Survival, germinability and fungal colonization of dimorphic achenes of the annual weed *Galinsoga parviflora* buried in the soil

F J ESPINOSA-GARCÍA, R VÁZQUEZ-BRAVO & M MARTÍNEZ-RAMOS
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Xangari, Morelia, Michoacán, México

Received 4 February 2003
Revised version accepted 14 April 2003

Summary

Galinsoga parviflora (Asteraceae) is a widespread annual weed that produces capitula containing both disc achenes with pappus and ray achenes without pappus. The latter are dispersed within a winged structure formed by capitulum bracts. We buried both achene types in an agricultural soil to be exhumed regularly to investigate whether they differed in survival, germinability and fungal colonization in the soil seedbank. Ray achenes remained viable longer than disc achenes, with different loss rates for the achene types. In both cases, loss rate was very high for the first 10 months, and then loss rates for the achene types tended to level off and even converge by the end of the observation period. The percentage of remaining viable disc achenes was always *c*. 10–15% lower than that of the ray achenes, except on the first and last sampling dates. Germination percentages for viable ray and disc achenes before burial and after exhumation were not statistically different during most of the observation period, except for that between 100 and 200 days of burial (mid-autumn–winter). There, germination of disc achenes reached 26.4% after 126 days of burial, whereas germination of ray achenes was close to zero. In addition, after 779 days, the germinability of ray achenes was 21.3%, whereas it was 0% for disc achenes. Surface-disinfected viable disc and ray achenes had low infection rates (0–15%) for both fungi and bacteria during the observation period. The fungal and bacterial infection peaks for both achene types were asynchronous. In general, the expected difference (lower infection rate for ray achenes) was not observed for fungal or bacterial infection.

Keywords: *Alternaria alternata*, fungal colonization, achenes, *Fusarium oxysporum*, *Galinsoga parviflora*, heteromorphic, seed, germination.

Introduction

Galinsoga parviflora Cav. (Gallant soldier) (Asteraceae) is an annual species that is considered a very serious major weed in more than 20 countries (Holm *et al*., 1979). It is a strong competitor with a number of crops and *G. parviflora* harbours crop pests and pathogens (Lordello *et al*., 1988; Mertelik & Mokra, 1998). It is also invasive, colonizing new ground where it is able to persist. One characteristic that enables *G. parviflora* persistence is the ability of the achenes to remain viable within the soil. The formation of a persistent seedbank has been inferred from studies of seedling emergence patterns (Martínez-Ghersa *et al*., 2000). However, there are no studies of *G. parviflora* seed longevity within the soil and the behaviour of its dimorphic achenes has not been documented in such environment. This knowledge would be important in the management of this cosmopolitan weed.

A number of weeds produce dimorphic sexual propagules that have different patterns of dispersal, dormancy and germination (Becker, 1912, cited in Salisbury, 1942; Forsyth & Brown, 1982; Corkidi *et al*., 1991; Joley *et al*., 1997; De Clavijo, 2001; and reviews by Mandák, 1997; Koyama, 1998). However, the behaviour of dimorphic sexual propagules in the soil seedbank has seldom been explored. Dimorphic achenes of *Heterotheca latifolia* Buckley differed greatly in their survival and behaviour in the soil; *c*. 55% of the shallowly buried disc achenes germinated after 40 days, whereas *c*. 20% of the

Correspondence: F J Espinosa-García, Centro de Investigaciones en Ecosistemas, UNAM, A.P. 27-3, Xangari, 58089, Morelia, Michoacán, México. Tel: (+52)-5-5623-2721; Fax: (+52)-5-5623-2719; E-mail: espinosa@oikos.unam.mx

ray achenes germinated under the same conditions (Venable & Levin, 1985). Less than 5% of the ray achenes buried at 1-cm depth germinated after 80 days of sowing, suggesting that *H. latifolia* forms a permanent seedbank at least with ray achenes. In contrast, multimorphic achenes of *Heterosperma pinnatum* Cav. do not form a permanent seedbank, and the depletion rate for the various achene types in the soil was quite comparable (Venable *et al.*, 1987). These studies, however, considered periods of 1 year or shorter, and they did not explore the sources of seed mortality within the soil.

