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The fate of *Datura ferox* seeds in the soil as affected by cultivation, depth of burial and degree of maturity

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SUMMARY

Seeds of *Datura ferox* were collected in soybean fields, grouped into four categories according to the degree of fruit maturity and placed just level with the soil surface or buried to a depth of 7 or 15 cm. Seed survival after 8 months was *c.* 30% when the seeds were left on the soil surface, but between 40 and 90% when the seeds were buried. The riper seeds were the more persistent. A similar pattern was observed after 20 months. Seedling emergence was negatively related with the degree of seed maturity and depth of burial, but it was never great enough to explain seed losses.

In another experiment seeds from ripe capsules were superficially sown and the soil was: (0) left undisturbed, (1) cultivated in late winter or (2) cultivated in late winter and late spring. In all cases there was a small flush of seedlings at the beginning of the first spring; other flushes occurred only after soil cultivation and were larger during the second spring than during the first. In the plots cultivated twice a year (2) the seedlings that emerged in the first spring represented *c.* 4% of the initial seed bank. Survival after 20 months was about 25% in all treatments. In an arable field under soybean cropping the seedling flushes during the spring months were related to the pattern of soil cultivation. The seedlings that emerged after crop drilling represented *c.* 18% of the seed bank (estimated before drilling). Implications for weed management are discussed.

INTRODUCTION

Datura ferox L. (Solanaceae), a troublesome weed of soybean crops, is propagated solely by its seeds. Seeds show germination blockage when the capsules reach ripeness in late autumn and previous studies with this species have shown a connection between inhibitors and seed dormancy (Soriano, Sánchez & Eilberg, 1964; Burkart & Sánchez, 1969; De Miguel, 1980; Sánchez, De Miguel & Eyherabide, 1981). Seeds buried in the soil lose their dormancy sooner than those kept in dry storage (Soriano, Eilberg & Suero, 1971; Adámoli, Goldberg & Soriano, 1973) or on the soil surface (Soriano *et al.*, 1971). Adámoli *et al.* (1973) suggested that seed imbibition is a fundamental factor in the breakage of dormancy. In agreement with this hypothesis it was found that dormancy can be broken rapidly if the seeds are stored in a water-saturated atmosphere (De Miguel & Soriano, 1974) and, during this treatment, a reduction in the level of endogenous inhibitors was observed (De Miguel, 1980).

Both seed mortality and germination are important variables in the construction of demographic models of plant populations (e.g. Cavers, 1983). In the case of *D. ferox*, little is known about the dynamics of seed banks under field conditions. Early studies (e.g. Soriano *et al.*, 1971) have suggested that seeds of *D. ferox* depend on burial for dormancy breakage, but it is not known to what extent this conclusion is independent of the degree of maturity attained by the seeds which, on the other hand, is regulated by the length of the crop cycle. Only rough estimations are available of seed mortality in the soil. The experiments described here were carried out in order to investigate the effects of cultivation system, depth of burial and degree of seed maturity on seed survival and germination.

MATERIALS AND METHODS

Seeds of *Datura ferox* were collected in soybean fields in Rojas province of Buenos Aires (34° 06′ S and 60° 25′ W). Seeds were grouped into four categories according to the degree of fruit maturity (Table 1). Seeds were soaked for 48 h and given a saturating pulse of red light, then the seeds were incubated in darkness under alternating temperatures – 20°C/15 h, 30°C/9 h (for details, see Sánchez *et al.*, 1981). Germination percentages were recorded after 7 days and viability of ungerminated seeds was checked using the tetrazolium chloride method (Moore, 1972).

Expt 1

Seeds were buried in recently-cultivated soil in Luján, province of Buenos Aires (34° 37′ S and 59° 10′ W) on 25 July 1984. Baskets of 12 cm diameter × 20 cm made with 1 cm-plastic mesh fabric were introduced into holes dug in the field and filled with soil up to 15, 7 or 0·5 cm from the ground surface. Seeds were carefully distributed into the baskets and soil was added up to 0·5 cm from the ground surface level for the deeper sowings (15 and 7 cm). The number of seeds introduced per basket was adjusted for each category to give 100 viable seeds. Experimental design was a factorial combination of degree of maturity (4), depth of burial (3) and duration of burial (2), with three replicates per treatment. Seedlings were counted periodically and removed. Half of the baskets were collected after 8 months (first autumn), and half after 20 months (second autumn). Seeds were recovered manually and their viability was tested as indicated above.

