

## A Comparative Study of Germination Ecology of Four *Papaver* Taxa

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- **Background and Aims** Comparative studies of closely related taxa can increase understanding of adaptations and changes in seed dormancy and germination preferences in an evolutionary perspective. For such studies, a method to describe and compare the performance of taxa in a general way is needed. The germination ecology of four *Papaver* taxa was studied with the aim of describing and comparing their responses to different seasonal temperature regimes.
- **Methods** Germination of *Papaver argemone*, *P. rhoeas*, *P. dubium* ssp. *dubium* and *P. dubium* ssp. *lecoqii* was investigated in three different artificial climates over 2.5 years. Seeds were collected in southern Sweden, and samples from different populations were used as replicates of taxa.
- **Key Results** Despite substantial intra-taxon variation, there were clear taxon-specific responses. Most germination occurred in the warmest climate. In general, the warmer the climate the more germination occurred in autumn instead of spring. *Papaver argemone*, phylogenetically most distant from the other taxa, was, in contrast to the others, restricted to germinating only at lower temperatures.
- **Conclusions** Seed dormancy and germination may be described by dormancy pattern, germination preferences and dormancy strength. The general dormancy pattern was a common feature for these taxa and therefore probably an evolutionary conservative character. Germination preferences varied between taxa, resulting in different temperature optima and intervals for germination, and dormancy strength was to some extent taxon-specific, but highly variable. The dormancy pattern explained how the taxa can perform as winter annuals in warmer climates, but mainly as summer annuals in colder climates. Hence, there is no need to interpret the within-taxon temporal differences in seedling emergence as local adaptations. In the field, an entire seed cohort will not germinate during a single season. Instead, emergence will be distributed over several seasons, regardless of local climate, weather and soil cultivation methods.

**Key words:** Annual weed, germination ecology, morphophysiological dormancy, *Papaver argemone*, *Papaver dubium*, *Papaver rhoeas*, Papaveraceae, poppy, seed dormancy, Sweden, summer annual, winter annual.

### INTRODUCTION

Seed characteristics, germination preferences and seed dormancy patterns have been proposed as tools for understanding evolutionary patterns (Martin, 1946; Baskin and Baskin, 2004; Nikolaeva, 2004). Because of bio-molecular methods, knowledge of phylogenetic relationships is increasing (e.g. APG, 2003), and we regard it as meaningful to study differences and similarities among documented, closely related taxa in order to increase understanding of adaptations and changes in seed dormancy and germination preferences. One difficulty when comparing seed dormancy and germination between taxa is the intra-taxon variation (Probert *et al.*, 1985; Schütz and Milberg, 1997; Andersson and Milberg, 1998; Keller and Kollman, 1999; Pezzani and Montaña, 2006). Variation within a taxon may depend on genetic differences, local weather during growth of mother plants and maturation of seeds, seed position on the mother plant, soil quality, or other naturally occurring factors. To be able to draw conclusions on a general level, for example for modelling or predicting changes in emergence pattern following climate change, knowledge about a taxon, including its variation, is needed. The general taxon performance within an area

can be studied by using seed batches from different populations as replicates of the taxon.

From an ecological perspective, germination can be viewed as being dependent on seed dormancy, germination preferences, and the interaction between these two characteristics and local climate and weather. We define seed dormancy here as a seed character that prevents germination, even if suitable germination conditions prevail. For ecological interpretations we consider that seed dormancy should be regarded as a continuous property of a seed batch (even though it is not known whether it is a continuum or an on–off property for a single seed); the degree of dormancy for a seed batch can be reduced, and, for some species, induced again, in response to environmental events and/or time. In this paper, we use ‘dormancy strength (weak–strong)’ for a general description of a seed batch or taxa, and ‘degree of dormancy (low–high)’ for describing any specific moment on the continuous scale.

The germination timing of the four *Papaver* taxa occurring as weeds in southern Sweden was investigated: *P. argemone*, *P. rhoeas*, *P. dubium* ssp. *dubium* and *P. dubium* ssp. *lecoqii*. The origin of these taxa is probably within south-eastern Europe, Anatolia and the eastern Mediterranean region (Kadereit, 1990). *Papaver rhoeas* is a close relative of the two *P. dubium* subspecies, while *P. argemone* is more distantly related; it is closer to

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*Roemeria* (which is not established in Sweden; Jonsell, 2001) than to the other *Papaver* studied here (Kadereit *et al.*, 1997; Carolan *et al.*, 2006). The four taxa often co-occur in various combinations, including all together, both in Sweden (Jonsell, 2001) and in England (McNaughton and Harper, 1960). Hybrids are rare in nature, and artificial inter-specific crosses either fail completely or reproduction of the hybrids usually fails (McNaughton and Harper, 1964). Even though all four taxa occur as weeds (e.g. Roberts and Boddrell, 1984; Jonsell, 2001), *P. rhoeas* is the only one regarded as being among the most serious weeds on a global scale (Holm *et al.*, 1997). Nowadays, *P. argemone* is, due to sensitivity to herbicides, a minor weed (Jonsell, 2001), often found only on the edge of agricultural fields (personal observation).

*Papaver rhoeas* emerges in both autumn and spring in England (e.g. Roberts and Feast, 1970) as well as in Sweden (Baskin *et al.*, 2002). In England, *P. dubium* is reported as being mostly a summer annual by McNaughton and Harper (1964), in contradiction to Roberts and Boddrell (1984) who found *P. argemone*, *P. dubium* ssp. *dubium* and *P. dubium* ssp. *lecoqii* emerging throughout the year, when seeds were mixed with soil and the soil was disturbed three times a year. However, seedlings were most common in autumn and infrequent in the middle of summer and winter. The four taxa were compared here by subjecting seeds from southern Sweden to three different artificial climates and two different times for dispersal.

## MATERIALS AND METHODS

### Collection

Sixteen seed batches of the four *Papaver* taxa were collected (Table 1). For each seed batch, mature capsules of approx. 30 plants were used (in two cases where plants were scarce, approx. ten), and the seeds were well mixed. Two batches per taxon were collected in summer and two in autumn, using the same sites for the two occasions, with the exception of *P. dubium* ssp. *lecoqii*, which is rare in Sweden (Jonsell, 2001) and for which we could

TABLE 1. Origin of batches of *Papaver* seeds in southern Sweden during 2002

Taxon	Site	Coordinates	Date
<i>P. argemone</i> L.	Alvastra	58°17'N, 14°39'E	15 July 24 August
	Ledberg	58°26'N, 15°28'E	15 July 24 August
<i>P. rhoeas</i> L.	Starby	58°27'N, 14°52'E	19 July 26 October
	Strå	58°24'N, 14°54'E	19 July 26 October
<i>P. dubium</i> ssp. <i>dubium</i> L.	Knivinge	58°29'N, 15°29'E	17 July 25 August
	Tolefors	58°25'N, 15°29'E	17 July 25 August
<i>P. dubium</i> ssp. <i>lecoqii</i> (Lamotte) Syme	Glänås	58°20'N, 14°50'E	17 July 25 August
	Alvastra	58°18'N, 14°39'E	25 August
	Vadstena	58°27'N, 14°53'E	25 August

not find two sites with ripe seeds in summer. *Papaver dubium* ssp. *dubium* and *P. dubium* ssp. *lecoqii* were distinguished by colour of the dried latex: brown to black and red, respectively (Kadereit, 1989). All sites were within agricultural areas in southern Sweden, and for each taxon there were at least 4 km between the sites used. Seeds were kept indoors (approx. 20 °C, 35 % relative humidity) for 1 week before the onset of experimentation.