Microorganisms have frequently been found within weed seeds either as seed-borne pathogens or apparently innocuous colonizers (Kremer, 1993; Espinosa & Vázquez, 1994). Although there is presumptive evidence of fungi as seedbank depletion agents (Kremer, 1993), there are no studies showing the possible importance of fungi as mortality agents in the seedbank dynamics of species with heteromorphic propagules. A differential susceptibility to soil microorganisms among morphs could be hypothesized because of the presumed differences in permanence within the soil among heteromorphic propagules.

The aim of this study was to quantify the longevity and germinability of the dimorphic achenes of *G. parviflora* within the soil and explore the role of soil fungi that colonize those achenes.

To determine whether differences in survival existed between these types of achenes, we buried achenes in a field of lucerne and recovered them periodically over 839 days. In addition, we performed germination tests to determine whether the viable achenes were ready to germinate once that they had been exhumed. We also determined susceptibility to soil fungi colonization for both achene types, because fungi are a cause of mortality of seeds in soil (Kremer, 1993; Baskin & Baskin, 1998). Thus, differences between achene types in their ability to survive in the soil might be correlated with susceptibility to fungi.

Materials and methods

Study species

Galinsoga parviflora is predominantly an agricultural weed in central Mexico, where it supposed to have originated (Canne, 1977). It produces capitula with both ray achenes, without a pappus, or, less frequently with a rudimentary pappus formed by four to six readily falling, short-barbed bristles half as long as the scales from disc achenes (Salisbury, 1942; Espinosa & Sarukhán, 1997; Rzedowski & Rzedowski, 2001), and disc achenes with a pappus formed by a crown of scales (Fig. 1). Capitula have three to eight ray flowers and 15–50 disc ones in the Valley of México (Espinosa & Sarukhán, 1997; Rzedowski & Rzedowski, 2001). Thus, around 15–20% of the achenes come from ray flowers. Although ray achenes have no pappus or only a rudimentary one, they are dispersed within a winged structure formed by capitulum bracts (Espinosa & Sarukhán, 1997). Ray achenes are slightly larger than disc achenes (2.0 mm vs. 1.7 mm). Achenes have no dormancy when they are produced in autumn but they require light to germinate (Van Rooden *et al.*, 1970; Baskin & Baskin, 1981, 1998). Achenes germinate well over a range of temperatures 10–35°C (Mes, 1954, cited in Andersen, 1968). Ray achenes have higher germination percentages and rates than those from the disc achenes (Rai & Tripathi, 1987). The achene dimorphism and their differential behaviour in germination could suggest that both achene types have different behaviour in the seedbank.

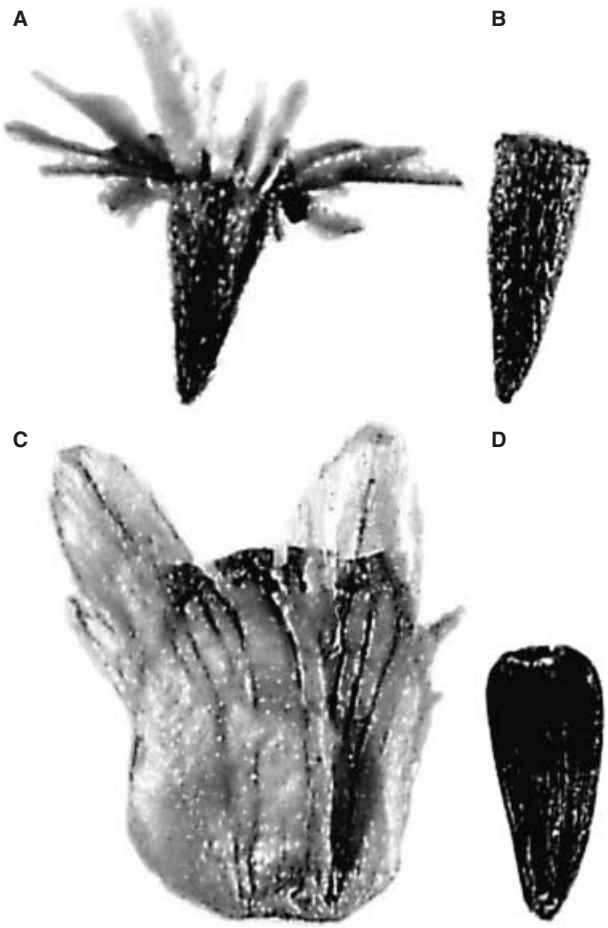

Fig. 1 Disc achenes of *Galinsoga parviflora* with intact pappus (A) and with the pappus removed (average length: 1.7 mm; average weight: 0.26 mg) (B). Ray achenes covered by capitulum bracts (C) and without cover (average length: 2.0 mm; average weight: 0.23 mg) (D).