Expt 2

In the same field, nine experimental plots (1 m × 1 m) were sown on 25 July 1984 with 1000 seeds belonging to category C and (0) left undisturbed, (1) cultivated once a year (in late winter) or (2) cultivated twice a year (in late winter and late spring). Cultivations were

Table 1. *Characteristics of the seeds of* Datura ferox *used in the experiments. Four samples of 50 seeds each were used for seed tests*

Seed category	Date of collection	Characteristics of the fruit	Germination* (%)	Viability** (%)
A	7 May 1984	green, closed F.W. ≤20 g	5	60
B	7 May 1984	green, closed F.W. >20 g	1	81
C	7 May 1984	green, partially open	0	94
D	28 June 1984	yellowish, partially open	0	93

* Calculated as (G/T) × 100; ** calculated as [(G + Z)/T] × 100, where G = number of germinated seeds, Z = number of non-germinating seeds classed as viable in the tetrazolium test; and T = total number of incubated seeds.

undertaken to a depth of *c.* 18 cm with a reversible 12-inch mouldboard plough followed by a rotary cultivator. Seedlings of *D. ferox* were counted periodically and removed. Twenty months after the experiment started five 25 cm × 25 cm × 20 cm deep soil samples were taken in each plot for seed density evaluation. Each sample was cut into two sections, 10 cm thick, and processed as in Expt 1. Cultivations produced some displacement of seeds in the horizontal plane. The horizontal distribution of seedlings was assumed to reflect that of the seeds in the soil bank. Therefore, to calculate the actual size of the seed bank in the case of the cultivated plots, the value obtained from soil sampling was corrected by using the proportion of seedlings emerged outside the original boundaries of the plots.

Seedling emergence in a soybean field

In a commercial field in Rojas a 60 m^2 area heavily infested with *D. ferox* was defined after soybean harvest on June 1984. During the period of observation the area was managed in the same manner as the rest of the field; cultivated with a disc harrow on 6 August and ploughed on 28 September and on 20 November for seed bed preparation. Seedling density was determined periodically in 40 quadrats (0·7 m × 0·7 m) placed in the area at random; after each assessment all the seedlings present in the plot were removed. Seed bank density was estimated in November (before sowing soybean) with 25 soil samples taken in the area at random. Each sample consisted of four 12 cm diameter × 20 cm cylinders of soil. The sampling method was as described in Van Esso, Ghersa & Soriano (1986). Seed recovery and seed tests were done as indicated above.

RESULTS

Expt 1

There was a large effect of both burial and degree of seed maturity on seed survival in the soil (Table 2). When seeds were kept on the soil surface for 8 months, less than one third of the original seeds were recovered (Fig. 1*a*). Seed decline was much less when seeds were buried at 7 or 15 cm (Fig. 1*b, c*). Seed survival was positively related to the degree of seed maturity (Fig. 1*a-c*; Table 2). In no case was seedling recruitment large enough to explain seed losses. Seeds from unripe capsules (categories A and B) produced significantly more seedlings than those from completely ripe fruits when seeds were kept on the soil surface (Fig. 2*a*; Table 3), but even in this case, no more than 20% of the original seeds gave rise to seedlings. Seeds buried to a depth of 7 cm produced only a few seedlings (Fig. 2*b*) and those buried at 15 cm did not produce any.

Recovery of viable seeds decreased after 20 months (Table 2). The general pattern of seed survival paralleled that of the first sampling (Fig. 1*d-f*), and it is remarkable that nearly all seeds from completely ripe fruits were still present 20 months after they were buried. No seedlings appeared in this second period of observations.

