Effect of burial depth and soil water regime on the fate of *Lithospermum arvense* seeds in relation to burial time

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Received 13 May 2008
Revised version accepted 20 August 2008

Summary

Lithospermum arvense is an increasing annual weed in winter crops of the semiarid region of southern Argentina under low impact tillage systems, an agricultural practice that has become popular in recent years. Seed distribution in the soil profile under conventional tillage will change when reduced tillage is implemented, thus affecting the germination microenvironment. The effect of seed burial depth and soil water regime on field germination, enforced dormancy, innate dormancy and seed decay was studied in relation to burial time in a field experiment. In addition, the effect of burial depth on seed germination and seedling emergence was examined under laboratory controlled conditions. Field germination of buried seed ranged from 55% to 65% for shallow (2 cm) and from 5% to 30% for greater depths (20 cm). Enforced dormancy levels were significantly higher among deeper seeds. The amount of innate dormant seeds was reduced to $<10\%$ after a year of burial. *Lithospermum arvense* seedbanks can be classified as short-term persistent. Germination in the laboratory was unaffected by burial depth, while seedling emergence reduction was adequately described by a sigmoidal model. Results indicate that agricultural practices that accumulate *L. arvense* seeds near the soil surface enhance seedling recruitment.

Keywords: winter annual weed, seedbank, field germination, seedling emergence, enforced dormancy, innate dormancy, seed decay, seed longevity.

CHANTRE GR, SABBATINI MR & ORIOLI GA (2009). Effect of burial depth and soil water regime on the fate of *Lithospermum arvense* seeds in relation to burial time. *Weed Research* **49**, 81–89.

Introduction

Lithospermum arvense L. (= *Buglossoides arvensis* (L.) I.M. Johnston) is a dicotyledonous facultative winter annual weed, a native of Eurasia where a progressive decline in this species was observed during recent decades due to long-term agricultural intensive cultivation (Bischoff, 2005; Hulina, 2005). In the United States, it is a commonly widespread weed and it is especially troublesome in winter crops (Whitson, 2004).

In Argentina, this species is also a common weed in the semiarid area of the Buenos Aires Province, specially in winter crops under low impact tillage systems (non-inversion or no tillage) (Lamberto *et al*., 1997; Chantre *et al*., 2005), a practice that has become popular in intensive agricultural systems of Argentina in recent years (Fabrizzi *et al*., 2005).

Vertical seed distribution in soils under conventional tillage (Van Esso *et al*., 1986) will change when low impact tillage practices are implemented (Yenish *et al*., 1992; Hoffman *et al*., 1998; Cardina *et al*., 2002). In fact, high concentrations of seeds in the upper layers of the soil produce more synchronous germination periods than deeper buried seeds (Ghersa & Martínez-Ghersa, 2000). In addition, seeds on/near the soil surface are subjected to a higher pressure of natural predators (Louda, 1989) and they are exposed to greater fluctuations in environmental conditions, which may promote a faster rate of seed decay (Taylorson, 1970).

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At the time of seed dispersal, the environmental conditions are frequently unsuitable for seedling survival. Thus, many weed species rely on innate mechanisms that avoid germination immediately after shedding (Nikolaeva, 1977; Baskin & Baskin, 1989; Schütz *et al*., 2002). Different weed species thus have different temporal patterns of germination (Leguizamón *et al*., 2008). A freshly matured dormant seed is said to have innate dormancy (Harper, 1957) or primary dormancy (Karssen, 1982; Hilhorst, 1995; Baskin & Baskin, 1998). Germination inhibition of non-dormant seeds due to unfavourable environmental conditions was defined by Harper (1957) as enforced dormancy. Many researchers (Popay & Roberts, 1970; Roberts & Feast, 1972; Harper, 1977) have found that enforced dormancy is an important survival mechanism that allows seeds to remain ungerminated in the soil until the environmental constraints are removed.

At seed maturity, *L. arvense* seeds (nutlets) show some kind of physiological dormancy, thus requiring seed exposure to high summer temperatures (after-ripening period) for dormancy release (Baskin & Baskin, 1998). Burial experiments with *L. arvense* showed that seed viability in the field was preserved for 2 or 3 years (Svensson & Wigren, 1986).

In semiarid regions, soil water availability is an important environmental factor that may influence seedbank dynamics. Due to the fact that the semiarid area of the Buenos Aires Province is characterised by an erratic precipitation regime, the effect of the fluctuations in soil water content could significantly influence field germination of *L. arvense* seeds.

The soil seedbank is the source of annual weed infestations in crop production systems (Buhler *et al*., 1997), so to improve weed management techniques it is of overwhelming importance to increase the level of knowledge on seed fate in response to changes in the germination environment (Chauhan *et al*., 2006). Therefore, the main objective of this study was to compare the effect of two contrasting seed burial depths and soil water regimes on field germination, enforced dormancy, innate dormancy and seed decay after different times of burial. In addition, a complementary experiment was performed in order to study the effect of burial depth on seed germination and seedling emergence under laboratory controlled conditions.

