

Weed seedling emergence and seed survival: separating the effects of seed position and soil modification by tillage

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Summary

Tillage causes both vertical redistribution of weed seeds and changes in soil physical properties. These two factors are rarely distinguished in studies of the impact of tillage on seedling emergence or seed survival. In this study, seeds of *Chenopodium album* L., *Amaranthus retroflexus* L., and *Abutilon theophrasti* Medik. were planted at particular depths in pots of undisturbed or stirred soil to separate these effects. Emergence and survival data were analysed by non-linear regression to determine the nature of significant differences between treatments. Emergence increased with slight burial and then decreased exponentially at greater depths. Average emergence over all depths was generally greater in tilled soil than in untilled soil, particularly for *C. album* and *A. retroflexus*. Seed survival approached a maximum with increasing depth. Average survival of seeds that did not produce emerged seedlings was greater in tilled soil than in untilled soil for *C. album* and *A. retroflexus*. Thus, tillage affects emergence and seed survival of weeds through changes in soil conditions independently of effects resulting from redistribution of seeds in the soil profile.

Introduction

Several studies have shown that soil disturbance often increases the emergence of weed seedlings (Chancellor, 1964a; Banting, 1966; Roberts & Dawkins, 1967; Roberts & Feast, 1972; Froud-Williams *et al.*, 1984). However, when seeds are mostly near the soil surface owing to deliberate sowing or seed shedding from a natural population, seedling density is often higher in untilled conditions (Egley & Williams, 1990; Teasdale *et al.*, 1991; Mohler & Callaway, 1992). Moreover, Roberts & Feast (1972) found that the difference between emergence rates in disturbed and undisturbed soil increased with increasing depth of planting, probably as a result of movement of seeds towards the surface during soil stirring. Interpretation of the effects of soil disturbance on seed germination and seedling emergence is thus complicated by the vertical redistribution of seeds that occurs during soil disturbance.

The fate of weed seeds in an agricultural environment is determined by several factors, including the availability of germination cues such as light, water and fluctuating temperatures (Chancellor, 1985; Baskin & Baskin, 1987), the presence of seed predators and pathogens (Brust & House, 1988), and the ability of new germinants to emerge from the soil. All of these factors are affected by depth in the soil profile. However, because placement of seeds into the soil usually requires substantial soil disturbance, previous studies have not separated the effects of soil disturbance on the environment of seeds and seedlings from the effects of seed position in the soil profile. This distinction is critical for understanding how tillage acts on weed populations. Tillage clearly affects the soil in ways expected to promote germination and emergence, yet the vertical redistribution of seeds by tillage implements is apparently sufficient to ex-

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plain the general patterns of weed density observed in field experiments (Mohler, 1993).

In general, viable seeds near the surface are lost from the soil by germination and mortality more rapidly than those deeper in the soil (reviewed in Mohler, 1993), probably because near-surface conditions are more suitable for germination (Banting, 1966) and pathogens and predators (Taylorson, 1970). For most weed species the optimum depth for emergence is less than 2 cm (Mohler, 1993), and the maximum depth from which emergence can occur is often less than 6 cm (Chancellor, 1964b; Froud-Williams *et al.*, 1984).

Morton & Buchele's (1960) study of the energy needed for a mechanical seedling to emerge from various soil conditions provides data relevant to the emergence of seedlings from tilled and untilled soil. They found that seedlings needed more energy to emerge from compacted soil, especially when the soil had dried to form a surface crust. Greater energy was also required to emerge from a deeper location. As tillage of soil reduces its mechanical strength, more seedlings would be expected to emerge, and to emerge from greater depths, in tilled soil than in untilled soil. However, less soil:seed contact in the loose soil produced by tillage might lead to less germination and therefore less emergence than in untilled soil.

The purpose of this study was to quantify the effects of soil disturbance on the fate of weed seeds and seedlings independent of effects caused by the depth of seeds in the soil profile. This was accomplished by precision insertion of seeds at various depths into stirred and unstirred soil using an apparatus that produced a minimum of soil disturbance over and around the seeds.

