

Dormancy patterns in buried seeds of *Datura ferox* and *D. stramonium*

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Seasonal changes in seed dormancy of *Datura ferox* L. and *D. stramonium* L. were studied during 2 years in seeds buried in the field and compared with changes in dormancy of dry-stored seeds. Dormancy levels were evaluated by measuring the germination of exhumed and dry-stored seeds under 32:27°C (nondormant seeds) or 32:12°C (relatively dormant seeds). Levels of relative or full dormancy did not change during 2 years of dry storage in either species. Seed burial at 20 cm accelerated after-ripening, and primary dormancy disappeared earlier than at 5 cm. However, burial depths greater than 10 cm prevented germination in situ. This inhibition was not due to smaller daily fluctuations of soil temperature with increasing depth, since seeds buried at 20 cm and kept at 32:12°C also failed to germinate. Transferring seeds to shallower soil layers allowed their germination. Cyclic seasonal changes in dormancy were found in buried seeds of *D. ferox* but not in *D. stramonium*. In *D. ferox*, dormancy was alleviated during the winter and germinability was maximal in early spring; the increase in dormancy was preceded by high late spring - summer temperatures. In *D. stramonium* most seeds near the soil surface germinated in the field in a brief flush in early winter, at temperatures under which *D. ferox* did not germinate.

Key words: *Datura*, germination, dormancy, buried seeds, temperature.

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Les auteurs ont comparé les changements saisonniers dans la dormance des graines de *Datura ferox* L. et de *D. stramonium* L. pendant 2 ans, en observant des graines enterrées au champs et des graines conservées au sec en laboratoire. Le degré de dormance a été évalué en mesurant la germination de graines exhumées et de graines gardées au sec à 32:27°C (graines non dormantes) et 32:12°C (graines relativement dormantes). Chez les graines des deux espèces conservées au sec, le degré de dormance totale ou relative n'a pas varié beaucoup au cours des deux années de conservation. Chez les graines enterrées à 20 cm, la post maturation est plus rapide et la dormance primaire disparaît plus tôt que chez celles enterrées à 5 cm. Cependant, l'enfouissement à une profondeur supérieure à 10 cm empêche la germination in situ. Cette inhibition ne peut être reliée à de plus petites fluctuations de la température quotidienne du sol avec l'augmentation de la profondeur, puisque les graines enterrées à 20 cm et conservées à 32:12°C n'arrivent pas non plus à germer. Le fait de transférer ces graines à des couches de sol plus superficielles déclenche leur germination. On trouve des variations cycliques dans les changements de dormance chez les graines enterrées du *D. ferox* mais non chez celles du *D. stramonium*. Chez le *D. ferox*, la dormance diminue pendant l'hiver et la germinabilité atteint un maximum de bonne heure au printemps, alors que l'augmentation de la dormance fait suite aux hautes températures de la fin du printemps et de l'été. Chez le *D. stramonium* la plupart des graines voisines de la surface du sol germent sur le champ au cours d'une brève période au début de l'hiver à des températures au dessous desquelles le *D. ferox* ne peut germer.

Mots clés : *Datura*, germination, dormance, graines enterrées, température.

[Traduit par la Rédaction]

Introduction

Datura ferox L. and *D. stramonium* L. are troublesome annual weeds of summer crops. In recent years field infestation by these species is increasing all over the world (Ballare *et al.* 1987; Weaver 1986). In Israel, *D. ferox* in particular contaminates irrigated cotton fields, where its eradication is extremely difficult. As in other annual weeds that reproduce only by seed, the success of *D. ferox* and *D. stramonium* as weeds is determined by seed persistence in the soil, which in turn is related to the rate of seed decay and to the adaptive seasonal changes in the level of seed dormancy in the field. It is well known that buried seeds of several summer and winter annuals go through an annual cycle of decreased and increased dormancy periods (Baskin and Baskin 1985; Karssen 1982). In the summer annuals, dormancy is alleviated during the winter, and secondary dormancy is induced during the autumn. Thus,

seedlings emerge during spring and early summer (Baskin and Baskin 1980, 1989; Courtney 1968; Karssen 1980-1981). Although the adaptive significance of these seasonal changes in seed dormancy is evident, the identity of the factors inducing the gradual changes in seed dormancy in the soil is less clear. Usually, these changes are attributed to the seasonal variation in temperature (Karssen 1980-1981). On the other hand, germination of the nondormant seeds may also show temporal patterns that are related to seasonal variation of different limiting environmental factors, such as temperature (King 1966; Thompson and Grime 1983), soil moisture and precipitation regime (Stoller and Wax 1973), or factors such as cultivation practices (Soriano *et al.* 1968) and burial depth (Holm 1972).

In the case of *D. ferox* and *D. stramonium*, information on the fate of buried seeds, seasonal patterns of dormancy, and the relationship between emergence and environmental conditions in the field is relatively scarce (Soriano *et al.* 1970;

Adamoly *et al.* 1974; Stoller and Wax 1973, 1974). However, this information is a prerequisite for the formulation of integrated efficient management programs for their control. Thus, in this work a comparative study was carried out on the germination of seeds of both *Datura* species that were buried in the field or under controlled environmental conditions.