Table 2. *Factorial analysis for data of seed survival* (*Treatment means are given in Fig. 1*)

Source of variation	D.F.	F	P
Sampling (8–20 months); S	1; 48	4·4	<0·05
Depth (0–7–15 cm); D	2	34·6	<0·001
Degree of seed maturity; M	3	7·5	<0·01
S × D	2	<1	>0·05
S × M	3	<1	>0·05
D × M	6	1·1	>0·05
S × D × M	6	1·5	>0·05

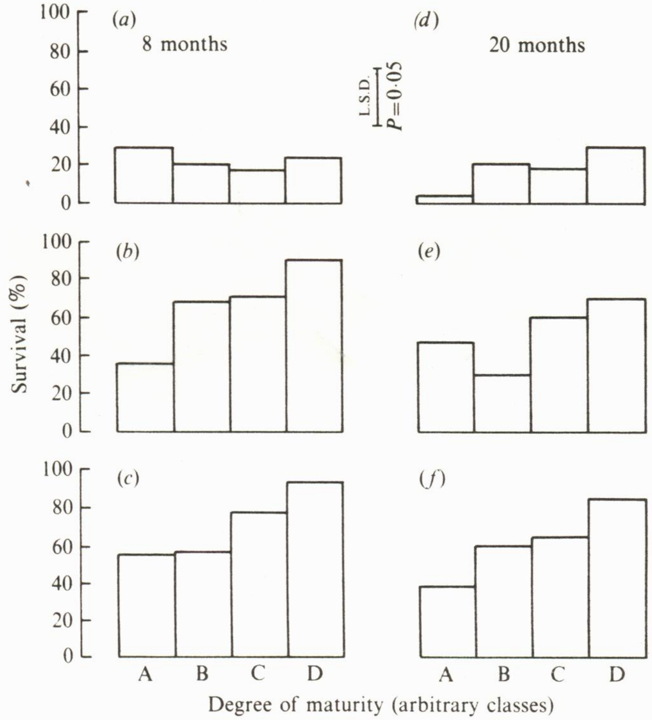

Fig. 1. The influence of degree of seed maturity and depth of burial on seed survival. (*a* and *d*) seeds left on the soil surface; (*b* and *e*) seeds buried at 7 cm; (*c* and *f*) seeds buried at 15 cm (Expt 1).

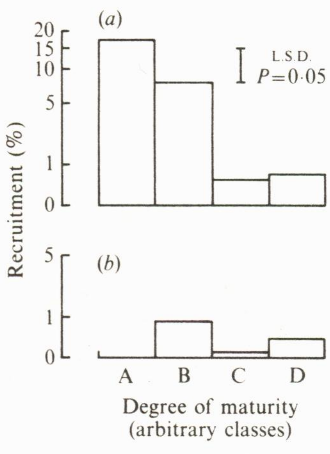

Fig. 2. The influence of degree of seed maturity and depth of burial on the proportion of seeds that gave rise to seedlings during the first 8 months (Expt 1). (*a*) seeds left on the soil surface; (*b*) seeds buried at 7 cm.

Expt 2

In the experimental plots seedling emergence was clearly associated with soil cultivation. In all cases there was a small flush of emergence at the beginning of the first spring (late September and October). Other flushes occurred only following soil cultivation and were larger during the second spring than during the first (Fig. 3). In plots cultivated twice a year,

Table 3. *Factorial analysis for data of seedling emergence (Treatment means are given in Fig. 2). The numbers of seedlings (x) were transformed by ln (x+1) before analysis*

Source of variation	D.F.	F	P
Depth* (0–7 cm); D	1; 40	63·2	<0·001
Degree of seed maturity; M	3	17·0	<0·001
D × M	3	15·3	>0·001

* The third level of the factor 'depth' was omitted in the analysis since no seedlings emerged from seeds buried at 15 cm.