Materials and methods

The effect of depth of burial and soil water regime on the fate of buried seeds of *L. arvense* in relation to burial time was studied in a field experiment conducted at the experimental station of the CERZOS (38°39′54′S 62°13′58′W), Universidad Nacional del Sur and CONICET, located in Bahía Blanca, Buenos Aires Province, Argentina. The soil of the experimental area was a sandy loam with an organic matter content of 1.4%. Two depths of burial were selected in order to simulate a contrasting seed stratification situation in the soil profile, and two different water regimes were applied to reproduce possible differences in soil water content due to the erratic rainfall regime of the region. In addition, a laboratory experiment was performed in order to study the effect of burial depth on seed germination and seedling emergence. Seeds of *L. arvense* were collected at maturity in late spring, in December 2004 and 2005, from a wheat field located close to Bahía Blanca. Both seed lots belonged to the same population. After harvest, seeds were separated manually from matured plants and stored under laboratory conditions until the initiation of the experiments. Laboratory storage temperature was 20 ± 3°C.

Field experiment

The effect of depth of burial and soil water regime on the seed fate of *L. arvense* was studied in a field experiment carried out between 2005 and 2007 and repeated during 2006–2007 but using a different time-frequency of exhumation. The experiment was performed using a completely randomised factorial design with three replicates. Treatments consisted of seeds buried at 2 and 20 cm under two different fluctuating water regimes, rain-fed (RAINF) and rain-fed plus irrigation (IRRIG), exhumed at different time intervals. Each treatment (combination of a given burial depth, soil water regime and time of burial) was applied to a mesh bag containing 50 seeds.

Seeds collected during late spring in December 2004 were placed in bags which were buried on 20 February 2005 and exhumed from the field at intervals of 75, 120, 180, 240, 330, 390, 480, 620 and 724 days after burial. During 2006–2007, bags containing seeds harvested in December 2005 were buried on 24 January 2006 and exhumed at intervals of 70, 165, 307, 411 and 520 days after burial. A total of 5400 and 3000 seeds were exhumed during the 2005–2007 and 2006–2007 burial periods, respectively.

The 10 × 10 cm bags were made of permeable nylon mesh to create natural soil conditions (water, air diffusion and microorganisms). A localised drip irrigation system was used for water addition in the IRRIG regime. Irrigation was performed every 2 weeks and the amount of added water was estimated in order to simulate a 50% average increase of rainfall with respect to the previous 2 weeks rain events. The bags were 1.5 m from each other, in order to avoid possible interference between soil water regimes.

The exhumed seeds were washed to remove the soil and the number of germinated and non-germinated seeds was determined at the time of sampling. Regardless of seedling emergence, *in situ* germinated seeds were classified as 'field germination'. Non-germinated seeds were incubated (see *Germination protocol*) and the seeds that germinated were considered to be under an 'enforced dormancy' state (*sensu* Harper, 1957). After incubation, the seeds that did not germinate were bisected and treated with a solution (0.1%) of tetrazolium chloride (2,3,5-triphenyltetrazolium chloride) in order to assess viability. Viable seeds (red stained embryos) were considered to be under an 'innate dormancy' state (*sensu* Harper, 1957), while unstained embryos indicated physiologically decayed seeds. In addition, seed predation by insects and mammals was determined by visual inspection under a dissection microscope. The sum of physiologically decayed plus predated seeds was identified as 'decayed seeds'. All the proportions were related to the original number of seeds placed in the bags (50 seeds).

The differentiation between 'field germination' and 'decayed seeds' categories after a long time period of seed burial was based on seed pericarp visual features (opened pericarps were observed only in germinated seeds).

Field temperature was recorded every 2 h using temperature data loggers (Thermochron Ibuttons, Model DS1921G-F50; Maxim Integrated Products, Inc.). Rainfall data was obtained from a meteorological station located in the experimental field.

Separate statistical analysis was performed on the basis of total seeds for (i) field germination; (ii) enforced dormancy (germination in the laboratory at 15/6°C); (iii) innate dormancy (viable ungerminated seeds) and (iv) decayed seeds (physiologically decayed plus predated seeds). Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. Both non-transformed and arcsine-transformed data were examined. Data transformation improved homogeneity; therefore, ANOVA was performed on square-root arcsine-transformed seed percentage data.

Germination protocol

A germination protocol was performed in order to evaluate *L. arvense* germination by placing seeds evenly in a 9 cm diameter Petri dish containing two layers of Whatman No. 1 filter paper, moistened with 5 mL of distilled water. Dishes were sealed with parafilm and placed in an incubator at an optimal fluctuating germination temperature of 15/6°C (Baskin & Baskin, 1998). The incubator was equipped with cool white fluorescent light providing a photosynthetic photon flux density of 80 μmol m^{-2} s^{-1} for 12 h day^{-1}. The number of germinated seeds was counted 21 days after the start of the experiment, with the criterion for germination being visible protrusion of the radicle.

