Seed-bank dynamics of the tropical weed *Sida rhombifolia* (*Malvaceae*): incidence of seedling emergence, predators and pathogens

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Abstract

Arrowleaf sida (*Sida rhombifolia*) is a tropical weed that grows in disturbed areas. Its control by hand pulling and mowing are only partially effective because arrowleaf sida is difficult to pull and quickly sprouts after cutting. We studied the seed-bank dynamics of *S. rhombifolia* in the region of Campinas, São Paulo State, Brazil for 2 years, following a known number of seeds placed artificially at five burial depths. Predators and pathogens were responsible for the loss of *c.* 40% of the seeds during the first year of the experiment. The importance of predation declined with depth. Mortality due to fungal attack did not differ among the burial depths, except for seeds placed at the surface (where it was negligible). Seedling emergence only occurred during the first year, after the beginning of the rainy period and when the study area was still free of a dense vegetation cover. Seedlings did not emerge from depths greater than 5 cm. We conclude that seedling emergence and death are significant causes of seed losses from the seed bank of *S. rhombifolia* but their relative importance is highly dependent on depth of burial.

Introduction

Sida rhombifolia (*Malvaceae*) is a common weed that grows throughout the tropical, subtropical and warm temperate regions of both the Old and the New World (Holm *et al.*, 1997). It is a short-lived perennial subshrub that reproduces only by seeds. The seeds (1.5–2.0 mm long) exhibit physical dormancy that can be broken by scarification (Cardoso, 1990). Certain attributes of the species, like the development of a long and resistant root system and its capacity to sprout vigorously if cut, make this weed a successful invader of pastures, abandoned lands and roadsides (Lorenzi, 1991; Holm *et al.*, 1997). It is a reported weed of 34 crops, including sugar cane, maize, bananas, beans, coffee, cotton, soybean and rice. It has become an increasing weed problem with the advent of reduced or no-tillage cropping systems (Smith *et al.*, 1992; Holm *et al.*, 1997).

Information about seed banks is needed to elucidate plant population dynamics. This includes estimates of the probabilities that seeds entering the soil meet certain fates (Teo-Sherrell *et al.*, 1996). Although the loss of seed viability in soil frequently represents much of the total mortality of plants (Cavers, 1983; Chambers and MacMahon, 1994), the relative importance of the sources that influence seed survival is largely unknown (Lonsdale, 1993; Horvitz and Schemske, 1994; Hulme, 1994). The persistence or transience of soil seed-banks varies among plant species and environments, depending on factors that influence seed dormancy, microbial attack or predation by granivores (Crist and Friese, 1993).

Seed predation has been widely studied and there are several reviews about this source of mortality (e.g. Janzen, 1971; Louda, 1989; Sallabanks and Courtney, 1992; Hulme, 1998a; Crawley, 2000; Hulme and Benkman, 2002; Moles and Westoby, 2003). Compared to most other plant parts, seeds have a very high nutritious value by unit volume; hence they provide a rich food supply for animals that exploit this potential resource (Janzen, 1971; Fenner, 1985; Hulme, 1998a; Hulme and Benkman, 2002). Studies in many temperate woodlands and grasslands show that post-dispersal seed predation rates are extremely variable in space and time (Crawley, 2000). Studies in tropical regions show that seed predation may be very severe

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(e.g. Piñero and Sarukhán, 1982; De Steven and Putz, 1984; Becker and Wong, 1985; Álvarez-Buylla and Martínez-Ramos, 1990; Blate *et al.*, 1998). However, and contrary to the expectation that the rates of post-dispersal seed predation would be higher towards the tropics, Moles and Westoby (2003) found no significant relationship between seed predation and latitude. In managed agro-ecosystems, seed predation can be influenced by crop species (Heggenstaller *et al.*, 2006), tillage regime (Cromar *et al.*, 1999; Nisensohn *et al.*, 1999) and cropping practices such as crop residue management (Cromar *et al.*, 1999).