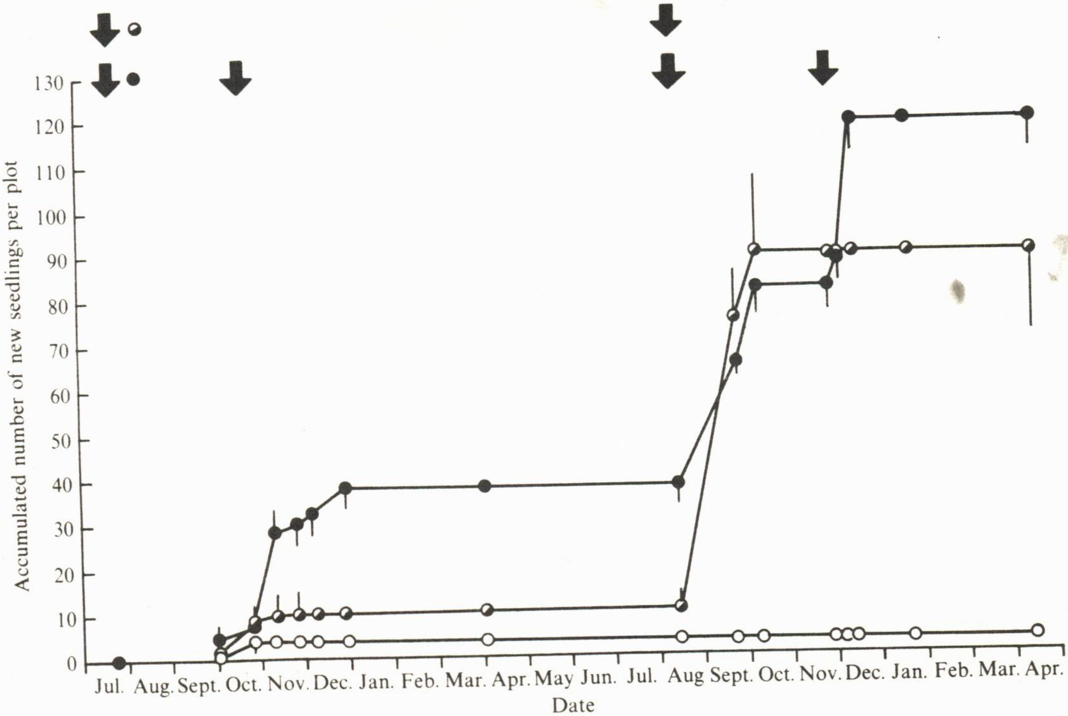

Fig. 3. Seedling emergence in the experimental plots (Expt 2). Treatments were : (○) no tillage; (◑) ploughed once a year and (●) ploughed twice a year. Arrows indicate dates of ploughing, thin bars represent ±1 s.e.m. (n = 3).

in a sequence which resembles the tillage system of a soybean/soybean rotation, 3·6% of the original seeds gave rise to seedlings in the first spring. Seed survival after 20 months was 23, 21 and 28% for uncultivated, with one cultivation and with two cultivations per year systems respectively (Table 4). All the seeds were in the 0 – 10 cm horizon in the uncultivated plots; in the cultivated plots the seeds were also unevenly distributed in the soil profile (Table 4).

Field observations

In the field, seedling emergence began in early October, during fallow, and ceased 1 month later (Fig. 4). In the surveyed area there were *c.* 80 seeds m^{-2} after ploughing before sowing the crop. Most of these seeds germinated in the laboratory after exposure to red light and under alternating temperatures (Table 5). Another flush of seedling emergence began soon

Table 4. *Seed recovery after 20 months and vertical distribution of seeds in Expt 2. Standard deviations are given in parentheses*

	No tillage	Ploughed* once a year	Ploughed* twice a year
Recovery (seeds per plot)	231 (138)	214 (10)	284 (81)
seed density (0–10 cm) / seed density (10–20 cm)	1:0	7·5(±2·6):1	1·7(±0·2):1

* Actual figures of seed density were multiplied by the ratio between the total number of seedlings emerged and the number of seedlings emerged within the original boundaries of the plots.

