

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

Gema Cruz-Mazo, Eduardo Narbona* & M. Luisa Buide

Área de Botánica, Dpto. Biología Molecular e Ingeniería Bioquímica, Universidad Pablo de Olavide, Ctra de Utrera, Km 1, E-41013 Sevilla, Spain (*corresponding author's e-mail: enarfer@upo.es)

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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-

phism is 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).

Dimorphic germination behaviour is found in some heterocarpic Asteraceae species (Venable & Levin 1985a, Tanowitz *et al.* 1987, Beneke *et al.* 1993, Larson & Kiemnec 1997, Chmielewski 1999, El-Keblawy 2003, Ruiz de Clavijo 2005, Brändel 2007). However, in other species, achenes do not show differences in germination behaviour (Schütz & Milberg 1997, Imbert 1999, 2002). Furthermore, intraspecific variation in the dimorphic pattern of germination has been found (Rocha 1996, Brändel 2004).

In this paper, three closely related taxa of the genus *Scorzonerooides* (formerly known as *Leontodon* subg. *Oporinia*, Asteraceae), were chosen to compare differences in the degree of heterocarpy between annual species growing in different types of unpredictable habitats. *Scorzonerooides* comprises 29 taxa occurring in the Euro-Mediterranean area (Greuter *et al.* 2006). Based on their nrDNA and cpDNA sequences, *S. palisiae*, *S. salzmännii*, 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 heterocarpy and disturbed habitats, i.e., unpredictable, and the association between heterocarpy and an annual life cycle. Nevertheless, *S. palisiae* and *S. salzmännii* are found in Mediterranean environments, whereas the studied populations of *S. muelleri* are found in semi-arid 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 *Scorzonerooides* 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

Scorzonerooides palisiae, *S. salzmännii* 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). *Scorzonerooides palisiae* plants bear around 45 achenes per capitula, whereas *S. salzmännii* and *S. muelleri* bear around 58 and 73 achenes per capitula, respectively.

Scorzonerooides palisiae and *S. salzmännii* grow in open fields, pine and oak woodlands, or agricultural lands borders at altitudes of up to 350 m (Talavera 1987, Izuzquiza 1991). *Scorzonerooides palisiae* is endemic in SW of Iberian Peninsula and N Morocco and *S. salzmännii* is endemic in N Morocco, although they do not co-occur (Finch & Sell 1976, Izuzquiza 1991, 1998). *Scorzonerooides 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 arranged randomly, and the arrangement was changed twice a week to maintain identical conditions. The dishes were

Table 1. Location and climatic characteristics of the studied populations of the three taxa of *Scorzoneroides*.

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

^a 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. salzmannii*), 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. salzmannii*) 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. salzmannii*, 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 *Scorzonerooides* 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. salzmannii* (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

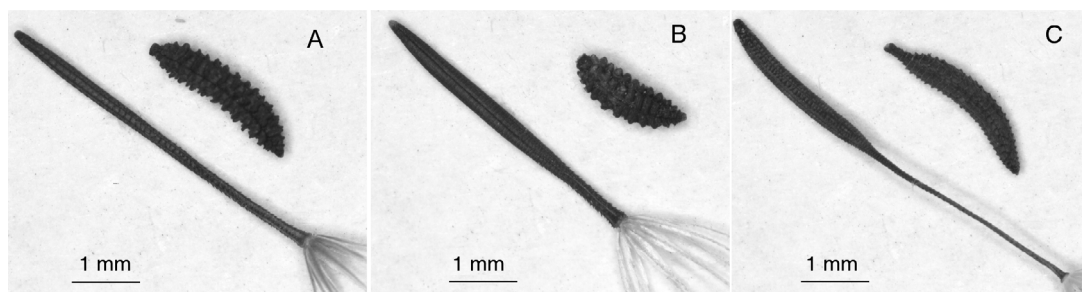


Fig. 1. Heteromorphic achenes of (A) *Scorzoneroideis palisiae*, (B) *S. salzmannii*, and (C) *S. muelleri*. For each taxon, central achenes are represented on the left, and peripheral on the right.