Pot burial experiment

Seeds collected in 2004 were dry-stored in a growth chamber at 24°C until after-ripening was completed (98% of germination at 10°C after 6 months of storage). These seeds were used to study the effect of burial depth on seed germination and seedling emergence under laboratory controlled conditions.

Samples of 25 seeds of *L. arvense* were sown at 0, 1, 3, 5, 7 and 10 cm depth in 10 cm diameter × 12 cm height cone-shaped plastic pots filled with soil. The soil used was extracted from the experimental field and it was previously sieved (1 mm mesh) in order to remove pre-existing seeds. Pots were placed in the incubator at 10°C with a 12-h photoperiod and watered daily in order to maintain adequate soil moisture for a 30-day time period. At the end of the experiment, the proportion of emerged seedlings was assessed by the observation of the appearance of the cotyledons on the soil surface. Afterwards, the soil was gently removed from the pots and the number of germinated seeds was counted. Length measurements of non-emerged seedlings were obtained in order to estimate the average length of the hypocotyls. Final germination and emergence were calculated from viable seeds. Tetrazolium chloride was used to test viability of ungerminated seeds.

A randomised complete-block design with five replications was used. Each replication was arranged on a different shelf in the incubator and considered as a block. Germination and emergence data was arcsine-transformed prior to the statistical analysis in order to improve homogeneity. A Boltzmann sigmoidal model:

$$y = a + (b - a)/(1 + \exp(c - x)/d)) \qquad (1)$$

where y, the emergence %; x, the burial depth (cm); a, b, c and d, the estimated parameters, was fitted to non-transformed emergence data in order to describe seedling emergence reduction as a function of burial depth increase.

Results

Field experiment

Square-root arcsine-transformed seed percentage data and statistical results for the effect of burial depth and soil water regime on field germination, enforced dormancy, innate dormancy and decayed seeds of *L. arvense* in relation to burial time during 2005–2007

and 2006–2007, respectively, are shown in Figs 1 and 2. Seed percentage trends of the seed fate components are presented in Figs 3 and 4.

Field germination was influenced by the interaction between time and depth of burial (Figs 1A and 2A). The amount of *in situ* germinated seeds was markedly higher at 2 cm than at 20 cm depth (Figs 3 and 4). As expected for a winter annual species, as field temperature decreased during late autumn and early winter (Fig. 5), the amount of germinating seeds of *L. arvense* increased. By mid-winter (August 2005), when field temperature averaged 9°C, seeds buried at 2 and 20 cm germination averaged 49% and 24%, respectively, for both soil water regimes (Fig. 3). In July 2006, similar germination figures were obtained for shallow buried seeds during the 2006–2007 burial period (Fig. 4A,C), but only an average of 5% was observed at 20 cm depth of burial (Fig. 4B,D).

The enforced dormancy component of the seed fate was influenced by the interaction between time and depth of burial and between time of burial and soil water regime during the 2005–2007 burial period (Fig. 1B). For seeds buried at 2 cm, the proportion of seeds under enforced dormancy was reduced from *c*. 45 to 10% between May and August 2005, mainly due to a field germination peak (Fig. 3A,C). Regardless of the soil water regime, seeds

