

Natural weed seed burial: effect of soil texture, rain and seed characteristics

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Abstract

Trials were carried out to investigate natural weed seed burial in a no-till agricultural system. With this aim, 30 important weed species were selected to explore if, and to what extent, seed vertical movement is conditioned by soil texture, cumulative rainfall or by seed characteristics. Without soil tillage, the vertical position of the seeds was only a few millimetres below the surface, but it was dependent on soil texture. Seed burial was much slower (and to lesser depths) in clay soils than in sandy soils. Seeds reached greater depths after 1 year in sandy soil (10% >6 mm) than in clay soils (2% >6 mm). Burial dynamics were also influenced by rainfall and seed weight. The amount of rain necessary to halve weed seeds observable on the soil surface was a function of the soil texture and seed weight; linear regressions between total rainfall amounts and seed weight showed that the slope of the relationship increased as the sand component of the soil decreased (21.1, 35.4 and 39.4 in sandy, loam and silty-clay soil, respectively). A polynomial regression, carried out in sandy soil, between 1000-seed weight and their burial capacity showed an inverse relation ($P > 0.05$) between these two parameters. Seed shape and coat microsculpture also influenced movement, but only minimally.

Keywords: no-till, seed bank, seed burial, seed characteristics, weed ecology

Introduction

Weed infestation dynamics depend on quantity (Forcella, 1992), structure (Myers *et al.*, 2004) and horizontal distribution of the seed bank (Wiles and

Brodahl, 2004), as well as seed-bank allotments in various soil layers (Grundy *et al.*, 1996). This last feature is particularly important because only the seeds near the soil surface are able to germinate and emerge (Grundy *et al.*, 2003), even though this depth-mediated inhibition is inversely proportional both to the seed weight (Benvenuti *et al.*, 2001) and soil particle size density (Benvenuti, 2003). Much of the seed bank is non-active because of hypoxia (Benvenuti and Macchia, 1995) and low rates of gaseous diffusion in soil, which limit germination and can even induce secondary dormancy (Baskin and Baskin, 1985). An additional ecological consequence of vertical distributions of seed banks is that long residence of seeds on the soil surface favours their predation (Jacob *et al.*, 2006).

From the beginnings of agriculture, many tillage techniques have been conceived with the aim of improving the physical characteristics of the soil, but they always have had a significant effect on seed burial. Indeed, seed-bank distribution depends both on the depth (Yenish *et al.*, 1992) and kind (Cousens and Moss, 1990) of soil tillage. Ploughing typically causes greater accumulation of seeds at deep depths than other tillage systems (Mohler *et al.*, 2006). Alternative cropping techniques based on a no-till strategy have been increasing for several decades. A growing interest in agroecosystem management based on no-till systems was prompted for economic (Patterson *et al.*, 1980), energetic (Uri, 1998), ecological (Holland, 2004) and agronomic (Slepetiene and Slepetys, 2005) reasons.

In no-till systems, the annually produced seed rain tends to remain on the soil surface (Clements *et al.*, 1996; Sissons *et al.*, 2000). Unfortunately, in such systems, high germination rates occur for some weed species because there are no physical obstacles to seed–gas environments (Benvenuti, 2003). Only a few species, such as some members of the *Gramineae* (= *Poaceae*) (Peart and Clifford, 1987, Collins and Wein, 1997) and *Geraniaceae* (Stamp, 1984), are able to self-bury their seeds utilizing their hygroscopic awns. Although these particular cases of self-burial are well

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known, the extent to which non-specialized weed seeds are able to bury themselves passively is not known, except for observations of seeds falling into soil cracks (Chambers and MacMahon, 1994). Given that seeds on the soil surface are exposed to raindrop impact, and that the kinetic energy of raindrop impact (van Dijk *et al.*, 2002) likely is proportional to the size of the drops (Jameson and Kostinski, 2001), rain may be an important factor that pushes seeds into the soil matrix.

The vertical distribution of seeds in natural habitats with little soil disturbance may be explained partly by seed size (Bekker *et al.*, 1998). Whether soil texture and seed characteristics (shape and coat microsculpture) regulate burial is not clear. Possibly one of the evolutionary strategies of some plants, before the advent of agriculture, was the modification of their seed morphology to permit rapid entry into soil, avoiding typical biotic and abiotic injuries common on the soil surface (Cromar *et al.*, 1999). The idea of the present work originated from the hypothesis that rainfall facilitates the entry of seeds into the soil matrix, and that vertical seed distributions can depend on both seed and soil characteristics. In fact, as the degree of cohesion of particles in the soil strongly depends on their size (Marshall *et al.*, 1996), this feature very likely can mediate soil penetration by seeds. The only experimentation regarding this problem was conducted in natural ecosystems (Chambers *et al.*, 1991) and showed that soil texture was involved in diversifying the rapidity and intensity of seed burial. Consequently, the lack of information about natural seed burial of common weeds inspired the present work, which was devoted to vertical seed movement in no-till cropping systems. In summary, the aims of the present work were to investigate: (1) whether seeds are capable of being buried following simple rainfall action; (2) if soil texture can be an important factor in this process; and (3) if a relationship exists between natural burial and seed characteristics of various weed species.