By contrast, experiments attempting to measure the effects of soil pathogens on the depletion of seed banks are scarce. This type of organism can be responsible for the death of seeds directly through necrotic action or indirectly through the production of toxic metabolic wastes (Burdon, 1987). Vulnerability to pathogen attack may be higher in physiologically active seeds than in dormant ones, and can increase with seed age and tegument deterioration (Burdon and Shattock, 1980). Studies where this source of mortality was evaluated (e.g. Crist and Friese, 1993; Lonsdale, 1993; Myster, 1997; Leishman *et al.*, 2000; Blaney and Kotanen, 2001, 2002; Schafer and Kotanen, 2003, 2004; O'Hanlon-Manners and Kotanen, 2006) showed that the mortality of seeds due to pathogen effects is highly variable, depending on the plant under study or on the characteristics of the habitat.

For weed seed-banks it is also important to know the fate of the seeds at different burial depths, because different cultural practices modify the spatial distribution of the seeds into the soil. Spatial heterogeneity is very common in soil seed-banks although it is more evident in cultivated soils (Dessaint *et al.*, 1991; Fumanal *et al.*, 2008). The pattern of seed distribution within a field generally follows the direction of crop rows and the greatest diversity of weed species is found at the edges (Cavers and Benoit, 1989). The vertical distribution of seeds depends on the treatment given to the soil: under reduced tillage, the seeds are concentrated in the upper horizons, while under conventional tillage the seeds are mostly found at intermediate depths (Roberts, 1981; Cavers and Benoit, 1989; Hoffman *et al.*, 1998; Benvenuti, 2007).

The aim of this study was to evaluate the fate of the seeds of the tropical weed *S. rhombifolia* over 2 years, at five different depths of burial, in the region of Campinas, São Paulo State, Brazil.

Materials and methods

Study site

The experiment was conducted on an abandoned hectare of the Experimental Field of the Centro de Pesquisas Biológicas e Aplicadas (CPQBA), Campinas, São Paulo State, Brazil (22°48′S, 47°07′W). The mean annual precipitation in the region is 1490 mm, about 80% of which falls between November and March. The temperature fluctuates slightly during the year, averaging 21.8°C. The soil is a red latosol of high clay content (>60% clay, 2.4% organic matter, pH 5.3). The selected area was mowed and the mowed residue was removed from the site before the beginning of the experiment. The area was used principally for sugar cane culture until 1986, and had not been cultivated since then. The old field vegetation consisted of a dense community of weeds dominated by grasses.

Field experiment

Seeds were harvested from plants of *S. rhombifolia* growing around the Campinas University Campus from August to November 1995. Mericarps were separated in groups of 50 each, removing those with evident signs of predation, and were kept in paper bags at 5°C until their burial in the field. In September 1996, ten parallel transects spaced 8 m apart, were established at the study area. Within each transect, eight sampling units spaced 3 m apart were marked with plastic flags. The sampling units consisted of five cylindrical holes of 10 cm diameter at five different depths: surface (0), 2, 5, 10 and 20 cm. The cylindrical holes were distributed at the centre and tips of an imaginary cross of arm length of 1 m. The position of the burial depth was randomized within each sampling unit. Fifty mericarps of *S. rhombifolia* were buried unprotected in the soil at each hole (a total of 20,000 seeds) using a circular 1-cm plastic mesh of 10-cm diameter at the bottom of the hole in order to mark the depth of the burial. The removed soil was placed back into the holes, a small amount at a time, without exerting pressure in order to avoid soil compaction. The position of each hole was marked by aligning a galvanized wire ring (10-cm diameter) having one leg (5-cm long) attached.

As a control, before the field experiment installation, ten soil cores of diameter 10 cm and depth 20 cm were sampled at random points. Soil cores were subdivided into portions referring to 0–2, 2–5, 5–10 and 10–20 cm depth (total = 40 samples). Soil samples were processed identically to the process of *S. rhombifolia* seed recovery described below.

Seedling emergence

The number of seedlings emerging at each sampling unit was recorded every 2 weeks for 2 years. Seedlings were removed once they had been registered.