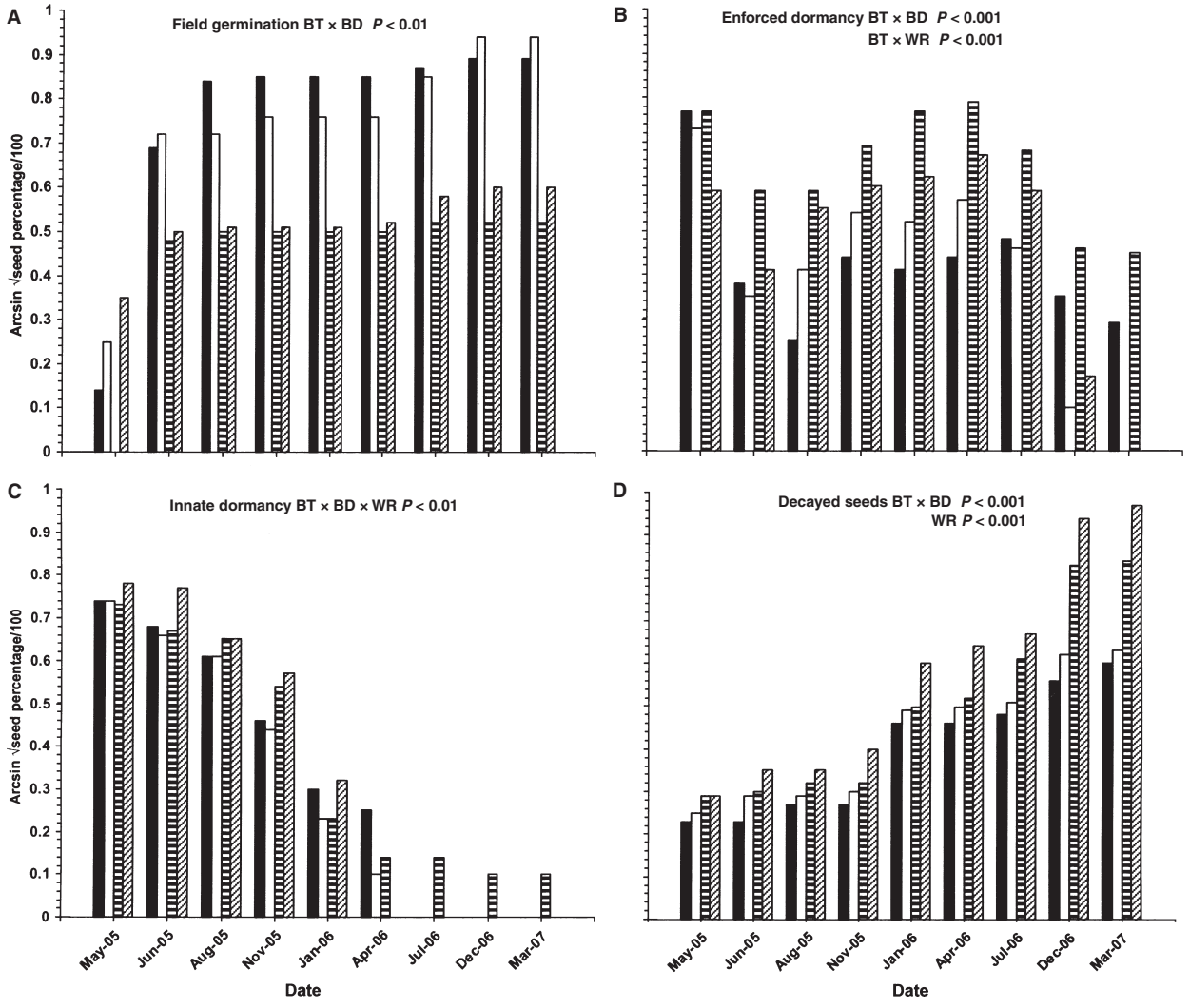

Fig. 1 Square-root arcsine-transformed seed percentage data showing the effect of depth of burial (BD) and soil water regime (WR) on field germination, enforced dormancy, innate dormancy and decayed seeds of *Lithospermum arvense* in relation to burial time (BT) during 2005–2007 burial period. Seeds were buried at 2 cm under a rain-fed (filled bars) and rain-fed plus irrigation (empty bars) water regimes, and at 20 cm under rain-fed (horizontal line bars) and rain-fed plus irrigation (diagonal line bars). In the top, significant interactions and main factors effects of ANOVA results for the different components of the seed fate are shown. SED (73 d.f., for comparison of field germination means for BT × BD interaction) = 0.07. SED (73 d.f., for comparison of enforced dormancy means for BT × BD and BT × WR interactions) = 0.06. SED (73 d.f., for comparison of innate dormancy means for BT × BD × WR interaction) = 0.04. SED (73 d.f., for comparison of decayed seeds means for BT × BD interaction) = 0.03. SED (73 d.f., for comparison of decayed seeds means for WR factor) = 0.01.

