Seed Dormancy, After-ripening and Light Requirements of Four Annual Asteraceae in South-western Australia

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Received: 25 June 2002 Returned for revision: 8 August 2002 Accepted: 30 August 2002 Published electronically: 16 October 2002

The role of dormancy, temperature and light in the regulation of seed germination of four annual Asteraceae from south-western Australia was investigated. The experiments aimed to identify after-ripening patterns, and to relate these to climatic conditions of the habitat in which the species occur. Seeds of all species were strongly dormant at maturity and maintained high levels of dormancy for time periods corresponding to the duration of summer in south-western Australia. Dry after-ripening was promoted best by temperatures lower than those prevailing in the dry season, although differences among storage temperatures were mostly insignificant. Germination percentages were highest at average winter temperatures (15 °C). A logistic model revealed significant differences in germinability among species, but not between incubation temperatures or light and dark treatments across species. Three species with seeds >0.5 mg germinated better in darkness than in light, whereas germination in darkness was almost inhibited in the species with the smallest seeds (0.14 mg). The course of dormancy loss, tested over a range of fluctuating incubation temperatures (7–30 °C), showed that seeds of three species came out of dormancy first at temperatures that prevail in south-western Australia during the winter (10–15 °C). Seeds from one species, introduced from South Africa, first lost dormancy at the lowest temperature (7 °C). All species showed after-ripening patterns of Type 1, typical of species growing in Mediterranean climates. The germination characteristics of the investigated species can be interpreted as ensuring that initial growth and establishment occur during the winter growing season, thereby avoiding the hot and dry summer conditions that follow seed dispersal.

Key words: Asteraceae, Australia, annuals, seed dormancy, after-ripening patterns, germination, light, Millotia myosotidifolia, Podotheca gnaphalioides, Podotheca chrysantha, Ursina anthemoides.

INTRODUCTION

Seed dormancy can serve to synchronize germination so that the probability of seedling survival is optimized (Harper, 1977; Baskin and Baskin, 1998). Since environmental conditions prevailing at the time of seed dispersal are frequently not suitable for seedling survival, many species rely on mechanisms that prevent germination immediately after shedding. In south-western Australia, where the climate is Mediterranean, the chance of a seedling becoming established is largely restricted to the rainy and moderately cool winter (Lamont et al., 1993; Bell, 1999). As seeds of many species ripen and are dispersed at the end of the rainy season, a postponement of germination is required for several months until the onset of the next rainy season when soil moisture is available to seedlings for a prolonged time period. Many studies have shown that primary dormancy, temperature and light play pivotal roles as components of germination-timing strategies in Mediterranean climates (e.g. Thompson, 1973a; Thanos et al., 1989; Bell et al., 1993; Schütz, 1999a).

Primary dormancy can be regarded as a major factor in preventing germination during the summer after occasional showers in Mediterranean climates. Seeds of many Australian species require several months’ storage before germination is possible (Bell, 1999). Dormancy may be strong and be alleviated only slowly, resulting in a period of dormancy that coincides with the average length of the unfavourable season, or else dormancy is weak but is combined with an inability to germinate at high temperatures. The duration of primary dormancy may change in relation to the after-ripening conditions. Suitable conditions for the relief of dormancy are often those that prevail in the habitat of a species or population during the unfavourable season. Indeed, dry and warm storage frequently promotes after-ripening of seeds in species of warm and arid climates (Mott, 1972; Thompson, 1973a; Baskin and Baskin, 1998; Pérez-Fernández et al., 2000). It has been observed that the relationship between the changing dormancy level and the temperature range for germination differs in response to regional climatic conditions. As seeds pass out of dormancy, three patterns of changes in the temperature requirements for germination can be distinguished (Vegis, 1964; Baskin and Baskin, 1994). Seeds of some species germinate first at low temperatures, but with additional loss of dormancy the maximum temperature for germination increases (Type 1). Seeds of other species first gain the ability to germinate at high temperatures, but with additional loss of dormancy the minimum temperature for germination decreases (Type 2). In a third group of species, seeds start to germinate first at intermediate temperatures, but with additional loss of...
dormancy they germinate at higher and lower temperatures (Type 3). Vegis (1964) suggested that Type 1 is an adaptation to a hot, dry season, Type 2 to a cold, unfavourable season and Type 3 to a hot, arid summer and a cold winter. Knowledge of dormancy syndromes in species of warm and seasonally dry climates is scarce and, as noted by Bell et al. (1993), there is a paucity of research on after-ripening and the influence of various storage regimes on seed germination of south-western Australian species.