### Germination experiment

For each treatment (described below), five Petri dishes (5 cm diameter) with 40 seeds in each were used. Ten millilitres of quartz sand (0.35 mm grain size; Baskarpsand 35, AB Baskarpsand, Habo, Sweden) and 3.8 mL deionized water were poured into each dish. The dishes were put on a vibrator to smooth the surface before seeds were placed on the substrate. Petri dishes were sealed with Parafilm. Dishes used for dark treatments were individually wrapped in aluminium foil, directly after seeds had been put on the substrate, and not opened before the end of the experimental period. During experiments, additional water was added when necessary to dishes in treatments with light.

Seeds were subjected to annual temperature cycles, representing three different climates: cold, intermediate and warm (Table 2). Seven temperature environments were used: three constant temperatures, –12 °C (LabRum AB, Stockholm, Sweden), 0 °C (Gram, Denmark) and 5 °C (ADU 200, Styrprojektering AB, Sweden), and four daily alternating, 15/5, 20/10, 25/15 and 30/20 °C day/night with 2 h linear transference between the maximum and minimum temperatures (Rubarth Apparatebau, Laatzen, Germany). All environments had light for 12 h d<sup>-1</sup>, coinciding with the higher temperature in daily alternating environments [daily alternating and 5 °C: 32–66 μmol m<sup>-2</sup> s<sup>-1</sup> with R:FR ratio 3.5–4.4; 0 °C and –12 °C: 29–44 μmol m<sup>-2</sup> s<sup>-1</sup> with R:FR ratio 1.6–2.1 (SKP 200, sensor SKP 215 and SKR 100, sensor SKR 110, Skye Instruments Ltd, Llandrindod Wells, UK)]. Dishes were randomly placed on shelves during incubation, and were rearranged randomly when checked. Each seed batch was subjected to one treatment simulating summer dispersal (beginning with the last 60 d of summer) and another

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

Season	Time (d)	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

simulating autumn dispersal (beginning with the middle 30 d of autumn) in each climate (Table 2). Experiments ran so that they included 30 d of the third winter after dispersal, i.e. the length of an experiment was 810 or 900 d for seeds beginning cycles with autumn or summer, respectively. Seeds were also subjected to the same environment for 900 d, namely 5/5, 15/5, 20/10, 25/15 or 30/20 °C.

There was one set of five dishes with light during daytime and five sets with continuous darkness in each annual cycle and each continuous temperature. Dishes subjected to light were checked for seedlings once a week over the first 2 months, every second week until day 510, and then every fourth week until the end of the experiment. Five dishes within the dark under constant temperature regimes were opened after each of 60, 270, 480, 690 and 900 d, and in annual cycles after each summer and winter. Seeds treated with light were regarded as having germinated upon root protrusion. Germination in the dark had frequently to be calculated from the number of empty seed coats. Some dishes with long incubation time in darkness at higher temperatures had dried out when opened; such dishes were directly discarded and not included in any evaluation.

#### Viability

Viability was checked at the beginning of the study by subjecting seeds to incubation on sand as above but with gibberellic acid solution (GA<sub>3</sub>, 1000 mg L<sup>-1</sup>; BDH Electran®, VWR International Ltd, Lutterworth, UK) instead of deionized water. Temperatures used were 15/5 or 25/15 °C, depending on the taxon, with light during daytime. Incubation continued until germination ceased. Three dishes with 50 seeds each were used for each seed batch.

During experiments, apparently dead seeds (moist and/or overgrown with mould) were counted and removed. At the end of the study, all dishes containing ungerminated seeds were placed without cover at room temperature for about 1 week, causing them to dry out completely. Thereafter, 3.8 mL GA<sub>3</sub> was added to each dish. Dishes were transferred several times between higher and lower temperatures (the number of times depending on response rates) for about 6 months, when possible germination was regarded as having been achieved. Seedlings were removed as they emerged during incubation. Remaining ungerminated seeds were considered dead.

#### Phenology

Seeds were sown outside in Ledberg, close to one site used for collection of *P. argemone* (Table 1), 1 week after collection. For each seed batch, five pots, each with 50 seeds, were used. Plastic pots (11 cm diameter) were filled with 0.4 L moist quartz sand (Baskarpsand 35) and the seeds were placed on the surface. A hollow in the ground, 0.15 m deep, was filled with ceramic clay pellets 2–6 mm in diameter (AB Svenska Leca, Linköping, Sweden) and the pots were buried to such a depth that the surface of the sand was at the same level as the surface

of the surroundings. The pots were protected from direct wind, rain and sunshine, but the sand was kept moist during the experiments. Temperature was measured with TinytagPlus (Intab; Stenkullen, Sweden) every hour. The pots were checked for seedlings at least twice a month (if snow-free) for about 2.5 years, until 4 December, 2004.

#### Calculations and analysis

In the germination study, seeds scored as dead during the study and seeds that did not germinate during a GA<sub>3</sub> test at the end of the experiments were excluded from calculations of germination. For the phenology study, the numbers of emerged seedlings are reported as fractions of the number of seeds sown.

Analyses of variance of results from continuous temperature regimes and annual cycles were performed with Statistica (StatSoft Inc., 2002) on arcsine-transformed data. One seed batch was regarded as one replicate. Categorical predictors were: taxon, temperature, light condition and collection time for continuous regimes, and taxon, climate, light condition, collection time and starting point for annual cycles. Time was treated as a continuous variable with five measured points: after 60, 270, 480, 690 and 900 d for continuous regimes, and each summer and winter for annual cycles. For each light treatment, the five dishes used were randomly distributed to one point in time each before analysis. For interpretation, special attention was paid to the factor 'taxon' and interactions including 'taxon', to evaluate possible differences between taxa. *Papaver dubium* ssp. *lecoqii*, which was not replicated during summer collection (Table 1), was omitted from ANOVA.

## RESULTS

#### Mortality

Fresh seeds germinated to 99.0% (range 96.7–100%,  $n = 150$ , for seed batches) when incubated with GA<sub>3</sub>. During experiments or in final GA<sub>3</sub> tests a total of 1.1% of all seeds were scored as dead. Severe mortality occurred only for *P. argemone* at 30/20 and 25/15 °C at continuous temperature regimes in light, where 34.0 and 16.9% ( $n = 800$ ), respectively, were scored as dead; this was observed as dead seeds, mostly during the last year, and low germination in GA<sub>3</sub> when tested after 900 d. In a parallel study, viability was good (average 95% of 320 seeds tested) for the same seed batches of *P. argemone* when incubated for 480 d in light at 30/20 or 25/15 °C.