Materials and methods

Plant material

Seeds of 30 species (see Table 2) were collected in crop fields during each year from 2003 through 2005. The species were selected on the basis of their importance as weeds and also due to the varied shape and size of the seeds of the different species. Annual seed collections allowed use of fresh seeds during each experimental period. The seeds (or fruits, as in the cases of *Asteraceae* or *Gramineae*) were extracted from mature plants, air-dried, cleaned and stored in glass

jars under standard conditions (20°C and *c.* 12% humidity).

Field experiments

The trials were conducted at Asciano (near Pisa, Italy; 43°43'N, 10°26'E) in a silty-clay soil classified as a Xerofluvent (USDA-SCS, 1961). The soil's chemical and physical characteristics are summarized in Table 1. At the beginning of October of each of 3 years (2003, 2004 and 2005), seeds of the 30 weed species were spread on the soil surface, following harvest of no-till silage corn each year. Soils were not tilled so that natural burial potential could be determined.

To assess the effect of soil texture on natural seed burial under identical rainfall conditions, small plots with different soil textures were created in these fields. Beginning in autumn 2002, 50 × 50 × 10 cm (length × width × depth) holes were dug and filled with sandy or loam soils (Table 1). By 2003, the introduced soils reached the same level of compaction (data not shown) as the adjacent silty-clay soil.

The pre-existing seed banks in the soils of the experimental plots were low (<2000 seeds m⁻²) and, overall, they were composed of weed species not used in the experiments. Field invasion of the tested weeds during the 3-year experiments was prevented by manual elimination after emergence. The number of holes (plots) dug and filled in 2002 was three times that necessary in a single experimental year. This allowed use of new plots each year and avoided effects of residual seeds from the preceding experiments. The seeds of mixtures of five species were distributed in each plot. Species composition of each mixture was determined according to shape and size characteristics, which facilitated later identification during successive counting operations. Thus, 54 plots were used each year (3 replications, 3 soil types, 6 mixtures each composed of 5 of 30 species). In the central area of each plot, a smaller area (30 × 30 cm) was identified where seeds were uniformly distributed on the soil surface. Seed densities ranged from 900 seeds (10 000 seeds m⁻²) for large-seeded species to 9000 seeds (100 000 seeds m⁻²) for small-seeded species.

Table 1. Chemical and physical characteristics of the soils used for the field trials. The sand and loam soils were introduced artificially, whereas the silty-clay soil was the natural soil of the experimental field

Soil types	Sand (%)	Clay (%)	Lime (%)	CaCO ₃ (%)	pH	Organic matter (%)
Sand	92	3	5	5.2	7.6	0.4
Loam	67	15	18	3.9	7.2	1.3
Silty-clay	29	28	43	5.7	7.7	1.6

Seed burial

October through February was chosen as the most suitable time for the experiments for two reasons: it is the wettest portion of the year at the site; and low temperatures during this period prevent seed germination, which would have hindered observation of the natural seed burial. Germination also was inhibited through primary dormancy typical of fresh seeds (Andersson and Milberg, 1998) and the sub-optimal seed–soil contact (Collis-George and Hector, 1966) of surface-applied seeds.

To prevent seed predation, specially designed units protected the small areas (30 × 30 cm) used for seed distribution on the soil surface. These units were comprised of a frame (30 × 30 cm) whose sides were enclosed by 1-cm plastic mesh. The top of the frame was covered by large-meshed (1 cm) plastic netting that prevented birds or other large granivores from entering, but did not appreciably alter the kinetic energy of raindrops reaching the soil (data not shown). Underground seed predation was prevented by the use of a common soil sterilant (active ingredient, benfuracarb), and invertebrate predation was virtually absent because of the low temperature during the winter periods (personal observation).