The effect of light on seed germination varies and has been interpreted in two ways. One series of studies has shown greater germination in light than in darkness, but with the importance of light decreasing with seed mass (e.g. Koller et al., 1964; Milberg et al., 2000). The ecological interpretation is that light acts as a depth-sensing cue, preventing germination too deep in the soil. Another series of studies has shown that light prevents germination (Thanos et al., 1989, 1991; Bell et al., 1995; Morgan, 1998). This has been interpreted as a means to avoid seed germination on the soil surface, a strategy that is reasonable in situations where the soil dries rapidly (Thanos et al., 1989; Bell, 1993, 1999; Bell et al., 1995; Rokich and Bell, 1995; Richards and Lamont, 1996). We believe that both germination syndromes could have evolved, but in areas differing in drought risk, and that Mediterranean soils are more likely to dry out faster than temperate soils.

Current knowledge suggests the following predictions regarding dormancy and germination behaviour of short-lived, herbaceous Asteraceae occurring in Mediterranean south-western Australia: (1) dormancy is strong and is alleviated slowly (Bell, 1999); (2) after-ripening is promoted best by high summer temperatures, i.e. those prevailing in the habitat of a species during the dry season (Bell et al., 1993; Baskin and Baskin, 1998); (3) germination is greatest at average expected winter temperatures (Bell et al., 1995); (4) seeds show a Type 1 after-ripening pattern, i.e. they begin to germinate first at temperatures prevailing in their original habitat during winter (Vegis, 1964; Baskin and Baskin, 1998); and (5) germination is greater in darkness than in light, but the light requirement increases in smaller seeds (Bell, 1993, 1999; Plummer and Bell, 1995).

These predictions were investigated in two experiments conducted on four annual Asteraceae in which (1) germination was tested in light after varying periods of warm and dry storage at a wide range of temperatures, and (2) germination was tested, in both light and darkness, after different lengths of time in one of three storage tempera-

### MATERIALS AND METHODS

#### Study species

*Millotia myosotidifolia* is an annual herb, 16–30 cm tall, whose achenes are narrowly cylindric, strigillose and measure 3 × 0.3 mm. The pappus consists of 15–30 erect, barbeate bristles. The species occurs in sandy soils and has been recorded in New South Wales, South Australia, Victoria and Tasmania (Marchant et al., 1987). *Podotheca gnaphalioidei* is an erect or decumbent annual up to 0.5 m tall, with disc florets but no ray florets. The achenes are obovoid, 3–5 × 0.5 mm, and equipped with four to six plumose bristles. The species occurs on sand, clay and loam, among low open woodland and in shrubland (Marchant et al., 1987). *Podotheca chrysanthi* is an erect, slightly branched annual herb up to 0.5 m tall with numerous florets. The achenes are 3 × 0.6 mm, obovoid and shortly stipitate. The pappus bears eight to ten barbellate bristles. It occurs on sandy soils above limestone and in wet depressions amongst open woodland. *Ursinia anthemoides* is an erect annual herb up to 0.5 m tall with yellow ray and disc florets. The achenes are terete, narrowed at the base, 5 × 0.7 mm, ribbed and black, with a basal tuft of hairs and a pappus consisting of five ovate, petal-like scales. The species is native to South Africa, but is now widespread in south-western Australia, being especially abundant on roadsides and wasteland (Marchant et al., 1987). Average seed mass for the seeds used was 0.14 mg for *M. myosotidifolia*, 0.64 mg for *P. gnaphalioidei*, 0.60 mg for *P. chrysanthi* and 1.8 mg for *U. anthemoides*.

#### Collection and storage of achenes

Achenes were collected during November 1996 from single populations of the four species in Perth, south-western Australia (Table 1). They were dried for a few days and, after cleaning, stored in paper bags [relative humidity (RH) 40–60 %] at approx. 20 °C in the laboratory until initial tests commenced 10 (expt 1) or 32 d later (expt 2).