Seed recovery and assessment

At 1, 3, 5, 7, 10, 14, 19 and 24 months after burial, one sampling unit from each transect was randomly selected and the five soil cores were removed (ten replicates at each sampling date). The soil cores were transported to the laboratory and sieved through a 1 mm mesh screen under a water jet. Seeds were recovered by gently picking them from the remnant soil samples. Recovered seeds with holes or bites were classified as predated seeds. The seeds that appeared undamaged were washed in a 1% sodium hypochlorite solution for 5 s, followed by two rinses in sterile distilled water to eliminate surface contamination, and were incubated at 24°C on moist filter paper in Petri dishes (ten seeds per Petri dish). Surface sterilization was unlikely to have affected subsequent seed dormancy. According to Crist and Friese (1993), immersion lasting less than 60 s allows insufficient time for dry seeds to absorb the solution. After 10 d, those seeds covered with fungal mycelium and soft to the touch were registered as decomposed. Fungi were isolated in pure culture (agar–malt 12%) and were identified at the Department of Phytopathology, Piracicaba, São Paulo University. Germinated (non-dormant) seeds were easily detected by protrusion of the radicle through the seed coat and were registered as viable seeds. The remaining seeds were tested for viability. Seeds were dissected longitudinally, immersed in a 1% tetrazolium chloride solution and left in the dark at room temperature for 2 h. Embryos and cotyledons were then examined carefully for staining.

As a control, at each sampling date a viability test was conducted from a stock of seeds kept in the laboratory in paper bags at room temperature. Five samples of 20 seeds each were used for this purpose by means of the procedure described above.

Statistical analysis

Data analysis was performed using the general linear modelling procedure of SYSTAT (Wilkinson, 1990). The analysis employed split-plot factorial ANOVA designs with soil depth used as a random blocking factor and nested inside sampling date. Separate ANOVAs were performed for each survival category: viability, seedling emergence, predation and fungal attack. Differences among averages were tested with Tukey's multiple comparison tests. Data were expressed relative to the initial viable seed fraction and were normalized by square root arcsin transformation prior to analysis.

Results

Initial controls

No seeds of *S. rhombifolia* were recovered from the soil sample controls, and visual inspection of the vegetation carried out before the clearance of the area revealed that the species was represented by very few individuals. Based on these facts, we assume there is negligible probability that seeds recovered from the experiment are different from those buried artificially.

More than 55% of the seeds collected from the plants of *S. rhombifolia* were dead. About 15% of the mericarps were discarded from the experiment because they exhibited conspicuous signs of predation, such as holes or bites that were easily detected by visual inspection. Of the remainder, 48% were non-viable according to the tetrazolium test. Externally, the non-viable seeds seemed undamaged, but when they were dissected, a jelly mass with remains of the embryo and cotyledons was observed. Therefore, although it would have been preferable to discard the non-viable seeds from the experiment, they were incorporated because it was impossible to detect them by external signs.

The percentage viability of the seeds kept in the laboratory remained unchanged with time. No significant differences were registered among the eight controls carried out during the 2 years of study ($F_{7,32} = 0.351$; $P = 0.923$). Accordingly, the results are expressed relative to this initial viable fraction.

Seed-bank dynamics

Seed losses from the bank, as a result of predation, fungal attack and seedling emergence began soon after seed burial. In consequence, the proportion of viable seeds that remained in the bank diminished sharply during the first 3 months of burial. After that, almost all recovered seeds were viable and preserved their viability for at least 2 years (Fig. 1). Also, a high proportion of seeds disappeared during the 2 years of study, particularly at the surface. One month after burial, 42.7% of the surface seeds were missing, while only 2.5% of the buried seeds were not accounted for. On the final sampling date, the percentage of missing seeds was 71.2 and 15.1% for surface and buried seeds, respectively. Viable seeds progressively lost their dormancy along the 2 years of study. Only 10% of the seeds sown were able to germinate according to the initial viability control. With time, seeds gradually lost their dormancy and at the beginning of the second year almost 90% of the seeds were non-dormant (Fig. 2).
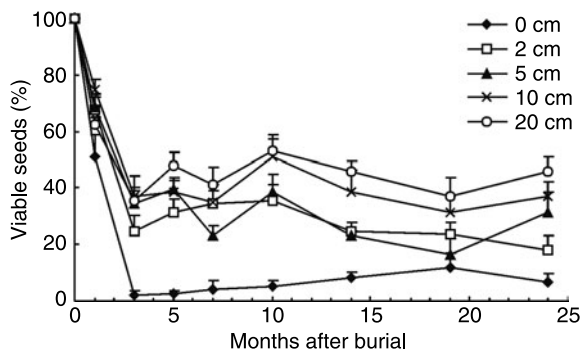
Figure 1. Percentage of viable seeds recovered from artificially buried seeds of *Sida rhombifolia*. Seeds were placed at five burial depths during a 24-month experiment (mean + SE).