Seed retrieval

In each of the three experimental years, soils were sampled twice: once about halfway through the experiment (late December) and again at the end of the experimental period (late February). The samplings were done by means of a custom-designed metal probe able to obtain small intact cylindrical cores (4 cm in diameter and 5 cm long), because breakage of the cores would have prevented observation of the effective dynamics of seed burial. The operation of this probe is based on a two-part opening device in the apical section. This works by means of a longitudinal hinge that rotates the two external semicylinders, thus extracting an internal metallic cylinder containing the soil core. This extractable cylinder is cut transversely on 350 of the total 360° by thin slits (0.2 mm) spaced 2 mm apart. In this way, it was possible to obtain precisely the soil layer required by using a thin, but rigid, metallic blade able to cut the soil core, and inserting it into the slits in the metallic cylinder described above. In the case of the larger seeds, the separation of the soil micro-layers was carried out very carefully, avoiding the cutting of the seeds and favouring their movement upwards or downwards according to the seed's position in one layer or another. In each of the above mentioned 54 areas, five cores were taken. Each of the various micro-horizons of the soil core was washed under running water using a metallic mesh (0.1 mm) filter for seed retrieval.

Seed characteristics

The seeds were classified in six different categories according to their relative shape (spherical, hemispherical, flattened, elongated, pyramidal and discoidal) and in three categories according to seed-coat surface (smooth, alveolar and coarse). This classification was performed by observing the seeds under an optical stereomicroscope (Model Optech Biostar 5, Optech Scientific Instruments, Thame, Oxfordshire, UK) at 40 ×. Seed weight was determined by weighing 1000 seeds, chosen randomly, according to ISTA rules for seed testing (ISTA, 1999).

Calculation of rain level to induce 50% of weed seed burial

After distributing seeds in the plots, the percentage of seeds still observable on the soil surface after rainfall events was carefully monitored with the aid of a magnifying lens. Monitoring was performed weekly in the first month and monthly thereafter. For each species and type of soil, rainfall levels (mm) needed to cause 50% burial (seeds no longer observable on the soil surface) were calculated by means of linear regressions between the percentage of seeds that had disappeared from the soil surface (y axes) and level of cumulative rainfall (x axes). Finally, the rain values for 50% burial for each weed species were compared to the corresponding 1000-seed weights and fitted through linear regressions.

Statistical analysis

The experimental design was a randomized complete block with three replications. Data were analysed as a three-way factorial, with soil texture, cumulative rain and years as the main factors. After a homogeneity test of variance, arc-sin transformation was necessary for percentage data. Appropriate data were subjected to analysis of variance (ANOVA) using the Student–Newman–Keuls test ($P < 0.05$ and $P < 0.01$) for mean separations (least-significant difference, LSD). The degree of seed burial was obtained by calculating the weighted means according to the following formula: $D = \Sigma(n_i \times d_i) / \Sigma n_i$, where D = weighted mean; n_i = number of seeds at a given depth; d_i = mean depth of the soil layer considered and n_i = total number of seeds.

Burial values were plotted with the corresponding 1000-seed weight and fitted with a Boltzman polynomial regression. The deviations between expected and real values were used to identify over- or underestimations of burial of the various weed species grouped according to the relative seed characteristics in terms of shape and seed-coat microstructure. For each statistical analysis, commercial software (CoStat, CoHort Software, Minneapolis, USA) was used.

Results

Most rainfall events during the experimental periods were <20 mm (Fig. 1). However, higher intensity rainstorms did occur: five in the period 2003–2004, six in 2004–2005 and five in 2005–2006. Overall precipitation was just less than 400 mm during the first trial period (2003–2004), whereas almost 500 mm occurred in each of the two later periods.

Soil texture showed a crucial influence on seed burial (Fig. 2), as indicated by its high level of significance ($P < 0.01$). On the contrary, the statistical analysis of the ‘year’ factor was not significant, probably due to the fact that the amount of rainfall in the trial periods was similar, even though rainfall was

100 mm lower in the 2003–2004 period than the mean of the two following years. This lack of significance permitted grouping of the data together, which are shown as an average across the 3-year experimental period for each soil type. The silty-clay soil strongly hindered the vertical movement of seeds, to the extent that >90% were still at or near the soil surface (0–2 mm) at the end of winter (Fig. 2). The remaining buried seeds showed very limited movement; i.e. 5%