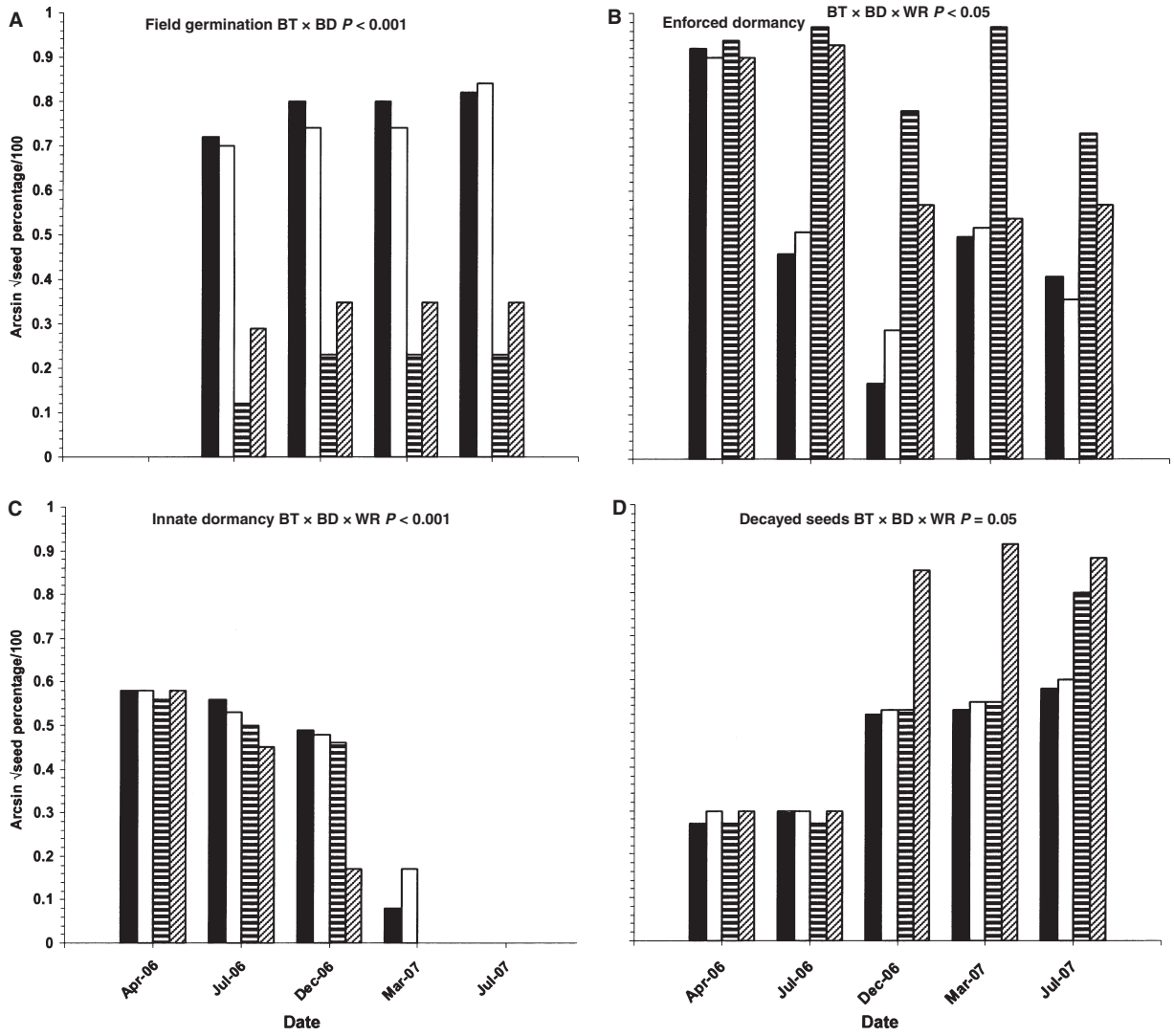

Fig. 2 Square-root arcsine-transformed seed percentage data showing the effect of depth of burial (BD) and soil water regime (WR) on field germination, enforced dormancy, innate dormancy and decayed seeds of *Lithospermum arvense* in relation to burial time (BT) during 2006–2007 burial period. Seeds were buried at 2 cm under a rain-fed (filled bars) and rain-fed plus irrigation (empty bars) water regimes, and at 20 cm under rain-fed (horizontal line bars) and rain-fed plus irrigation (diagonal line bars). In the top, significant interactions and main factors effects of ANOVA results for the different components of the seed fate are shown. SED (41 d.f., for comparison of field germination means for BT × BD interaction) = 0.08. SED (41 d.f., for comparison of enforced dormancy means for BT × BD × WR interaction) = 0.08. SED (41 d.f., for comparison of innate dormancy means for BT × BD × WR interaction) = 0.03. SED (41 d.f., for comparison of decayed seeds means for BT × BD × WR interaction) = 0.10.

buried at 20 cm showed higher levels of enforced dormancy, as evidenced by lower field germination percentages. In late spring (December 2006), enforced dormant seeds averaged 15% and 2%, for RAINF and IRRIG seeds, respectively (Fig. 3). Observed results for seeds buried in January 2006 (Figs 2B and 4) also showed higher values of enforced dormancy for deeper buried seeds, mainly under a RAINF regime.

Innate dormancy was influenced by a second-order interaction between burial time, depth of burial and soil water regime (Figs 1C and 2C). For seeds buried in February 2005, 6 months later (by mid-winter), the proportion of innate dormant seeds averaged 35% of the population (Fig. 3). As field temperature increased during spring and after exposure to high summer temperatures (Fig. 5), dormancy levels were markedly reduced, so in July 2006 only 2% of RAINF seeds buried at 20 cm remained dormant (Fig. 3B). Results for seeds buried in January 2006 show that the amount of innate dormant seeds exhumed during winter 2006 averaged 25% for all seed environments. As seen before, dormancy levels were clearly reduced by exposure to high summer temperatures, being almost negligible by March 2007 (Fig. 4).