Seedling emergence

Seed output due to successful germination occurred during the rainy period (November–February) of the first year of the experiment, when vegetation cover was still scarce. Seedlings emerged only from seeds placed at the surface and at 2 and 5 cm of burial depth ($F_{28,288} = 3.769$; $P = 0.0001$ for the date × soil depth interaction) (Table 1). No emergence was registered after the first year, when the area was completely covered by a dense layer of grasses and dicot weeds (Fig. 3). At the seventh month of burial, unsuccessful germination (seeds with the radicle extended) caused 1.1 and 3.1% of seed losses at the 10 and 20 cm samples, respectively. This minor cause of mortality was not included in the analysis.

Seed predation

Signs of post-dispersal seed predation, such as holes or bites, were found mainly during the summer of the

Table 1. Results of the split-plot ANOVAs for the main seed fates of *Sida rhombifolia* at Sao Paulo State. Seeds were exhumed at eight sampling dates from five depths of burial

Factor	df	Emergence F	Predation F	Pathogens F	Viability F
Date	7	7.06*	10.30*	83.19*	64.12*
Depth	4	7.51*	6.17*	20.08*	105.28*
Date × depth	28	3.77*	2.41*	6.82*	4.24*

* $P < 0.001$.

first year of the experiment, under hot and rainy conditions, decreasing in importance with burial depth ($F_{28,288} = 2.413$; $P = 0.0001$ for the date × soil depth interaction) (Table 1). A second but minor peak of predated seeds was observed in the second year of sampling (Fig. 3). Several adult insects (mostly Carabidae and Formicidae) and larvae were collected from the soil samples.

Figure 3. Main seed-bank losses (expressed as the percentage of initially viable seeds) of *Sida rhombifolia*. Seeds were artificially buried at five depths for 2 years. For clarity, error bars are not shown.
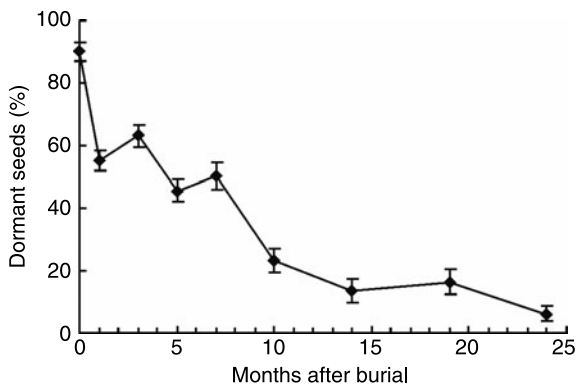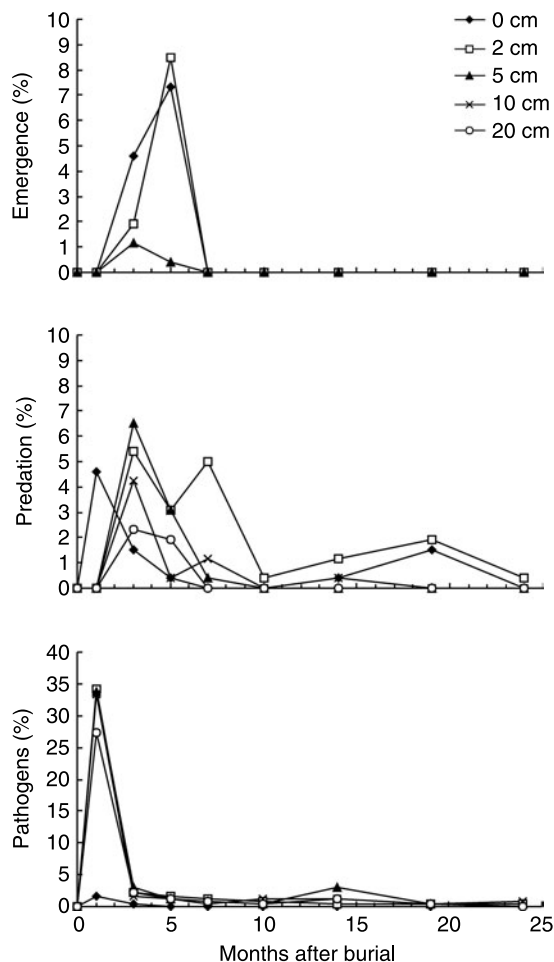

Figure 2. Percentage of dormant seeds of *Sida rhombifolia* (relative to the number of viable seeds recovered) during 2 years of burial. Values are the mean (± SE) of the five burial depths.