Experimental procedures

Galinsoga parviflora achenes were collected in November 1991 at the Instituto de Investigaciones Agrícolas, Forestales y Pecuarias (INIFAP) Research Station Rancho Santa Lucía, in Texcoco, Estado de México, 19°17′N latitude and 98°53′W longitude. They were then dried, sorted into disc and ray achenes and put in 5 cm × 5 cm organza (fine mesh cloth) bags. Each bag with ray achenes contained 56 mg (243 ± 11 SD achenes); each bag with disc achenes contained 62 mg of them (239 ± 18 SD achenes). We prepared 100 bags of each achene type that were closed by sewing and joined in pairs (disc–ray achenes) with a 20-cm nylon string to facilitate recovery from the soil.

The Rancho Santa Lucía used to be a dairy ranch, with most of its land dedicated to growing lucerne (*Medicago sativa* L.), maize (*Zea mays* L.) and other forage crops. Currently, it is an agricultural research station. The soil is a sandy clay loam with 2.5% organic matter. The climate is subhumid temperate with rain from summer to autumn, according to the Köppen climatic classification (García, 1968). The rainy season starts in early June and ends in mid-October or early November. The experiment was carried out within a 50 m × 100 m plot near the centre of a lucerne field cultivated in rows for seed production. Nomenclature for *G. parviflora* follows Rzedowski and Rzedowski (2001).

On 22 July 1992, paired bags of achenes were buried 10 cm deep between the lucerne rows separated from other pairs by 5 m starting from one extreme of the plot. The germination peak for *G. parviflora* in field conditions occurs 1 or 2 weeks after the beginning of the rainy season. At each sampling date over 863 days (28.7 months), five randomly chosen bag pairs were exhumed. Exhumed bags were allowed to dry at room temperature before they were processed. We considered firm achenes as viable because the soft ones usually were empty or decayed, presumably by microbes (Bouwmeester & Karssen, 1993). Firm achenes were counted and separated into two groups, one to estimate germinability and the other to obtain mycobiota. Survival was estimated by counting all remaining firm achenes at each sampling date for the whole period. However, we were only able to perform germinability and mycobiota assays for 12 sampling dates over the first 458 days of burial and two later dates, those for 779 and 839 days. The achene drying, sorting and counting exposed the seeds to daylight at least 15 days before they were sown in Petri dishes under fluorescent light mixed with daylight. This exposure was enough to fulfil the *G. parviflora* achenes light requirements, because for this species light after ripening or storage is required for germination (Mes, 1956, cited in Andersen, 1968; Baskin & Baskin, 1981). Achenes were germinated in water-agar (1% wt/*V*) in an incubator at 25°C for 7 days. Mycobiota was obtained by disinfection of the achene surface with 3% sodium hypochlorite for 1 min, rinsing with sterile water and plating the achenes on malt-agar followed by incubation at 25°C for 7 days. This procedure eliminated all the soil organisms from the achene surface that did not colonize the seed. We considered that the only fungi capable of reducing seed survival in the soil were those able to penetrate the seedcoat (Baskin & Baskin, 1998).

Germination and mycobiota assays were performed in Petri dishes, each one with 25 (sometimes 20) firm achenes from each exhumed bag. We used five bags to obtain 125 achenes, when possible, that were distributed in five Petri dishes. Fungi were isolated and identified using standard mycological techniques (CMI, 1968) and specialized literature (Booth, 1971; Ellis, 1971; Barnett & Hunter, 1972). The achenes producing bacterial colonies were counted but we made no attempt to identify bacteria to the genus or species level.

Statistical analysis

We used analysis of deviance (ANDEVA) to test isolated and interactive effects of time and achene type on soil seed survivorship. In this analysis we used a logistic model of the type $Y = e^{(A + bT + cT^2 + dt \cdot AT + fT^2 \cdot AT)} / [1 + e^{(A + bT + cT^2 + dT \cdot AT + fT^2 \cdot AT)}]$, where Y is the proportion of achenes remaining in the soil, A is the Y-intercept (both achene types have the same intercept at $Y = 1.0$ at time 0), b is main slope, c is a quadratic term that defines the shape of the curve, and d and f are the terms defining the interaction between time (T) and achene type (AT). When c is negative, the shape of the curve is convex, and when c is positive the curve is concave; if $c = 0$ the curve is a straight line. A binomial error was assigned to the dependent variable and a logit-link function was used to linearize the model (Crawley, 1993). ANDEVA was performed using the statistical package GLIM 3.77 (Royal Statistical Society, 1985). Overdispersion was corrected by dividing the deviance values by a scale factor as indicated by Crawley (1993). Comparisons between germinability of achene types after different periods of burial were carried out using the Yate's corrected chi-square test (Sokal & Rohlf, 1979).