of the 6-month central and peripheral achenes of *S. palisiae* were $73\% \pm 5.0\%$ and $28\% \pm 3.5\%$, 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 \times 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 ($66\% \pm 2.0\%$ and $21\% \pm 3.8\%$, respectively, Table 3). The germination of the central 6-month achenes of *S. muelleri* was $51\% \pm 5.4\%$, and this was not significantly different from that of the peripheral achenes ($37\% \pm 3.9\%$, Table 3). Again, the mean germination percentage of the populations and the interaction between the achene type \times 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 ($92\% \pm 1.3\%$ and $90\% \pm 1.8\%$, 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 percent-

ages than the peripheral achenes ($76\% \pm 4.1\%$ and $63\% \pm 1.3\%$, 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 ($94\% \pm 1.0\%$ and $83\% \pm 2.8\%$, respectively, Table 3). In this species, the mean germination percentages of the populations were statistically different, but the significant interaction between achene type \times 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

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

Table 2. Mean weight \pm SE (mg) of 10 groups of 20 achenes of the three taxa of *Scorzoneroideis*.

Achene type	<i>S. palisiae</i>	<i>S. salzmannii</i>	<i>S. muelleri</i>
Central	7.9 ± 0.12	5.9 ± 0.11	4.9 ± 0.14
Peripheral	8.1 ± 0.11	$4.7 \pm 0.04^{***}$	5.0 ± 0.24

*** = significant differences at $p < 0.001$, Mann-Whitney test.

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.

Source of variation	df	Six-months achenes				More than one year achenes			
		Deviance	Residual df	Residual dev.	p	Deviance	Residual df	Residual dev.	p
<i>S. palisiæ</i>									
Population	1	0.39	30	361.95	ns	0.256	46	8.188	ns
Achene type	1	220.82	29	141.13	<0.0001	0.395	45	7.793	ns
Achene type × population	1	0.11	28	141.02	ns	1.699	44	6.094	<0.001
<i>S. salzmannii</i>									
Achene type	1	69.44	6	6.63	<0.0001	2.876	6	1.694	<0.01
<i>S. muelleri</i>									
Population	1	10.29	38	354.34	ns	0.278	54	55.857	ns
Achene type	1	34.05	37	320.29	ns	10.060	53	45.797	<0.01
Achene type × population	1	10.09	36	310.20	ns	0.011	52	45.786	ns

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 involucre 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. palisiæ* 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 compositae 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

