Germination patterns of dimorphic achenes in three related species of *Scorzoneroides* (Asteraceae, Lactuceae) growing in different environments

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*Scorzoneroides palisiae*, *S. salzmannii*, and *S. muelleri* (Asteraceae) are phylogenetically close annuals with dimorphic achenes. Although these three species are characteristic to areas with some degree of disturbance, *S. palisiae* and *S. salzmannii* grow in Mediterranean environments, whereas *S. muelleri* preferentially grows in semi-arid environments. This study compared the germination characteristics of central and peripheral achenes subjected to different storage times. Both central and peripheral achenes of the three *Scorzoneroides* species were completely dormant immediately after dispersal. This dormancy was reduced after six months in dry storage, and practically disappeared after more than a year in storage. Six-month central achenes of *S. palisiae* and *S. salzmannii* displayed lower dormancy levels than peripheral achenes did, producing a mixed germination pattern. However, 6-month central achenes of *S. muelleri* displayed the same dormancy levels as those of peripheral achenes. Furthermore, there was a nearly significant negative correlation among germination and the annual aridity index in the studied populations. We suggest that this increase in dormancy may be interpreted as an adaptation to semi-arid ecosystems.

Key words: adaptation, dormancy, heterocarpy, Mediterranean, seed ecology, weed germination

Introduction

Seed heteromorphism and heterocarpy are the production of seeds or fruits with different shapes or behaviour by the same plant (Venable 1985). Some authors have hypothesized that heterocarpy supposes an evolutionary strategy to extend dispersal in time and space (Venable & Lawlor 1980, Ellner 1986). This would reduce the impact of environmental spatiotemporal variability on plant reproductive success, i.e., a bet-hedging strategy (Venable & Levin 1985a). Such a strategy may be advantageous in natural environments with temporal or spatial heterogeneity, i.e., unpredictable habitats (Venable *et al*. 1995), such as frequently disturbed habitats and arid or semi-arid environments (El-Keblawy 2003 and references therein). In these variable environments, seed heteromor-
Phylogeny and Evolution of Heterocaryous Asteraceae

Heterocaryous seed forms are more common in annuals than perennials (Harper 1977, Plitmann 1986, Imbert 2002). Most recognized cases of species with heteromorphic seeds belong to the Asteraceae family, and usually involve differences between central and peripheral achenes (Zohary 1950, Imbert 2002). Commonly, central achenes have a higher dispersal capacity through beaks, pappi, or spines (Rocha 1996, Ruiz de Clavijo 2001, 2005, Imbert 2002) and have lower dormancy, as compared with peripheral achenes. However, peripheral achenes have a lower dispersal capacity, and present some degree of dormancy (Baskin & Baskin 1976, Ruiz de Clavijo 2001, 2005, Imbert 2002, but see Brändel 2004).


In this paper, three closely related taxa of the genus Scorzoneroides (formerly known as Leontodon subg. Oporinia, Asteraceae), were chosen to compare differences in the degree of heterocaryous between annual species growing in different types of unpredictable habitats. Scorzoneroides comprises 29 taxa occurring in the Euro-Mediterranean area (Greuter et al. 2006). Based on their nrDNA and cpDNA sequences, S. palisiae, S. salzmannii, and S. muelleri are closely related species that fall into a group comprising mainly annuals with dimorphic achenes (Samuel et al. 2006, G. Cruz-Mazo unpubl. data). All three species grow in areas with some degree of disturbance, thus fulfilling the association between heterocaryous and disturbed habitats, i.e., unpredictable, and the association between heterocaryous and an annual life cycle. Nevertheless, S. palisiae and S. salzmannii are found in Mediterranean environments, whereas the studied populations of S. muelleri are found in semiarid areas. Although both types of environments may be considered unpredictable, inter-annual variation in precipitation has been demonstrated to increase with decreasing annual precipitation or increasing aridity (Arroyo et al. 2006). For this reason, S. muelleri, which grows in more arid populations, is expected to show a different behaviour. Specifically, we expect prolonged seed dormancy in this species, as this is thought to be an adaptation to environmental uncertainty in desert annuals (Philippi 1993). Specifically, we tried to address the following questions:

1. What are the morphological differences between the two achene types?
2. Is there any difference in the germination behaviour of central and peripheral achenes in each of the three Scorzoneroides species?
3. Is the germination behaviour of the two achene types maintained at different storage times from dispersal?
4. Is the different degree of aridity among populations influencing the behaviour of the two achene types?