Materials and methods

The species chosen for the study were *Amaranthus retroflexus* L. (redroot pigweed), *Chenopodium album* L. (lambsquarters) and *Abutilon theophrasti* Medik. (velvetleaf). All are widespread and economically important weed species (Bridges, 1992), but they differ in seed size (0.4, 0.7 and 10 mg respectively, Mohler, 1996), germination characteristics (Mohler & Teasdale, 1993) and response to burial depth (reviewed in Mohler, 1993).

The experiment consisted of a completely randomized design, with three species, two 'tillage' regimes (tilled, untilled) and either five (*A. theophrasti*) or six planting depths (*C. album* and *A. retroflexus*) (Table 1). The experiment was repeated, with trials beginning in July and August of 1994 at a site near Ithaca, New York. Weather conditions differed greatly between the two trials. The August trial received 181 mm of rain, with 155 mm during the period in which 95% of the seedlings emerged. In contrast, the July trial received only 84 mm of rain, and only 35 mm during the period in which 95% of the seedlings emerged.

In October 1993, plastic pots (12.5 cm deep, 25 cm top diameter) were set into a tile drained bed, leveled and filled with soil. After settling, the soil level inside and outside the pots was the same. The soil was a sandy loam with pH 6.9 and 6.3% organic matter. It had been collected from a site that was free of the weed species used in the experiment, and was passed through 1.2-cm-mesh hardware cloth to remove large stones. Use of pots was necessary to prevent entrance of seeds from the surrounding soil, and to ensure complete recovery of seeds remaining at the end of the experiment. However, the experiment

Table 1. Design of the experiments

Species	Replications	Depths (cm)	Pots	Trial	Seeds/ injection	Seeds/ pot
<i>Amaranthus retroflexus</i>	3	(0, 0.5, 1.0, 1.5, 2.0, 2.5)	36	July Aug	10 15	80 120
<i>Chenopodium album</i>	3	(0, 0.5, 1.0, 1.5, 2.0, 2.5)	36	July Aug	10 15	80 120
<i>Abutilon theophrasti</i>	4	(0, 0.5, 1.0, 2.0, 4.0)	40	July Aug	6 6	48 48

used unsterilized field soil, and was conducted under natural field conditions.

Soil in the tilled treatment was broken and turned thoroughly with a trowel shortly before seeding. In both trials the soil was slightly moist when turned. The soil was smoothed by hand and gently firmed by dropping a 1075-g weight from 5 cm on to a wooden circle (350 g, 22 cm diameter). The resulting surface was similar to that produced by rolling well-worked soil of good tilth.

A. theophrasti seeds were 1993 stock obtained from F. & J. Seed Service, Woodstock, IL, USA. *A. retroflexus* and *C. album* were taken from bulk seed collections consisting of about fifty plants from a single local population. *A. retroflexus* seeds were collected in 1993. *C. album* seeds from 1993 were used in the July trial; 1992 seeds (with a higher laboratory germination rate) were used in the August trial.

To minimize soil disturbance during planting, seeds were planted using an injection apparatus, which consisted of a funnel and a brass tube clamped in a groove machined into the 45° angle of a combination square. Tubes for *A. retroflexus* and *C. album* had a 2.7-mm outside diameter and 1.7-mm inside diameter. *A. theophrasti* tubes had a 4.5-mm outside diameter and a 3.9-mm inside diameter. The tube was inserted to the correct depth for a particular injection using graduations marked on the outside of the tube. A metal rod was placed in the tube to prevent it from filling with soil during insertion. The rod was subsequently removed and used to push seeds out the end of the tube. A clip prevented the rod from protruding beyond the end of the tube. The tube and rod were carefully removed along the angle of entry after injection of seeds. In tilled pots, the soil collapsed behind the injector tube as it was removed, so the soil was gently levelled to even the surface at the top of the hole. In untilled pots, removal of the tube left a distinct tunnel in the soil, so a wooden dowel the same diameter as the tube was gently inserted and the soil surface firmed with a finger. Pebbles that could damage the tube and whose movement would disturb the soil, and large cracks that could modify seed depth, were avoided when positioning the injector.

The large labour requirements of the injection procedure prohibited individual placement of seeds. Seeds were injected at eight locations in each pot. The number of seeds planted at each

location varied between species and trials (Table 1), depending on the expected rate of emergence from the optimal planting depth. Typically 0–4 seedlings emerged from each injection location, although often not at the same time.