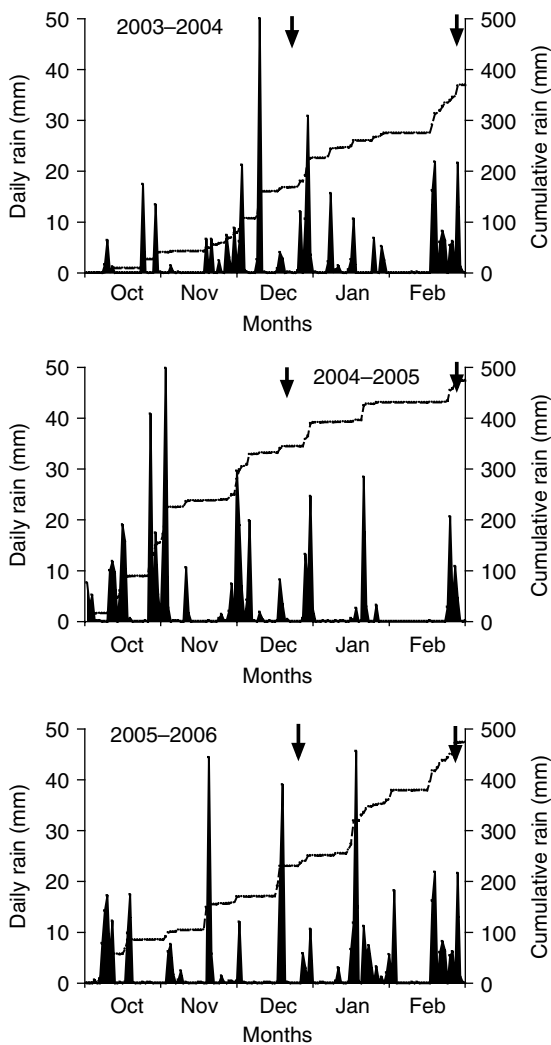


Figure 1. Rainfall (daily and cumulative) during each of the three experimental periods from October to February, 2003–2006. Arrows indicate the time of soil sampling for the weed seed burial evaluation.

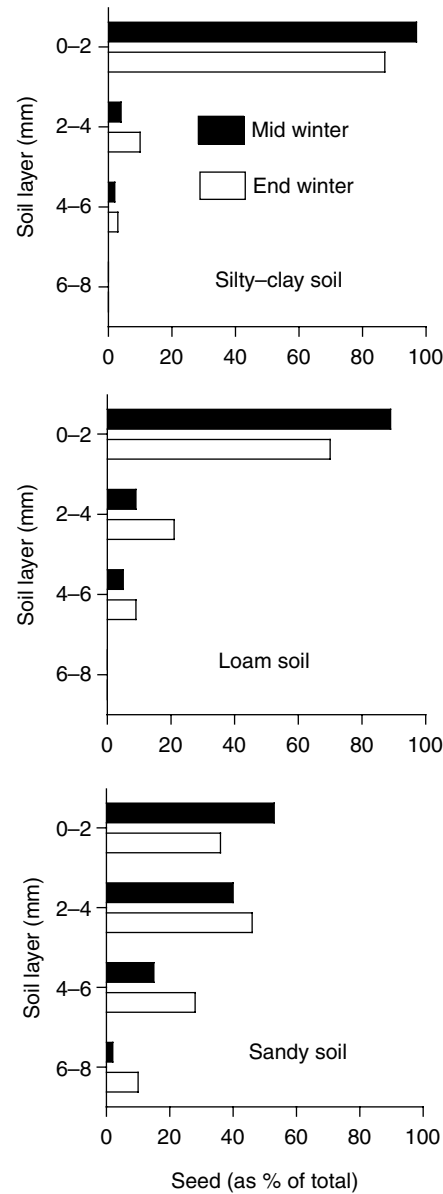


Figure 2. Effect of soil texture (silty-clay, loam and sand) on the natural seed burial dynamics of 30 species after two different sampling periods, at mid winter (December) and the end of winter (February). The data are expressed as percentages of the total seeds of the different weed species initially dispersed on soil surfaces.

were found at 2–4 mm, and 2% were retrieved from 4–6 mm.

Loam soil also obstructed downward movement of seeds, although to a lesser extent than the silty-clay. For example, seed distribution by the end of winter in silty-clay matched that of loam at mid winter, which indicated that downward seed transport was faster in loam than silty-clay soils. By winter's end in loam soil, about 70% of the seeds remained at the shallowest horizon (0–2 mm), 20% at 2–4 mm and 10% at 4–6 mm.

In neither silty-clay nor loam soils did seeds of any species go beyond 6 mm of burial depth. However, this depth was overcome easily in the sandy soil; about 2% occurred at 6–8 mm by mid winter and 10% at winter's end. In this case, vertical movement of seeds was both more rapid (almost half the seeds were already below the surface layer in mid winter) and more intense, given that at the end of winter, the soil horizon with the highest concentration of seeds (about 50%, $P > 0.01$) was that immediately below the surface (2–4 mm). Interestingly, however, after a year of burial the seeds tended to maintain their vertical position because additional periods of rainfall made no difference in further downward movement (data not shown). This indicates that equilibrium was reached in pure physical terms; i.e. overlying energy (rainfall energy decreasing with depth) equalled underlying resistance (cohesion of soil particles).

