining seeds at the end of the last treatments was checked by warm stratification (30/20°C) in darkness for three months before a

germination test at 20/10°C in light. Seeds already at 30/20°C at the end of the study were directly transferred to 20/10°C in light. For seeds not germinating during 20/10°C incubation, the warm stratification was repeated before a new test.

RESULTS

Fresh seeds

Fresh seed germinated to a large extent (Fig. 1), thus; the initial degree of dormancy was low. Light promoted germination, but was not an obligatory requirement for germination. No germination occurred at 30/20°C.

Warm or cold stratification

Germination increased after warm stratification, and this was especially pronounced in darkness where initial germination was low (Fig. 1). Cold stratification reduced germination; one seed batch, Fouriesbourg, did not germinate at any of the tested temperatures after 3 or 6 months of cold stratification, while the other, Roundvlei, showed a clear reduction of germination in response to cold stratification when tested at 25/15 or 20/10, but not at 15/5°C (Fig. 1). No germination occurred at 30/20°C after any of the stratification treatments. No germination occurred during warm stratification, but 0.028% germinated during cold stratification.

Embryo lengths

Average embryo lengths for fresh seeds were 0.21 (SD 0.043) and 0.23 (SD 0.042) mm for the Fouriesbourg and Roundvlei seed batches, respectively. There was no detectable difference in embryo lengths between fresh seeds and seeds stratified at 5°C or 30/20°C in darkness for 9 months. At the end of the study, after 1.5 years, un-germinated seeds in light treatments remained only at 15/5 and 30/20°C. Embryos were significantly (t-test: $p < 0.01$) longer at 30/20°C in light (0.28, SD 0.060 and 0.58, SD 0.098 mm for

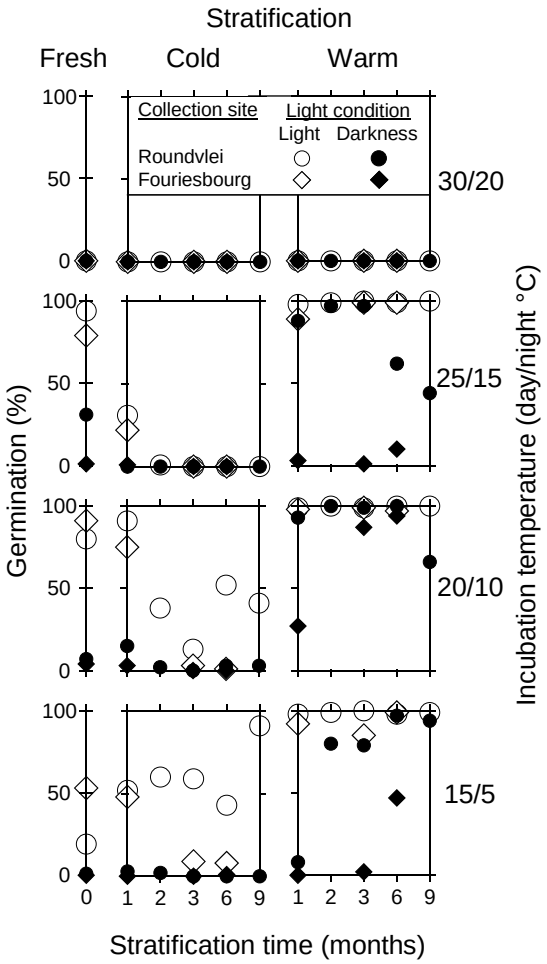


Figure 1. Germination of two populations of Papaver aculeatum, *collected at Roundvlei and Fouriesbourg in South Africa, when fresh and after various periods of cold or warm stratification.*

Fouriesbourg and Roundvlei, respectively) compared to when fresh. Otherwise, there was no difference in embryo lengths between fresh seeds and remaining un-germinated seeds.