#### Experiment 1: after-ripening patterns

After-ripening patterns were investigated in a thermogradient incubator (Rubarth Apparatebau, Laatzen, Germany). This incubator has 12 parallel chambers...
(443 × 24 × 25 mm), covered with lids of transparent polycarbonate sealed with rubber o-rings, cut in an aluminium block. The construction principles of this type of incubator are described in detail by Ekstam and Bengtsson (1993). Seeds were sown on water-saturated filter paper strips (Schleicher and Schüll, no. 595) resting on a layer of polythene granules. De-ionized water was added to the chambers until the granules and the filter paper were just afloat, but not inundated. The incubator was equipped with warm white fluorescent light providing a photon flux density (PFD) of 25 μmol s⁻¹ m⁻² at seed level for 12 h d⁻¹.

Batches of 50 achenes were sown at six positions within each chamber of the thermogradient incubator, representing temperature regimes of 12/2, 15/5, 20/10, 25/15, 30/20 and 35/25 °C (corresponding to average temperatures of 7, 10, 15, 20, 25 and 30 °C, respectively). Two replicates, in randomly chosen chambers, were run in this experiment. Maximum and minimum temperatures were kept constant for 6 h, and heating and cooling periods were of the same duration. The light period started 3 h before the maximum temperature had been reached. Germination tests were performed in the light using fresh achenes (10 d after harvest) and using achenes stored dry at 25 °C for 80, 215 and 532 d.

Experiment 2: The effect of storage temperature and light on germination

Achenes were placed in transparent sealed plastic boxes on a double layer of filter paper and stored dry at constant temperatures of 5 (70 % RH), 15 (70 % RH) or 25 °C (45 % RH). At the beginning of each month the lid was removed and the filter paper was wetted with de-ionized water to simulate the occasional showers that may occur during the dry season (Baskin and Baskin, 1994). The boxes were kept open until the filter paper had dried out completely.

Germination tests were performed in light and darkness at 10 and 25 °C after 0, 40 and 126 d of storage under controlled conditions (corresponding to 32, 72 and 156 d after collection) and, additionally, at 15 °C after 126 d. Batches of 50 seeds of each species were placed in 5-cm Petri dishes on filter paper (Schleicher and Schüll, no. 595) wetted with de-ionized water. Experiments were performed with three replicates. Petri dishes intended for dark treatments were wrapped immediately in a double layer of aluminium foil. Seeds were stored and germination tests carried out in cooled incubators (Rubarth Apparatebau). The incubators were equipped with warm white fluorescent light providing a PFD of 20–30 μmol m⁻² s⁻¹ at seed level for 12 h d⁻¹.

Duration of experiments

The duration of the germination tests in both experiments ranged from 4 to 7 weeks. After the first 4 weeks, experiments were terminated when 7 d had passed without any further germination. Germinated achenes were counted every second day in the light treatments, whereas counts in the dark treatments were made every second week with the aid of dim green light. Achenes were judged to have germinated if at least 1 mm of the radicle was visible. In the calculation of germination percentage, dead seeds, which were identified based on their softness and brownish embryo colour, were excluded. Hence, germination is expressed as a percentage of viable seeds.

Data analyses

The data of expt 2 were analysed using a generalized linear model, available in ‘GENMOD’ (SAS, 1996), with a logit link function and a binomial error structure, followed by a likelihood ratio test. The model included the factors ‘light-level’ (light and darkness), ‘incubation temperature’ and ‘species’. The Williams method was used to account for overdispersion. In the preliminary analysis, a full model, including all main factors and all interactions, was computed. In a second step, the full model was reduced by restricting the data set to match an interpretable ecologically feasible situation. That is, seeds that were stored dry at a mean summer temperature prevailing in south-western Australia (25 °C), and thereafter incubated at winter temperatures, representing the average of daily mean (15 °C) and daily minimum (10 °C) temperatures in winter. Hence, data obtained from seeds kept at storage temperatures of 5 and 15 °C were omitted from this analysis, as were data of seeds incubated at 25 °C. This statistical test was performed with germination data 156 d after collection, a time-span approximating the duration of the hot and dry season in the Perth region. As it was not our intention to interpret interactions of species with light-level, ‘species’ was nested within ‘light-level’ to increase the number of degrees of freedom. Data obtained with recently matured achenes and with achenes 72 d after collection were not treated statistically because of too little germination.