#### Continuous temperature regimes

Soon after experiments were begun, some germination (<25%) occurred in light at all temperatures tested, except 30/20 °C (Fig. 1). Temperature preferences differed between taxa (Table 3); *P. argemone* germinated mostly at the lower and *P. rhoeas* and *P. dubium* ssp. *dubium* at the higher temperatures tested (Figs 1 and 2). In the course of time, the magnitude of inter-taxon differences

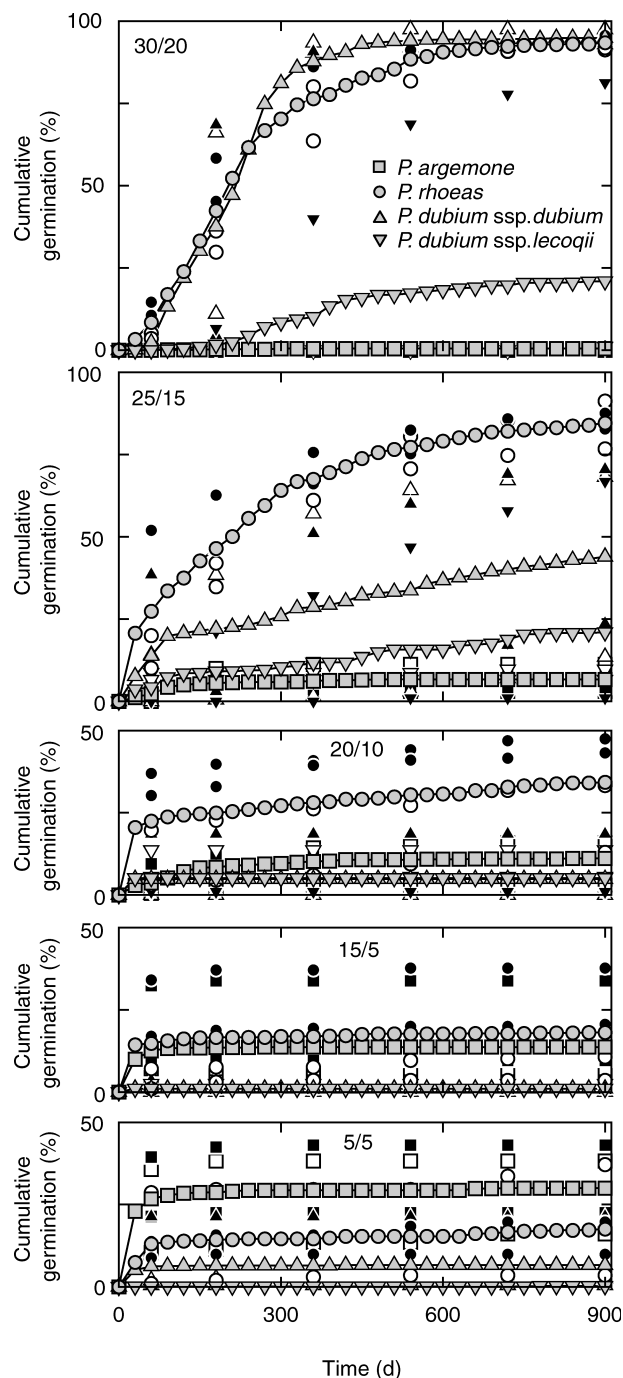


FIG. 1. Cumulative germination of four *Papaver* taxa when subjected to five different temperature regimes (day/night °C shown in graphs) and provided with light during daytime. Four seed batches were collected from each taxon: shaded symbols are taxon averages. Open and closed symbols indicate batches collected in summer and autumn, respectively, on a few separate occasions.

increased when germination for *P. rhoeas* and *P. dubium* ssp. *dubium* increased at the higher temperatures in light (Fig. 1).

Time of collection was a significant explanatory factor for all taxa (Table 3); seeds collected in autumn germinated to a higher extent than those collected in summer (Figs 1

TABLE 3. ANOVA of germination results of *Papaver* seeds collected 2002 in southern Sweden and subjected to five continuous temperature regimes for 900 d

Factor	d.f.	MSS	F	P
Intercept	1	0.276	10.5	0.001
Time	1	1.606	61.1	0.000
(1) Taxon	2	2.157	82.1	0.000
(2) Temperature	4	1.335	50.8	0.000
(3) Light condition	1	8.421	320.5	0.000
(4) Collection	1	0.492	18.7	0.000
Taxon × Temperature	8	0.835	31.8	0.000
Taxon × Light	2	0.894	34.0	0.000
Taxon × Collection	2	0.075	2.9	0.058
Temperature × Light	4	1.109	42.2	0.000
Temperature × Collection	4	0.019	0.7	0.589
Light × Collection	1	0.097	3.7	0.056
Taxon × Temperature × Light	8	0.594	22.6	0.000
Taxon × Temperature × Collection	8	0.031	1.2	0.319
Taxon × Light × Collection	2	0.010	0.4	0.696
Temperature × Light × Collection	4	0.014	0.5	0.711
(1) × (2) × (3) × (4)	8	0.014	0.6	0.822
Error	539	0.026		

Seeds of each taxon were collected from two populations and on two occasions, one seed batch was considered one replicate. Time was treated as a continuous variable with five independent points.

(1) *P. argemone*, *P. rhoeas* or *P. dubium* ssp. *dubium*; (2) 5/5, 15/5, 20/10, 25/15 or 30/20 °C, day/night; (3) light during daytime or continuous darkness; (4) summer or autumn.

and 2). The importance of the taxon × light interaction (Table 3) was a result of the relative difference between taxa in germination achieved, being more pronounced in light than in darkness, even though *P. rhoeas*, overall, germinated the most and *P. argemone* the least in both light conditions (cf. Fig. 1 and Fig. 2). The taxon × temperature × light interaction was an important explanatory factor (Table 3) because *P. dubium* ssp. *dubium* germinated less at 25/15 than at 30/20 °C in light (Fig. 1), but about the same at the two temperatures in darkness (Fig. 2).

Only one of the four seed batches of *P. dubium* ssp. *lecoqii* (Alvastra, Table 1) germinated more than 15% when provided with light. All germination for this taxon occurred in light at higher temperatures (Fig. 1). In darkness, germination for *P. dubium* ssp. *lecoqii* was approx. 10% for the Alvastra seed batch (Table 1) at continuous 25/15 °C after 480 d or longer, and the dishes opened after 480 d at 30/20 °C had 3% germination. Otherwise, germination of *P. dubium* ssp. *lecoqii* in darkness was less than 1% regardless of seed batch, temperature level and time in treatment.

#### Responses to different climates

Light condition, time, climate, taxon, starting point and time of collection were all important explanatory factors (Table 4). Light condition was the single most important factor (Table 4), with much more germination in light (Fig. 3) than in darkness (Fig. 4). Overall, the warmer the climate the more germination occurred, both in light (Fig. 3) and in darkness (Fig. 4). In general, the taxa

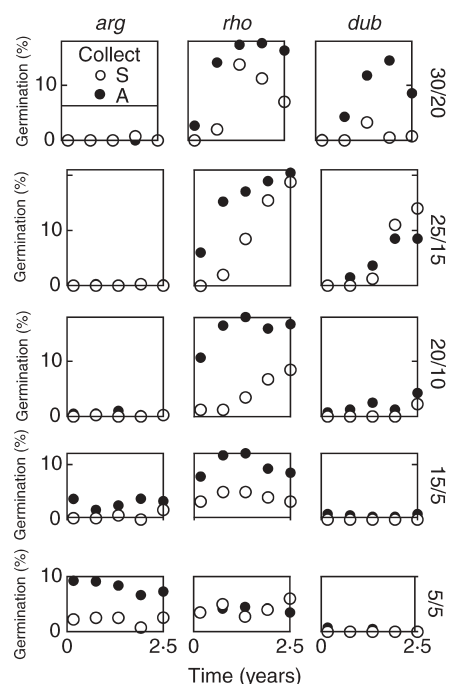


FIG. 2. Germination in continuous darkness of seeds of three *Papaver* taxa [*P. argemone* (*arg*), *P. rhoeas* (*rho*) and *P. dubium* ssp. *dubium* (*dub*)] collected during the summer (S) or autumn (A), and subjected to five different continuous temperature regimes (5/5, 15/5, 20/10, 25/15 or 30/20 °C, day/night). The study continued for 900 d. Each point shows the average germination reached at one point in time of two seed batches from different sites. *Papaver dubium* ssp. *lecoqii* was also included in the study, and germination was approx. 10% after 480 or more days at 25/15 °C for one of four seed batches, otherwise zero or nearly zero.

differed (Table 4), with *P. rhoeas* germinating most, and *P. argemone* and *P. dubium* ssp. *dubium* least and about the same. Seed batches collected during the autumn germinated more than those collected in the summer (Fig. 3).