Our objectives were (i) to describe the seasonal pattern of *Datura* seedling emergence in infested fields, in relation to the size of the seed bank; (ii) to examine their ability to emerge from increasing depths of burial; (iii) to study dormancy changes in seeds buried at different depths; and (iv) to examine the effects of simulated cultivation on the behaviour of seeds.

Materials and methods

Ripe fruits of *Datura ferox* L. and *D. stramonium* L. were harvested in cotton fields near Palmachim and Kvutzat Yavne (coastal plain of Israel) during November 1984. Mature (black) seeds were stored in open containers at room temperature.

Field experiments

Field experiments were conducted in a cotton field at Kvutzat Yavne. The soil is a heavy aluvium (clay 43%, silt 22%, and sand 35%) with 6% lime. Data on temperature and precipitation were obtained from the meteorologic station at Kvutzat Yavne.

Seedling emergence of *D. ferox* was followed during April–August 1985 in a cotton field in which wheat had been grown in the previous winter. No herbicides were applied before cotton sowing. Emergence was observed in 13 plots (2 m long × 1 m wide) located between the cotton rows. Seedlings were counted every 2 weeks. The seed bank was sampled in nine plots at the end of the crop season, before the onset of seed dispersal by *D. ferox*. Ten samples, 10.5 cm in diameter and 10 cm in depth, were taken randomly from each plot. The total area sampled from each plot was 865 cm². Each sample was washed with running water to recover nongerminated seeds. Based on these data the number of seeds/m² was calculated. The recovered seeds were placed on two layers of filter paper in 9-cm Petri dishes with 7 mL of deionized water (pH 7) and germinated under the optimal conditions of 30:20°C (12 h : 12 h) and continuous illumination from fluorescent cool white (Sylvania) lamps, providing 80 μE m⁻² s⁻¹ at Petri dish level. Data on emergence and seed-bank size of individual representative plots are presented.

Phytotron experiments

Experiments under controlled conditions were performed in the Phytotron of the Faculty of Agriculture, The Hebrew University of Jerusalem, Rehovot (Ofir and Koller 1974). Germination was carried out under daily thermoperiods of 32:27°C or 32:12°C and long days (LD, 16 h). Seeds were sown in drained plastic pots filled with soil from Kvutzat Yavne, at depths of 5 cm (20 × 20 × 7 cm pots) or 20 cm (15 × 15 × 25 cm pots). Pots were randomly arranged under the different conditions and watered once a day. Seedling emergence was recorded every 2 days. Since no germination was observed at the 20-cm depth, germinability of seeds recovered after washing the soil was determined 3 weeks after sowing in Petri dishes kept in light at 30:20°C.

Burial experiments

In all burial experiments seeds of *D. ferox* and *D. stramonium* were sown between 13 and 23 January 1985 in wire-net trays (20 × 20 × 5 cm), on a 1-cm layer of soil, and buried in the field-experiment plot (20 × 30 m) at the indicated depths. The number of seeds in each tray was 100 and 150 for *D. ferox* and *D. stramonium*, respectively. Seedling emergence was recorded every 2 or 4 weeks.

Dormancy changes of buried seeds

Sixty wire-net trays with seeds of each species were buried at a depth of 5 or 20 cm, respectively, and exhumed at monthly intervals

until January 1987. At each exhumation three trays, randomly selected for each species and burial depth, were taken out, placed in drained plastic pots (20 × 20 × 7 cm), and transferred to the Phytotron with a thermoperiod of 32:27°C and LD. Care was taken not to break the soil cores to avoid seed exposure to light. In cores taken from the 20-cm depth the upper layer of soil was removed so that the final soil cover thickness was 5 cm. After 1 month at 32:27°C the pots were transferred to more extreme alternating temperatures (32:12°C) for another month. At each exhumation date dry seeds stored under room conditions were sown as controls at the 5-cm depth in similar plastic pots containing soil. The controls remained for 2 months under 32:27°C or 32:12°C, or for 1 month in 32:27°C before transferring them to 32:12°C for another month. Trays containing seeds buried in the field or dry-stored sown seeds were randomly arranged during exposure to the different conditions in the Phytotron. At the end of the 2 months of treatment the soil was washed with running water to retrieve the seeds. Seeds missing from buried-sown seeds were defined as nonviable seeds that decayed in the field or in the Phytotron during the experiment. Germination percentages were calculated out of the total number of viable seeds (e.g., those seeds that germinated in the field or in the Phytotron, or were ungerminated but hard and intact at the time of exhumation).

Simulation of cultivation

Seeds were sown in wire-net trays at the end of January 1985. The trays were buried in the field so that the seeds were covered with 1 or 20 cm of soil. Ten and 19 months following burial (October 1985 and July 1986, respectively), five randomly selected trays of each species were exhumed from the 20-cm depth and reburied at 1-cm depth. Seedling emergence was recorded. Ungerminated seeds were recovered by washing at the end of the experiment, and the germination percentage was calculated out of the total number of viable seeds buried in each tray.