One-way ANOVAs were used to detect possible significant differences (5 % level of significance) among storage temperatures on germination after 156 d of dry storage. Light and dark treatments within each species and each incubation temperature (10 and 15 °C) were analysed separately. When ANOVA indicated a significant treatment effect, a Tukey multiple comparison test (HSD-test) was performed to determine which treatment means differed significantly. Seed germinability at the temperature regarded initially as optimal for after-ripening (25 °C) was compared with germinability at 15 °C. Data were arcsin-transformed prior to this analyses to achieve better distribution properties.

RESULTS

Experiment 1: after-ripening patterns

Fresh seeds of the four species were strongly dormant (Fig. 1). After 80 d storage, only a few seeds germinated at low and medium temperature regimes. Germination had increased by 215 d, with minor species-specific peaks at temperatures between 7 and 20 °C. In each species these peaks coincided with the temperature peaks at which the highest germination percentages were achieved after 532 d of storage.
Podotheca gnaphalioides showed the highest germination percentage at an average temperature of 20 °C, P. chrysantha at 15 °C, Millotia myosotidifolia at 10–20 °C and Ursinia anthemoides at 7 °C. Germination after 215 d was restricted to temperatures between 7 and 20 °C in M. myosotidifolia and P. chrysantha, and 7 (temperatures below this were not tested) and 25 °C in U. anthemoides. Only achenes of P. gnaphalioides germinated to some extent at 30 °C (Fig. 1). Germination at the optimum temperatures were between 50 and 75 % for all species. Hence a considerable fraction of achenes remained dormant irrespective of environmental conditions.

Dormancy loss had occurred by 532 d of storage (Fig. 1). At their specific optimum temperature, all species attained germination of between 80 and 100 %. Although germination increased at the higher temperatures with time of storage, the shape of the germination curves did not change substantially in any of the species. However, after 532 d of storage, germination also occurred at higher temperatures in M. myosotidifolia, P. chrysantha and U. anthemoides, and a greater proportion of P. gnaphalioides seeds germinated at temperatures between 20 and 30 °C (Fig. 1).

Experiment 2: the effect of storage temperature and light

None of the recently matured achenes in the four species germinated when incubated at 25 °C, and very few did so at 10 °C, in light or in darkness (Table 2). After 40 d of storage at 25 °C, germination percentages in the light fell below the values attained in recently harvested achenes in all species (Table 2). Germination was slightly higher in achenes stored at 15 °C. After 126 d of controlled storage, germination percentages had increased considerably, but a fraction of the seeds remained ungerminated in all species (Fig. 2). Overall, germination was highest in P. gnaphalioides, followed by P. chrysantha, U. anthemoides and M. myosotidifolia. The most conspicuous result was that germination was inhibited almost completely in all species at an incubation temperature of 25 °C, except in seeds of P. gnaphalioides stored at 15 °C that germinated to about 50 % in darkness (Fig. 2).

The logistic model representing a situation with a high (summer) ripening temperature (25 °C), and lower incubation (winter) temperatures, revealed highly significant differences among species, but there was no significant effect of light and incubation temperature across species on germination. A significant incubation temperature \times species interaction was due to lower germination of P. chrysantha and P. gnaphalioides at 10 °C than at 15 °C, whereas overall germination of U. anthemoides and M. myosotidifolia was higher at 10 °C (Table 3). The rank order in germinability of the four species was the same across all storage temperatures. Likewise, there was little difference within species in the response to light across the incubation temperatures.