Results

Achene survival in the soil

At each sampling date the proportion of viable ray achenes was always higher than that of the disc achenes

(Fig. 2). Both curves describing achene loss through time were concave, indicated by a significantly positive quadratic term (Fig. 2, Table 1). The main and quadratic loss rates for disc achenes were different from those for ray achenes, as indicated by the significant interaction between time and achene type (Table 1). In both cases, the loss was very great during the first 10 months, and then it tended to level off and even converge for both achene types by the end of the observation period. For most sampling dates the difference between the achene types was *c*. 10–15%, with fewer disc achenes remaining firm, except at the first and last sampling dates (Fig. 2).

Germinability of viable achenes after different periods of burial

Percentage germination before burial and after 22 and 33 days of burial was higher for ray achenes, although the differences were not statistically significant ($\chi^2 = 1.18$, $P = 0.28$; $\chi^2 = 0.65$, $P = 0.42$; $\chi^2 = 0.43$, $P = 0.51$, respectively), and then it decreased to near zero for both achene types (Fig. 3). Later on, ray achenes germinability remained close to zero. However, germination of the disc achenes started to increase and reached a peak of 26.4% after 126 days of burial ($\chi^2 = 20.44$, $P < 0.00001$). Afterwards, germination decreased again to close to zero from 253 to 458 days of burial (Fig. 3). The germination peak for disc achenes started in mid-autumn, at the end of the rainy season, and finished in winter. We were not able to perform germination trials for the period between 459 and 778 days. However, after 779 days, by the end of summer, the germinability of ray achenes was 21.3% whereas the disc achenes did not germinate ($\chi^2 = 19.04$, $P < 0.00001$); both types of achenes converged at *c*. 50% in their germinability after 839 days of burial.

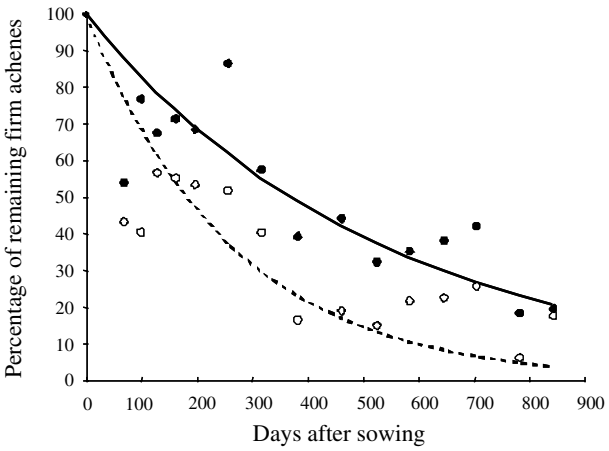

Fig. 2 Remaining firm achenes of *Galinsoga parviflora* after different periods of burial. Solid circles: ray achenes; continuous line: predicted logistic model for ray achenes with Y-intercept = 1.0, $b = -0.0008$, $c = 0.000006$. Open circles: disc achenes; broken line: predicted logistic model with Y-intercept = 1.0, $b = -0.0139T$, $c = 0.000003$ (see 'Materials and methods' for details of the models).

Table 1 Results of the analysis of deviance performed to individual and interactive effects of time (T, linear term; T^2, quadratic term) and achene type (AT) on survival of *Galinsoga parviflora* seeds in soil. Total deviance (R^2) explained by the model was 85%*

Factor	Deviance (approx. χ^2)	d.f.	R^2	P
T	119.1	1	0.68	<0.001
T^2	13.5	1	0.08	<0.001
$T \times AT$	10.0	1	0.06	<0.005
$T^2 \times AT$	5.2	1	0.03	<0.025
Residual	27.0	23		
Total	174.9	27		

*Probability distribution is binomial, with a logit-link function and a 74.43 scale parameter.