Effect of burial depth on emergence

Seeds were buried at depths of 1, 2.5, 5, 7.5, 10, 15, and 20 cm in wire-net trays as described above. A randomized block design was used in this experiment, with three replicates. Emergence percentages were calculated out of the total number of buried seeds.

Seed weight

Seed coats were carefully removed with thin forceps. Dry weights of decoated and intact seeds were determined in three replicates of 10 seeds each, after drying at 80°C in a forced-air oven for 24 h.

Statistical analysis

All data on percent germination or seedling emergence were arcsin transformed before statistical analysis. Data from the burial depth experiment were subjected to analysis of variance (ANOVA).

Results

Patterns of *D. ferox* emergence

The pattern of seedling emergence in *D. ferox* and its relationship to the size of the seed bank was examined in 1985, from April through August, in an infested cotton field (Fig. 1). Great variability was found among plots in the number of seedlings emerged per unit area. Thus, emergence in each plot was expressed as a percentage of the total number of seedlings emerged during the season. Patterns of seedling emergence were quite uniform and occurred in well-defined waves in all plots. The first and largest wave occurred from the end of April to mid-May, shortly after the first irrigation and was followed by two smaller waves, each after consecutive irrigations. Seedling emergence stopped at the end of July, even though irrigations continued. The size of the seed bank varied greatly between plots (Fig. 2). The number of intact seeds that were found in the upper 10-cm layer at the end of the crop season varied between 70 and 3222 seeds/m².

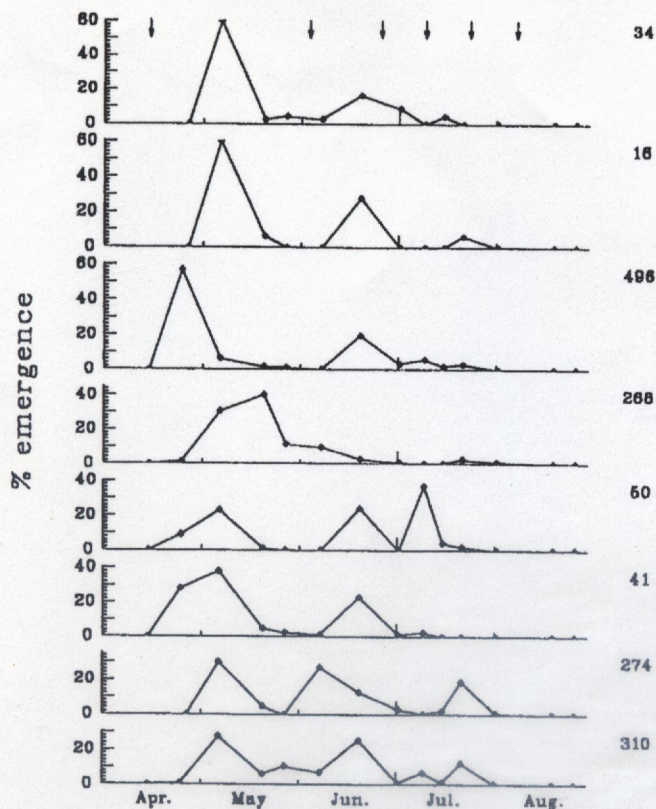


FIG. 1. The time course of emergence of *D. ferox* seedlings in a cotton field during the crop season (1985). Results are from eight different representative plots. Total sum of seedlings emerged per square metre in each plot during the season is at the right of each graph. Time of irrigation is indicated by arrows.

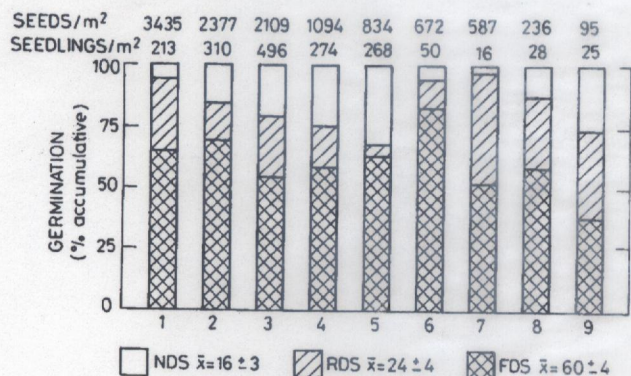


FIG. 2. Distribution of level of dormancy in the seed bank of *D. ferox* at the beginning of the cotton growth season (1985). Each column represents one plot. Seeds/m² was measured as emerged seedlings plus ungerminated viable seeds found at the end of the season per square metre. NDS, nondormant seeds emerged in the field during the season; RDS, relatively dormant seeds germinated under optimal germination conditions (30:20°C, light); FDS, fully dormant seeds that did not germinate in the field nor under optimal germination conditions.