The most important second-order interaction was climate  $\times$  light (Table 4); the difference between the warm climate and the other two was relatively larger when seeds were subjected to light than to continuous darkness. Several second-order interactions that included 'taxon' were of importance. The taxon  $\times$  climate interaction was a significant explanatory factor (Table 4) due to *P. argemone*, compared with *P. rhoeas* and *P. dubium* ssp. *dubium*, showing a relatively small difference in level of germination among the three different climates (Figs 3 and 4). The importance of taxon  $\times$  start is a result of *P. rhoeas* being the only taxon with substantially more germination after a summer than after an autumn start in the annual cycles. Taxon  $\times$  light and taxon  $\times$  collection were both a result of *P. rhoeas* differing more, but in the same way, to different light conditions and times of collection than the other taxa.

There were three significant third-order interactions that included 'taxon'. Taxon  $\times$  climate  $\times$  light was a result of *P. dubium* ssp. *dubium* germinating more and less than *P. argemone* in the warm and cold climates, respectively, in light (Fig. 3), while the two taxa germinated to the same magnitude in the climates in darkness (Fig. 4).

TABLE 4. ANOVA of germination results of *Papaver* seeds collected 2002 in southern Sweden

Factor	d.f.	MS	F	P
Intercept	1	0.530	23.1	0.000
Time	1	2.266	99.0	0.000
(1) Taxon	2	0.871	38.1	0.000
(2) Climate	2	2.226	97.3	0.000
(3) Light condition	1	11.824	516.7	0.000
(4) Collection	1	0.172	7.5	0.006
(5) Starting point	1	0.214	9.3	0.002
Taxon $\times$ Climate	4	0.270	11.8	0.000
Taxon $\times$ Light	2	0.086	3.8	0.024
Taxon $\times$ Collection	2	0.010	0.4	0.653
Taxon $\times$ Start	2	0.272	11.9	0.000
Climate $\times$ Light	2	1.056	46.1	0.000
Climate $\times$ Collection	2	0.050	2.2	0.115
Climate $\times$ Start	2	0.083	3.6	0.027
Light $\times$ Collection	1	0.047	2.1	0.151
Light $\times$ Start	1	0.184	8.0	0.005
Collection $\times$ Start	1	0.039	1.7	0.193
Taxon $\times$ Climate $\times$ Light	4	0.112	4.9	0.001
Taxon $\times$ Climate $\times$ Collection	4	0.009	0.4	0.827
Taxon $\times$ Climate $\times$ Start	4	0.014	0.6	0.643
Taxon $\times$ Light $\times$ Collection	2	0.005	0.2	0.801
Taxon $\times$ Light $\times$ Start	2	0.126	5.5	0.004
Taxon $\times$ Collection $\times$ Start	2	0.080	3.5	0.031
Climate $\times$ Light $\times$ Collection	2	0.027	1.2	0.314
Climate $\times$ Light $\times$ Start	2	0.076	3.3	0.036
Climate $\times$ Collection $\times$ Start	2	0.019	0.8	0.433
Light $\times$ Collection $\times$ Start	1	0.010	0.4	0.513
(1) $\times$ (2) $\times$ (3) $\times$ (4)	4	0.013	0.6	0.692
(1) $\times$ (2) $\times$ (3) $\times$ (5)	4	0.012	0.5	0.728
(1) $\times$ (2) $\times$ (4) $\times$ (5)	4	0.010	0.4	0.789
(1) $\times$ (3) $\times$ (4) $\times$ (5)	2	0.057	2.5	0.083
(2) $\times$ (3) $\times$ (4) $\times$ (5)	2	0.001	0.04	0.963
(1) $\times$ (2) $\times$ (3) $\times$ (4) $\times$ (5)	4	0.011	0.5	0.760
Error	647	0.023		

The seeds were subjected to three different artificial climates for 900 d, with two different artificial times for dispersal (i.e. starting points in annual cycles). Seeds of each taxon were collected from two populations and on two occasions, one seed batch was considered one replicate. Time was treated as a continuous variable with five independent points.

(1) *P. argemone*, *P. rhoeas* or *P. dubium* ssp. *dubium*; (2) cold, intermediate or warm; (3) light during daytime or continuous darkness; (4) summer or autumn; (5) summer or autumn.

Taxon  $\times$  light  $\times$  start and taxon  $\times$  collection  $\times$  start were both a result of *P. rhoeas* exhibiting more pronounced responses to start and collection in light than in darkness, and taxon  $\times$  collection  $\times$  start also by *P. argemone* showing a substantial difference between summer and autumn collections in darkness but not in light (cf. Fig. 3 and Fig. 4). Fourth- and fifth-order interactions were of minor importance (Table 4).

Of the four seed batches of *P. dubium* ssp. *lecoqii* only the Alvastra seed batch (Table 1) germinated to 40–80%, which occurred during the second and third autumns in the intermediate and warm climates (Fig. 3). In darkness, the maximum germination for *P. dubium* ssp. *lecoqii* was 2–5% for the same seed batch in the warmest climate at the two last points in time. Otherwise, germination for this taxon