Seedlings were counted in the July trial 15–23 days and 27–35 days after planting. In the August trial counts were made 4–9 days after planting and weekly thereafter for 3 more weeks. As weeds were counted they were clipped close to the soil surface and removed.

To evaluate the survival of the seeds that did not produce emerged seedlings, at the end of the August trial, all soil was removed from the pots, and dried at 49 °C in a forced draft oven. *C. album* and *A. retroflexus* seeds were recovered by elutriation (Gross & Renner, 1989). Trial elutriations of known numbers of seeds showed that the procedure recovered 97% (SE ± 0.7%) of the seeds. *A. theophrasti* seeds were recovered by washing the soil through a 1.0-mm-mesh screen. The seeds of all three species were counted, examined and crushed for inspection of the endosperm. Damaged seeds and seeds with powdery or darkened endosperm were scored as non-viable. Estimates of the initial proportion of viable and dead seeds were made from samples of the original seed stocks by the same procedure.

A curve of the form

$$E_i = (a_i + b_i D) e^{(-c_i D)} \quad (1)$$

was fitted to emergence data for each species trial using non-linear least squares regression (StatSoft, 1994), where E_i represents the proportion of seeds that produces emerged seedlings in tillage treatment i , D represents the planting depth, a_i , b_i and c_i are fitted constants ≥ 0 and e is the base of the natural logarithms. Differences between tillage treatments were assessed by fitting data for each species trial to successively reduced forms of eqn (1), in which first parameter c , then b , then a , was forced to a common value. Significant differences between successively reduced models were determined by an F -test ($\alpha = 0.05$) on the change in the residual sum of squares (Gomez & Gomez, 1984; Ascard, 1994). The pooled variance among replicates was used as the denominator of the F -ratio rather than the usual sum of squared error from the regression, as the former provides an estimate of error that is independent of the particular model.

The observable fate of seeds can be described by the equation.

$$I = A + V + N + M \quad (2)$$

where I is the initial pool of viable seeds, A represents seeds that produce emerged seedlings, V represents dormant viable seeds remaining in the soil, N represents non-viable seeds remaining in the soil and M represents missing seeds (i.e. those that were eaten, decomposed or germinated but failed to emerge). We define seed survival, S , as

$$S = V/(I - A)$$

Seed mortality is the complement of survival, and thus is here considered to include germination without emergence. Survival data were fitted to the equation

$$S_i = f_i + g_i(1 - e^{-h_i D}) \quad (3)$$

where S_i represents the proportion of seeds surviving in tillage treatment i , D represents the planting depth, f_i , g_i , and h_i are fitted constants ≥ 0 and e is the base of the natural logarithms (Mohler, 1993). Models of different complexity were compared in the same way as for the emergence curves.

The estimated average emergence and survival from a seed pool uniformly distributed over 2.5 cm (*A. retroflexus* and *C. album*) or 4 cm (*A. theophrasti*) was used to compare tillage treatments and trials. Average emergence was computed as

$$\bar{E}_{ij} = D_{ijn}^{-1} \sum_k^{n-1} 0.5 \cdot (\bar{E}_{ijk} + \bar{E}_{ijk+1}) \cdot (D_{ijk+1} - D_{ijk})$$

where \bar{E}_{ijk} and D_{ijk} are the mean emergence and planting depth for depth k in tillage treatment i and trial j , and n is the number of depths. Average survival was estimated similarly. Differences between tillage treatments within trials and between trials for each tillage treatment were tested using the jack-knife procedure (Sokal & Rolf, 1981)

Results

Emergence was less in the untilled than in the tilled treatment for most of the species trials (Fig. 1, Table 2), the primary exception being *A. theophrasti* in the August trial. For the untilled

Table 2. Estimated average proportion of seeds that produced emerged seedlings, assuming a seedbank uniformly distributed over the top 2.5 cm (*C. album* and *A. retroflexus*) or 4.0 cm (*A. theophrasti*) of soil (see text), and ratio of emergence in untilled conditions to that in tilled conditions