Germination of *Datura* seeds is enhanced by daily alternations of temperatures with amplitudes greater than 5°C (O. Reisman-Berman, unpublished data). Thus, by germinating the seeds recovered from the sampled soil cores under optimal conditions (30:20°C, light), it was possible to divide the

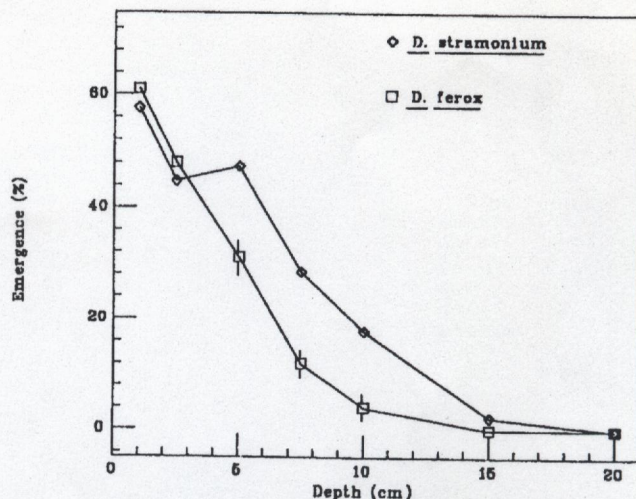


FIG. 3. The effect of burial depth on the emergence of *D. ferox* and *D. stramonium* seedlings. Emergence was recorded in the field from the date of sowing (January 1985) to January 1987. Values are the average of three replicates. Bars indicate SE.

TABLE 1. Seed weight of *D. ferox* and *D. stramonium*

	<i>D. stramonium</i>	<i>D. ferox</i>	Ratio ^a
Intact seeds (mg)	11.7 ± 0.5	15.5 ± 0.5	0.76**
Decoated seeds (mg)	5.1 ± 0.5	7.5 ± 0.5	0.68*
Seed coat (%)	56.3	50.4	1.12

^aRatio of *D. stramonium* to *D. ferox*. Values are means ± SE of three replicates of 10 seeds each. * and ** indicate significant differences (Student's *t*-test) at *P* = 0.05 and *P* = 0.01, respectively.

TABLE 2. Germination (mean ± SE) of dry-stored *D. ferox* and *D. stramonium* seeds as affected by different temperature regimes

Burial depth ^a (cm)	Temperature ^b (°C)	Germination (%)	
		<i>D. ferox</i>	<i>D. stramonium</i>
5	32:27	11 ± 2	5 ± 2
5	32:12	68 ± 5	63 ± 7
20	32:27	2 ± 1	2 ± 1
20	32:12	13 ± 2	2 ± 1

^aNo significant (*P* = 0.05) differences in germination at 5 cm were found during 22 months of dry storage, and the results from monthly sowings were pooled for each temperature treatment (e.g., 22 × 3 replicates). At 20-cm depth, seeds were tested after 22 months of dry storage, with 4 replicates for each treatment.

^bEach temperature treatment lasted 2 months.

viable soil-seed population at the beginning of the season into three subpopulations (Vegis 1964; Harper 1982): (i) nondormant seeds (NDS): seeds that germinated and emerged during the season; (ii) relatively dormant seeds (RDS): potentially nondormant seeds that germinated under optimal conditions, but they did not germinate during the season in the field (seeds with conditional or enforced dormancy); and (iii) fully dormant seeds (FDS): viable seeds that did not germinate, even under optimal conditions (innately dormant seeds).

This estimation of the seed bank at the beginning of the cotton season is based only on the persisting viable seeds and does not include seeds that decayed during the season. A large proportion of the seed bank was fully dormant at the end of the season, and this proportion was relatively constant for the different plots (60 ± 4%). However, the proportion of RDS

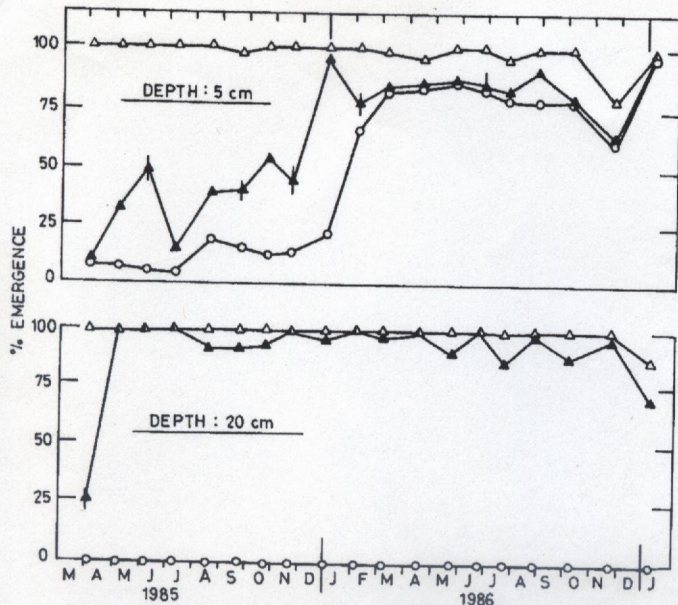


FIG. 4. Time course of dormancy changes in seeds of *D. stramonium* buried in January 1985 at 5 or 20 cm. O, accumulated emergence percentages in the field until the time of exhumation and transferring to the Phytotron. The exhumed seeds remained in the Phytotron for 1 month under daily thermoperiods of 32:27°C (▲) and then were transferred to 32:12°C for another month (△). Values are the average of three replicates. Bars indicate SE.

