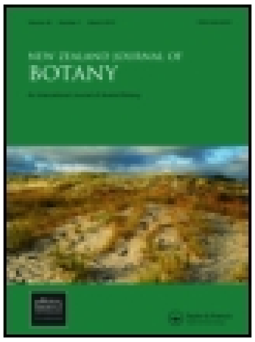

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R. L. Hill , A. H. Gourlay & R. J. BARKER

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Survival of *Ulex europaeus* seeds in the soil at three sites in New Zealand

R. L. HILL*
A. H. GOURLAY
R. J. BARKER†
Landcare Research
P.O. Box 69
Lincoln, New Zealand

*Present address: Richard Hill & Associates, P.O. Box 4704, Christchurch, New Zealand.
Email: Hillr@crop.cri.nz

†Present address: Department of Mathematics and Statistics, University of Otago, P.O. Box 56, Dunedin, New Zealand.

Abstract Seed banks are a major factor in the persistence of perennial, woody, leguminous weed species. The longevity of seeds of *Ulex europaeus*, (gorse) in the soil at three sites was determined, and the implications of these results for the selection of biological control agents for the weed are discussed. Locally collected seeds were buried in bags at depths ranging from 2.5 cm to 15 cm at three climatically distinct sites. Seeds were recovered and germinated over a 10-year period to estimate the dormancy characteristics and viability of *U. europaeus* seed banks at the three sites. The decline in the seed bank conformed to a linear model using an exponential transformation. Seeds survived longer when buried deeper, but this influence was weak. The main determinant of seed survival was the time elapsed since burial. Results indicate that the dynamics of the seed bank vary from site to site. Thus, the view that *U. europaeus* seeds last almost indefinitely in the seed bank may be exaggerated, at least in some sites. At two sites, the number of viable seeds buried at a depth of 5 cm declined to 10% of the original number within 10 years of burial and to 1% within 20 years. By contrast, data from the third site suggested that in some places seed could survive many decades in the seed bank. Almost all seeds recovered from the soil were viable, and losses from the seed bank were probably due to germination. Local climatic conditions or local genotype may explain the variation in seed longevity between sites, although this study could not examine the relative importance of these factors. Seed-feeding biological control agents reduce *U. europaeus* seed rain, and these may influence the population dynamics of the weed within several decades in areas where the rate of seed decline in the soil is rapid.

Keywords *Ulex europaeus*; seed; seed bank; gorse; climate

INTRODUCTION

Long-lived seed banks form a reservoir of dormant individuals that often vastly outnumber the growing plants in a population. This seed bank provides the population with a refuge in time, a source for reinvasion of the habitat long after the parent plants have died. It also gives the population the capacity to weather adverse environmental conditions and to take advantage of environmental change. The development of such a dormant life stage is a characteristic of plants that colonise unpredictable, disturbed habitats (Harper 1977; Auld 1986; Baker 1989), and many of the most difficult-to-control weeds of arable farming and of plantation forestry have such seed banks. Seed banks directly influence temporal and spatial patterns of seedling emergence (Louda 1989). Therefore, understanding the dynamics of the seed bank is important, not only to interpreting the role that a species plays in community ecology, but also to designing sustainable control strategies for a weed. Seed banks become depleted over time through seed germination and mortality, but are replenished by seed input. Reducing seed production by biological control could potentially exhaust the seed bank over time, leading to patchiness or

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localised extinction of the weed. Significant depletion of the seed bank would increase the effectiveness of other control techniques such as plant competition (T. R. Partridge et al. unpubl. data) or targeted use of herbicides.

Studies of seed banks are often conducted by inferring seed bank dynamics from seedling emergence patterns (Rees & Long 1993). Experiments designed to directly measure seed mortality by burying seeds have been conducted for 140 years (Baker 1989; Burnside et al. 1996), but relatively rarely. Most have concentrated on seeds of grassland plants or weeds of arable agriculture, and there have been few studies on seeds of long-lived woody perennials (Auld 1986; Baker 1989; Crawley 1990).