Species	Trial	Untilled	Tilled	Significance†	Ratio untilled:tilled
<i>Chenopodium album</i>	July	0.025	0.082	***	0.30
	Aug.	0.045	0.109	*	0.41
	Sig.†	NS	NS		
<i>Amaranthus retroflexus</i>	July	0.070	0.170	**	0.41
	Aug.	0.176	0.206	NS	0.85
	Sig.†	***	NS		
<i>Abutilon theophrasti</i>	July	0.188	0.402	***	0.47
	Aug.	0.316	0.303	NS	1.04
	Sig.†	***	**		

Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

Table 3. Estimated average survival of seeds, assuming a seedbank uniformly distributed over the top 2.5 cm (*C. album* and *A. retroflexus*) or 4.0 cm (*A. theophrasti*) (see text), and ratio of survival in untilled conditions to that in tilled conditions, August trial

Species	Untilled	Tilled	Significance†	Ratio untilled:tilled
<i>Chenopodium album</i>	0.501	0.603	*	0.83
<i>Amaranthus retroflexus</i>	0.236	0.572	***	0.41
<i>Abutilon theophrasti</i>	0.686	0.702	NS	0.98

Significance: * $P < 0.05$; *** $P < 0.001$; NS, not significant.

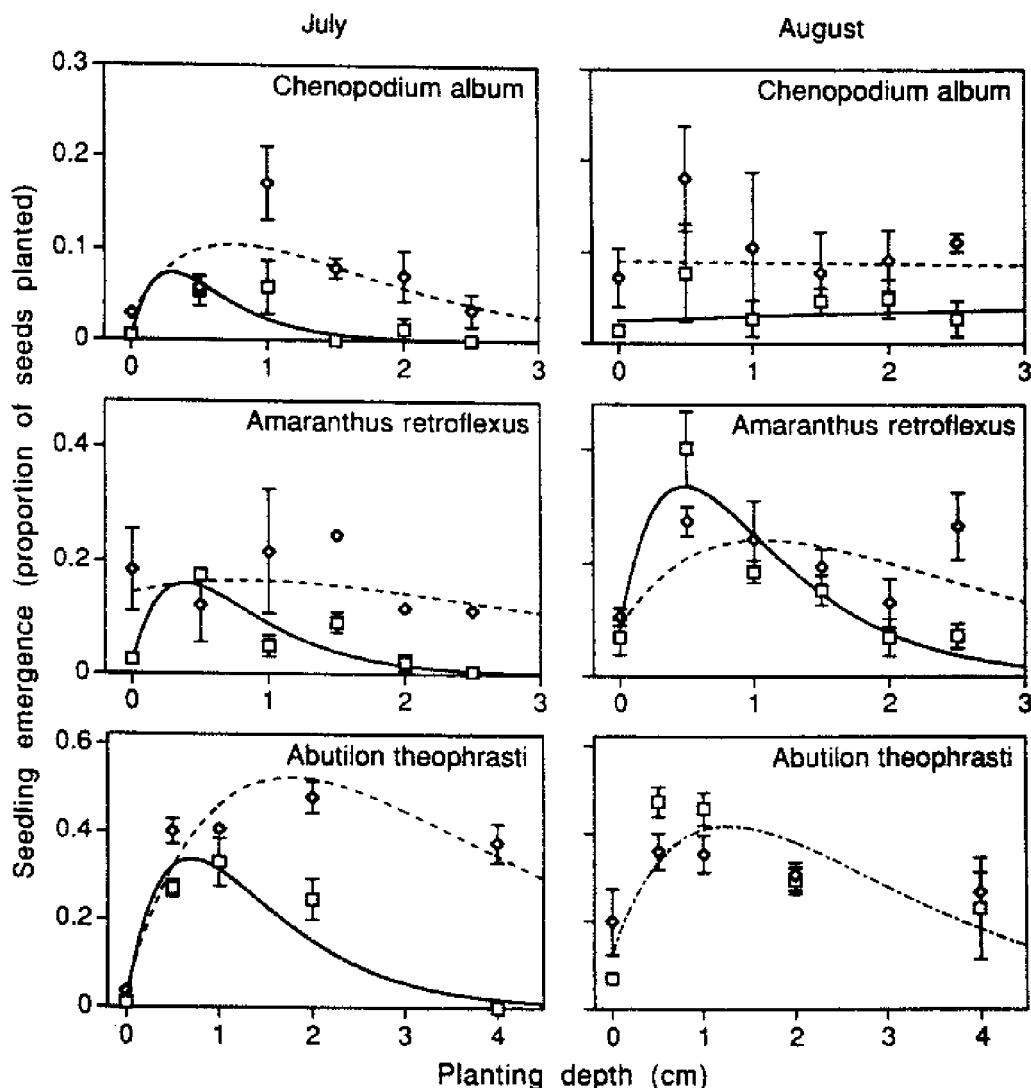


Fig. 1 The proportion of seeds that produced emerged seedlings for each species and trial. Fitted curves follow eqn (1). ◇, Tilled; □, untilled; ---, model for tilled; —, model for untilled; — — —, model for both.