and NDS varied greatly between plots (range of RDS: 8 to 48%). Thus, the great differences in emergence among plots were probably caused by two factors: (i) the absolute size of the seed bank, and (ii) differences in the level of relatively dormant seeds in the seed fraction that was not fully dormant. Similar observations have been reported on the dormancy and fate of *D. stramonium* seeds in the field (Stoller and Wax 1974).

Sowing depth and emergence

Seedling emergence decreased in both *Datura* species with increasing sowing depth ($F = 22.43$; $df = 5, 24$; $P = 0.001$), and no emergence occurred from depths below 10 cm (Fig. 3). However, *D. stramonium* had a larger ability ($F = 4.96$; $df = 1, 24$; $P = 0.035$) to germinate and to emerge from greater depths than *D. ferox*. This ability has been related to greater seed size (King 1966; Froud-Williams *et al.* 1984). However, this was not the case with *D. stramonium*, since its seeds are significantly ($P < 0.05$) smaller than *D. ferox* seeds (by 24 and 32%, for intact and decoated seeds respectively; Table 1). The proportion of seed coat from total seed weight was approximately the same in both species.

Dormancy changes in buried seeds

Time courses of seed dormancy in *D. stramonium* and *D. ferox* were studied in seeds buried in the field at 5- or 20-cm depths and compared with those in seeds that were dry stored under room conditions. Again, differences in the proportion of seeds that germinated in the Phytotron at 32:27°C or 32:12°C (small vs. large daily temperature alternations) were used as a qualitative indication of changes in dormancy level during burial or dry storage. In this case seeds that germinated in the field or shortly after transferring them to 32:27°C were considered as NDS, or as RDS if they germinated under

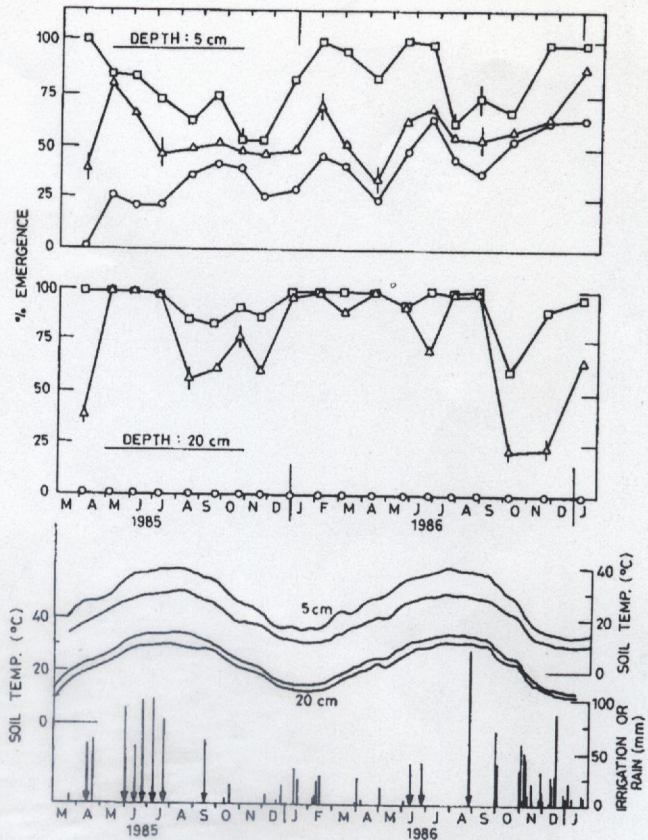


FIG. 5. Time course of dormancy changes in seeds of *D. ferox* buried on January 1985 at 5 or 20 cm depth. O, accumulated emergence percentages in the field until the time of exhumation and transferring to the Phytotron. The exhumed seeds remained in the Phytotron for 1 month under 32:27°C (△) and then were transferred to 32:12°C for another month (□). Values are the average of three replicates. Bars indicate SE. Maximal and minimal soil temperature at 5 and 20 cm, and amount of precipitation (bars) during the period 1985–1987 are shown at the bottom of the figure. Arrows indicate irrigation time, and their height represents amount in millimetres.

32:12°C. Viable seeds that did not germinate even under 32:12°C were considered as FDS.