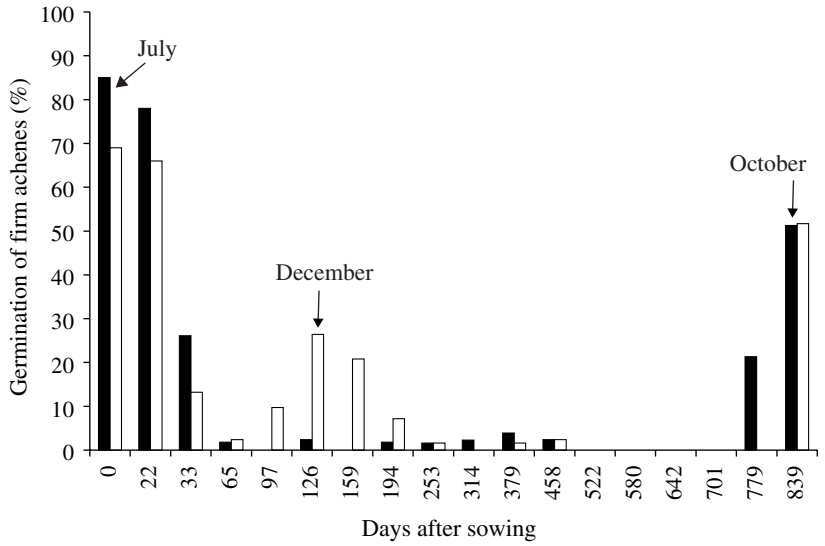

Fig. 3 Germination percentage of *Galinsoga parviflora* firm achenes retrieved from the soil after different periods of burial. Solid bars represent ray achenes and those empty, disc achenes. Statistical comparisons are given in the text.

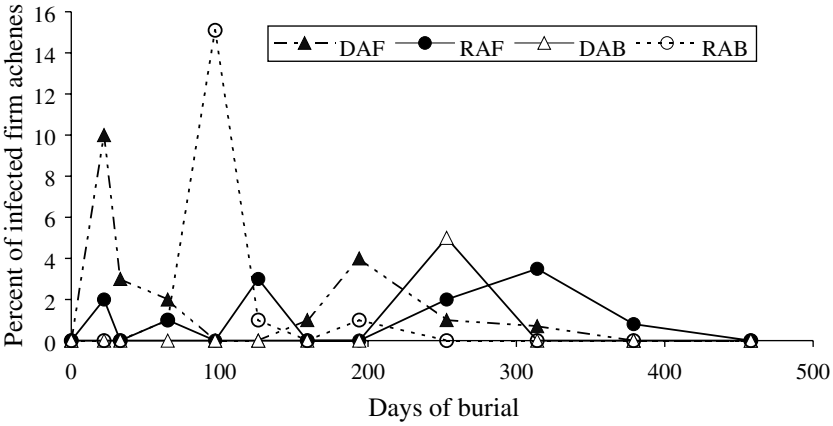

Fig. 4 Percentage of infected *Galinsoga parviflora* firm achenes retrieved from the soil after different periods of burial. Calculations were based on the number of firm achenes infected of the total firm achenes recovered from burial. DAF, disc achenes infected by fungi; RAF, ray achenes infected by fungi; DAB, disc achenes infected by bacteria; RAB, ray achenes infected by bacteria.

Infection percentage for exhumed viable achenes

Both achene types showed low infection percentages for both fungi and bacteria throughout the observation period. Disc achenes had 10% infection by fungi compared with 2% for ray achenes in the first sampling date, although this difference was not statistically significant ($\chi^2 = 3.05$, $P = 0.08$). Afterwards, the fungal infection peaks for both achene types were asynchronous (Fig. 4). Bacterial infection was 15% in the ray achenes exhumed after 3 months of burial compared with no infection for disc achenes for the same period ($\chi^2 = 24.98$, $P < 0.0001$) (Fig. 4). Bacterial infection for ray achenes decreased to zero after this peak and remained practically the same during the whole observation period. The disc achenes had no bacterial infection for the whole period, except for a 4% infection peak at 250 days (NS). Thus, the expected difference (lower infection rate for ray achenes) was not observed for fungal or bacterial infection. The fungi isolated from the surface-disinfected achenes were *Alternaria alternata* (Fr.) Keissler and *Fusarium oxysporum* Schlecht.