Material and methods

Plants and study area

Scorzoneroides palisiae, S. salzmannii and S. muelleri are annuals with a basal rosette and branched stems ending in a capitulum with ligulate yellow flowers. Seeds germinate in autumn, and plants overwinter as rosettes and flower from February to May. The three taxa are self-incompatible, they are pollinated by insects, and achene maturation takes place 8–10 days after pollination (G. Cruz-Mazo unpubl. data). Scorzoneroides palisiae plants bear around 45 achenes per capitula, whereas S. salzmannii and S. muelleri bear around 58 and 73 achenes per capitula, respectively.

Scorzoneroides palisiae and S. salzmannii grow in open fields, pine and oak woodlands, or agricultural lands borders at altitudes of up to 350 m (Talavera 1987, Izuzquiza 1991). Scorzoneroides palisiae is endemic in SW of Iberian Peninsula and N Morocco and S. salzmannii is endemic in N Morocco, although they do not co-occur (Finch & Sell 1976, Izuzquiza 1991, 1998). Scorzoneroides muelleri grows in steppes and agricultural land borders at altitudes...
between 30–1300 m, and is distributed in SE of Iberian Peninsula, S of Morocco and Algeria (Izuzquiza 1991). In general, the three taxa occur on disturbed or nitrified soils (Talavera 1987, Izuzquiza 1991, Cruz-Mazo per. obs.). The achenes of *S. palisiae* were collected from six populations in SW Spain, and those of *S. muelleri* were collected from seven populations in SE Spain and in Morocco (Table 1). Because of the restricted distribution area (Izuzquiza 1998, G. Cruz-Mazo pers. obs.), data from only a single population of *S. salzmannii* were available (N Morocco, Table 1). The climate is characterized as Mediterranean pluviseasonal-oceanic with a dry sub-humid ombrotype in the area where the populations of *S. palisiae* and *S. salzmannii* were located, and Mediterranean xeric-oceanic with a semi-arid ombrotype in the area where the population of *S. muelleri* was (Rivas-Martínez 1987).

**Characteristics of the achene**

Matured achenes were collected from different populations of the three species to observe the presence of pappus and to compare the mass of central and peripheral achenes. Due to the small mass of achenes, 10 groups of 20 achenes were weighed for each species to the nearest 0.01 mg.