Change between warm and cold stratification

When seeds were subjected to alternating warm and cold stratifications, full germination was achieved in light when warm stratification was the last treatment before germination test; this response occurred at the same temperatures as for fresh seeds and for seeds subjected to only warm stratification (*c.f.* Fig. 1 and Fig. 2). After cold

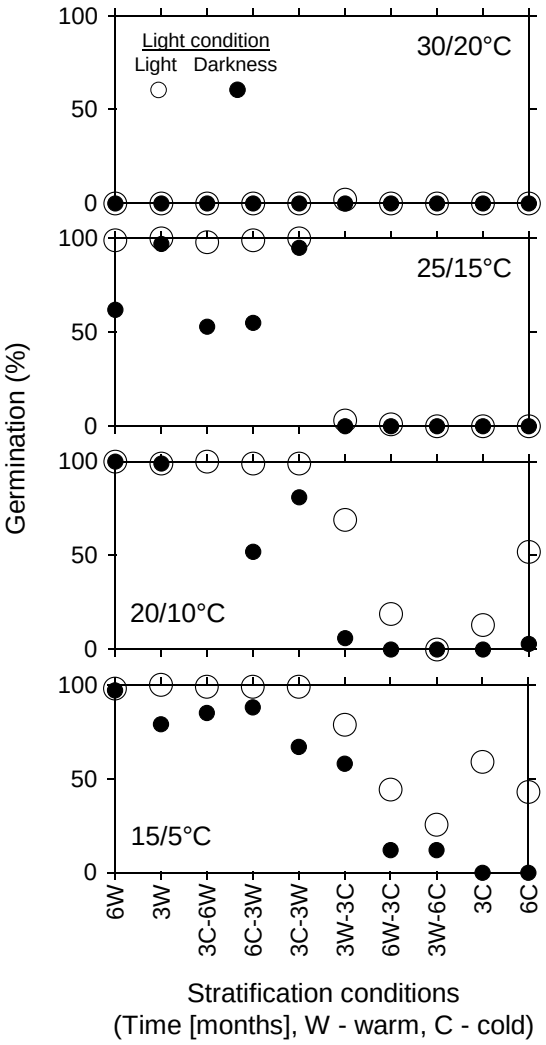


Figure 2. Germination of Papaver aculeatum*, collected at Roundvlei in South Africa, after combinations of cold and warm stratification.*

followed by warm stratification there was also germination in darkness (Fig. 2). In treatments with warm stratification followed by cold, germination was reduced to the same magnitude as when seeds were subjected to only cold stratification (Fig. 2). The dishes to be used for a test at 20/10°C in darkness after three weeks cold followed by six weeks warm stratification were lost. Germination during stratification occurred

exclusively when warm stratification was followed by cold; 2.35% of these seeds germinated.

Annual temperature cycles

For the treatments beginning at 25/15°C (*i.e.* intermediate climate starting with summer) or 20/10°C (*i.e.* warm climate starting with autumn and cool climate starting with summer) nearly full germination occurred within four weeks (Fig. 3). Seeds being subjected to a summer start (30/20°C) in the warm climate delayed germination until transferred to early autumn; 25/15°C (Fig. 3). When subjected to an intermediate climate with autumn start, the Roundvlei seeds germinated to about the same extent during the first autumn and the following spring, while the Fouriesbourg seeds germinated exclusively in autumns (Fig. 3). In the cold climate with autumn start, the Roundvlei seeds batch germinated in spring, and the Fouriesbourg very little (Fig. 3).

Dry storage

There was no detectable difference between fresh seeds and seeds dry stored for up to nine months in most test conditions. However, after nine months of dry storage, 4 and 9% for the Fouriesbourg and Roundvlei seed batches, respectively, germinated in light at 30/20°C, compared to no germination at that temperature when fresh.

Gibberellic acid

There was no detectable germination difference between fresh seeds incubated with GA_3 or de-ionized water within ten weeks of incubation. Seeds subjected to GA_3 at 30/20°C were kept for 540 days. At that time, the Roundvlei and Fouriesbourg seed batches had reached 81 and 53% germination, respectively. For the seeds at 30/20, without GA, the corresponding figures were 0.5 and 1.5%. Most germination (75%) in GA at 30/20°C occurred between days 105 and 300.