Discussion

This study confirms the Martínez-Ghersa *et al.* (2000) inference that *G. parviflora* forms a permanent seedbank. It also shows that its achenes can remain viable within the soil for more than 2 years. We also found that the achene morphs differ in their longevity and loss rate from the seedbank. These traits may help to explain the persistence of this species in all the places in the world that it has invaded.

The higher survival in the seedbank of ray achenes agrees with a hypothesis that has been used to understand dimorphisms in sexual propagules. Risk-spreading has been frequently used to explain the behaviour of heteromorphic seeds (Mandák, 1997; Koyama, 1998). Within the risk-spreading explanations, the high risk–low risk (HRLR) hypothesis has been proposed to explain dimorphism in sexual propagules (Venable, 1985). One particular expectation under the HRLR hypothesis is that the low risk (LR) morph has higher permanence within the soil than the high risk (HR) morph because the latter germinates readily. The pattern found with *G. parviflora* agrees with this expectation, although the differences in loss rate in soil was not as high as that obtained for *H. latifolia* (Venable & Levin, 1985). These authors used both types of viable achenes, and after 40 days of shallow burial, about 45% of the disc achenes compared with 75% of ray achenes did not germinate. This difference is twice as much as that found for *G. parviflora* achenes during the whole burial period. In the case of *H. latifolia*, achene types differ greatly in morphology, particularly in the pericarp, whereas for *G. parviflora*, ray and disc achenes are very similar in weight, length and morphology, the pappus being the main difference (Fig. 1). It would be interesting to test whether the differential magnitude between achene morphs is correlated with the differences in achene type behaviour in the seedbank. It would also be interesting to determine if the small differences between the morphs have been the result of selection in a predictable agricultural environment by comparing the behaviour of achenes of a *G. parviflora* population that grows in other environments. For example, selection of *Heterosperma pinnatum* at contrasting sites produced different patterns of achene morphology and behaviour (Venable *et al.*, 1987).

The germinability for both achene types was not statistically different during the first 72 days of burial. The expected pattern for an HRLR species was that ray achenes would have delayed germination, i.e. longer dispersal in time, whereas the disc achenes would have immediate or only a short period before germination (Corkidi *et al.*, 1991; Venable & Brown, 1993). The first 72 days of burial were at odds with that expectation, but later on, the behaviour of both achene types was

according to the expected pattern until the completion of 458 days of burial. However, the germinability peak observed for disc achenes was modest (26% of the supposedly viable achenes germinated), indicating that the majority of those remaining were dormant. For a weed of agriculture, such as *G. parviflora*, whose propagules are buried and brought to the surface by ploughing, this would mean that disc achenes also persist for almost as long as ray achenes. Neither did the germinability of both achene types in the two last sampling dates conform to the expectations for an HRLR species: after 779 days of burial, all firm disc achenes remained dormant whereas more than 20% of firm ray achenes germinated and then, after 839 days of burial, both achene types showed the same level of germination. The differences in survival in the soil and in germinability between the *G. parviflora* achenes may suggest that the fitness differences between the morphs are not as high as those found for HRLR species, at least for the period when the achenes remain within the soil. This suggestion should be viewed with caution because other studies with *G. parviflora* have shown that at low and medium nutrient levels, seedlings from ray achenes survive better than those from disc achenes, but the reverse is true in high nutrient levels (Rai & Tripathi, 1987). In addition, the same study shows that ray achenes have higher protein and energy content than that of disc achenes. These two findings agree with an HRLR pattern. We did not investigate the dispersal of both achene types and we are not aware of a published study on this subject. However, disc achenes are first dispersed from the capitula and, later on, ray achenes with their bracteal enclosure, when most ray achenes have been detached from the capitulum. Ray achenes require more shaking or wind blowing to become detached than for disc achenes (F. Espinosa-García, unpubl. obs.). This pattern would also agree with an HRLR syndrome if the differences in detaching time would result in different dispersal distances between achene types.

For both achene types our results suggest that the non-dormant character shown by unburied achenes (Van Rooden *et al.*, 1970; Baskin & Baskin, 1981, 1998) is lost once they are buried. This acquired dormancy lasted for variable periods and once it was broken, it apparently could be induced again. The germinability peak for disc achenes started in mid-autumn and concluded in midwinter. This would coincide with the winter cycle crop, and thus it is possible that most *G. parviflora* plants colonizing winter-irrigated crops would have originated from achenes with pappus. Unfortunately we do not have data to find out if the germinability peak started again the following autumn. If this were the case, disc achenes would have shown germinability cycles such as those found in other species (Baskin & Baskin, 1998). In contrast, ray achenes apparently do not show germinability cycles.