The 30 species were characterized by very variable 1000-seed weights (Table 2), ranging from 0.003 g for *Orobancha ramosa* to 11.33 g for *Galium aparine*. Since significant seed burial was observed only in sandy soil, the calculations of the relationships between seed characteristics and burial capacity were carried out only with this soil type. Burial depths reached across species varied widely and ranged from the 1.3 mm of *Galium aparine* to 9.4 mm for *Orobancha ramosa*. Burial levels of the smallest seeds were relatively deep, as in the case of *Papaver rhoeas* (6.9 mm), *Spergula arvensis* (6.6 mm), *Portulaca oleracea* (6.3 mm) and *Stellaria media* (6.3 mm), while very limited burial depths were observed for the larger seeds, such as those of *Abutilon theophrasti* (1.4 mm), *Convolvulus arvensis* (1.5 mm) and *Datura stramonium* (1.8 mm). Whatever the case, rain-induced seed movement tended to be < 1 cm in these temperate sandy soils. This seed movement is somewhat less than that occurring in the wet tropics, where rainfall levels are notably higher (Kellman, 1978).

An attempt was made to assess the functions that can describe the possible associations between seed weight and burial tendency. A Boltzman sigmoidal equation significantly ($P < 0.005$) showed an inverse relation between unit seed weight and relative capacity of burial (Fig. 3).

Regression analysis (Fig. 4) established a correlation between the unit weight of seeds of the various species and the cumulative amount of rain required to

halve the number of seeds on the soil surface. The slopes of the regressions relative to each of the three soil types summarize the rapidity with which the seeds are buried due to the kinetic energy of rainfall. Larger seeds like those of *Galium aparine*, *Convolvulus arvensis*, *Abutilon theophrasti* and *Datura stramonium* need ≥ 300 mm of rain to undergo 50% burial both in the loam and clay-loam soils.

However, vertical seed movement was mediated not only by the relative weight but also by seed shape (Fig. 5) and seed-coat sculpture (Fig. 6). Spherical seed shape favours natural seed burial (Fig. 5). On the contrary, the flattened seed shape appears to play a crucial role to hinder vertical movement. Alveolar and smooth (in this case with less evidence) seed-coat sculptures were associated with the seed movement towards the deeper soil layers (Fig. 6). On the contrary, the coarse seed-coat sculpture showed a negative effect upon seed burial capacity.

Discussion

The dependence of the vertical movement of the seeds on soil particle size (i.e. soil textural class) confirms what has been discovered previously in a natural ecosystem (Chambers *et al.*, 1991). The influence of soil texture on seed movement may be associated with the colloidal component of the soil. High cohesive forces of smaller (clay) soil particles form in the presence of bivalent and trivalent cations, causing attraction to one another (Marshall *et al.*, 1996) and, thereby, form possible barriers to the raindrop-induced gravitational movement of seeds. However, only the smallest seeds have a tendency to be buried in the soil. Moreover, the inverse relation found by Bekker *et al.* (1998) between seed size and relative longevity indicated that species with small seeds tend to form more persistent seed banks than larger-seeded species. This is true to the extent that this parameter is considered to be a valid indicator of the persistence of seeds in the soil (Thompson *et al.*, 1993). Consequently, in absence of soil tillage (natural ecosystems and no-till agroecosystems), the smallest seeds tend to be buried more rapidly, therefore avoiding those predation phenomena common on the soil surface (Ghersa and Martínez-Ghersa, 2000).

The typical oxygen limitation in the soil matrix that surrounds buried seeds (Benvenuti and Macchia, 1995) can also have a role in longevity, because seed decay strongly depends on oxidation rates of enzymatic pools (Hendry, 1993). However, this strategy seems to be effective particularly in cases of soils that have little colloidal activity (i.e. sands), thus making the seed presence on the soil surface very much a transitory stage. This idea is supported by the differences among slopes ($P < 0.01$) of the linear regressions (Fig. 4).