Levels of relative or full dormancy of both *D. ferox* and *D. stramonium* did not change during 22 months of dry storage (Table 2). Under 32:27°C, germination of dry-stored seeds buried at 5- or 20-cm depths was very low. However, an increase in the daily temperature fluctuation to 32:12°C greatly promoted germination of seeds buried at 5 cm, but did not induce germination at those buried at 20 cm (Table 2). Contrary to the constant levels of dormancy observed in dry-stored seeds, different time courses of dormancy change were observed in seeds buried in the field during the same period (Figs. 4, 5). Seeds of *D. stramonium* buried at 5 cm remained relatively dormant for almost 11 months of burial, as indicated by low emergence in the field (<20%) and by the small enhancement of germination observed during this period after transferring to 32:27°C (20–30% additional germination (Fig. 4). However, the remaining seed fraction (about 60%) was not fully dormant, since the seeds completely germinated when transferred from 32:27°C to 32:12°C. Dormancy breakage in the field occurred during January 1986, as evidenced by the more or less simultaneous seedling emergence from 60 to 70% of the ungerminated buried seeds. The remaining frac-

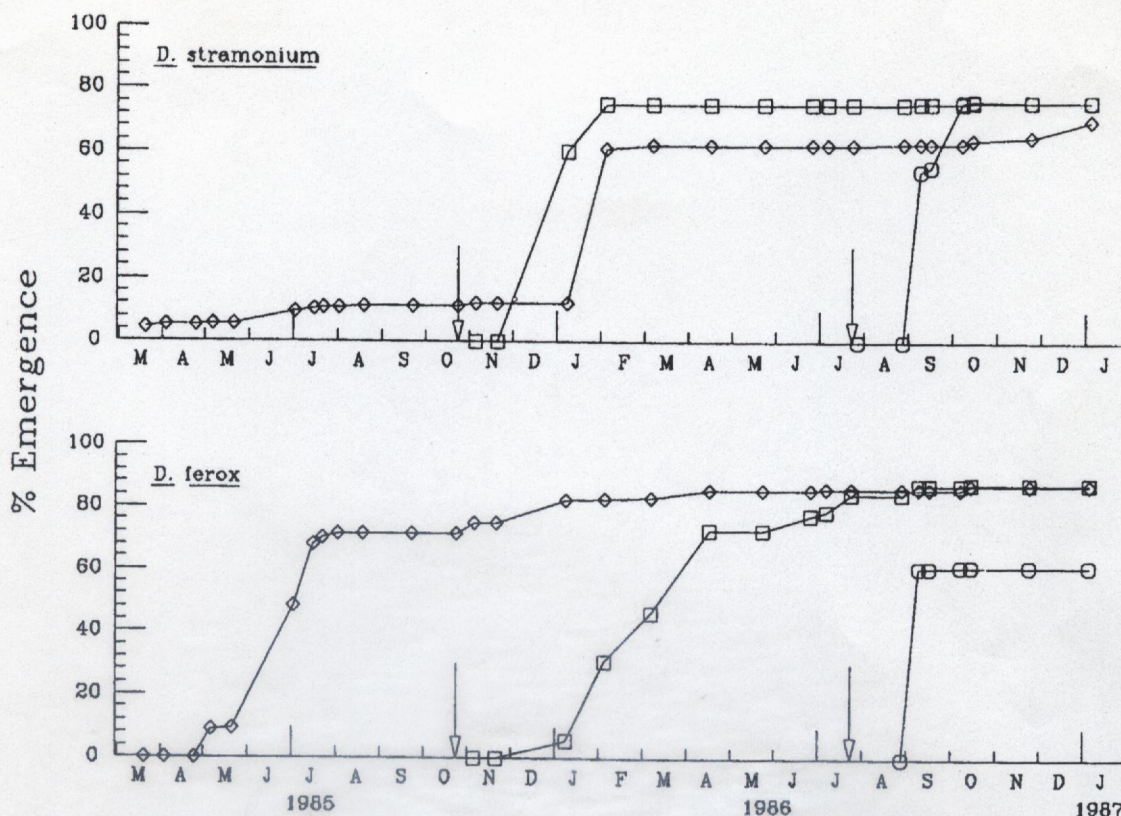


FIG. 6. Time course of seedling emergence from *D. ferox* and *D. stramonium* seeds buried at 20 cm, exhumed, and reburied at 1 cm, 10 (□) and 19 (○) months after initial burial (January 1985). ◇, emergence from seeds buried at 1 cm. Arrows show date of exhumation and reburial. Bars indicate SE.

tion (about 20%) remained relatively dormant and germinated if transferred to 32:12°C. In the field this fraction germinated during the following winter (January 1987). Thus, all the viable seeds of *D. stramonium* that were buried at 5 cm reached germination after 2 years of burial. On the other hand, seeds buried at 20 cm did not germinate at all during the 2 years of burial in the field (Fig. 3). However, these seeds were not dormant, since they fully germinated when transferred to 32:27°C or 32:12°C. In fact, during the first year of burial, seeds at 20 cm were even less dormant than seeds buried at 5 cm depth (Fig. 4). Furthermore, their level of relative dormancy decreased 3 months after burial compared with 11 months in seeds buried at 5 cm.