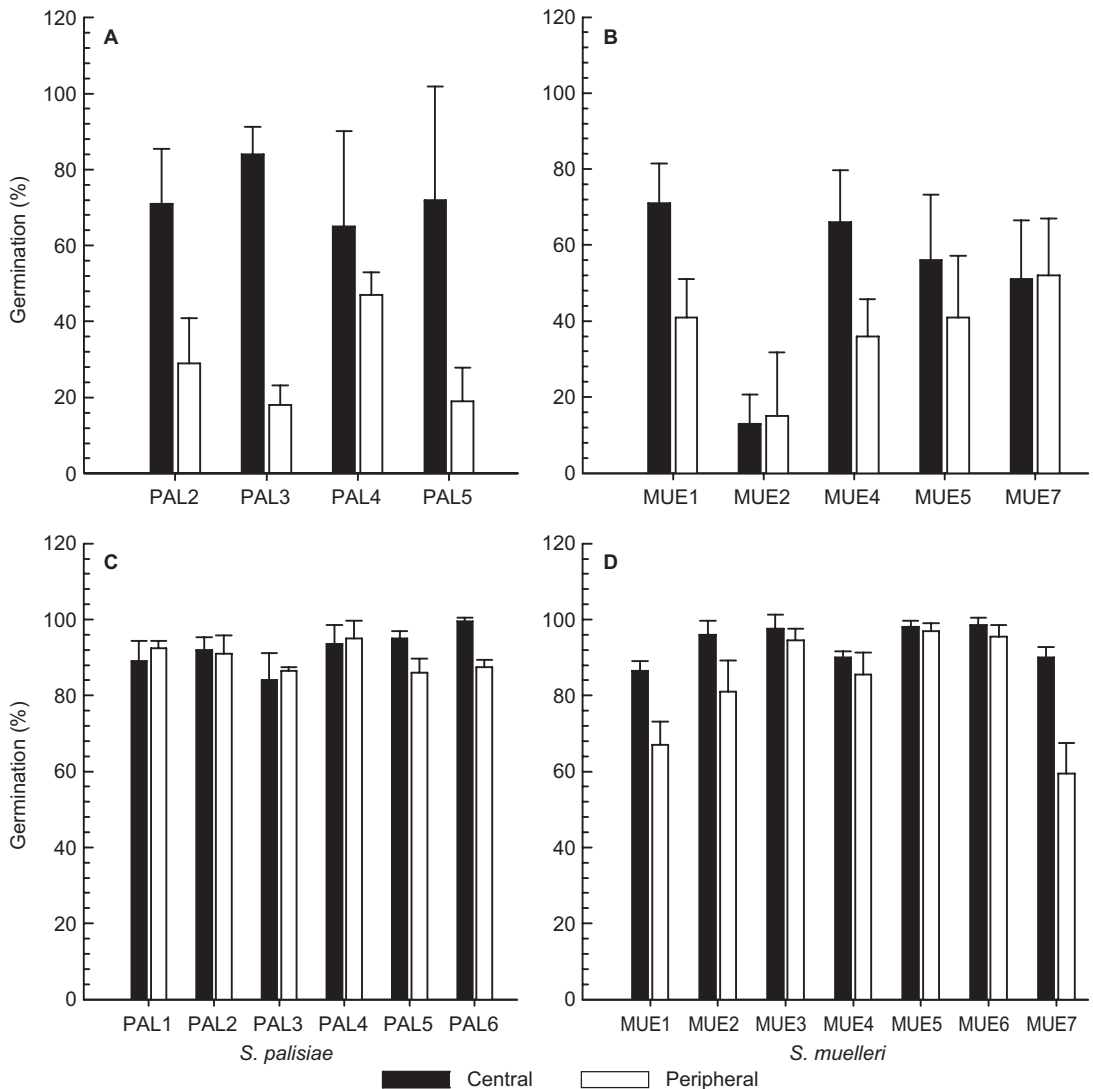


Fig. 2. Germination percentages of central and peripheral achenes of the different populations of *Scorzoneroideis palisiae* and *S. muelleri* after six month of dry storage (**A**, **B**), and after more than one year of dry storage (**C**, **D**). Means + 95% CIs are shown.

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 *Scorzoneroideis* 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 *Scorzoneroideis* 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 were therefore similar to peripheral. Thus, the expected difference in dormancy between the two achene types used as an adaptation strategy in

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, Gutterman & Evenary 1994). 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, Claus & 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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References

Adondakis, S. & Venable, D. L. 2004: Dormancy and germination in a guild of Sonoran desert annuals. — *Ecology* 85: 2582–2590.