Table 2. List of the tested weed species and the relative seed characteristics in terms of shape, coat microsculpture, 1000-seed weight and seed natural burial depth in sandy soil after the rain periods of 5 months. Means are followed by \pm standard errors, and least-significant difference (LSD) values are reported

Weed species	Family	Seed shape	Seed-coat microsculpture	1000-seed weight (g)	Seed burial depth (mm)
<i>Abutilon theophrasti</i> Medicus	Malvaceae	Spherical	Smooth	8.73 \pm 0.812	1.4 \pm 0.1
<i>Alopecurus myosuroides</i> Hudson	Graminaceae	Flattened	Smooth	1.866 \pm 0.105	2.5 \pm 0.2
<i>Amaranthus retroflexus</i> L.	Amaranthaceae	Discoidal	Smooth	0.486 \pm 0.062	5.8 \pm 0.2
<i>Capsella bursa-pastoris</i> (L.) Med.	Brassicaceae	Spherical	Smooth	0.092 \pm 0.071	5.2 \pm 0.2
<i>Cardamine hirsuta</i> L.	Brassicaceae	Spherical	Smooth	0.85 \pm 0.008	5.2 \pm 0.3
<i>Chenopodium album</i> L.	Chenopodiaceae	Spherical	Smooth	0.51 \pm 0.055	5.5 \pm 0.3
<i>Cirsium arvense</i> (L.) Scop.	Asteraceae	Elongated	Smooth	1.693 \pm 0.166	2.4 \pm 0.2
<i>Convolvulus arvensis</i> L.	Convolvulaceae	Spherical	Smooth	9.84 \pm 1.121	1.5 \pm 0.1
<i>Cuscuta campestris</i> L.	Convolvulaceae	Spherical	Coarse	2.78 \pm 0.183	3.0 \pm 0.2
<i>Datura stramonium</i> L.	Solanaceae	Flattened	Smooth	8.211 \pm 0.791	1.8 \pm 0.1
<i>Digitaria sanguinalis</i> (L.) Scop.	Graminaceae	Flattened	Smooth	0.528 \pm 0.063	5.1 \pm 0.3
<i>Echinochloa crus galli</i> (L.) Beauv.	Graminaceae	Hemispherical	Smooth	1.923 \pm 0.127	3.3 \pm 0.3
<i>Euphorbia helioscopia</i> L.	Euphorbiaceae	Spherical	Alveolar	3.41 \pm 0.245	2.8 \pm 0.2
<i>Galium aparine</i> L.	Rubiaceae	Spherical	Coarse	11.33 \pm 0.174	1.3 \pm 0.1
<i>Geranium dissectum</i> L.	Geraniaceae	Spherical	Coarse	2.315 \pm 0.273	2.8 \pm 0.1
<i>Malva sylvestris</i> L.	Malvaceae	Spherical	Smooth	2.063 \pm 0.092	3.7 \pm 0.2
<i>Melilotus officinalis</i> L.	Fabaceae	Spherical	Smooth	2.33 \pm 0.192	3.5 \pm 0.2
<i>Orobanche ramosa</i> L.	Orobanchaceae	Spherical	Alveolar	0.003 \pm 0.001	9.4 \pm 0.2
<i>Papaver rhoas</i> L.	Papaveraceae	Elongated	Alveolar	0.083 \pm 0.016	6.9 \pm 0.3
<i>Plantago lanceolata</i> L.	Plantaginaceae	Elongated	Smooth	0.773 \pm 0.076	5.7 \pm 0.3
<i>Polygonum convolvulus</i> L.	Polygonaceae	Pyramidal	Smooth	1.496 \pm 0.241	4.2 \pm 0.3
<i>Polygonum persicaria</i> L.	Polygonaceae	Discoidal	Smooth	3.21 \pm 0.218	2.5 \pm 0.2
<i>Portulaca oleracea</i> L.	Portulacaceae	Spherical	Coarse	0.092 \pm 0.007	6.3 \pm 0.3
<i>Rumex crispus</i> L.	Polygonaceae	Pyramidal	Smooth	3.45 \pm 0.256	2.4 \pm 0.2
<i>Setaria viridis</i> L.	Graminaceae	Hemispherical	Coarse	2.34 \pm 0.194	3.4 \pm 0.2
<i>Sinapis arvensis</i> L.	Brassicaceae	Spherical	Smooth	1.745 \pm 0.202	5.1 \pm 0.3
<i>Solanum nigrum</i> L.	Solanaceae	Flattened	Smooth	0.805 \pm 0.092	5.4 \pm 0.4
<i>Sorghum halepense</i> (L.) Pers.	Graminaceae	Elongated	Smooth	5.143 \pm 0.518	2.0 \pm 0.2
<i>Spergula arvensis</i> L.	Caryophyllaceae	Discoidal	Smooth	0.234 \pm 0.041	6.6 \pm 0.2
<i>Stellaria media</i> L.	Caryophyllaceae	Pyramidal	Smooth	0.396 \pm 0.047	6.3 \pm 0.4
		LSD		0.67	0.8