Seeds of *D. ferox* buried in the field at 5 cm were dormant for 4 months following burial (Fig. 5). Onset of emergence occurred in May 1985 and increased gradually, reaching 60% by the end of the experiment (22 months from burial). The initial gradual increase in emergence was concomitant with a decrease in the germination observed following the transfer to 32:27°C. After August 1985, the additional germination obtained under those conditions was very small (10% average). On the other hand, the fraction of the FDS showed a cyclic change with time. Germination under 32:12°C gradually decreased during the summer (after April 1985), reaching a minimum in the autumn (between October and November 1985). During the following winter, dormancy gradually disappeared. In the next summer (2nd year of burial), however, secondary dormancy was induced again, as shown by the increase in the fraction of FDS. This dormancy lasted from

July to October and disappeared again during late autumn and early winter.

Seeds buried at 20 cm did not germinate in the field, but they also showed cyclic changes in their dormancy level (Fig. 5). Three months after burial the seeds were still relatively dormant, and most of the seed population (about 60%) germinated only under extreme alternating temperatures (32:12°C). Dormancy breakage occurred after 4 months of burial, as indicated by the fact that all seeds germinated after transferring to 32:27°C. Secondary dormancy was induced at the same time as in seeds buried at 5 cm. Concomitantly with the reduction in germination of seeds planted at 5 cm, there was a great decrease in the germination at 32:27°C (ca. 40%) and a smaller decrease at 32:12°C (ca. 20%). During the 2nd year of burial, induction of secondary dormancy was delayed and dormancy was stronger, but it was maintained for a shorter time. Thus, contrary to *D. stramonium*, burial of *D. ferox* seeds in the field induced cyclic changes in their dormancy level. Dormancy level increased during the late summer months and autumn, and decreased during early winter. On the other hand, in both species, burial at 20 cm reduced seed dormancy but at the same time prevented germination.

A remarkable fact found in this experiment was that in both *Datura* species the proportion of missing (unaccounted) seeds out of the seeds buried in the field was relatively constant through the 22 months of the experiment (about 25 and 10% for seeds buried at 5 and 20 cm, respectively). Moreover, this proportion was similar to that recorded in the controls sown in the Phytotron at the different temperature treatments (about

15%). Thus, it probably represents the fraction of the nonviable seeds in our collections. This assumption is supported by the fact that ca. 15–20% of dry-stored seeds of both species did not germinate *in vitro* under conditions optimal for germination (O. Reisman-Berman, unpublished data). The slightly higher proportion of unaccounted seeds buried at 5 cm than at 20 cm was probably due to more unfavorable conditions at 5 cm depth (water shortage, bird predation, etc.).

Simulation of cultivation

To examine the behavior of buried seeds that are brought to the soil surface by cultivation, seeds were sown in trays at a depth of 1 or 20 cm at the end of January 1985. After 10 or 19 months of burial the trays buried at 20 cm were recovered and reburied at 1 cm. In *D. ferox* the main wave of emergence from seeds initially buried at 1 cm occurred 5 months after burial, and emergence reached 80% (Fig. 6). Seeds brought to the soil surface from the 20-cm depth in the autumn (October 1985) started to emerge 3 months later, after December–January rains, and emergence gradually increased during the winter. The slower rate of emergence of *D. ferox* during autumn probably resulted from the greater relative dormancy of the buried seed population at this time of the year and from the lower winter temperatures (Fig. 5). Seeds that were brought to the soil surface in the summer (July 1986), at the time that dormancy was at the lowest level (Fig. 6), germinated immediately after irrigation. Unlike *D. ferox*, seeds of *D. stramonium* buried at 1 cm remained dormant for a year, and low emergence (15%) was observed till January 1986 (Fig. 6). At the beginning of February 1986 dormancy was broken and most of the seed population germinated. This time course of emergence was similar to that observed for seeds buried at 5 cm (Fig. 4). Earlier emergence was observed from seeds buried at 20 cm and brought to the soil surface in October 1985, compared with seeds buried near the soil surface. This finding emphasizes the fact that in *D. stramonium* dormancy is alleviated during burial at the depth of 20 cm (Fig. 4). Although *D. stramonium* seeds were nondormant when exhumed in October, germination did not occur immediately after the exhumation owing to the lack of rain during November 1985. On the other hand, emergence after the second exhumation occurred shortly after irrigation, and the time course was similar to that observed in *D. ferox*.

In both species the proportion of seeds that did not germinate out of the exhumed seeds or out of the seeds buried near the soil surface was about 20%, as in the other burial experiments.

Discussion

Seed burial has a dual antagonistic effect on the seed of *D. ferox* and *D. stramonium*. While increasing depth of burial inhibits their germination (Fig. 3), at the same time it also alleviated dormancy (Figs. 4–6). Apparently, burial at the 20-cm depth accelerated after-ripening processes, and primary dormancy of *D. stramonium* and *D. ferox* declined earlier than in seeds buried at 5 cm or dry stored. A faster alleviation of dormancy in buried seeds of *D. ferox* compared with dry-stored seeds was reported by Soriano *et al.* (1970). In this species, imbibition of the buried seeds was required for breakage of dormancy, but not contact with the soil itself (Adamoly *et al.* 1974).