Pathogen attack

One month after burial, and coinciding with the beginning of the rainy season, a large proportion of seeds were dead due to fungal attack. After that time, mortality caused by fungi diminished gradually, reaching values near to zero in the second year of sampling (Fig. 3). Pathogens infested preferentially the buried seeds ($F_{28,288} = 6.817$; $P = 0.0001$ for the date $\times$ soil depth interaction) (Table 1). If surface seeds are removed from the analysis, fungal attack was equally important at all burial depths ($P = 0.728$). Seeds were mostly infected by *Alternaria alternata*, *Fusarium semitectum* and *F. oxysporum*.

Discussion

Seed-bank input

According to our observations, a great number of seeds produced by *S. rhombifolia* die before being dispersed. Conspicuous damage on the seeds, such as holes or bites, was observed on *c*.15% of the seeds collected. Moreover, the high proportion of non-viable seeds, not detectable by external signs and incorporated into the experiment, may be attributable to the action of sucker hemiptera, whose association with the family *Malvaceae* was outlined long ago by Janzen (1969). If this is the case, pre-dispersal seed predation would account for the loss of more than 55% of the seeds produced naturally by *S. rhombifolia* in the region.

At the same location of the present study, six species of herbivores (mostly Curculionidae) were isolated from the reproductive structures of *S. rhombifolia*, including seeds. Germination tests confirmed that predated seeds were unable to germinate (Mello and Souza, personal communication). In addition, at the area of seed collection, many adults of *Dysdercus* sp. (Heteroptera, Phyrrocoridae) were observed. Species of the genus *Dysdercus*, known as 'cotton stainers', inhabit tropical and subtropical areas all over the world and are primarily seed feeders (Kohno and Bui Thi, 2006). In Brazil, cotton stainers are associated with 53 species of plants, most of them of the family *Malvaceae*, including *Sida* spp. (Azevedo-Ramos *et al.*, 1991).

Seed-bank losses

Seedling emergence

In the present study, seed output from the soil due to seedling emergence was mainly registered during the rainy period of the first year of the experiment, and at low proportions. Several factors may explain this result. Like most species of *Malvaceae*, *S. rhombifolia* produces seeds with a water-impermeable seed coat. The seeds remain in a state of physical dormancy until the coat is made permeable by scarification or some unknown factor in natural conditions (Van Assche and Vandelook, 2006). In our experiment, when the rainy period began, a high proportion of the seeds remained dormant. During the second year of study most of the seeds were non-dormant, but at this time the study area was completely covered by a dense layer of grasses and dicot weeds. It is possible that, like many weeds, seeds of *S. rhombifolia* are highly successful in germinating in disturbed areas (e.g. after the clearance of the area at the beginning of the experiment) but are unable to germinate with a dense cover of vegetation. Burial depth was also important for seedling emergence. Seedlings only emerged at depths up to 5 cm and our results agree with those reported by Smith *et al.* (1992) who observed experimentally that seedlings of this species only emerged when seeds were buried between 0 and 5 cm of depth. Arrested germination was observed at the seventh month of burial. Some undetermined environmental circumstance during that period (although we have no record of surface emergence) or the manipulation of the samples could have initiated the germination of these seeds.

Pathogens

The incidence of fungi on seeds peaked soon after burial, being equally important at all burial depths, but very low at the soil surface. However, it is known that abundance of fungal propagules decreases with soil depth (Christensen, 1981) and in consequence a higher proportion of seed decay is expected in the upper layers of soil. Our results suggest that seed-borne fungi, and not soil fungi, may be responsible for seed decay in the soil. Burdon (1987) argues that infrequent reports of pre-dispersal seed losses due to pathogen attack in non-crop plants is due to the effects of the dry and near sterile conditions in which many seeds are normally held prior to their release from the parent plant. But many propagules of saprophytic or pathogenic fungi can be associated with seeds or seed appendages. For example, Kirkpatrick and Bazzaz (1979) isolated 28 fungal species from seeds of four colonizing annuals of early successional habitats and Prete *et al.* (1984) identified 18 species of fungi from seeds of several weeds that grow in São Paulo State, near the region of Campinas, where this experiment was conducted. It is reasonable to assume that propagules of opportunistic and relatively non-specific fungi, such as *Alternaria* and *Fusarium*, may have travelled attached to the pericarp or seed coat, and infested the seeds when more appropriate conditions of humidity and temperature for fungal growth were met in the soil.