The clear lack of burial capacity of weeds with relatively large seeds, especially in clay soils, could limit the persistence of these species. Indeed, near-surface seed banks tend to be more subject to the wide

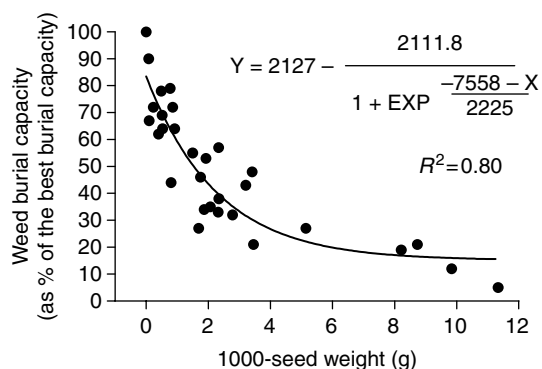


Figure 3. Polynomial regression between weed seed burial capacity (as % of the greatest depth reached) and the relative 1000-seed weight. Data are for the sandy soil.

ranges of natural (predation, thermal stress, pathologies) and agronomic (contact with herbicides) disturbances. Therefore, they are more likely to be short lived. However, a fact worth noting is that larger seeds are less photosensitive, which suggests that light response and seed mass possibly co-evolved (Milberg *et al.*, 2000). This relationship could be associated with the fact that in larger seeds, which are less likely to be buried, the perception of light via phytochrome (Casal and Sánchez, 1998) is a signal of secondary importance.

On the other hand, irrespective of seed size, the no-till agricultural systems do not enable the typical photostimulation of the seed bank (Gallagher and Cardina, 1998). Consequently, the vertical micro-distribution of the seeds is essential in order to be reached by the light, depending on the fluctuating physical characteristics of the soil in terms of humidity and porosity (Tester and Morris, 1987). On the other hand, small seeds, capable of even a minimum burial, typically undergo an increase in light perception (Ballarè *et al.*, 1992), defined as the very low fluence

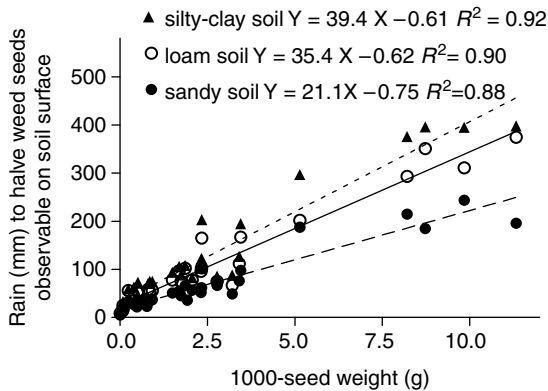


Figure 4. Linear regression between the amount of rain (millimetres) necessary to halve the number of weed seeds observable on the soil surface and the relative 1000-seed weight (g). The regression equations and the relative R^2 values for silty-clay, loam and sandy soils are reported.

response (VLFR) of photomorphogenesis, above all in the presence of nitrates (Milberg, 1997).

Despite the fact that the 1000-seed weight and soil texture were important parameters governing seed burial, they were not the only factors involved, since seed shape also influenced burial. Indeed, flattened seeds appear predisposed to lie on the soil surface. Perhaps such hindering is logical for flattened seeds, as this form has the greatest surface contact with the underlying soil, possibly causing seeds to ‘float’ on the soil more so than seeds with other shapes. If true, this coincides with observations that several grass species, often with flattened seeds, tend to form transitory seed

banks (Thompson, 1987) and that grass seed banks in natural ecosystems are concentrated on the soil surface (Traba *et al.*, 2004).

The additional role played by alveolar micro-sculpture on seed movement is unknown, but it possibly facilitates the sliding of seeds into the soil with the help of micro-droplets of water held in alveolar grooves, which tend to reduce friction with the soil particles. Often, weed species that have an alveolar seed coat tend to create persistent seed banks, perhaps as a function of their faster burial, which prevents soil-surface predation and/or germination. Some examples of persistent species with alveolar seeds are *Papaver rhoeas* and *Euphorbia helioscopia* (Roberts and Feast, 1973), as well as *Orobanchaceae* species (López-Granados and García-Torres, 1999). On the other hand, in the latter case, it is logical to envisage that the evolutionary strategy towards root parasitism induced a parallel co-evolution in the production of seeds adapted to easy vertical movement towards the roots of the host plant. In this case, burial is not only useful for the persistence of the seeds, but is essential for survival, since germination is only possible close to the roots of the host plant (Joel *et al.*, 1990), thus implying an absolute need for seed burial. In other words, the experimental trials showed that the seed of this species is the ideotype for easy burial in that it includes all the positive characteristics in terms of size, shape and seed-coat microsculpture. On the contrary, the coarse seed-coat hindered the vertical movement of the seeds, given that its relative roughness tends to create frictional forces with the soil matrix. In this case, there appears to have been a