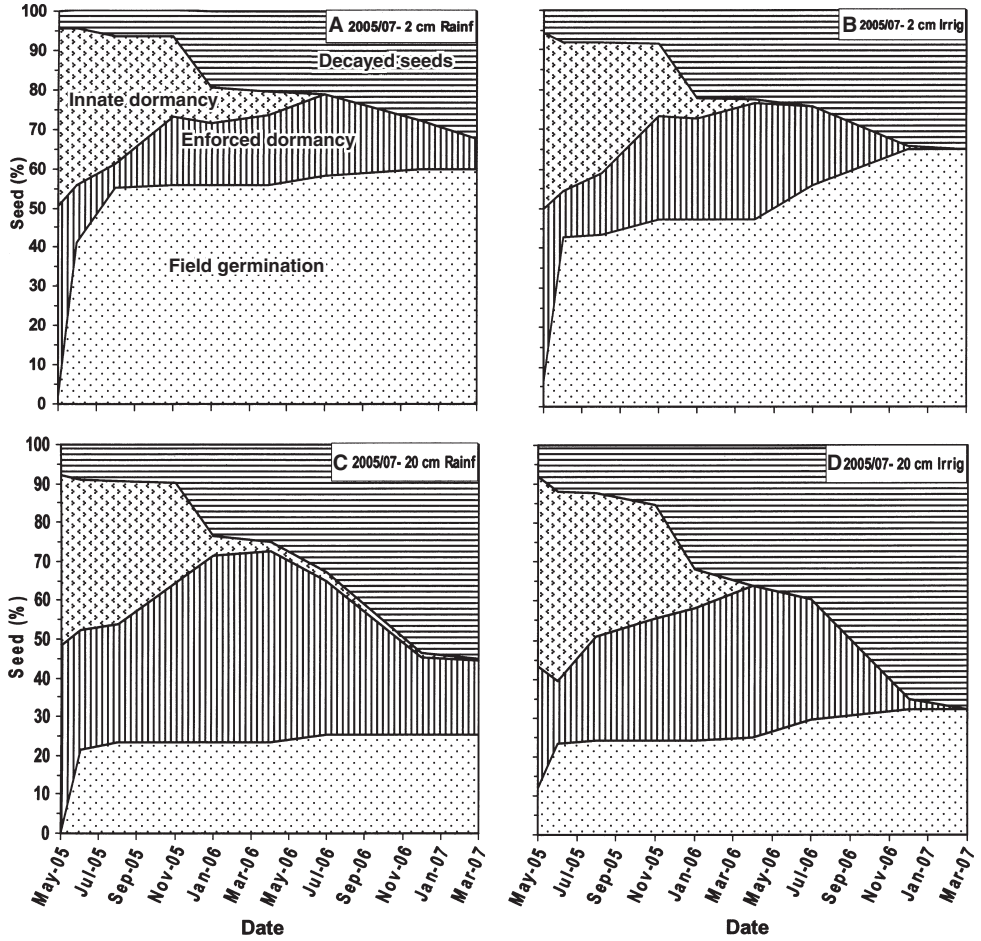

Fig. 3 Seed fate (field germination: dots; enforced dormancy: vertical line; innate dormancy: arrows; decayed seeds: horizontal line) of *Lithospermum arvense* in relation to depth of burial (2 and 20 cm), soil water regime (RAINF, rain-fed; IRRIG, rain-fed plus irrigation) and burial time in 2005–2007.

The seed decay component was influenced by the interaction between time and depth of burial during 2005–2007 and also by the applied soil water regime (Fig. 1D). Seed decay was essentially ruled by seed senescence and probably also by soil microorganism attack, due to the fact that seed predation was negligible, as no evidence was detected by visual inspection under the dissection microscope. Regardless of seed environment, seed decay increased with burial time. From 480 days of burial (July 2006), until the end of the evaluation period, the amount of physiologically decayed seeds was higher for deeper buried seeds (Figs 1D and 3). Concomitantly, in March 2007, seed decay values for IRRIG seeds were 15% higher than for RAINF seeds at 20 cm depth of burial. During 2006–2007, seed decay was influenced by the interaction between burial time, depth of burial and soil water regime (Fig. 2D). A fast rate of seed decay was observed after July 2006 (165 days of burial) in IRRIG seeds buried at 20 cm compared with the other seed environments (Fig. 4). In fact, the amount of decayed seeds observed after 307 days of burial (December 2006) was *c*. 55% for deeper buried IRRIG seeds and 25% for the rest of the seed environments (Fig. 4).

Pot burial experiment

At the end of the 30-day experiment, seed germination was unaffected by burial depth and averaged 98% ($P > 0.05$). In contrast, seedling emergence was highly influenced by burial depth increase ($P < 0.001$).