The effect of storage temperature on germinability was obvious after 126 d. Overall, dormancy loss was highest in seed-lots kept at 15 °C in all species (Fig. 2). In almost all...
cases, seeds stored at 15 °C germinated better, or equally well, compared with seeds stored at 25 °C. The 16 pairwise comparisons of germination percentages (Table 4) between the two storage temperatures yielded significant differences in four cases, although two of these were relatively small. It was only the two Podotheca species that exhibited substantial differences, and only in light at an incubation temperature of 10 °C (Table 4, Fig. 2). Moreover, there were no consistent germination patterns across species or across incubation temperatures. For instance, a higher proportion of seeds of P. gnaphalioides incubated at 10 °C germinated in light when stored at 15 °C than when stored at 25 °C, whereas germination was higher in darkness in seeds stored at 25 °C than in those stored at 15 °C. In most cases, storage

**Table 2. Germination percentages (mean ± s.e.) of achenes of four Asteraceae from south-western Australia when recently matured, and after 40 d dry storage at 15 or 25 °C**

<table>
<thead>
<tr>
<th>Storage temperature (°C):</th>
<th>–</th>
<th>15</th>
<th>25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Storage duration (d):</td>
<td>0</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Incubation temperature (°C)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Millotia myosotidifolia</td>
<td>10</td>
<td>2.2 ± 0.6</td>
<td>1.1 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Podotheca chrysantha</td>
<td>10</td>
<td>5.9 ± 4.4</td>
<td>6.6 ± 4.4</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>P. gnaphalioides</td>
<td>10</td>
<td>2.9 ± 1.2</td>
<td>5.2 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Ursinia anthemoides</td>
<td>10</td>
<td>9.7 ± 1.0</td>
<td>11.2 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Germination tests were conducted at 10 and 25 °C in light and darkness.

**Table 3. Results of the logistic model applied to the germination data obtained for four annual Asteraceae from south-western Australia after 150 d of dry storage at 25 °C**

<table>
<thead>
<tr>
<th></th>
<th>NDF</th>
<th>DDF</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>1</td>
<td>32</td>
<td>0.69</td>
<td>0.412</td>
</tr>
<tr>
<td>Incubation temperature</td>
<td>1</td>
<td>32</td>
<td>1.13</td>
<td>0.295</td>
</tr>
<tr>
<td>Species (nested within light-level)</td>
<td>6</td>
<td>32</td>
<td>41.42</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Light × incubation temperature</td>
<td>1</td>
<td>32</td>
<td>0.54</td>
<td>0.468</td>
</tr>
<tr>
<td>Incubation temperature × species</td>
<td>6</td>
<td>32</td>
<td>9.99</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

The factor ‘species’ was nested within the factor ‘light-level’ resulting in an increment of nominator degrees of freedom from 3 (n – 1) to 6 (2n – 1). NDF, Nominator degrees of freedom; DDF, denominator degrees of freedom.
at 5 °C reduced subsequent germination, except in *U. anthemoides*, where germination percentages were almost equal in seeds kept at 5 and 15 °C, in light and darkness.

**DISCUSSION**

*Primary dormancy and its alleviation*

Our first prediction, that seeds are strongly dormant at maturity and dormancy becomes alleviated only slowly, was confirmed for all four species investigated. We can surmise that ineffective germination during the first summer is prevented as the period of dormancy coincided well with the average length of the unfavourable season for seedling establishment in south-western Australia. Maintenance of dormancy under high temperatures is vital for species in Mediterranean-climate Australian habitats because occasional summer rainfall can provide sufficient moisture for germination, but not enough to carry seedlings into the next winter period when rainfall is more reliable (Bell *et al.*, 1999).

The levels of primary dormancy in fresh seeds and the temporal course of dormancy loss were markedly similar in the four species studied. By comparison, primary dormancy was much lower, and dormancy was lost rapidly in seeds of eight Asteraceae from south-eastern Spain, a region with climatic conditions similar to those in south-western Australia (Schütz, 1999b). Thus, dormancy loss in the Spanish species occurred long before the end of the dry season, with the result that only the upper temperature limit prevented untimely germination in late summer. Unfortunately, little information about initial dormancy levels is available for species from south-western Australia. In almost all previous studies, seeds were stored dry for prolonged, or even unknown, time periods before the onset of experiments (e.g. Bell, 1993; Plummer and Bell, 1995; Peishi *et al.*, 1999). Moreover, different storage periods were not combined with a range of incubation temperatures that are necessary to identify the dormancy syndromes under investigation in the present study. Germinability differed considerably in three annual Western Australian Asteraceae after different periods of time, ranging from weak primary dormancy and its rapid loss in one species, to a strong and long-lasting dormancy in the other two species (Peishi *et al.*, 1999).