**Variability in achene germination**

Matured achenes from capitula of the first branching level were taken from 30 random plants per population. For each population, the seeds were mixed and kept in paper envelopes in the dark under laboratory conditions (ca. 22 °C, relative humidity = 50%–70%) until the beginning of the germination studies (hereafter referred to as “dry storage”). In all our experiments, four replicates of 50 achenes each were sown. These replicates were placed on permanently moist Whatman no. 1 filter paper in Petri dishes, and incubated in a germination chamber at 18/21 °C, in the dark/light for 13/11 h, respectively. Preliminary tests had shown that these experimental conditions are optimal for germination. The dishes were Table 1. Location and climatic characteristics of the studied populations of the three taxa of *Scorzoneroides*.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>locality (country)</th>
<th>Code</th>
<th>Coordinates</th>
<th>Altitude (m a.s.l.)</th>
<th>Mean annual temp. (°C)</th>
<th>Mean annual precip. (mm)</th>
<th>Annual aridity indexa</th>
<th>Substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. palisiae</em></td>
<td>Monesterio, Badajoz (Spain)</td>
<td>PAL1</td>
<td>37°54´N, 6°13´W</td>
<td>515</td>
<td>17.1</td>
<td>766</td>
<td>1.16</td>
<td>Slate</td>
</tr>
<tr>
<td></td>
<td>Villaverde, Sevilla (Spain)</td>
<td>PAL2</td>
<td>37°35´N, 5°52´W</td>
<td>17</td>
<td>17.8</td>
<td>524</td>
<td>1.75</td>
<td>Clay</td>
</tr>
<tr>
<td></td>
<td>Alcalá, Sevilla (Spain)</td>
<td>PAL3</td>
<td>37°20´N, 5°51´W</td>
<td>35</td>
<td>18.1</td>
<td>543</td>
<td>1.41</td>
<td>Clay</td>
</tr>
<tr>
<td></td>
<td>Puebla, Sevilla (Spain)</td>
<td>PAL4</td>
<td>37°11´N, 6°4´W</td>
<td>19.0</td>
<td>532</td>
<td>1.53</td>
<td>Sand</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Arroyo Plata, Huelva (Spain)</td>
<td>PAL5</td>
<td>37°40´N, 6°14´W</td>
<td>273</td>
<td>15.8</td>
<td>810</td>
<td>1.07</td>
<td>Slate</td>
</tr>
<tr>
<td></td>
<td>Almodóvar, Córdoba (Spain)</td>
<td>PAL6</td>
<td>37°48´N, 5°1´W</td>
<td>121</td>
<td>17.0</td>
<td>598</td>
<td>1.05</td>
<td>Slate</td>
</tr>
<tr>
<td><em>S. salzmannii</em></td>
<td>Larache (Morocco)</td>
<td>SAL1</td>
<td>35°7´N, 6°9´W</td>
<td>50</td>
<td>17.6</td>
<td>719</td>
<td>1.69</td>
<td>Sandstone</td>
</tr>
<tr>
<td><em>S. muelleri</em></td>
<td>Tabernas, Almería (Spain)</td>
<td>MUE1</td>
<td>37°2´N, 2°25´W</td>
<td>400</td>
<td>17.9</td>
<td>220</td>
<td>4.19</td>
<td>Marl</td>
</tr>
<tr>
<td></td>
<td>Turrillas, Almería (Spain)</td>
<td>MUE2</td>
<td>37°4´N, 2°18´W</td>
<td>425</td>
<td>17.8</td>
<td>240</td>
<td>3.79</td>
<td>Gypsum</td>
</tr>
<tr>
<td></td>
<td>Albánchez, Almería (Spain)</td>
<td>MUE3</td>
<td>37°17´N, 2°10´W</td>
<td>472</td>
<td>15.2</td>
<td>425</td>
<td>2.05</td>
<td>Sandstone</td>
</tr>
<tr>
<td></td>
<td>Castaños, Almería (Spain)</td>
<td>MUE4</td>
<td>37°8´N, 2°2´W</td>
<td>338</td>
<td>17.5</td>
<td>255</td>
<td>3.17</td>
<td>Gypsum</td>
</tr>
<tr>
<td></td>
<td>Rioja, Almería (Spain)</td>
<td>MUE5</td>
<td>36°55´N, 2°27´W</td>
<td>147</td>
<td>18.0</td>
<td>231</td>
<td>3.87</td>
<td>Marl</td>
</tr>
<tr>
<td></td>
<td>Albox, Almería (Spain)</td>
<td>MUE6</td>
<td>37°21´N, 2°0´N</td>
<td>241</td>
<td>18.3</td>
<td>296</td>
<td>3.17</td>
<td>Sandstone</td>
</tr>
<tr>
<td></td>
<td>Tafraoute (Morocco)</td>
<td>MUE7</td>
<td>30°1´N, 9°2´W</td>
<td>980</td>
<td>19.6</td>
<td>281</td>
<td>4.5</td>
<td>Schist</td>
</tr>
</tbody>
</table>

* Annual aridity index = Annual potential evapotranspiration/Mean annual precipitation (data from the nearest bioclimatic stations in Rivas-Martínez et al. 2004).
inspected daily, and the number of germinated seeds was recorded (i.e., those with an emerged radicle greater than 0.2 mm). The trials lasted for a period of 43 days, until the number of germinated achenes stabilized (i.e., no newly germinating achenes were found). However, the dishes were checked for a further 20 days to confirm that no more germination had occurred (Baskin & Baskin 1998). Non-germinated achenes were pinched with forceps to see if the embryos were firm, which confirmed that they were still alive. Previously, we confirmed the viability of achenes using the tetrazolium test (Grabe 1970). Dead achenes were excluded from the calculation of germination percentages (Baskin & Baskin 1998).