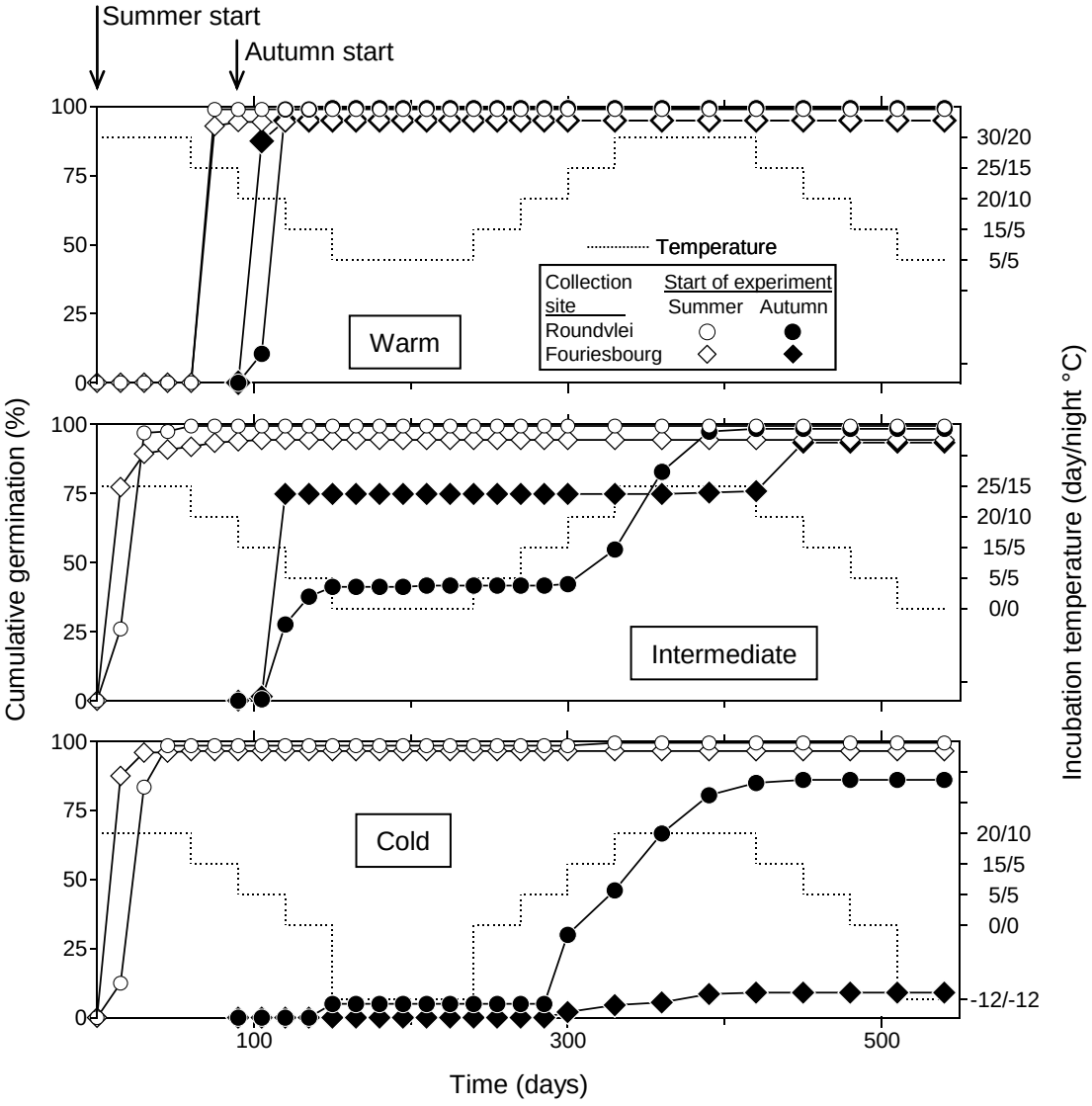


Figure 3. Cumulative germination of two populations of Papaver aculeatum*, collected at Roundvlei and Fouriesbourg in South Africa, when subjected to three different artificial climates and two starting points in annual cycles; summer and autumn. Seeds were provided with light during daytime.*

Viability

During the study, 0.14% of the total number of tested seeds scored dead. At the end of the study, 98.7% of the 694 remaining seeds germinated when tested at 20/10°C in light after being stratified at 30/20°C in darkness for one or two periods of three months.