The low incidence of fungal and bacterial infection in the two types of achenes does not help to explain the differential achene survival or germinability. According to the optimal plant defence theory (Rhoades, 1985), we expected higher susceptibility to infection in disc achenes, because they were likely to remain for less time within the soil than ray achenes, which in turn, would be better defended and thus, less susceptible to the soil microbes and animals. We did not observe the expected difference, but rather minor and asynchronous infection peaks with cycles in the case of fungi. The species that colonized the achenes in the soil (both types were free of fungi before their burial), *Alternaria alternata* and *Fusarium oxysporum*, are common fungal soil phytopathogens and can be isolated from apparently uninfected mature weeds (Valarini & Spadotto, 1995) and various viable weed seed species (Kremer *et al.*, 1984; Espinosa & Vázquez, 1994). The infection cycles might have been due to differential susceptibility of individual achenes to these phytopathogens, where some achenes were killed, some became susceptible and perhaps others just carried fungi that behaved as endophytes within their tissues (Bose, 1956; Kremer *et al.*, 1984).

The *G. parviflora* achene types differ in their survival in the seedbank: viability of ray achenes in the soil lasts longer than disc achenes. In addition, the germinability patterns between achene types are different. However, this species does not display the typical HRLR syndrome found in other species with dimorphic propagules when the achene behaviour in the seedbank is considered, although the dispersion pattern, the survival of seedlings originating from disc and ray achenes (Rai & Tripathi, 1987) agree with the HRLR hypothesis. A possible explanation for the absence of the typical HRLR pattern for the achenes in the soil, could be that the aboveground behaviour of achenes and seedlings derived from them is not correlated with their underground behaviour, and that the HRLR hypothesis is more applicable to life cycle stages rather than to achenes in soil. Another possibility would be that agricultural selection on *G. parviflora* reduced the differences between morphs in the population studied here, and that in some other populations, selection results in different patterns from the one found here. Thus, our population would only represent one point along a spectrum of possibilities.

Acknowledgements

We wish to thank Yolanda García Rodríguez for her technical assistance and Heberto Ferreira for his com-

puter assistance. We are grateful for the observations made by Dr Alma Orozco and Dr Ken Thompson on an earlier version of this manuscript. This project was partially funded by the grant CONACYT-1172-N902.

References

Andersen RN (1968) *Germination and Establishment of Weeds for Experimental Purposes*, 77. W.F. Humprey Press, Geneva, NY, USA.

Barnett HL & Hunter BB (1972) *Illustrated Genera of Imperfect Fungi*, 3rd edn. Burgess Publishing Company, Minneapolis, MN, USA.

Baskin JM & Baskin CC (1981) Temperature relations of seed germination and ecological implications in *Galinsoga parviflora* and *G. quadriradiata*. *Bartonia* **48,** 12–18.

Baskin CC & Baskin JM (1998) *Seed Biology: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA, USA.

Booth C (1971) *The Genus* Fusarium. Commonwealth Mycological Institute, Kew, Surrey, UK.

Bose SR (1956) *Alternaria* within the pericarp of the wheat seed. *Nature* **178,** 640–641.

Bouwmeester HJ & Karssen CM (1993) Annual changes in dormancy and germination in seeds of *Sisymbrium officinale* (L) Scop. *New Phytologist* **124,** 179–191.

Canne JM (1977) A revision of the genus *Galinsoga* (Compositae: Heliantheae). *Rhodora* **79,** 319–389.

CMI (1968) *Plant Pathologist's Pocketbook*. Commonwealth Mycological Institute, Kew, UK.

Corkidi L, Rincón E & Vázquez-Yanes C (1991) Effects of light and temperature on germination of heteromorphic achenes of *Bidens odorata* (Asteraceae). *Canadian Journal of Botany* **69,** 574–579.

Crawley MJ (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford, UK.

De Clavijo ER (2001) The role of dimorphic achenes in the biology of the annual weed *Leontodon longirrostris*. *Weed Research* **41,** 275–286.

Ellis, MB (1971) *Dematiaceous Hyphomycetes*. CAB International, Wallingford, Oxon, UK.

Espinosa GFJ & Sarukhán J (1997) *Manual de Malezas del Valle de México*, 83–84. Universidad Nacional Autónoma de México y Fondo de Cultura Económica, México.