On or near the soil surface (0 and 1 cm depth) all of the seedlings emerged, while a reduction of 84% was observed at a 5 cm burial depth (Fig. 6). Seedling emergence reduction at increasing burial depths was adequately described by a Boltzmann sigmoidal model (Fig. 6). According to the model, 50% reduction of seedling emergence should be achieved at 3.5 cm, while at 7 cm it should be 3%; 4% of emergence was observed from that depth of burial (Fig. 6). No emergence was observed at 10 cm, and the average length of non-emerged hypocotyls was 4.5 ± 2.3 cm ($n = 25$).

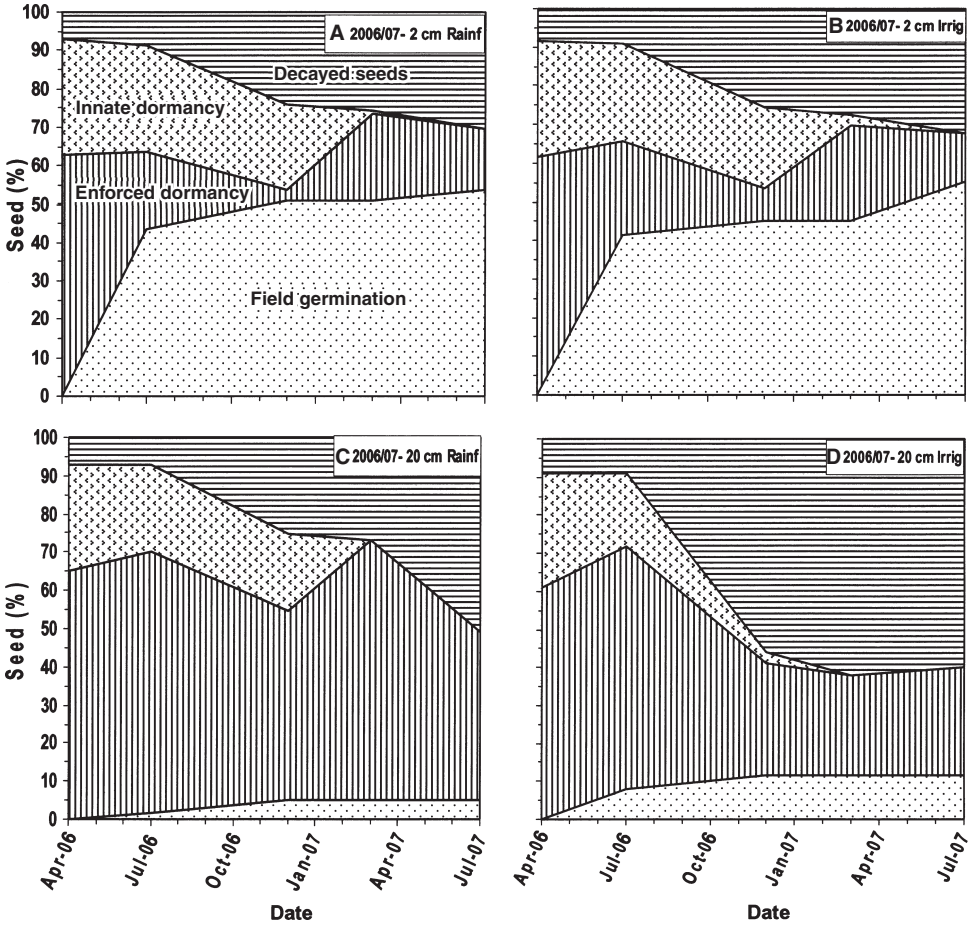

Fig. 4 Seed fate (field germination: dots; enforced dormancy: vertical line; innate dormancy: arrows; decayed seeds: horizontal line) of *Lithospermum arvense* in relation to depth of burial (2 and 20 cm), soil water regime (RAINF, rain-fed; IRRIG, rain-fed plus irrigation) and burial time in 2006–2007.

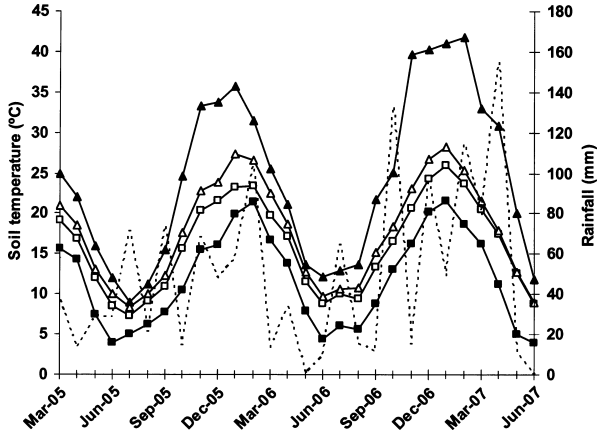

Fig. 5 Maximum (triangles) and minimum (squares) soil temperatures measured at 2 cm (filled symbols) and 20 cm (open symbols). Rainfall data (dotted lines) was recorded at the experimental field from March 2005 until June 2007.