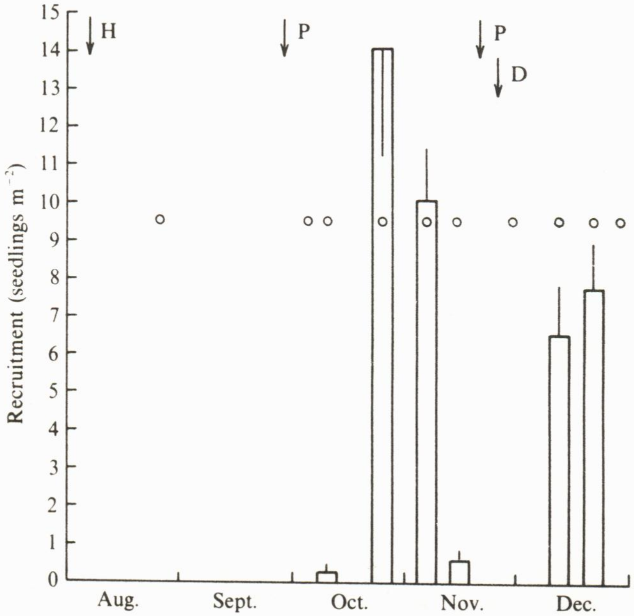

Fig. 4. Seedling emergence in the field. H: cultivated with a harrow disc; P: ploughed; D: soybean drilling; (○) counting. Thin bars represent ±1 s.e.m. (n = 40).

Table 5. *Number and physiological condition of* D. ferox *seeds in the soil immediately before soybean drilling (late November)*

Depth	Seed density (m^{-2})* L.L.	$\bar{X}$	U.L.	Germination (%)†	Viability (%)†
0–6	(18·1)	37·8	(62·6)	86	98
6–12	(10·7)	22·7	(37·3)	85	94
12–18	(9·8)	19·9	(32·1)	93	100
Total	(38·6)	80·4	(132·0)		

* Raw data (x) were transformed by $\sqrt{x + 0{\cdot}5}$ before analysis; backtransformed means are presented and lower and upper 95%-confidence limits are given between brackets (n = 25).

† Calculated as explained in Table 1 over the total number of seeds recovered from each depth.

after the soybean crop had been sown and ceased by late December (Fig. 4). These seedlings represented 18% of the seeds present in the soil bank in late November.

DISCUSSION

Seed germination

Both degree of maturity and cultivation affected seed behaviour in the soil. The riper seeds produced more seedlings when the soil was cultivated (Fig. 3) than when they were either kept on the soil surface (Figs 3 and 2*a*) or buried at a constant depth (Fig. 2*b*). The stimulatory effect of simulated cultivations has been reported previously for *D. ferox* (Soriano *et al.*, 1971) and other weed species (Chancellor, 1964; Wesson & Wareing, 1969; Roberts & Potter, 1980; Roberts, 1984; Froud-Williams, Chancellor & Drennan, 1984). Cultivations can incorporate seeds into the soil where continuous imbibition accelerates the rate of loss of dormancy (Adámoli *et al.*, 1973; De Miguel & Soriano, 1974) or alternatively bring seeds with a low degree of dormancy to the surface soil. Near the soil surface, temperature fluctuations and light, both known to stimulate *D. ferox* germination (Soriano *et al.*, 1964; Burkart & Sánchez, 1969), might fulfil germination requirements. This view is consistent with the results of germination tests (Table 5), and also with the clear association between seedling flushes and soil disturbance observed in Expt 2 (Fig. 3) and in the field (Fig. 4). Loss of dormancy of buried seeds is also suggested by the observation that, as reported by Soriano *et al.* (1971), greater seedling emergence occurred in the second spring than in the first (Fig. 3). Wilson (1985), who buried seed populations of *Avena fatua* in successive years, so that the behaviour of different aged populations could be compared in the same season, also noted that most spring emergence occurred in the second spring after sowing.