To investigate variations in germination behaviour between peripheral and central achenes in different populations, some experiments were carried out using achenes subjected to different storage times from dispersal.

1. Germination of freshly matured achenes. The existence of dormancy in recently dispersed achenes was tested in PAL2, PAL3, PAL4, and PAL5 (S. palisiae), in SAL1 (S. salzmanii), and in MUE1, MUE2, MUE4, MUE5, and MUE7 (S. muelleri) (see Table 1 for abbreviations). This experiment was carried out using achenes collected in the spring of 2006, which were sown within seven days of harvest (Baskin & Baskin 1998).

2. Germination of achenes after six months in dry storage, (hereafter, 6-month achenes). Achenes from the same populations used in the previous experiment were stored for a period of six months, and then germinated in the germination chamber.

3. Germination of achenes after more than a year in dry storage, (hereafter, 1-year achenes). Achenes from PAL1, PAL2, PAL3, PAL4, PAL5, and PAL6 (S. palisiae), and MUE1, MUE2, MUE3, MUE4, MUE5, and MUE6 (S. muelleri) were collected during April–May 2004, and sown in October 2005. Achenes from SAL1 (S. salzmanii) and MUE7 (S. muelleri) were collected in April 2003, and sown in October 2005.

**Data analysis**

In each of the three species, the weights of achenes were compared using the Mann-Whitney test (Zar 1999) due to lack of non-normality and heterogeneous variances.

The final germination proportion was analyzed to assess the germination response. The intraspecific variability of the germination percentage of S. palisiae, S. salzmanii, and S. muelleri achenes was analyzed using a Generalized Linear Model (GLM) with a quasi-binomial error distribution and a probit link function. We used quasi-binomial functions instead of a binomial error structure to correct for data over-dispersion applying the F test for the analysis of deviance (Crawley 2005). Analyses were performed with R ver. 2.5.0 (R Development Core Team 2007). The sequential Bonferroni test was applied to control for experiment-wise type I error produced by multiple comparisons (García 2004). A Pearson correlation was used to reveal whether the germination percentage of the achenes was dependent on aridity index (Table 1).

**Results**

**Characteristics of the achene**

In the three Scorzoneroides species, the central and peripheral achenes were highly dimorphic. The central achenes were thinner and had a pappus with 10, (rarely 9 or 11), plumose hairs, while the peripheral achenes were thicker, shorter, and had no pappus (Fig. 1). The weight of both types of achenes was statistically similar in S. palisiae and S. muelleri, but the central achenes were heavier than the peripheral achenes in S. salzmanii (Table 2).

**Variability in achene germination percentage**

None of the freshly matured achenes germinated in any of the populations of the three species tested. Achenes after 6 months in dry storage germinated, but presented different degrees of dormancy. The mean germination percentages
of the 6-month central and peripheral achenes of *S. palisiae* were 73% ± 5.0% and 28% ± 3.5%, respectively, and this difference was statistically significant (Table 3). The mean germination percentage of the populations was not statistically different (Table 3). The interaction between the achene type × population was not significant, which indicates that the differences in germination percentages between the two achene types were homogeneous in all populations (Table 3 and Fig. 2A). In the sole population of *S. salzmannii*, the mean germination percentage of the 6-month central achenes was significantly higher than that of the peripheral achenes (66% ± 2.0% and 21% ± 3.8%, respectively, Table 3). The germination of the central 6-month achenes of *S. muelleri* was 51% ± 5.4%, and this was not significantly different from that of the peripheral achenes (37% ± 3.9%, Table 3). Again, the mean germination percentage of the populations and the interaction between the achene type × population were not statistically different (Table 3 and Fig. 2B).