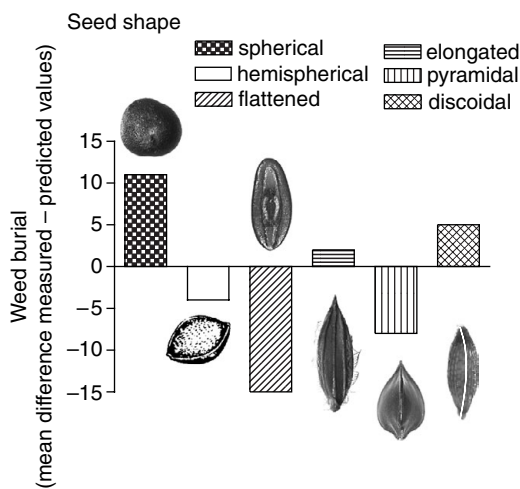


Figure 5. The mean differences between measured and predicted values of the burial performance shown by Boltzman sigmoidal equation illustrated in Fig. 3. Weed seed species were grouped in six different categories as a function of the relative seed-shape characteristics.

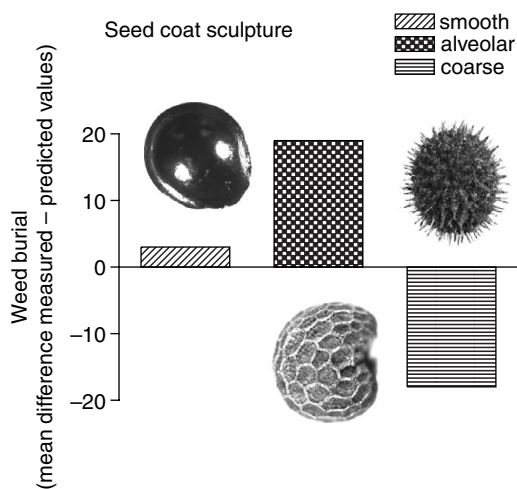


Figure 6. Mean differences between measured and predicted values of the burial performance from the Boltzman sigmoidal equation shown in Fig. 3. Weed seed species were grouped in three different categories, according to the relative seed microsculpture characteristics.

difference in evolutionary dynamics not addressed by easy seed burial. The ecological role of the coarse seed-coat is probably due to an epizoochory seed-dispersal strategy that favours attachment to the coats of vertebrate animals (Couvreur *et al.*, 2004). In summary, the capacities of burial and dissemination by adhesion are incompatible, and might result from different selective processes.

Conclusions

Despite the fact that the seed bank tends to concentrate on the surface in the absence of soil tillage, as in natural ecosystems, its effective micro-distribution in the more superficial soil layers strongly depends both on soil texture and seed characteristics. Both of these factors determine rapidity and depth of burial. However, the depths reached by seeds distributed on the soil surface are in the region of a few millimetres, whereas typical depth-mediated germination inhibition occurs when seeds are buried centimetres in soil (Benvenuti *et al.*, 2001). Therefore, natural burial probably can play a role in germination only in cases of species with photosensitive seeds, as buried seeds still can perceive light through a few millimetres of soil (Benvenuti, 1995).

Despite clay soil being the least suitable for penetration by weed seeds, it still may foster persistent seed banks. Other physical conditions can compensate for limited seed burial by inhibiting germination rates or promoting dormancy (Benvenuti and Macchia, 1995) via the low oxygen diffusion typical of clay soils (Benvenuti, 2003). In these cases, there are relatively low levels of emergence in the field (Leblanc *et al.*, 2004), thereby preventing seed-bank losses.

In general, the no-till method likely favours the development of younger seed banks, irrespective of soil texture. The lower degree of depth-mediated inhibition in no-till may increase the percentage of active seed bank, thereby reducing the amount of older seeds. Besides the limited distance from the soil surface of the naturally buried seed bank, there is also the favourable contact with oxygen, which is one of the main factors involved in ageing and loss of vitality in seeds (Hendry, 1993). The present observations are consistent with the hypothesis that the absence of soil tillage can reduce the mean age of the viable seed bank.

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