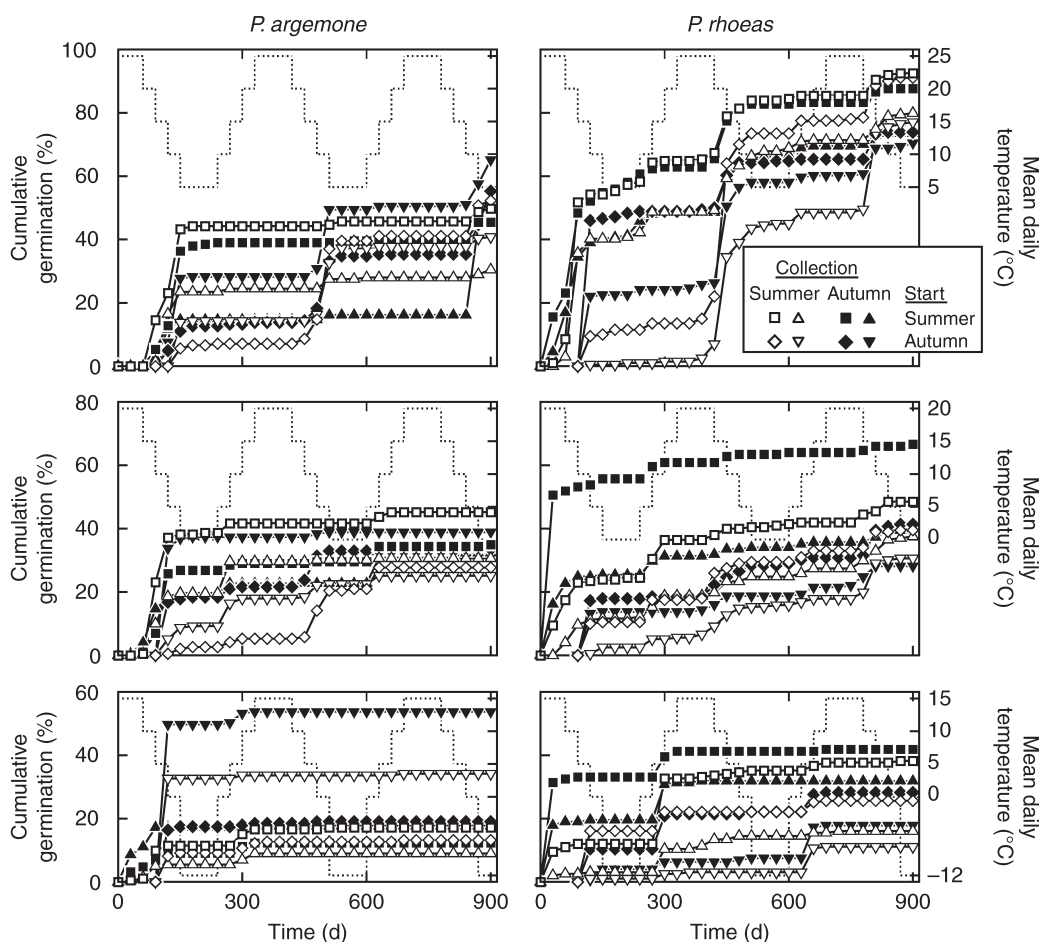


FIG. 3. Germination of four *Papaver* taxa when subjected to three different artificial climates and provided with light during daytime. Four seed batches were collected from each taxon. Seed batches were collected either during summer or autumn [each symbol shape (triangles, squares or circles) shows one collection site], and all were subjected to two starting points in the annual cycles: summer and autumn.

was less than 10% and 1% in light and darkness, respectively, regardless of seed batch, climate and time in treatment.

The temperature outdoors in Sweden was between the cold and the intermediate artificial climates (cf. Fig. 3 and Fig. 5), with the last summer during the study at a mean daily temperature close to the cold artificial climate. Emergence outdoors was generally low; *P. rhoeas* and *P. argemone* emerged most, *P. dubium* ssp. *dubium* little (Fig. 5) and *P. dubium* ssp. *lecoqii* nearly not at all (2%). Emergence outdoors occurred mainly during the first and second autumns and during the first spring (Fig. 5).

#### Germination time and temperatures

There was a general difference between *P. argemone* and the other three taxa regarding germination temperatures, with *P. argemone* not germinating at high temperatures, resulting in later germination during autumn (Figs 3 and 5). During autumn in the warm climate, *P. argemone* germinated at 15/5 and 20/10 °C, *P. dubium* ssp. *lecoqii* and *P. rhoeas* at 25/15 °C, and *P. dubium* ssp. *dubium* at 25/15 °C and also at 30/20 °C in late summer (Fig. 3). In the intermediate climate, *P. argemone* germinated at

15/5 °C and the other three taxa at 20/10 °C during autumn, while spring germination was limited to 5/5 and 15/5 °C for *P. argemone*, *P. rhoeas* and *P. dubium* ssp. *dubium*. By contrast, *P. dubium* ssp. *lecoqii* did not germinate during spring (Fig. 3).

## DISCUSSION

#### Variation within taxon

On several occasions there were larger differences in cumulative germination within taxa rather than between them (Figs 1 and 3). Part of the intra-taxon variation depended on the collection date (Tables 3 and 4) or starting point in the cycles (Table 4), but there were also substantial differences between seed batches collected on the same day and subjected to the same treatment (Figs 1 and 3). Especially large differences within a taxon were found in *P. dubium* ssp. *lecoqii*: of four seed batches only one germinated to a substantial extent at any of the circumstances tested (Figs 1 and 3). Pronounced differences occurred also within *P. dubium* ssp. *dubium* (Fig. 3), even though the two sites used for this taxon were the two most adjacent sites used (Table 1).

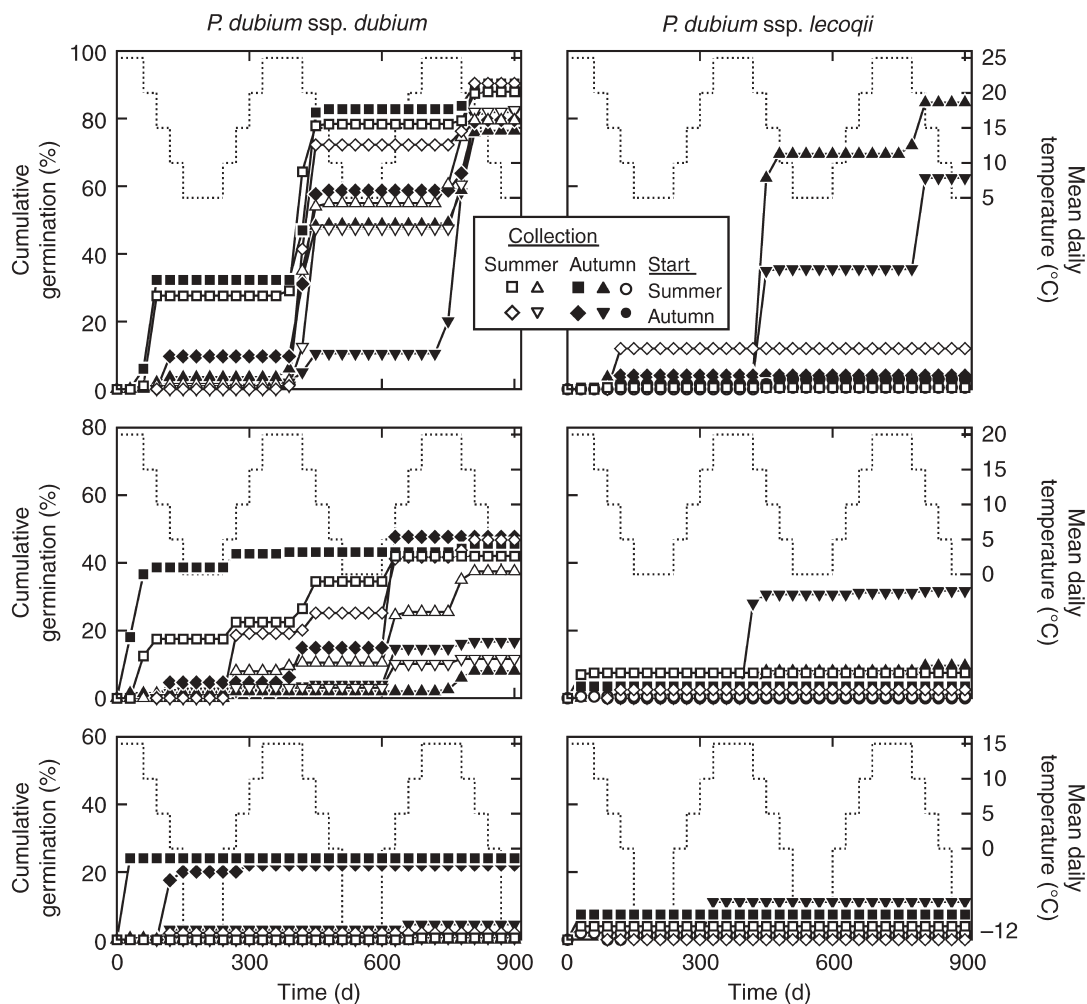


FIG. 3. Continued.