- Arroyo, M. T. K., Chacon, P. & Caviares, L. A. 2006: Relationship between seed bank expresión, adult longevity and aridity in species of *Chaetanthera* (Asteraceae) in central Chile. — *Annals of Botany* 98: 591–600.
- Baskin, C. C. & Baskin, J. M. 1998: *Seeds: ecology, biogeography, and evolution of dormancy and germination*. — Academic Press, San Diego.
- Baskin, J. M. & Baskin, C. C. 1976: Germination dimorphism in *Heterotheca subaxillaris* var. *subaxillaris*. — *Bulletin of the Torrey Botanical Club* 103: 201–206.
- Beatley, J. C. 1974: Phenological events and their environmental triggers in Mojave Desert ecosystem. — *Ecology* 55: 856–863.
- Beneke, K., Van Rooyen, M. W., Theron, G. K. & Van der Venter, H. A. 1993: Fruit polymorphism in ephemeral species of Namaqualand: III. Germination differences between the polymorphic diaspores. — *Journal of Arid Environments* 24: 333–334.
- Brändel, M. 2004: Dormancy and germination of heteromorphic achenes of *Bidens frondosa*. — *Flora* 199: 228–233.
- Brändel, M. 2007: Ecology of achene dimorphism in *Leontodon saxatilis*. — *Annals of Botany* 100: 1189–1197.
- Chmielewski, J. G. 1999: Consequences of achene biomass, within-achene allocation patterns, and pappus on germination in ray and disc achenes of *Aster umbellatus* var. *umbellatus* (Asteraceae). — *Canadian Journal of Botany* 77: 426–433.
- Claus, M. J. & Venable, D. L. 2000: Seed germination in desert annuals: and empirical test of adaptive bet hedging. — *The American Naturalist* 155: 168–186.
- Crawley, M. J. 2005: *Statistics. An introduction using R*. — John Wiley & Sons, Chichester.
- El-Keblawy, A. 2003: Effects of achene dimorphism on dormancy and progeny traits in two ephemerals *Hedypnois cretica* and *Crepis aspera* (Asteraceae). — *Canadian Journal of Botany* 81: 550–559.
- Ellner, S. 1986: Germination dimorphism and parent-offspring conflict in seed germination. — *Journal of Theoretical Biology* 123: 173–185.
- Finch, R. A. & Sell, P. D. 1976: *Leontodon*. — In: Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds.), *Flora Europaea*, vol. IV: 310–315. Cambridge University Press, Cambridge.
- Forsyth, C. & Brown, N. A. C. 1982: Germination of the dimorphic fruits of *Bidens pilosa* L. — *New Phytologist* 90: 151–164.
- García, L. V. 2004: Escaping the Bonferroni iron claw in ecological studies. — *Oikos* 105: 657–663.
- Grabe, D. F. 1970: *Tetrazolium testing handbook for agricultural seeds*. — Contribution No. 29 to the Handbook on Seed Testing, Association of Official Seed Analysts, North Brunswick.
- Greuter, W., Gutermann, W. & Talavera, S. 2006: A preliminary conspectus of *Scorzoneroides* (Compositae, Cichorieae) with validation of the required new names. — *Willdenowia* 36: 689–692.
- Gutterman, Y. & Evenari, M. 1994: The influences of amounts and distribution of irrigation during the hot and