**Temperature optimum for after-ripening**

Our second prediction was that after-ripening is best promoted at high temperatures, and it was based on what appeared to be a general consensus (Thompson, 1973a; Bell *et al.*, 1993; Baskin and Baskin, 1998; Peishi *et al.*, 1999). That is, the warmer the storage environment the greater the loss of dormancy (Murdoch and Ellis, 2000).

Temperatures regarded as suitable for after-ripening (omitting heat shock) may range from 25 to 70 °C in species of warm and seasonally arid habitats (Mott, 1972; Bell *et al.*, 1993). Our results, however, indicate that a considerable degree of after-ripening may be achieved at lower temperatures (15 °C). The surprising lack of a greater effect of the 25 °C storage temperature in our experiment may lie in a time period of dry after-ripening too short to bring about marked differences between storage temperatures of 15 and 25 °C. In our experiment, the water content in seeds stored at 15 °C was probably appropriate for after-ripening (approx. 5–12 %), even after 126 d of dry storage, and had thus not yet reached values where after-ripening is severely restricted (Simpson, 1990; Probert, 2000). In another study on south-western Australian Asteraceae, seeds stored at 25 and 38 °C germinated better than seeds stored at 5 and 15 °C, but only after about 8 months of storage (Peishi *et al.*, 1999). In this study, a drop in germinability in seeds stored at 15 °C coincided well with an increase in seed water content from 5–9 % initially to more than 12 % after about 10 months, while the water content of seeds stored at 25 °C had changed little during a storage period of 10 months.

We did not test storage temperatures higher than 25 °C. However, higher storage temperatures could have led to differences in germinability within the storage period of 126 d, as temperatures corresponding to the maximum temperatures (>40 °C) occurring in the field during summer in warm and seasonally arid regions of Australia may accelerate after-ripening considerably (Mott, 1972; Peishi *et al.*, 1999).

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**Table 4.** Results of one-way ANOVAs comparing the effect of three storage temperatures on germinability of four annual Asteraceae from south-western Australia

<table>
<thead>
<tr>
<th>Incubation Condition:</th>
<th>Millotia myosotidifolia</th>
<th>Podothea gnaphaloides</th>
<th>P. chrysantha</th>
<th>Ursinia anthemoides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light, 10 °C</td>
<td>n.s.</td>
<td>**</td>
<td>***</td>
<td>n.s.</td>
</tr>
<tr>
<td>Light, 15 °C</td>
<td>**</td>
<td>*</td>
<td>**</td>
<td>n.s.</td>
</tr>
<tr>
<td>Dark, 10 °C</td>
<td>n.s.</td>
<td>**</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Dark, 15 °C</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

*‘A’ denotes statistical differences between storage temperatures (5, 15, 25 °C); ‘B’ denotes differences between 25 and 15 °C identified by means of an HSD-test.

*** P < 0·001; ** P < 0·01; * P < 0·05; n.s., not significant.*
**Temperature optima for germination**

The general impression that germination of south-western Australian seeds is highest at temperatures associated with the winter rainfall period (approx. 15 °C) (Bell et al., 1993) was confirmed by our data. Similar temperature optima were not only characteristic for a number of ‘everlasting daisies’ (Asteraceae), but also for most species of other taxa in south-western Australia (Bell et al., 1995), and for Asteraceae of the Mediterranean Basin (Schütz, 1999b).

An increasing fraction of seeds of the four species gained the ability to germinate at higher and lower temperatures with age, reflecting the potential of many Asteraceae to germinate over a range of average temperatures exceeding those that occur in their current habitats (Atwater, 1980; Baskin and Baskin, 1998; Schütz, 1999b). The wide range of germination temperatures is in contrast to species in many other plant families occurring in south-western Australia that remain largely ungerminated at lower and, particularly, at higher temperatures (Bell, 1993, 1994; Bell et al., 1995; Plummer and Bell, 1995).