The differences within each taxon, when being subjected to the same treatment (Figs 1 and 3), are regarded as a result of different dormancy strengths. Compared with a seed batch with weak dormancy, a seed batch with strong dormancy requires longer and/or closer to optimum and/or repeated environmental event(s) to reduce the degree of dormancy sufficiently to reach a specific germination fraction in any specific environment. It seems possible that large differences in dormancy strength within *Papaver* taxa are not rare. Grime *et al.* (1981) tested one seed batch of each of *P. argemone*, *P. rhoeas* and *P. dubium*: for *P. argemone*, no suitable germination environment was found, but for both *P. rhoeas* and *P. dubium*, germination occurred to a substantial extent at 5 °C in darkness, in contrast to results from other *Papaver* studies (Fig. 2; Milberg and Andersson, 1997; Baskin *et al.*, 2002). However, the study by Grime *et al.* (1981) did not aim to investigate dormancy, and seeds had been stored dry for some time before being tested; a treatment that we have observed, *per se*, reduces dormancy in *Papaver*, even though we have not seen such extensive germination (data not shown). Substantial differences of 10–40 % within a year (Baskin *et al.*, 2002) were also found among

*P. rhoeas* seed batches when collected at different sites within 15 km on the same day and sown outdoors at one single site.

Despite the variation within each taxon, taxon was an important exploratory factor for germination in annual cycles (Table 4). In addition, when subjected to a continuous temperature regime there were taxon-specific temperature preferences (Table 3). Therefore, it was relevant to investigate the differences in germination timing between taxa on a general level, instead of focusing on the specific fraction of germination at any single moment. It is also obvious that comparative studies need to include several seed batches per taxon studied to be able to reach sound conclusions regarding inter-taxon differences. Complementary to such extensive studies, some kind of general description of dormancy pattern and germination preferences may be used in order to evaluate potential differences between taxa or locally adapted types.

#### Seed dormancy classification

*Papaver* has relatively small embryos in comparison with the seeds (Martin, 1946), the embryos have to grow before

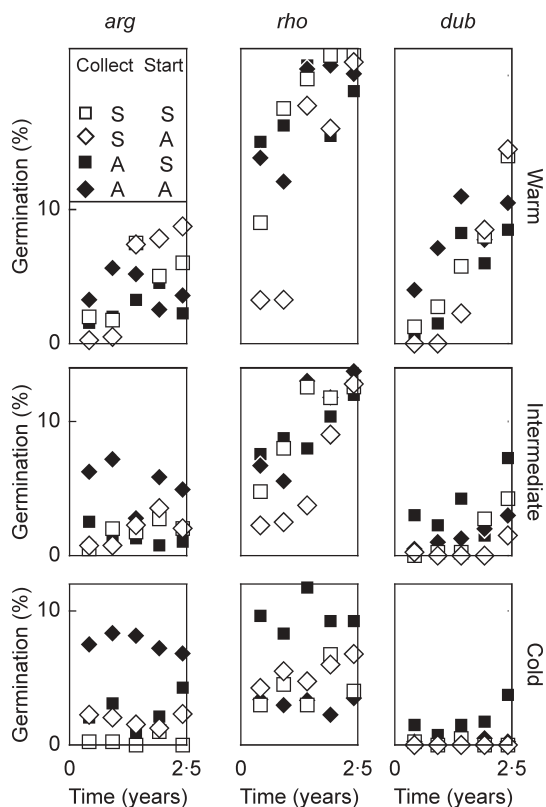


FIG. 4. Germination in continuous darkness of seeds of three *Papaver* taxa [*P. argemone* (*arg*), *P. rhoeas* (*rho*) and *P. dubium* ssp. *dubium* (*dub*)] collected in summer (S) or autumn (A). Seeds were subjected to three different artificial climates (cold, intermediate or warm: summer temperatures were 30/20, 25/15 or 20/10 °C, day/night, respectively) with two different artificial dispersal times, i.e. starting points in cycles: summer (S) or autumn (A). The study continued for 900 d, including three autumns and two springs. Each point shows achieved average germination at one point in time for two seed batches from different sites. *Papaver dubium* ssp. *lecoqii* was also included in the study, but germination was nearly zero in all darkness treatments.

germination and *Papaver* seeds imbibe easily. In accordance with this, *Papaver* has, according to the classification system proposed by Baskin and Baskin (2004), either (1) morphological dormancy (MD) or (2) some kind of morphophysiological dormancy (MPD), which means that (1) embryo growth and germination occur as one continuum within 4 weeks when seeds are placed in an environment suitable for germination or that (2) there is a (hypothetical) physiological inhibiting mechanism that has to be disarmed before germination can occur during any circumstances.

Seed dormancy of *P. rhoeas* is reduced when incubated in darkness at moderate temperatures (approx. 20–25 °C), and embryo growth and germination occur over a wide range of temperatures when provided with light during daytime (Milberg and Andersson, 1997; Baskin *et al.*, 2002). Therefore, as concluded by Baskin *et al.* (2002), *P. rhoeas* has non-deep simple MPD.

The present results provides evidence that the other three *Papaver* taxa studied also belong to the non-deep simple MPD dormancy described by Baskin and Baskin (2004), even though the experimental set-up in this study aimed

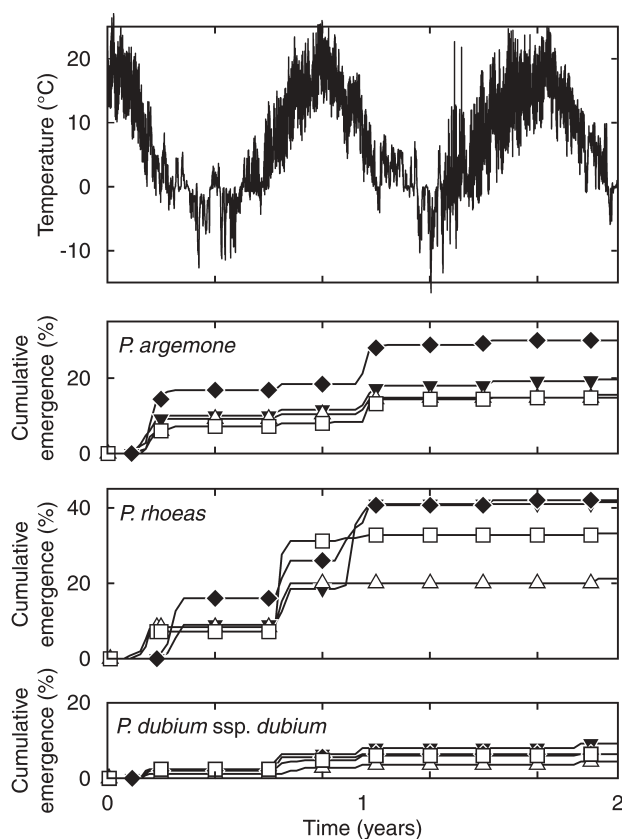


FIG. 5. Emergence, as a fraction of seed sown, of three *Papaver* taxa in southern Sweden. For each seed batch, 250 seeds were sown in pots outdoors 1 week after collection. Pots were kept moist and protected from direct wind, rain and sunshine. Closed and open symbols show seeds collected during summer and autumn, respectively, and squares and triangles show different sites used for collection (cf. Fig. 3). *Papaver dubium* ssp. *lecoqii* was also included in the study, but only 2.0% emerged.