- dry season on emergence and survival of some desert winter annuals plants in the Negev Desert. — *Israel Journal of Plant Sciences* 42: 1–14.
- Harper, J. L. 1977: *Population biology of plants*. — Academic Press, New York.
- Imbert, E. 1999: The effects of achene dimorphism on the dispersal in time and space in *Crepis sancta* (Asteraceae). — *Canadian Journal of Botany* 77: 508–513.
- Imbert, E. 2002: Ecological consequences and ontogeny of seed heteromorphism. — *Perspectives in Plant Ecology, Evolution and Systematics* 5: 13–36.
- Izuzquiza, A. 1991: A new species and two new combinations of *Leontodon* (Asteraceae, Hypochoeridinae). — *Nordic Journal of Botany* 11: 33–40.
- Izuzquiza, A. 1998: Algo acerca de la distribución de *Leontodon palisiae* Izuzquiza en Marruecos y algunas consideraciones sobre *L. salzmännii* (Schultz-Bip) Ball. — *Lagascalia* 20: 333–335.
- Larson, L. & Kiemnec, G. 1997: Differential germination by dimorphic achenes of yellow starthistle (*Centaurea solstitialis* L.) under water stress. — *Journal of Arid Environments* 37: 107–114.
- Lavorel, S., Debussche, M., Lebreton, J. D. & Lepart, J. 1993: Seasonal patterns in the seed bank of Mediterranean old-fields. — *Oikos* 67: 114–128.
- McEvoy, P. B. 1984: Dormancy and dispersal in dimorphic achenes of tansy ragwort *Senecio jacobaea*. — *Oecologia* 61: 160–168.
- McEvoy, P. B. & Cox, C. S. 1987: Wind dispersal distance in dimorphic achenes of ragwort, *Senecio jacobaea*. — *Ecology* 68: 2006–2015.
- Pake, C. E. & Venable, D. L. 1996: Seed banks in desert annuals: implications for persistence and coexistence in variable environments. — *Ecology* 77: 1427–1435.
- Philippi, T. 1993: Bet-hedging germination of desert annuals: beyond the first year. — *The American Naturalist* 142: 474–487.
- Plitmann, U. 1986: Alternative modes in dispersal strategies with an emphasis on herbaceous plants of the Middle East. — *Proceedings of the Royal Society of Edinburgh* 89: 193–202.
- R Development Core Team 2007: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna.
- Rivas-Martínez, S. 1987: *Memoria del mapa de series de vegetación de España*. — Instituto para la Conservación de la Naturaleza, Madrid.
- Rivas-Martínez, S., Penas, A. & Diaz, T. E. 2004: *Bioclimatic map of Europe: Bioclimates*. — Cartographic Service, University of León, León.
- Rocha, O. J. 1996: The effects of achene heteromorphism on the dispersal capacity of *Bidens pilosa* L. — *Israel Journal of Plant Sciences* 157: 316–322.
- Ruiz de Clavijo, E. 2001: The role of dimorphic achenes in the biology of the annual weed *Leontodon longirrostris*. — *Weed Research* 41: 275–286.
- Ruiz de Clavijo, E. 2005: The reproductive strategies of the heterocarpic annual *Calendula arvensis* (Asteraceae). — *Acta Oecologica* 28: 119–126.
- Samuel, R., Gutermann, W., Stuessy, T. D., Ruas, F. C. F., Lack, H. W., Tremetsberger, K., Talavera, S., Hermanowski, B. & Ehrendorfer, F. 2006: Molecular phylogenetics reveals *Leontodon* (Asteraceae, Lactuceae) to be diphyletic. — *American Journal of Botany* 93: 1193–1205.
- Schütz, W. & Milberg, P. 1997: Seed germination in *Lau-naea arborescens*: a continuously flowering semi-desert shrub. — *Journal of Arid Environments* 36: 113–122.
- Sheldon, J. C. & Burrows, F. M. 1973: The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. — *New Phytologist* 72: 665–675.
- Talavera, S. 1987: *Leontodon* L. — In: Valdés, B., Talavera, S. & Fernández-Galiano, E. (eds.), *Flora Vascular de Andalucía Occidental*, vol. III: 99–102. Ketres Editora, Seville.
- Tanowitz, B. D., Salopek, P. F. & Mahall, B. E. 1987: Differential germination of ray and disc achenes in *Hemizonia increscens* (Asteraceae). — *American Journal of Botany* 74: 303–312.
- Thompson, K. & Grime, J. P. 1979: Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. — *Journal of Ecology* 67: 893–921.
- Venable, D. L. 1985: The evolutionary ecology of seed heteromorphism. — *American Naturalist* 126: 577–595.
- Venable, D. L. & Brown, J. S. 1988: The selective interactions of dispersal dormancy and seed size as adaptations for reducing risk in variable environments. — *The American Naturalist* 131: 360–384.
- Venable, D. L. & Lawlor, L. 1980: Delayed germination and dispersal in desert annuals, escape in space and time. — *Oecologia* 46: 272–282.
- Venable, D. L. & Levin, D. A. 1985a: Ecology of achene dimorphism in *Heterotheca latifolia*. II. Demographic variation within populations. — *Journal of Ecology* 73: 743–755.
- Venable, D. L. & Levin, D. A. 1985b: Ecology of achene dimorphism in *Heterotheca latifolia*. I. Achene structure, germination and dispersal. — *Journal of Ecology* 73: 133–145.
- Venable, D. L., Dyreson, E. & Morales, E. 1995: Population dynamic consequences and evolution of seed traits of *Heterosperma pinnatum* (Asteraceae). — *American Journal of Botany* 82: 410–420.
- Zar, J. H. 1999: *Biostatistical analysis*. — Prentice-Hall, New York.
- Zohary, M. 1950: Evolutionary trends in the fruiting head of Compositae. — *Evolution* 4: 103–109.