treatment, emergence tended to be greater in the August trial (Table 2). In the tilled treatment, however, *A. theophrasti* had greater emergence in the July trial and emergence did not differ significantly for the other species.

Generally, emergence was less at the soil surface than when seeds were buried 0.5–1 cm deep (Fig. 1). In the untilled treatment of the July trial all three species showed a rapid decline in emergence as planting depth increased beyond 0.5 cm (Fig. 1). In contrast, all species emerged well

from the deepest planting depth in the tilled treatment.

In contrast with the July trial, emergence was less inhibited by deep planting in the August trial, even in the untilled treatment (Fig. 1). This was most noticeable for *A. theophrasti*, in which the emergence responses to depth in tilled and untilled treatments were indistinguishable.

Seed survival was generally low at the soil surface and rapidly increased to an asymptote as burial depth increased (Fig. 2). Seed survival at

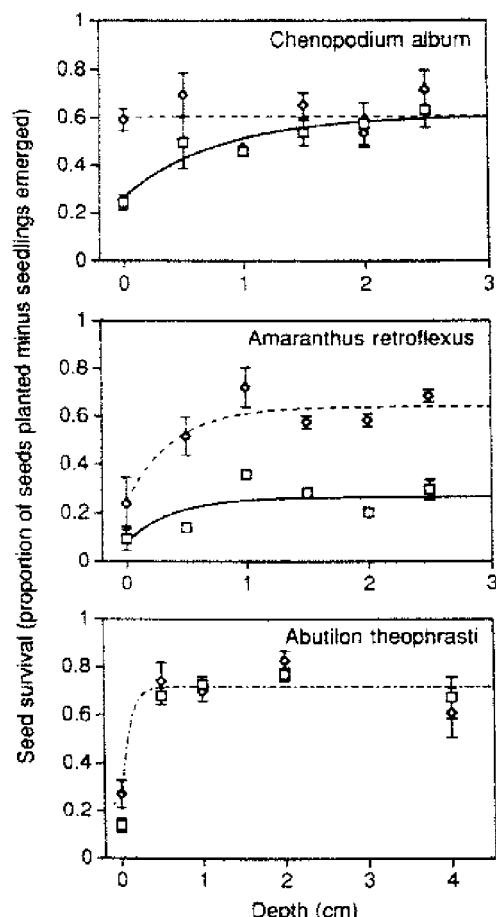


Fig. 2 Seed survival in the August trial. Fitted curves follow eqn (3). \square , Untilled; \circ , tilled; —, model for untilled; ---, model for tilled; ·····, model for both.

the soil surface and average seed survival were significantly higher in the tilled treatment for *A. retroflexus* and *C. album* (Fig. 2 and Table 3).

Discussion

The greater emergence in tilled soil relative to untilled soil (Fig. 1 and Table 2) agrees with previous work (Chancellor, 1964a; Roberts & Dawkins, 1967; Roberts & Feast, 1972; Froud-Williams *et al.*, 1984), but in the present study the result was solely due to differences in the condition of the soil and not the movement of seeds to the surface by tillage. The greater emergence in the untilled treatment for the August trial relative to the July trial (Table 2) was probably due to greater rainfall in August (see Materials and methods). Greater soil moisture probably promoted germination and reduced the resistance of soil to seedling emergence (Morton & Buchele, 1960). As wetting reduces the resistance of untilled soil more than tilled soil, emergence from the two treatments was more nearly equal in the August trial than in the July trial (Table 2). This was particularly true for *A. theophrasti*. The large seedlings of *A. theophrasti* may allow this species to break through compact untilled soil more easily than the two small-seeded species, at least when the soil is moist.