When seeds were buried and left undisturbed they produced virtually no seedlings (Fig. 2*b*). The high rate of recovery after 20 months (Fig. 1*e, f*) indicated that germination of the riper seeds remained blocked in the deeper horizons. However, in the case of the unripe seeds, low recruitment could have been a consequence of post-germination mortality. A lower degree of primary dormancy of the unripe seeds is suggested by the observation that some of them produced seedlings when maintained on the soil surfrace (Fig. 2*a*).

Even in the plots cultivated twice a year the seedlings represented only a small percentage (*c.* 4% in the first spring) of the seed bank. This figure is in accord with previous reports for other species (Roberts & Ricketts, 1979; Roberts, 1984) but is considerably lower than that observed in the soybean crop (*c.* 18%). This discrepancy could reflect the fact that the natural seed bank has a more heterogeneous population with regard to the degree of seed maturity and seed age.

Seed survival

Seed stocks declined fairly rapidly when kept on the soil surface (Fig. 1*a, d*). It is clear that losses of seeds by successful germination could not account for this fact (Fig. 2*a*). Lateral migration of seeds can be discarded as a source of seed losses since recovery of viable seeds was very similar in both baskets and plots, in spite of their contrasting edge:area ratio (Fig. 1*d* and Table 4).

Among the remaining possibilities are unsuccessful germination and seed predators. The latter is strongly suggested by the fact that in a previous trial (Soriano *et al.*, 1971) where the seeds were placed at the soil surface in cylinders lined with nylon cloth seed losses were substantially lower.

Seed decline was also important in cultivated plots; assuming an exponential pattern of decrease (Roberts & Feast, 1973*a, b*) the annual loss of viable seeds was about 50%. Similar rates were observed in cultivated land for other annual weeds (Roberts & Feast, 1973*b*;

Wilson, 1985). The number of seedlings emerged did not explain such losses. On the other hand, results from Expt 1 (Fig. 1*b, c, e, f*) showed that, as has been reported previously for *Avena fatua* (Wilson, 1981), *Alopecurus myosuroides* (Moss, 1985) and other arable weeds (Froud-Williams *et al.*, 1983), seed survival was greater when the ripe seeds were initially buried and then left undisturbed. It is possible that after cultivation seeds were encouraged to germinate but seedlings subsequently died before emerging, as suggested by Roberts & Potter (1980) and Roberts (1984).

Implications for weed management

The results show that in a programme aimed to control *D. ferox*, seed burial at the end of the growing season is not an adequate practice, especially if the weed seeds are allowed to complete ripeness in the previous crop (Fig. 1). Either the delay of ploughing until the beginning of the next spring coupled with minimal cultivation prior to sowing the crop, or even the complete avoidance of soil inversion, seem to be more rewarding strategies. These systems could maximise seed losses from the soil bank (Fig. 1) and also reduce the numbers of seedlings emerging within the crop cycle (Fig. 3).

With an annual decline for the seed bank similar to that observed in intensively cultivated soil (*c.* 50% per year, Expt 2), a demographic model predicted a steady increase of the population of *D. ferox* in a conventional soybean/soybean rotation (Ballaré, Scopel, Ghersa & Sánchez, 1987*b*). This result, and the observation that most seedling emergence occurred in the second spring after sowing (Fig. 3, and Soriano *et al.*, 1971), emphasises the importance of preventing new additions of seeds to existing reserves. Among the strategies available to achieve this objective are: (a) the adoption of cultivation systems that minimise seedling emergence during the crop cycle (e.g. avoiding soil inversion), (b) the use of effective herbicides, and (c) the elimination of a large proportion of seeds during crop harvesting. The simulations quoted above assumed a seedling control efficiency of 95%. This is now a common value in commercial soybean crops in Argentina (Ballaré *et al.*, 1987*a*), but higher efficiencies seem to be difficult to achieve at a reasonable cost. Combine-harvesters, on the other hand, can collect more than 90% of the fruits of *D. ferox*, but a widely variable proportion of the seeds are returned to the ground (Ballaré *et al.*, 1987*a*). It appears, therefore, that slight modifications in the cleaning units of the machines may be very valuable for controlling the annual input of seeds to the soil reserves.

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