Ulex europaeus (Fabaceae) (gorse) is a spiny shrub that can grow to 4 m tall. It is native to the western seaboard of continental Europe and the British Isles, where it is a characteristic component of acid heathland vegetation. These heaths are prone to episodic destruction by fire. *U. europaeus* can recolonise burnt areas quickly because it has a long-lived seed bank and fire breaks the dormancy of gorse seed (Chater 1931; Zabkiewicz & Gaskin 1978). It has been introduced to many other parts of the world, where it has become an invasive weed, out-competing young trees in plantation forests and excluding grazing animals from pastoral land. It competes poorly with pasture plants growing at high density (T. R. Partridge et al. unpubl. data), but cultivation or overgrazing can induce significant reinvasion of grasslands. In New Zealand, herbicides have been used extensively over the past 50 years to restore productive grazing pasture and to protect forest plantations (MacCarter & Gaynor 1980). However, the seed bank that remains buried in the soil can allow constant reinvasion, even where plants have been absent for many years. When plantation pine forests are harvested after 25–35 years, soil disturbance often results in the germination of buried seeds, even though *U. europaeus* may have been absent from the plantation for 15 years or more. These plants must be controlled before trees can be planted again. The environmental and economic costs and benefits of *U. europaeus* in New Zealand are discussed by Hill & Sandrey (1986).

There is anecdotal evidence that *U. europaeus* seed lasts many decades in the soil. Seedlings have been recorded germinating in areas many years after plants ceased to produce seed there, and the inference taken from such observations is that the seed fell from plants on site. However, as with all such accounts, there is little proof that the seed was not carried there at a later date. Although the bulk of *U. europaeus* seed falls close to the parent bush (Hill et al. 1996), some can disperse widely. Sem & Enright (1996) detected *U. europaeus* in the seed rain of a forest, even though there were no parent plants within 17 m of the site. Seed can be carried by flood waters, in fur and wool, and on machinery (Moss 1959). We cannot draw conclusions about the longevity of gorse seeds without reliable data on the age of those seeds.

There are only two formal studies that have estimated how long *U. europaeus* seed can survive in the soil in New Zealand. Moss (1959) sampled soil from fields in Taranaki that had been free of *U. europaeus* plants for known periods. Where gorse had been cleared by burning, Moss could not detect a *U. europaeus* seed bank after 28 years. In another study, Partridge (1989) measured the general seed bank under 5-m-high stands of kanuka (*Kunzea ericoides*). A significant population of *U. europaeus* seed remained buried deeply in the soil. Partridge (1989) concluded that this seed was shed by plants present on the site up to 100 years earlier.

Other studies have examined the density of *U. europaeus* seeds at different levels in the soil (Moss 1959; Ivens 1978; Zabkiewicz & Gaskin 1978; Rolston & Talbot 1980; Ogle-Mannering 1995). Ivens (1978) found 21% of seed buried 5–10 cm deep and 4% at 10–15 cm deep. Zabkiewicz & Gaskin (1978) found up to 90% of the seeds in the top 6 cm, but significant numbers of seeds can be present deeper in the soil. Across all studies, approximately 75% of seeds were found in the litter or the top 5 cm of soil. Individual seeds may be actively moved down through the profile by worms, but also fall through cracks created by soil desiccation and holes created by worms. Ants are known to transport seeds with elaiosomes deeply into nests, but this was not observed for gorse in England (Chater 1931) and is not a behaviour associated with ants in New Zealand. Seeds buried below 5 cm cannot germinate successfully (R. L. Hill & A. H. Gourlay unpubl. data) unless brought to the soil surface by disturbance.

In this paper we report an experiment designed to directly measure the lifespan of *U. europaeus* seeds buried in soil in New Zealand. It presents the survival patterns of locally collected seeds buried at 2 or 3 depths in three climatically distinct regions, and then recovered over a period of 10 years. The purpose of the study was to find out whether the probability of seed survival varied with age, depth, and site, and to estimate the survival rate of seeds at different sites. A suitable predictive model is fitted to the data. Gorse genotypes and field conditions varied between sites, but this study did not attempt to distinguish the relative importance of these factors in determining seed longevity. This information will be used in a simple model of the long-term population dynamics of *U. europaeus*, which is being prepared to evaluate the role of two seed-feeding insects as biological control agents for the weed in New Zealand (M. Rees & R. L. Hill unpubl. data).