Discussion

The field experiment showed that *in situ* germination was significantly reduced in deeper buried seeds but was unaffected by the soil water regime. Unlike the field experiment, high germination figures obtained in the laboratory indicated no specific requirements of fluctuating temperatures or light exposure for the germination of non-dormant seeds of *L. arvense*. Although the maximum burial depth tested in the pot burial experiment was 10 cm, these results suggest that the higher proportion of enforced dormant seeds and the low germination percentages found in seeds buried at 20 cm in the field could be caused by other external factors. Benvenuti (2003) linked the decrease in germination of seeds of *Datura stramonium* L. as burial depth increased to poor gas exchange in the environment surrounding buried seeds. In fact, it has been shown that high soil moisture, soil compaction, high microbial activity or poor soil structure may decrease soil oxygen concentration or inhibit gaseous movement within the soil (Ishii & Kadoya, 1991; Drew, 1992) so that toxic volatile fermentation products may accumulate around buried seeds and inhibit germination (Wesson & Wareing, 1969; Benvenuti & Macchia, 1995). Thus, germination inhibition in the field could be associated with a limited soil

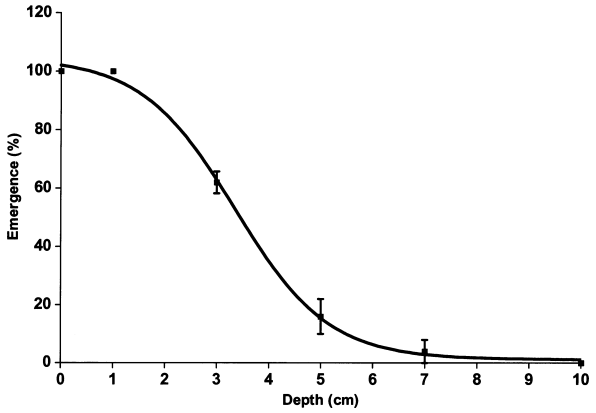

Fig. 6 Effect of depth of burial on seed germination and seedling emergence of *L. arvense* (30 days after sowing). Symbols = observed data; the vertical bars represent standard error. Solid line = fitted Boltzmann sigmoidal model [$y = a + (b - a)/(1 + \exp(c - x)/d)$], where estimated parameters are: $a = 104.50 \pm 3.736$; $b = 1.19 \pm 2.644$; $c = 3.35 \pm 0.144$; $d = 0.90 \pm 0.145$; $R^2 = 0.975$.

oxygen exchange situation, rather than the effect of temperature, light exposure or soil water content.

The laboratory experiment demonstrated that reduced seedling emergence as burial depth increased was mainly due to depth-mediated 'suicidal germination' probably caused by exhaustion of reserves (Zorner *et al*., 1984; Pierce & Cowling, 1991; Jansen & Ison, 1995). In fact, seedling emergence from different soil depths has been found to be proportional to seed energy reserves (Lafond & Baker, 1986).

No conclusive effect of burial depth or soil water regime was observed in relation to innate dormancy levels. However, the dormancy release process was clearly regulated by soil temperature. The high rate of innate dormancy release observed during the summer season indicates that dormancy loss progresses faster at high after-ripening temperatures, as was previously documented for *L. arvense* where higher rates and seed percentages of germination were found at increasing after-ripening temperatures (Chantre *et al*., 2006). Positive relationships between seed dormancy release rate and after-ripening temperatures have been described for many winter annual species (Foley, 1994; Allen *et al*., 1995; Christensen *et al*., 1998).

Our results suggest that under the evaluated environmental conditions, the proportion of viable seeds of *L. arvense* would be reduced after 2 years of burial to $< 10\%$ of the initial seed population, although a seed viability of 20% was found when high levels of enforced dormancy were imposed to deeper buried seeds under a RAINF regime (Fig. 3). The increased rate of seed decay observed in deeper buried seeds, also described by others (Zorner *et al*., 1984; Lonsdale *et al*., 1988), could be related to seed deterioration due to seed senescence and activity of soil microorganisms (Kremer, 1993) enhanced by the complementary water supply, as observed for IRRIG seeds during the 2006–2007 burial period. According to these results, *L. arvense* seedbanks could be classified as short-term persistent (Bakker *et al*., 1996) or persistent (type III), as described by Thompson and Grime (1979) for others facultative winter annual species.

Based on field and laboratory results we conclude that the increasing abundance of *L. arvense* under low impact tillage systems is related to the high amount of seeds located on/near the soil surface after dispersal, as cited for many other species (Yenish *et al*., 1992; Hoffman *et al*., 1998; Cardina *et al*., 2002). As a result of the implementation of these agricultural practices, *L. arvense* seed burial is not deep enough to induce high levels of enforced dormancy in the seed population. Therefore, most of *L. arvense* seeds are capable of germinating during late autumn and winter months after dispersal. Concomitantly, newly germinated seedlings are able to reach the soil surface before seed reserve exhaustion.

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