Espinosa GFJ & Vázquez BR (1994) Patrones de incidencia de hongos en semillas arvenses a través de 253 días de permanencia en un suelo agrícola. In: *Memorias del V Congreso Nacional de Micología*, Guanajuato, México, 27–30 November (ed. M Carvajal), 149. Sociedad Mexicana de Micología, México.

Forsyth C & Brown NAC (1982) Germination of the dimorphic fruits of *Bidens pilosa* L. *New Phytologist* **90,** 151–164.

García E (1968) Los climas del Valle de México. *Colegio de Postgraduados, Montecillo, México. Serie de Sobretiros* **6,** 1–34.

Holm LG, Pancho JV, Herberger JP & Plucknett DL (1979) *Geographical Atlas of World Weeds*. John Wiley & Sons, New York, USA.

Joley DB, Maddox DM, Mackey BE, Schöening SE & Casanave KA (1997) Effect of light and temperature on germination of dimorphic achenes of *Centaurea solsticialis* in California. *Canadian Journal of Botany* **75,** 2131–2139.

Koyama H (1998) Seed heteromorphism and timing of germination—their mechanisms and adaptive significance [in Japanese]. *Japanese Journal of Ecology* **48,** 129–142 (CAB Abstract no. 990304012).

Kremer RJ (1993) Management of weed seed banks with microorganisms. *Ecological Applications* **3,** 42–52.

Kremer RJ, Hughes IB, Jr & Aldrich RJ (1984) Examination of microorganisms and deterioration resistance mechanisms associated with velvetleaf seed. *Agronomy Journal* **76,** 745–749.

Lordello RRA, Lordello AIL & Paulo EM (1988) Multiplicao de *Meloidogyne javanica* em plantas daninhas. *Nematologia Brasileira* **12,** 84–92.

Mandák B (1997) Seed heteromorphism and the life cycle of plants: a literature review. *Preslia* **69,** 129–159.

Martínez-Ghersa MA, Ghersa CM, Benech-Arnold RL, Donough RM & Sánchez RA (2000) Adaptive traits regulating dormancy and germination of invasive species. *Plant Species Biology* **15,** 127–137

Mertelik J & Mokra V (1998) Tomato spotted wilt virus in ornamental plants, vegetables and weeds in the Czech Republic. *Acta Virologica* **42,** 347–351.

Rai JPN & Tripathi RS (1987) Germination and plant survival and growth of *Galinsoga parviflora* Cav. as related to food and energy content of its ray- and disc-achenes. *Acta Oecologica* **8,** 155–165.

Rhoades DF (1985) Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* **125,** 205–238.

Royal Statistical Society (1985) *GLIM Statistical Package, Version 3.77*. Royal Statistical Society, London, UK.

Rzedowski GC & Rzedowski J (eds) (2001) *Flora Fanerogámica del Valle de México*, 2nd edn, 876. Instituto de Ecología, A.C. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Páztcuaro (Michoacán), México.

Salisbury EJ (1942) *The Reproductive Capacity of Plants*, 31–32. G. Bell and Sons, London, UK.

Sokal RR & Rohlf FJ (1979) *Biometría. Principios y Métodos Estadísticos en la Investigación Biológica*. H. Blume Ediciones, Madrid, Spain.

Valarini PJ & Spadotto CA (1995) Identification of survival niches of phytopathogens in irrigated agriculture of Guaira, Sao Paulo State. *Pesquisa Agropecuaria Brasileira* **30,** 1239–1243.

Van Rooden J, Akkermans LMA & Van Der Veen R (1970) A study on photoblastism in sedes of some tropical weeds. *Acta Botanica Neerlandica* **19,** 257–264.

Venable DL (1985) The evolutionary ecology of seed heteromorphism. *American Naturalist* **126,** 577–595.

Venable DL & Brown JS (1993) Population dynamic functions of plant dispersal. *Vegetatio* **107/108,** 31–55.

Venable DL & Levin DA (1985) Ecology of achene dimorphism in *Heterotheca latifolia*. 1. Achene structure, germination and dispersal. *Journal of Ecology* **73,** 133–145.

Venable DL, Búrquez A, Corral G, Morales E & Espinosa F (1987) The ecology of seed heteromorphism in *Heterosperma pinnatum* in central Mexico. *Ecology* **68,** 65–76.