In all three species, achenes after 1 year in dry storage experienced a general increase in the germination percentage. Nearly all central and peripheral 1-year achenes of *S. palisiae* germinated (92% ± 1.3% and 90% ± 1.8%, respectively), and thus, the germination percentages of the two achene types were not significantly different (Table 3). The mean germination percentage was statistically similar among the populations (Table 3). However, similarities in germination between the two achene types were not found in all populations (Table 3 and Fig. 2C). The 1-year central achenes of *S. salzmannii* had significantly higher mean germination percentages than the peripheral achenes (76% ± 4.1% and 63% ± 1.3%, respectively, Table 3). In *S. muelleri*, the mean germination percentage of the 1-year central achenes was significantly higher than that of the peripheral achenes (94% ± 1.0% and 83% ± 2.8%, respectively, Table 3). In this species, the mean germination percentages of the populations were statistically different, but the significant interaction between achene type × population indicated that differences in the germination percentages between the two achene types were dissimilar in the populations studied (Table 3 and Fig. 2D).

Germination of 6-month central achenes decreased with an increase in the aridity index of the populations studied (Table 1), although the correlations were only marginally significant (*r* = −0.650, *p* = 0.058, *n* = 9). No respective correlation was found in both the 6-month peripheral achenes and the 1-year achenes.

### Discussion

*Scorzoneroides palisiae*, *S. salzmannii* and *S. muelleri* produced morphologically different achenes within the capitula: the central achenes

![Fig. 1](image). Heteromorphic achenes of (A) *Scorzoneroides palisiae*, (B) *S. salzmannii*, and (C) *S. muelleri*. For each taxon, central achenes are represented on the left, and peripheral on the right.

### Table 2. Mean weight ± SE (mg) of 10 groups of 20 achenes of the three taxa of *Scorzoneroides*.

<table>
<thead>
<tr>
<th>Achene type</th>
<th><em>S. palisiae</em></th>
<th><em>S. salzmannii</em></th>
<th><em>S. muelleri</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Central</td>
<td>7.9 ± 0.12</td>
<td>5.9 ± 0.11</td>
<td>4.9 ± 0.14</td>
</tr>
<tr>
<td>Peripheral</td>
<td>8.1 ± 0.11</td>
<td>4.7 ± 0.04***</td>
<td>5.0 ± 0.24</td>
</tr>
</tbody>
</table>

*** = significant differences at *p* < 0.001, Mann-Whitney test.
possessed a pappus, whereas the peripheral achenes did not. The central achenes are wind dispersed in their natural habitat, while peripheral achenes remain on the plant, and are partially covered by the involucral bracts (G. Cruz-Mazo & E. Narbona pers. obs.). In this type of dimorphism, described in a large number of composites, central achenes are usually lighter than peripheral achenes (reviewed by Imbert 2002). This has also been found in some species of *Leontodon*, which have the same pattern of weight differences (Ruiz de Clavijo 2001, Brändel 2007). However, in this study, *S. salzmannii* produced heavier central achenes, and no differences were found between the two achene types in *S. palisiae* and *S. muelleri*. The different morphologies of the achenes lead to a difference in dispersal capacity, which is better in the central achenes than in the peripheral achenes (Rocha 1996, Imbert 1999). In wind-dispersed composites, the most important variables that influence the dispersal capacity of the achenes are their weight and morphology, which includes the presence of specialized structures, such as pappi (Sheldon & Burrows 1973, McEvoy & Cox 1987). Both achene types of all three *Scorzoneroides* species were very light (around 0.3 mg), and thus, the only variable that seemed to affect the dispersal ability of the achenes was the presence or absence of a pappus. This strategy should be particularly advantageous for annual species growing in disturbed sites, because central achenes can colonize new sites or patches, and peripheral achenes can self-replace parent plants in the next generation (Harper 1977, McEvoy 1984).