to investigate germination timing, not to classify dormancy. First, because no environment led to substantial germination for fresh seeds (Fig. 1), MD is excluded. Second, fresh seed of all taxa responded positively to a reduction in temperature, during the first autumn, in the annual cycles (Fig. 3). Third, the non-deep simple MPD dormancy is the only type of MPD in the scheme that allows only one warm period for dormancy reduction (the other types have requirements of either warm plus cold, cold plus warm plus cold, or only cold). Thus, if the *Papaver* taxa should belong to any other kind of MPD, the first sign of reduced dormancy should have appeared at the earliest during or after the first winter (Fig. 3). However, full germination, which is needed to regard a treatment as successful in completely breaking dormancy (*sensu* Baskin and Baskin, 2004), was not achieved in this study. Therefore, the possibility of an as yet undescribed type of dormancy exists. However, an ongoing study indicates that environmental conditions suitable for dormancy reduction of *P. argemone* and the two *P. dubium* subspecies are similar to those for *P. rhoeas*, but requiring longer periods (data not shown). Thus, we conclude that seed dormancy classification should be non-deep simple MPD (Baskin and Baskin, 2004) for all



four taxa studied. Therefore, neither the dormancy classification scheme of Baskin and Baskin (2004) nor other classification systems proposed (Harper, 1957, 1977; Lang, 1987) can be used to separate differences in germination timing for the taxa studied. Furthermore, the non-deep simple MPD classification covers both species that reduce dormancy during a warm period and those that reduce dormancy during a cold period (Baskin and Baskin, 2004), and is therefore not informative when aiming to understand, compare or predict germination in an ecological perspective.

To facilitate comparisons, and also discussion, it is practical to structure the description of the process leading to germination. Assuming that seed batches are the study objects, it may be possible to describe species/populations by: (1) 'dormancy pattern', i.e. what are the environmental events that reduce and, if applicable, induce dormancy; (2) 'germination preferences', i.e. what environments are (or became during dormancy reduction) suitable for germination; and (3) 'dormancy strength', i.e. how much effort is needed to reduce dormancy.

#### Germination timing

Climate was a strong explanatory factor for germination (Table 4). The colder the climate, the more germination occurred in spring instead of autumn and the less germination occurred during the last year of the study (Figs 3 and 5). Germination in spring may be explained either by dormancy being reduced under cold conditions (0 °C), or by the seeds being on the way to germinate before winter, but the actual germination being postponed until suitable temperatures, or sufficient temperature in total, occurred in spring. In the cold climate, most germination occurred in the first autumn, but later in the study nearly all germination occurred during spring, and almost exclusively so for *P. rhoeas* (Fig. 3). Either *P. rhoeas* was the only taxon for which 20/10 °C (summer in the cold climate) was high enough for dormancy reduction, or the other taxa required longer times than 90 d for dormancy reduction at that temperature. Given that *P. rhoeas* is known to reduce dormancy within a time period of 12 weeks, albeit in darkness, at 20/10 °C, partly at 15/5 °C but not at 1 °C (Baskin *et al.*, 2002), the explanation that germination during spring is a result of germination being delayed during cold periods seems to be the most plausible.

Several species are reported as having dormancy cycles (e.g. Baskin and Baskin, 1985; Murdoch, 1998; Mennan and Nguajio, 2006), i.e. after dormancy reduction, induction of dormancy occurs, as a response to an environmental event, if circumstances acceptable for germination have not been present. Among species with reported dormancy cycles is *P. rhoeas* (Milberg and Andersson, 1997; Cirujeda *et al.*, 2006), in which dormancy is induced during cool periods, thus avoiding spring germination. In the intermediate and cold climates, germination occurred in autumn and in spring directly after transference from 0 to 5 °C (Fig. 3). Thus, seeds remaining ungerminated after autumn had a degree of dormancy low enough to allow at least some germination after the winter. This

may be the result of 0 °C and -12 °C being too low for induction of dormancy, or of only -12 °C being too low and an ongoing germination process continuing at 0 °C, but too slowly for germination during the winter period.

There was a difference between times of collection (Tables 3 and 4), with the late-collected seeds having weaker dormancy and therefore germinating more easily (Figs 1 and 3). Some species exhibit differences in germination characteristics depending on whether seeds are from plants that emerged during spring or autumn. For *Capsella bursa-pastoris* in Sweden (Baskin *et al.*, 2004) there was a difference observed when seeds were subjected to suboptimal conditions. Most germination occurred for seeds from mother plants that emerged in spring, but the difference was neutralized when seeds were subjected to optimal conditions or after a winter outdoors. For *Galium aparine* and *Brassica kaber* (syn. *Sinapis arvensis*) in Turkey (Mennan and Nguajio, 2006) there was a distinct difference in time for germination, with the seeds from spring mother plants mainly germinating earlier than those from autumn mother plants, even 2 years after collection. The emergence date for the plants used for our *Papaver* seed collections cannot be confirmed, but from field observations it is likely that the July (summer) and the remaining (autumn) collections were from mother plants that emerged during autumn and spring, respectively. For *Papaver*, the difference between summer- and autumn-collected seeds was only pronounced for initial germination; in treatments where additional germination occurred, the differences tended to level out with time (Fig. 3).

Regardless of collection time and starting point in cycles, time for germination, or emergence, was similar for all batches within a taxon (Figs 3 and 5). Therefore, differences in dormancy strength due to collection date for the four *Papaver* taxa studied here are probably explained by response to ripening circumstances and not an adaptation leading to two distinctly different generations. A stronger dormancy when ripening during a warmer period (summer) than during a cooler period (autumn) seems to be a proper adaptation to avoid germination during occasional periods with circumstances suitable for germination during summer, which would be important not least in the Mediterranean region, where these taxa probably evolved (Kadereit, 1990). This contrasts with *Avena fatua* for which a higher temperature during maturation reduces dormancy (Peters, 1982).

#### Comparison of taxa

Germination preferences differed between taxa. Compared with *P. rhoeas* and *P. dubium* ssp. *dubium*, *P. argemone* preferred lower temperatures for germination (Figs 1 and 3). When subjected to 30/20 °C for 900 d, full germination occurred for *P. rhoeas* and *P. dubium* ssp. *dubium*, and for one seed batch of *P. dubium* ssp. *lecoqii*, but there was no germination of *P. argemone* (Fig. 1), even though 30/20 °C as summer temperature was suitable for dormancy reduction for all taxa (Fig. 3). Mortality occurred exclusively for *P. argemone* subjected to 30/20 or 25/15 °C in light for more than 480 d. The

mortality may be an additional indicator that *P. argemone* requires lower temperatures for germination than for the others tested; for the other taxa, the viability of the remaining seeds was nearly 100 % after 900 d in light at 30/20 or 25/15 °C. The relative similarity in germination temperature preferences between *P. rhoeas* and *P. dubium* ssp. *dubium* compared with *P. argemone* is reflected in the close relationship between *P. rhoeas* and *P. dubium* ssp. *dubium* (Kadereit *et al.*, 1997; Carolan *et al.*, 2006).