DISCUSSION

Dormancy pattern and germination preferences

We define seed dormancy as a seed character that prevents germination even during good germination conditions, *i.e*. a character distinguished from non-germination because of the absence of factors required to evoke germination. It is not known whether seed dormancy of a seed is an on-off-character or a continuous character that can take any value between completely dormant and completely non-dormant. However, for ecological purposes we regard a seed batch, rather than a seed, as the study object, which we allude to when discussing dormancy in this paper. Regardless of the mechanisms leading to changing dormancy status in single seeds, a seed batch expresses changes that are observed as continuous changes in degree of dormancy. A decrease in degree of dormancy can therefore be observed as an increasing number of seeds germinating in a specific environment and/or as an increase of the range of environments where germination occurs.

Dormancy of *P. aculeatum* seeds was weak, and warm stratification easily decreased the degree of dormancy; after one month, full germination was achieved at 15/5°C in light, and warm stratification also led to increased germination in darkness (Fig. 1). No germination occurred at 30/20°C in light, even when dormancy was reduced, thus, that temperature was too high for germination. In contrast to warm stratification, cold stratification increased the degree of dormancy. This was obvious for seeds tested at 25/15°C in light: after one month of cold stratification germination was about 25%, and after two months or more germination was 0% (Fig. 1). At the cooler test temperatures, 20/10 and 15/5°C, induction of dormancy was not that obvious: only one of the seed batches, Fouriesbourg, reduced germination to (nearly) zero (Fig. 1). Thus, the two seed batches induced dormancy to different extents: Fouriesbourg to a

high extent, nearly completely inhibiting germination regardless of test environment, and Roundvlei moderately, still allowing some germination at the most preferable temperatures.

The dormancy pattern with decrease during warm periods and increase during cold periods was apparent for the Fouriesbourg seed batch, but not for the Roundvlei one, in the annual cycles (Fig. 3). In the intermediate climate, the majority of autumn-started Fouriesbourg seeds germinated soon after onset of incubation, while the rest remained un-germinated until the second autumn, meanwhile about half of the Roundvlei seeds germinated the first autumn and the other half during the spring and following summer in that climate (Fig. 3). The difference between the two batches can be explained by Fouriesbourg seeds more efficiently inducing dormancy (Fig. 1), and the remaining Fouriesbourg seeds germinated after reduction of dormancy during summer (Fig. 3). In the cold climate, few seeds germinated during the first autumn, while Roundvlei, but not Fouriesbourg, seeds germinated to a high extent the following spring and summer (Fig. 3). In that climate, summer temperature (20/10°C) was too low for dormancy reduction; no germination occurred during late summer and the last autumn, despite the fact that nearly all Fouriesbourg and some Roundvlei seeds still remained un-germinated.

When the Roundvlei seed batch was subjected to combinations of warm and cold stratifications (Fig. 2), it was shown that a change in degree of dormancy of *P. aculeatum* is not one-way but re-induction and re-reduction are possible. Such a dormancy pattern may lead to a dormancy cycle in the field, where seeds are prepared to germinate only during a restricted period of each year.

It is not rare with differences between seed batches of the same species. Sometimes such differences are, or seem to be, a result of local adaptation (*e.g.* Probert *et al.* 1985; Meyer & Allen 1999; Ramakrishnan *et al.* 2004) but sometimes differences observed are rather unpredictable variations (*e.g.* Schütz & Milberg 1997; Andersson & Milberg 1998). In the case of *P. aculeatum*, both seed batches were collected in the first half of summer, and the mother plants had probably emerged during autumn or winter. The two sites differ by Fouriesbourg having colder winters, and that population may have had a stronger impetus to restrict germination during a period with warmer weather during winter. However, one seed batch from each of the two sites is too little to use as a basis for inferring local adaptations; the difference observed could as well be a result of unexplained variation between populations and/or generations.