**After-ripening types**

After-ripening patterns revealed marked differences between the four species tested in the present study and Asteraceae in temperate Europe and North America, most of which germinate first at high and later at increasingly lower temperatures (Baskin and Baskin, 1993, 1998). Differences were also apparent between the three native Australian species studied and Asteraceae of the Mediterranean Basin. The Australian species commenced germination first at temperatures between 10 and 20 °C, but subsequently also germinated at higher and lower temperatures, whereas Asteraceae of the Mediterranean Basin germinated first at 7 and 10 °C and subsequently at increasingly higher temperatures (Schütz, 1999b; W. Schütz, unpubl. res.). It should be noted that both groups of Asteraceae, those collected in south-eastern Spain and those collected in the Perth region of Australia, were tested under the same experimental conditions, i.e. in light over a range of fluctuating temperatures between 7 and 30 °C. Nevertheless, we consider that both groups belong to after-ripening Type 1 as their seeds began to germinate first at temperatures representing winter conditions in their respective habitats. That is, the criterion for the assignment of species to dormancy types is their response to the range of temperatures occurring in their habitat and not their ability to germinate at higher or lower temperatures (Baskin and Baskin, 1998). After-ripened seeds of many Asteraceae of Mediterranean environments are capable of germinating at temperatures below the mean minimum winter temperatures of their habitat (Schütz and Milberg, 1997; Schütz, 1999b).

In contrast to the native Australian species, the naturalized species *U. anthemoides* commenced germination first at the lowest (7 °C) and subsequently at higher temperatures, thus showing after-ripening patterns typical of species in the Mediterranean Basin (Schütz, 1999b). We suspect that the germination responses of *U. anthemoides* to temperature reflect an adaptation to climatic conditions prevailing in the original distribution area of this species in South Africa, with winter rain, but with colder winters (at least in the uplands) than in south-western Australia. The difference in temperature preferences for germination between *U. anthemoides* and the native Australian species provides evidence that after-ripening requirements of naturalized species are related to the climatic conditions of their region of origin (Thompson, 1973b; Baskin and Baskin, 1998; Schütz, 1999a).

**Light requirement for germination**

The germination response to light was clearly related to seed weight in the species studied. *U. anthemoides* and *P. gnaphalioides*, the two species with the largest seeds, germinated better in darkness than in light, whereas germination in *M. myosotidifolia*, the species with the smallest seeds, was almost exclusively confined to light. Plummer and Bell (1995) showed a light requirement for germination in seeds weighing less than 0.5 mg of ten Asteraceae from south-western Australia, whereas the response varied among species with heavier seeds. These findings imply that light acts as a depth-sensing mechanism, thereby avoiding possible fatal germination of small seeds buried too deep in the soil, a response previously shown for many small-seeded temperate species (Grime, 1979; Milberg et al., 2000).

The difference between light and dark germination was comparatively small in the species with medium and large seeds. Either germination is inhibited by light in a fraction of the seeds, or light is unimportant for the regulation of germination in the Mediterranean species investigated, at least at the low irradiation levels used in most experiments. In *P. gnaphalioides*, high germination in darkness but no germination in light at a constant temperature of 25 °C (Fig. 2) may indicate the existence of a mechanism to avoid germination on the soil surface at high temperatures, whereas burial may ensure enough moisture for germination and seedling establishment.

**CONCLUDING REMARKS**

The dormancy and germination characteristics studied in the four species are likely to be those that regulate germination in the field. Nevertheless, the treatments chosen do not span the full range of conditions that seeds can experience in the field. For example, soil surface temperatures during summer might be much higher than those in our experiments, and after-ripening rates might thus have been underestimated since they increase with temperature. Nevertheless, the duration of primary dormancy of the four species coincided well with the average length of the unfavourable season for seedling establishment in south-western Australia and serves to prevent germination in the summer following seed shedding. From our results we can infer that the four annuals are able to accumulate a short-term persistent seed pool in the soil, but a seed carry-over after the first year seems to be restricted to a small proportion of seeds due to the lack of a light requirement in three of the species. However, the light-requiring small seeds of *M. myosotidi-
folia may be able to persist for a longer time in the soil seedbank. Burial experiments are required to determine how long seeds can survive under field conditions. Another problem that deserves further investigation is the complex interaction between seed dormancy status and temperature, relative humidity, and occasional wetting during the summer. Information on after-ripening processes in species from south-western Australia and other Mediterranean regions remains scarce.

ACKNOWLEDGEMENTS

We thank G. Rave for valuable help with statistics and the ‘Deutsche Forschungsgemeinschaft’ for financial support.

LITERATURE CITED