The significant interaction taxon  $\times$  collection  $\times$  start (Table 4) was partly a result of *P. argemone* germinating more after autumn than after a summer start for autumn-collected seeds in the cold climate (Fig. 3), while the other taxa did not differ with starting point in the cold climate, and all taxa, including *P. argemone*, germinated more after a summer start than after an autumn start in the intermediate and warm climates (Fig. 3). This pattern can be explained by a summer start at intermediate and warm climates including a period warm and long enough to lower the degree of dormancy and to lead to germination during autumn, and that the autumn start in the cold climate (5 °C) was well suited for germination for fresh seeds of *P. argemone* (Fig. 1). Because of stronger dormancy for the summer-collected seeds, the germination response directly after start in the cold climate occurred mostly for autumn-collected seeds (Fig. 3).

The differences in germination timing were mostly due to germination temperatures (Fig. 3), giving a later germination in autumn for *P. argemone*. However, germination in spring occurred simultaneously for all taxa (Fig. 3), showing that low temperatures did not restrict germination for *P. rhoeas* and *P. dubium*, as moderate temperatures did for *P. argemone*. Lack of germination at low temperatures in autumn for *P. rhoeas* and *P. dubium* was therefore probably a result of all possible germination occurring as soon as a suitable temperature was present, i.e. early during autumn for these two taxa.

Dormancy strength affected the overall response of the taxa. Even though *P. rhoeas* and *P. dubium* ssp. *dubium* germinated at similar temperatures (Fig. 4) and achieved nearly full germination after three autumns in the warm climate (Fig. 3), *P. dubium* ssp. *dubium* had its peak in germination during the second autumn whereas *P. rhoeas* germinated about equally in the first and the second autumns (Fig. 3). Thus, *P. rhoeas* had weaker dormancy than the other taxa. Other indications of *P. rhoeas* having the weakest dormancy are that this taxon was the only one that germinated during the second cycle in the cold climate (Fig. 3), most frequently germinated without a change of temperature condition (Fig. 1) and, to the highest degree, overcame the light preference for germination (Figs 2 and 4). Strongest dormancy was found in *P. dubium* ssp. *lecoqii*, which, despite the close relationship to *P. dubium* ssp. *dubium*, germinated very little (Fig. 3).

In an evolutionary perspective, it seems that the general dormancy pattern (dormancy reduction when warm) is a conservative character for the *Papaver* studied here. Germination temperature preferences have probably been adjusted when or after new taxa evolved, thus being less conservative than the general dormancy pattern.

Dormancy strength, although to some degree being taxon-specific, varied between seed batches (Fig. 3), seemingly being the most easily changeable character involved in germination. One *Papaver* species, *P. somniferum*, has been reported to have weak dormancy without a requirement for a warm period before germination (Bare *et al.*, 1978; Grime *et al.*, 1981). It is a closer relative to *P. rhoeas* and *P. dubium* than to *P. argemone* (Kadereit *et al.*, 1997; Carolan *et al.*, 2006). These results may depend on the fact that *P. somniferum* ssp. *somniferum*, which has been cultivated since ancient times, has lost its dormancy because of artificial selection. Bare *et al.* (1978) described their study object as a 'cultivated plant', and only *P. somniferum* ssp. *somniferum*, the cultivated type, is known to occur outside the Mediterranean region in Europe (Tutin *et al.*, 1964; Kadereit, 1986). Therefore, the population at Sheffield (Grime *et al.*, 1981) was probably naturalized *P. somniferum* ssp. *somniferum*, not the wild-type *P. somniferum* ssp. *setigetum*.

#### Field implications

The four *Papaver* taxa studied here are annual weeds, occurring in crop fields. Therefore, a substantial part of the seeds from each cohort can be assumed to be buried. They are known to persist in soil for at least 5 years (Roberts and Boddrell, 1984), and *P. dubium* and *P. rhoeas* survived to 91 and 84 %, respectively, after 11 years in soil (Salzmann, 1954). Reduction of dormancy of *Papaver* being buried in soil will normally not lead to germination (Fig. 4). This is to be expected, because a light requirement for germination, not seed dormancy, is probably the most important factor for forming persistent seed banks (Thompson *et al.*, 1997). *Papaver rhoeas* is known to show increased emergence in cultivated, compared with uncultivated, soil (Roberts and Feast, 1973) and it is possible to achieve 100 % germination of at least *P. rhoeas* using a combination of warm stratification in darkness and a germination test in cooler environments equipped with light (Milberg and Andersson, 1997; Baskin *et al.*, 2002). However, in the field, the entire cohort of any of the *Papaver* taxa studied here will not germinate during a single season (Figs 3 and 5), even if not buried in soil and thus prevented from germination by lack of light (Milberg and Andersson, 1997). Instead, the seed dormancy pattern in combination with germination requirements and dormancy strength distributes the emergence of a cohort over several seasons, regardless of local climate, weather and soil cultivation methods. From a weed management point of view, *P. rhoeas* is a problematic taxon (Holm *et al.*, 1997) that is frequently reported to show herbicide resistance (e.g. Paterson *et al.*, 2002; Durán-Prado *et al.*, 2004; Scarabel *et al.*, 2004). For the reasons described above, the old method of fallow practice, i.e. allowing germination but not flowering, would probably be the best to reduce the seed bank in heavily infested fields.

Because of the extensive variation within each of the taxa studied (Fig. 3), despite being collected within a relatively small area (Table 1), taxon-wise predictions about

germination, as fractions, are not possible. By contrast, the general response to climate and seasonal changes was distinct and taxon-specific (Fig. 3). Therefore, it should be possible to predict the relationship between autumn- and spring-germinated parts, and germination timing for seeds not buried in the soil, with relatively good certainty, from temperatures during the last year before the specific occasion, at least in climates where seeds remain imbibed for most of the year (cf. Fig. 3 and Fig. 5). For example, a warm summer would have resulted in extensive germination during autumn (because of the wide range of temperatures accepted for germination) and thus little germination would have been possible the following spring. However, if soil disturbance transfers seeds to the soil surface, germination can occur in a seemingly unpredictable pattern (Roberts and Boddrell, 1984) as a result of seed being subjected to suitable dormancy reduction circumstances but remaining ungerminated in soil until they are exposed to light (Milberg and Andersson, 1997).

As shown in this study, these *Papaver* taxa perform as winter annuals in warmer climates while spring emergence is an important factor in cooler climates (Figs 3 and 5). Therefore, changes in emergence pattern as a result of climate changes are also predictable: a warmer climate will decrease spring emergence, and increase autumn emergence, in relation to the present situation.

## CONCLUSIONS

Despite considerable variation within taxa, it was possible to establish taxon-specific responses as several seed batch per taxa were used. Present suggestions for seed dormancy classifications were not helpful for revealing differences in seed dormancy pattern, germination preferences and dormancy strength, at least not in an ecologically meaningful way. In an evolutionary perspective, we conclude that the general dormancy pattern is a conservative character for these *Papaver* taxa, that germination temperature preferences have been adjusted when or after new taxa evolved, and that dormancy strength is the most easily changeable character involved in germination. The general dormancy pattern explains how the taxa can perform as winter annuals in warmer climates, but mainly as summer annuals in colder climates. Hence, there is no need to infer local adaptations when interpreting within-taxon differences in temporal patterns of seedling emergence. Furthermore, the results suggest that the expected climatic change in cold temperate areas, from cooler to warmer, will lead to a transformation of *Papaver* phenology from a substantial fraction of summer annuals to mainly winter annuals.

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