Dormancy classification

To facilitate comparisons of germination ecology within and between species, it may be possible to use some kind of sorting of responses to evaluate similarities and differences. There are different ways suggested about how to classify seed dormancy, the most recent, and probably the most comprehensive, was presented by Baskin & Baskin (2004). According to this system the first, and therefore most important, feature for separating different kinds of dormancy is the use of selected kinds of seed and embryo morphology. *Papaver* seeds imbibe easily and have embryos that are small in comparison with the seed (Martin 1946). Such species are regarded as morphological dormant (MD), and can have a complementary physiological dormancy, not related to morphology, resulting in morphophysiological dormancy (MPD) (Baskin & Baskin 2004). Within the MPD class there are different sub-groups, *e.g. P. rhoeas* is regarded as having non-deep simple MPD (Baskin *et al.* 2002). However, Baskin & Baskin

(2006) have adjusted this view, and now regard the *P. rhoeas* seeds that germinated directly as belonging to the MD class, and the rest to non-deep simple MPD. Following this reasoning, the part of *P. aculeatum* that germinated directly when fresh had MD, and the rest non-deep simple MPD and thus, what differs between the two species is the MD/MPD ratio, with *P. aculeatum* having a much larger fraction of MD (Fig. 1) than *P. rhoeas* (Baskin *et al.* 2002; Karlsson & Milberg 2007). Therefore, that method allows detection of differences in readiness to germinate for fresh seeds, but not description and comparisons of other differences. Using different classification for different seeds in a seed batch, and allowing a single seed to pass between groups, make the system similar to Harper's system (1957, 1977), which allows sorting of what circumstances prevent germination at any single moment, but not sorting of species/populations into different groups following their general responses.

We think there is a need for other ways to evaluate and compare species or populations regarding dormancy and germination ecology, focusing on expressions in different environments rather than morphology and/or mechanisms. For example, not assuming that species with low embryo/seed ratio automatically should be regarded as dormant. Fresh *P. aculeatum* did germinate to a high extent (Fig. 1) so it seems illogical to call this complete dormancy when fresh, even if parted into different classes (*c.f.* Baskin & Baskin 2006). Also, species with fully developed embryos have a time lag – germination does not occur simultaneously with onset of incubation – but the mechanisms active during this period are not easily observed. We think that the minimum time, depending on species and environment, required for germination should be the lower limit for regarding seeds of that species as dormant, regardless if the processes within the seeds are visible or non-visible. In the case of *P. aculeatum*,

dormancy induction can occur after reduction in darkness (Fig. 2) but probably not after reduction in light, when embryos have elongated. Thus, it is not only dormancy reduction *per se* that is of ecological interest, but also during what circumstances the reduction takes place.

To describe germination ecology, a possibility would be to not use the term "dormancy" at all, but to study different environments necessary between dispersal and root protrusion as included in germination requirements. However, to facilitate comparison, and also discussion, we think it is practical to structure the description of the process. Assuming that seed batches are the study objects, it may be possible to characterise species/populations by three characteristics, hypothesised to be mutually independent seed characteristics: (i) dormancy pattern - described by the kinds of environmental events that reduce and, if applicable, induce dormancy, (ii) germination preference - described by the kinds of environments that are (or became during dormancy reduction) suitable for germination and (iii) dormancy strength - described by how much effort that is needed to reduce dormancy. Below is an example, where we compare *P. aculeatum* with published accounts of *P. rhoeas*.

Comparison of *P. aculeatum* with *P. rhoeas*

Dormancy pattern

The two species responded in the same way to warm incubation in darkness as pre-treatment, after which germination increased in the subsequent test (Fig. 2; Baskin *et al.* 2002). When *P. rhoeas* was subjected to annual changing temperatures, dormancy was reduced during warm periods and induced, even though not completely, during a following cold period (Milberg & Andersson 1997; Baskin *et al*. 2002; Cirujeda *et al*. 2006), as for *P. aculeatum* (Fig. 2). Thus, the two species have, as was hypothesized,

the same dormancy pattern: reduced by warmth, induced by coldness (*c.f.* Figs 1, 2 and Milberg & Andersson 1997; Baskin *et al*. 2002; Cirujeda *et al*. 2006, Karlsson & Milberg 2007).