Few previous studies have attempted to describe mathematically the response of seedling emergence to seeding depth. Baird & Dickens (1991) used a negative exponential model for emergence of *Diodia virginiana* L. after 4 days, but a quadratic for emergence after 14 days. Mohler (1993) fitted a negative exponential to data from several published studies, but this equation would fail to fit most of the data reported here. In contrast, eqn 1 appears to fit the trend in all data sets reasonably well (Fig. 1), and reduces approximately to the negative exponential when fitted to monotonically declining data

Table 4. Parameters of the emergence model (eqn 1) for *C. album*, *A. retroflexus* and *A. theophrasti* in the July and August trials. Equal values for parameters subscripted N (no tillage) and T (tillage) indicate that the model with a shared parameter was not significantly different at $P < 0.05$ from the model with separate parameters (see text)

	<i>C. album</i>		<i>A. retroflexus</i>		<i>A. theophrasti</i>	
Parameter	July	August	July	August	July	August
a_N	0.002	0.025	0.017	0.087	0.005	0.126
a_T	0.025	0.090	0.143	0.087	0.038	0.126
b_N	0.673	0.009	1.03	1.53	1.30	0.694
b_T	0.315	0.009	0.142	0.452	0.758	0.694
c_N	3.39	0.099	2.46	1.87	1.42	0.693
c_T	1.22	0.099	0.55	0.798	0.547	0.693
R^2	0.65	0.22	0.55	0.55	0.89	0.44

Table 5. Parameters of the seed survival model (eqn 3) for *C. album*, *A. retroflexus* and *A. theophrasti* in the August trial. Equal values for parameters subscripted N (no tillage) and T (tillage) indicate that the model with a shared parameter was not significantly different at $P < 0.05$ from the model with separate parameters (see text)

Parameter	<i>C. album</i>	<i>A. retroflexus</i>	<i>A. theophrasti</i>
f_N	0.264	0.080	0.205
f_T	0.602	0.241	0.205
g_N	0.348	0.187	0.512
g_T	0.005	0.400	0.512
h_N	1.27	2.58	10.2
h_T	1.27	2.58	10.2
R^2	0.48	0.83	0.75

sets. The variability between replications observed here (Fig. 1) is typical of experiments of this sort.

Parameters of eqn 1 are readily interpretable, and help explain the results of the study. The parameter a is the emergence of seeds located at the soil surface. It was generally small (Table 4), probably because seeds on the soil surface had difficulty imbibing and retaining sufficient moisture for germination. When differences in parameter a existed between tilled and untilled treatments, the value was always higher for tilled conditions (Fig. 1). This probably resulted from better seed:soil contact owing to seeds lodging between soil particles on the looser surface of the tilled treatment. Parameter b reflects the increase in emergence as a result of decreased desiccation when seeds are buried. For the four cases with a significant difference in b between treatments, b was greater in untilled conditions (Table 4). That is a given coverage by undisturbed soil apparently prevents desiccation more than an equivalent depth of the looser tilled soil. Parameter c reflects the exponential decline in emergence at greater planting depths. In the four cases in which c differed significantly between tillage treatments (all species in the July trial, and *A. retroflexus* in the August trial), it was greater for untilled conditions. This probably reflects greater physical resistance to emergence by a given depth of untilled soil relative to tilled soil.

The general pattern of emergence in response to depth of burial observed in this study agrees well with previous reports on these three species in the literature. Wiese & Davis (1967) found that peak emergence of *A. retroflexus* occurred at 0.6–1.2 cm and that few seedlings emerged

from deeper than 2.5 cm. Similarly, Chancellor (1964b) found that maximum emergence of *C. album* was from the 0- to 2-cm layer and that few seedlings emerged from deeper than 3 cm. Stoller & Wax (1973) did not test *A. theophrasti* at the soil surface, but found that emergence was greater at 2.5 than at 5.1 cm. In their study, a few seedlings emerged from seeds placed at 10.2 cm. Mester & Buhler (1991) observed that *A. theophrasti* emergence was highest at the surface, except at a relatively cool temperature (10 °C). However, their study was carried out in a growth chamber where drying of the soil surface was probably less rapid than in the field conditions of the study reported here.