Both central and peripheral achenes of the three *Scorzoneroides* species were dormant immediately after dispersal. This dormancy was reduced after 6 months in dry storage and practically disappeared after more than a year. Similar after-ripening has been observed in peripheral achenes of *Heterotheca subaxillaris* (Baskin & Baskin 1976). Several authors have proposed that pericarps of some heterocarpic composite taxa can influence achene germination (Forsyth & Brown 1982, Venable & Levin 1985b, Beneke et al. 1993). The three *Scorzoneroides* taxa studied are winter annuals. Germination of the achenes occurs in the autumn, plants develop

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Deviance</th>
<th>Residual df</th>
<th>Residual dev.</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. palisiae</em></td>
<td>1</td>
<td>0.39</td>
<td>29</td>
<td>141.13</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achene type</td>
<td>1</td>
<td>220.82</td>
<td>28</td>
<td>141.02</td>
<td>ns</td>
</tr>
<tr>
<td>Achene type x population</td>
<td>1</td>
<td>69.44</td>
<td>6</td>
<td>6.63</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td><em>S. salzmannii</em></td>
<td>1</td>
<td>10.29</td>
<td>38</td>
<td>354.34</td>
<td>ns</td>
</tr>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achene type</td>
<td>1</td>
<td>34.05</td>
<td>37</td>
<td>320.20</td>
<td>ns</td>
</tr>
<tr>
<td>Achene type x population</td>
<td>1</td>
<td>31.00</td>
<td>36</td>
<td>310.20</td>
<td>ns</td>
</tr>
<tr>
<td><em>S. muelleri</em></td>
<td>1</td>
<td>0.278</td>
<td>46</td>
<td>8.188</td>
<td>ns</td>
</tr>
<tr>
<td>Population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achene type</td>
<td>1</td>
<td>10.00</td>
<td>45</td>
<td>7.793</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Achene type x population</td>
<td>1</td>
<td>1.694</td>
<td>44</td>
<td>6.094</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>

**Table 3.** Analysis of deviance for the effect of achene type and population in the germination percentages of achenes sowed after six months, and after more than one year of dry storage. ns = not significant.
gradually during the winter, and flowering and dispersal takes place in late winter or early spring. Mid–late spring rains are frequent and abundant in the areas studied (Rivas-Martinez 1987), and therefore, the achenes can germinate in spring, increasing the probability of seedling death in hot late spring and summer. The dormancy of freshly matured achenes of all three Scorzonerooides taxa leads to transient seed banks during spring and summer (see Thompson & Grime 1979). Thus, the achenes gradually become active, allowing most to germinate in the autumn, when soil moisture conditions become favourable to the seedlings (Lavorel et al. 1993).

The germination behaviour of 6-month central and peripheral achenes was different in the three Scorzonerooides species. Central achenes of S. palisiae and S. salzmannii displayed lower dormancy levels than did peripheral achenes, whereas central achenes of S. muelleri displayed higher dormancy levels in central achenes, which where therefore similar to peripheral. Thus, the expected difference in dormancy between the two achen e types used as an adaptation strategy in

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**Fig. 2.** Germination percentages of central and peripheral achenes of the different populations of Scorzonerooides palisiae and S. muelleri after six month of dry storage (A, B), and after more than one year of dry storage (C, D). Means + 95%CIs are shown.
arid habitats (Venable & Lawlor 1980, Venable & Brown 1988) was found only in the two species found in Mediterranean climates. The populations of *S. muelleri* were in areas with the highest annual aridity index found in this study (see Table 1). Under these harsh conditions, germination becomes a decisive event, since germination in non-optimal periods has drastic consequences for the later vegetative phase (Beatley 1974, Guttner & Evenary 1999). Thus, the increase in dormancy found in the central achenes of *S. muelleri* could be a strategy to adjust their dormancy to semi-arid conditions (Adondakis & Venable 2000). This is because delayed germination increases the likelihood that some seedlings will survive when any unfavourable environmental events occur (Pake & Venable 1996, Clauss & Venable 2000).

The different populations of *S. palisiae* and *S. muelleri* analyzed showed a homogeneous germination pattern between central and peripheral 6-month achenes, but a different germination pattern in 1-year achenes. The variation among the populations can be explained by the different germination behaviour of the two achene types that were more than a year old, or simply by the different time needed to lose their dormancy (Baskin & Baskin 1998). To the best of our knowledge, our study is the first to analyze the germination patterns of two achene types in populations after different storage times from dispersal. Our data suggests that studies of germination behaviour of heteromorphic species should be investigated in more than one population to define any patterns.

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