When subjected to annual changing temperature cycles, despite the degree of dormancy being reduced during a warm period, germination also occurred during spring in annual cycles at not too warm climates both for *P. aculeatum* (Fig. 3) and *P. rhoeas*, and also for *P. argemone* and *P. dubium*, (Karlsson & Milberg 2007). Thus, even though cold stratification *per se* does not reduce the degree of dormancy, the dormancy pattern allows germination after a cold period when subjected to annual temperature changes.

Germination preferences

Their germination preferences differ by *P. aculeatum* not germinating at 30/20°C, regardless of pre-treatment (with the exception of 4-9% germination in light after nine months of dry storage, and when incubating in GA), while *P. rhoeas* has been shown to germinate, to some extent, at that temperature when fresh (4-11%, Karlsson & Milberg 2003) and considerably after a long incubation time (Karlsson & Milberg 2007). Thus, even though both species have their optimal germination temperature below 30/20°C, only *P. aculeatum* resists germination at that temperature (Figs 1, 2), giving the delay in germination for summer-dispersed seeds until early autumn in the warm artificial environment (Fig. 3), while the delay of germination of *P. rhoeas*, after onset of incubation when fresh, is not a result of germination requirements *per se* (Karlsson & Milberg 2007).

Dormancy strength

Fresh seeds of *P. aculeatum* germinated to a high extent when subjected to suitable environments (Fig. 1) while fresh seeds of *P. rhoeas* germinated very little (Baskin *et al*. 2002; Karlsson & Milberg 2003; Cirujeda *et al*. 2006). Furthermore, *P. aculeatum* easily reduced dormancy to its lowest level during warm stratification (Figs 1, 2), while *P. rhoeas* needed longer times (Baskin *et al*. 2002). Hence, the largest difference between these two species was in dormancy strength, with *P. aculeatum* having the weaker dormancy (Fig. 1) and *P. rhoeas* the stronger (Baskin *et al*. 2002). This difference leads to fundamental differences in germination ecology: *Papaver aculeatum* will germinate directly after dispersal if subjected to light at not too high temperature (Fig. 3), while *P. rhoeas* will stay dormant until a warm period has passed and reduced dormancy (Karlsson & Milberg 2007).

Implication for temporal and geographic distribution

Germination of both *P. aculeatum* and *P. rhoeas* is promoted by light (Fig. 1; Milberg & Andersson 1997; Karlsson & Milberg 2007), and *P. rhoeas* is known to form soil seed banks that persist for a long time (e.g. Salzmann 1954). Survival of *P. aculeatum* in soil has not been studied, as far as we know, but there are indications of the species forming soil seed banks as it is reported to suddenly occur on a site where it has not been seen before (van Wyk 2000); which can be explained by buried seeds being transferred to the soil surface after some time in the soil. Because of the weak dormancy of *P. aculeatum*, one can assume that virtually all seeds that are transferred to a soil's surface will germinate within a year.

The establishment of *P. aculeatum* in colder parts of the world may be restricted; with low germination after cold periods (Fig. 2) and 20/10°C being too low for dormancy reduction (Fig. 3), dispersal and germination after a first year with spring-

sown seeds could lead to a lack of germination analogous to the situation for autumn-started Fouriesbourg seeds in the cold climate (Fig. 3). There is little possibility for early summer dispersal in a cold climate (even if autumn-germinated seedlings survive winter, spring is short), thus, the summer-started seeds in the cold climate should not be treated as a realistic model for established populations. However, if seeds are spread to the warmer parts of the Americas, Europe and Asia, germination ecology *per se* should probably not limit the distribution of *P. aculeatum*, as is not the case for *P. rhoeas* which has spread from its origin at the east coast of the Mediterranean (Kadereit 1990) to become regarded as a weed in several, not too cold, parts of the world (Holm *et al.* 1997). It would be interesting to study responses to cold and alternating cold and warm incubation of *P. somniferum*, occurring as occasional summer annual as far north as in northern Scandinavia (Jonsell 2001). Because *P. somniferum* seems to have no, or weak, dormancy (Bare *et al.* 1978; Grime *et al.* 1981), it may respond similarly to *P. aculeatum*, and in such a case could indicate a possible distribution range.

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