Although *Datura* seeds became nondormant while buried in the soil, germination of seeds buried deeper than 10 cm was practically null (Fig. 3). A similar blockage of germination by burial was previously reported for *D. ferox* (Soriano *et al.* 1970) and *D. stramonium* (Stoller and Wax 1973, 1974), respectively, and is of common occurrence in other species (Karssen 1982; Roberts 1981). This inhibition has been attributed to the lack of promotive factors such as light and (or) temperature alternations at increasing depths in the soil (Karssen 1982; Bewley and Black 1981). In both *Datura* species, *in vitro* dark germination requires temperature fluctuations or temperature shifts greater than 5°C. (O. Reisman-Berman, unpublished data). On the other hand, in our field experiments, the amplitudes of daily temperature alternations at the 20-cm depth (Fig. 5) were smaller than 5°C. However, the lack of germination at 20 cm in the field was not only due to the small temperature fluctuations encountered by the seeds at that depth. Dry-stored seeds buried at 20 cm and left imbibed for 2 months under 32:12°C also failed to germinate at this depth, whereas complete germination was attained at 5 cm (Table 2). Thus, inhibition of germination of seeds buried at 20 cm was probably due to other factors acting at greater depths in the soil, such as volatile metabolites (acetaldehyde, ethanol, acetone) (Holm 1972), ethylene or nonvolatile allelopathic compounds, or high levels of CO₂ resulting from biologic activities (Karssen 1982). Involvement of gaseous or volatile compounds in the inhibition of *D. ferox* and *D. stramonium* germination has been suggested, since blockage of the seed hillum aperture prevents their germination but does not affect imbibition (Reisman-Berman *et al.* 1989). Extensive germination of both *Datura* species occurs whenever seeds are transferred to the upper layers of the soil, after a period of burial at 20 cm (Fig. 6) (Soriano *et al.* 1970). As mentioned before, this promotion might be due to a release from inhibiting factors present at greater depths. Moreover, germination may be promoted near the soil surface by the greater temperature fluctuations or by light acting through the very low fluence rate (VLFR) reactions of phytochrome (Cone and Kendrick 1986).

The larger ability of *D. stramonium* to germinate at depths of 5–10 cm compared with *D. ferox* (Fig. 3) may indicate a differential response to burial. In *D. stramonium*, germination is probably less inhibited, or alternatively, dormancy alleviation is greater during burial than in *D. ferox*.

A cyclic seasonal change in dormancy level was found in buried seeds of *D. ferox* (Fig. 5) but not in those of *D. stramonium* (Fig. 4). By comparing the time course of germinability and temperatures, it can be seen that dormancy decreased after exposure to decreasing soil temperatures, whereas trends of increasing dormancy were preceded by increasing temperatures during the spring and (or) summer. Transitions in dormancy level were gradual and occurred after relatively prolonged periods of low or high temperatures. Thus, the cyclic changes in dormancy in the field cannot be attributed to sudden shifts in soil temperature. Apparently long exposures to low or high temperature are necessary to induce the physiological changes in the seeds conducive to low or high dormancy, respectively. Similar seasonal changes in dormancy have been reported for other summer annuals, such as *Aphanes arvensis* (Roberts and Neilson 1982), *Ambrosia artemisiifolia* (Baskin and Baskin 1980), *Polygonum persicaria*, and *Senecio vulgaris* (Karssen 1980–1981). But, in *D. ferox* the seasonal fluctuations in the proportion of fully dormant seeds were much

less pronounced than in these species. This was particularly evident in seeds buried at 20 cm, in which the seasonal variation in dormancy was smaller, and a larger proportion of the seeds remained nondormant at the time of highest dormancy at 5 cm (Fig. 5). However, no cyclic changes in dormancy were reported by Soriano *et al.* (1970) for *D. ferox* during 18 months of burial at 20 cm in the field.

Alleviation of dormancy during the winter was achieved in both species after exposure to minimum temperatures of 8–15°C. These temperatures are relatively high compared with those reported for summer annuals from temperate regions (freezing or below freezing) (Baskin and Baskin 1980; Karssen 1980–1981). This difference may be explained by the tropical or subtropical origin of *D. ferox* and *D. stramonium* (Weaver and Warwick 1984). Nevertheless, seeds of *D. stramonium* were able to germinate during winter at temperatures around 10–15°C, under which *D. ferox* seeds did not germinate (Figs. 4, 5). Since this weed has followed man migrations since ancient times, it is possible that ecotypic adaptation has occurred to different climatic regions.

The prolonged longevity of *Datura* seeds (Toole 1946) and the fact that dormancy is enforced by burial are the major causes contributing to the difficult weed control of *D. ferox* and *D. stramonium*. Moreover, the great variability in the ratio of fully dormant to relatively dormant seeds in *D. ferox* (Figs. 2, 4) and *D. stramonium* (Fig. 4) (Stoller and Wax 1973, 1974) make the forecast of infestation based on the size of the seed bank a difficult task. Such a forecast requires a better understanding of the factors that modulate the level of dormancy in the seed bank.

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