Low seed survival at the surface in this study (Fig. 2) probably reflected a combination of desiccation of seedlings shortly after seed crack, and foraging by ground beetles (Brust & House, 1988), which were commonly observed in the pots. Significantly higher seed survival at the soil surface in the tilled treatment for the two small-seeded species (Fig. 2) may reflect the sheltering effect of seeds lodging between soil aggregates. As seed survival for all species in this study reached an asymptote around 1 cm depth (Fig. 2), the decline in emergence with increasing depth below 1 cm (Fig. 1) must have been due to a decrease in germination rather than a decrease in successful emergence of germinants. If germination had not decreased with depth, then the observed decrease in emergence with depth below 1 cm would have resulted in more dead germinants. These would have contributed to a decline in survival with depth, which was not observed. This result contrasts with that of Sanchez del Arco *et al.* (1995), who found that germination of *Avena sterilis* ssp. *ludoviciana* (Dur.) Gill

& Mayne was roughly constant with depth. These contrasting results probably relate to species-specific differences in germination cues.

Although the inspection and crush test for seed viability used here is approximate, it was probably reasonably accurate. Few seeds of these long-viable species would be expected to die from ageing in 1 month, and death from insect and fungal damage was detected by the procedure. Possibly some seeds died as a result of initiation of germination followed by subsequent desiccation, but most of these would show detectable changes in the seed coat or endosperm. This latter source of mortality would be greatest for the surface-planted seeds, as soil below the surface was continuously moist in the August trial. Modest additional undetected mortality of surface seeds would not affect the conclusions.

As the design of most seed survival experiments prevents seedling emergence, few studies provide comparable data on seed survival as it is defined here. Seed survival calculated from data in Roberts & Feast (1972) shows increased survival with greater mean depth for all 20 species tested. Similar calculations on data from other sources (Stoller & Wax, 1973; Dawson & Bruns, 1975; Moss, 1985) show that survival increases with depth for a variety of species, but that other responses are also common. In contrast to the greater survival of *C. album* and *A. retroflexus* seeds in the tilled treatment of this study (Table 3), Roberts & Feast's (1972) data show lower survival of *C. album* and all other species with tillage. However, regular stirring of the soil in their tilled treatment probably induced some fatal germination.

Parameters of the seed survival model (eqn 3) are interpreted as follows: f is seed survival at the soil surface, $(f + g)$ is the asymptotic survival that is approached with increasing depth and h is the exponential rate of increase in seed survival with depth. For all three species, there was no significant difference in the parameter h between tillage treatments (Table 5). For *C. album*, f and g differed between tillage treatments, but the asymptotic survival $(f + g)$ was similar (Fig. 2). Values of f and g also differed between tilled and untilled treatments for *A. retroflexus*. *A. theophrasti* showed no significant difference between tillage treatments in any of the parameters (Fig. 2).

Thus, changes in soil conditions owing to till-

age in some cases had little effect on seedling emergence and seed survival, but more often increased the probability that an individual completed one or the other of these life-history transitions. Results presented here indicate that shallow tillage of seeds initially on the soil surface may increase emergence because (1) shallow burial increased emergence and (2) tilled soil favoured emergence. In contrast, inversion of the soil by mouldboard ploughing would be expected to decrease emergence from seeds initially on the surface and to increase seed survival (1) by burying seeds beyond the reach of surface hazards (e.g. predation, desiccation) and (2) by changing the soil in a way that promotes survival. However, caution is recommended in extrapolating results from the short-term survival experiment presented here to the survival of seeds between seasons. Finally, in addition to emergence and seed survival, effects of tillage on a whole seedbank depend on the initial vertical distribution of the seeds and their movement by the tillage implement. Data from this study will be used to extend the vertically stratified seedbank model of Mohler (1993).