Post-dispersal seed predation

Predation was high in the first year of the experiment. The signs observed on the seeds suggest that invertebrates were the main agents of predation. Although we cannot assert that the carabids and ants collected from the soil samples were responsible for the registered seed predation, both groups of insects are reported as important consumers of seeds after dispersal (Tooley and Froud-Williams, 1999; Hulme and Benkman, 2002; Mauchline *et al.*, 2005; Honek *et al.*, 2006). During the second year of burial, mortality due to predation was significantly lower. It is possible that the decrease of seed predation reflects a dilution effect. By this time, more than 60% of seeds had disappeared, so seeds as a resource were sparse and more difficult to locate. Few studies have explicitly examined the effect of seed density on rates of seed predation, but, in an overwhelming field study on this issue, Harms *et al.* (2000) have unequivocally demonstrated density-dependent mortality on seeds and/or seedlings in 53 Panamanian tree species.

When burial depth is considered, almost all studies show that seed burial reduces post-dispersal seed predation, particularly for smaller seeds (Hulme, 1994, 1998b). In our study, the small seeds of *S. rhombifolia* were predated mainly on the surface and at burial depths above 10 cm, probably because burial protects seeds from granivores, particularly invertebrates (Hulme and Borelli, 1999).

Most of the studies that evaluate seed predation assume that missing seeds are the result of consumption by granivores. However, keeping in mind that we are probably underestimating the number of predated seeds, we opted to include the missing seeds of our study in a category apart because of the uncertainty of their fates. Chambers and MacMahon (1994) and Vander Wall *et al.* (2005) argue that secondary seed dispersal (e.g. movement of viable seeds following initial dispersal) is an important process in the reproductive cycle of many plants and consequently it is inappropriate to consider missing seeds as predated seeds. For example, it is not clear whether the *c.* 70% of missing seeds registered on the soil surface is attributable to an increment of seed predation and/or it is a consequence of abiotic factors, such as wind and rain.

In order to facilitate seed recovery, several studies used the seed-bag or seed-pot burial method (e.g. Lewis, 1973; Roberts and Neilson, 1981; Egley and Chandler, 1983; Sester *et al.*, 2006). However, this procedure has the effect of protecting seeds from predators and may elevate the levels of pathogens (Van Mourik *et al.*, 2005). We think that burying the seeds unprotected in the soil, as we did in our study, is a more realistic way of analysing seed survival, even though it may increase the proportion of missing seeds.

Our study constitutes the first attempt to evaluate the relative importance of the causes of seed-bank depletion of *S. rhombifolia*. We have shown that seedling emergence, fungi and predators reduce the soil seed-bank of the weed. This knowledge may provide insights for the management of the species. While seed predators and microorganisms cannot be expected to eliminate weed problems, their effects can be promoted with certain cultural practices, such as leaving crop residues to provide ground cover. This management technique has been shown to enhance seed predation levels because of the more stable environment and greater protection provided by the residue (Cromar *et al.*, 1999; Shearin *et al.*, 2008) and to increase soil moisture, which may favour infestation by pathogens (Schafer and Kotanen, 2003). Moreover, the absence of seedlings of *S. rhombifolia* when vegetation cover was high, suggests that this practice may also prevent establishment of the weed. Future studies should examine whether the presence of residues effectively enhances losses from the seed bank of *S. rhombifolia*.

Our results also indicate that the seed-bank dynamics of *S. rhombifolia* are highly dependent on burial depth. Seeds placed on the surface, seeds buried up to 5 cm depth and seeds buried deeper (10–20 cm) are exposed to different rates of seed losses. Tillage practices alter the vertical distribution of seeds in soil (Grundy *et al.*, 1999; Colbach *et al.*, 2000; Roger-Estrade *et al.*, 2001), so knowledge of seed fates at different burial depths is important as it can help us predict weed emergence patterns.

Acknowledgements

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