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References

- ASCARD J (1994) Dose-response models for flame weeding in relation to plant size and density. *Weed Research* **34**, 377–85.
- BAIRD JH & DICKENS R (1991) Germination and emergence of Virginia buttonweed (*Diodia virginiana*). *Weed Science* **39**, 37–41.
- BANTING JD (1966) Studies on the persistence of *Avena fatua*. *Canadian Journal of Plant Science* **46**, 129–40.
- BASKIN JM & BASKIN CC (1987) Environmentally induced changes in the dormancy states of buried weed seeds. *Pro-*

- seedlings 1987 *British Crop Protection Conference - Weeds*, Brighton, 695-706.
- BRIDGES DC (ed.) (1992) Crop losses due to weeds in Canada and the United States - 1992. Weed Science Society of America, Champaign, IL.
- BRENT GE & HOUSE GJ (1988) Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. *American Journal of Alternative Agriculture* 3, 191-25.
- CHANCELLOR RJ (1964a) Emergence of weed seedlings in the field and the effects of different frequencies of cultivation. *Proceedings Seventh British Weed Control Conference - Brighton*, 599-606.
- CHANCELLOR RJ (1964b) The depth of weed seed germination in the field. *Proceedings Seventh British Weed Control Conference - Brighton*, 607-13.
- CHANCELLOR RJ (1985) Tillage effects of annual weed germination. In: *World Soybean Research Conference III: Proceedings* (ed. R. Shibles), pp. 1105-11. Westview Press, Boulder, CO, USA.
- DAWSON JH & BRENS VF (1975) Longevity of barnyard grass, green foxtail, and yellow foxtail seeds in soil. *Weed Science* 23, 437-40.
- EILEY GH & WILLIAMS RD (1990) Decline of weed seeds and seedling emergence over five years as affected by soil disturbances. *Weed Science* 38, 504-10.
- FROUD WILLIAMS RJ, CHANCELLOR RJ & DRENNAN DSH (1984) The effects of seed burial and soil disturbance on emergence and survival of arable weeds in relation to minimal cultivation. *Journal of Applied Ecology* 21, 629-41.
- GOMEZ KA & GOMEZ AA (1984) *Statistical Procedures for Agricultural Research*, 2nd edn. John Wiley, New York.
- GROSS KL & RENNER KA (1989) A new method for estimating seed numbers in the soil. *Weed Science* 37, 836-9.
- MESTER TC & BUEHLER DD (1991) Effects of soil temperatures, seed depth, and cyanazine on giant foxtail (*Setaria faberii*) and velvetleaf (*Abutilon theophrasti*) seedling development. *Weed Science* 39, 204-9.
- MOHLER CL (1993) A model of the effects of tillage on emergence of weed seedlings. *Ecological Applications* 3, 53-73.
- MOHLER CL (1996) Ecological bases for the cultural control of annual weeds. *Journal of Production Agriculture* 9, 468-74.
- MOHLER CL & CALLAWAY MB (1992) Effects of tillage and mulch on the emergence and survival of weeds in sweet corn. *Journal of Applied Ecology* 29, 21-34.
- MOHLER CL & TEASDALE JR (1993) Response of weed emergence to rate of *Vicia villosa* Roth and *Secale cereale* L. residue. *Weed Research* 33, 487-99.
- MORTON CT & BUCHELE WF (1960) Emergence energy of plant seedlings. *Agricultural Engineering* 41, 428-31, 453-55.
- MOSS SR (1985) The survival of *Alopecurus myosuroides* Huds. seeds in soil. *Weed Research* 25, 201-11.
- ROBERTS HA & DAWKINS PA (1967) Effect of cultivation on the numbers of viable weed seeds in soil. *Weed Research* 7, 290-301.
- ROBERTS HA & FLAIST PM (1972) Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research* 12, 316-24.
- SANCHEZ DEL ARCO MJ, TORNER C & FERNANDEZ OLIN ANILLA C (1995) Seed dynamics in populations of *Avena sterilis* ssp. *huloviciana*. *Weed Research* 35, 477-487.
- SOKAL RR & ROLF FJ (1981) *Biometry*, 2nd edn. Freeman, New York.
- STATSOFT (1994) STATISTICA for the Macintosh. StatSoft, Tulsa, OK, USA.
- STOLLER EW & WAX LM (1973) Periodicity of germination and emergence of some annual weeds. *Weed Science* 21, 574-80.
- TAYLORSON RB (1970) Changes in dormancy and viability of weed seeds in soils. *Weed Science* 18, 265-9.
- TEASDALE JR, BESTL CE & POTTS WF (1991) Response of weeds to tillage and cover crop residue. *Weed Science* 39, 195-9.
- WIESE AF & DAVIS RC (1967) Weed emergence from two soils at various moistures, temperatures, and depths. *Weeds* 15, 118-21.

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