MATERIALS AND METHODS

Study sites

Ulex europaeus is an agricultural and silvicultural weed in most of New Zealand. Seeds were buried at three sites that represented widely different climate types within that distribution. At the Mt Albert Research Centre in Auckland (36°54′S, 174°44′E), a plot was established in a basalt-derived topsoil over a clay subsoil, on a sloping area of *Pennisetum clandestinum* (kikuyu grass) that was mown infrequently. Seeds were buried at Totara Flat, on the northern West Coast of the South Island (42°18′S, 171°37′E) in a stony silt loam under a closely mown lawn of ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) growing at the headquarters of a plantation forest. After four years this lawn was abandoned and then was mown infrequently. The site at Lincoln, Canterbury (43°39′S, 172°28′E) was established in a silt loam under a ryegrass/white clover sward that was mown infrequently. Records from New Zealand Meteorological Service stations near the three sites were used to describe the climate generally prevailing during the trial (Table 1). Records were not complete. The climate station at Auckland (Owairaka) adjoined the study site, and the station at Lincoln (Broadfield) was approximately 1 km away. The station at Totara Flat was within metres of the study site but ceased operation four years into the study, so records for the 10 years prior to the last reading are used. Records for the Lincoln station were incomplete (Table 1). No soil temperatures were available from Totara Flat. It was assumed that conditions prevailing at Reefton, 25 km from Totara Flat, but with similar climate and soil type, were similar to those at Totara Flat. Soil temperatures from Reefton are recorded in Table 1.

Table 1 Monthly temperatures and rainfall prevailing at three sites during the study. Meteorological data were not available for Totara Flat after 1988. Soil temperatures representative of Totara Flat were recorded 25 km away at Reefton.

	Period	Jan	Jul	Mean annual
Auckland				
Total rainfall (mm)	1985–95	87.0	148.0	1236.0
Mean air °C	1985–95	19.4	10.8	15.0
Mean daily grass min °C	1985–95	12.6	3.1	7.6
Mean 10 cm soil °C	1985–95	20.1	9.6	14.9
Mean 20 cm soil °C	1985–95	21.0	10.7	15.9
Lincoln				
Total rainfall (mm)	1985–95	36.0	51.0	588.0
Mean air °C	1987–95	17.0	6.0	11.7
Mean daily grass min °C	1985–95	9.5	−1.3	4.7
Mean 5 cm soil °C	1987–90	17.6	3.2	10.6
Mean 10 cm soil °C	1987–95	16.2	3.6	10.4
Mean 20 cm soil °C	1987–90	18.5	5.3	11.8
Totara Flat				
Total rainfall (mm)	1979–88	178.0	191.0	1989.0
Mean air °C	1979–88	16.0	5.9	11.3
Mean daily grass min °C	1979–88	8.2	−1.4	3.9
Mean 10 cm soil °C	1985–95	16.6	4.2	10.8
Mean 20 cm soil °C	1985–95	17.9	5.3	11.9

Experimental design

Mature pods were collected from *U. europaeus* plants growing within 5 km of the Auckland and Lincoln study sites, and within 50 km of Totara Flat. Pods were stored in paper bags and allowed to dehisce naturally. Random samples of 100 intact seeds were combined with 100 g of sieved soil obtained from the site, and placed in sewn nylon mesh bags (42 squares cm^{-2}) measuring 10 × 10 cm. Bags allowed micro-organisms to be active near the seeds, but excluded larger insects and worms. At each site, a 3 × 3 m plot was established. Within that plot, the top 2 cm layer of turf was removed, and 36 (30 at Lincoln) equidistant 15-cm-diameter holes were cut to a depth of 15 cm below the surface using an augur. A 15-cm length of 15-cm diameter "Drainflo" perforated plastic drainage pipe was placed in each hole. Soil was returned to the hole and compacted, as far as possible to the same degree as undisturbed soil. Bags of seed were placed at different depths within each pipe, and the turf was replaced. Bags were buried in 1985 at 3 and 10 cm deep at Auckland and Totara Flat and 2.5, 7, and 15 cm deep at Lincoln. To examine variation within sites, each plot was divided into three sub-plots (10 or 12 cylinders per sub-plot). At varying intervals over 10 years, one cylinder was randomly selected from each sub-plot at each site. Bags were retrieved, and the final depth of each bag within the soil profile was recorded. Samples were taken at six-monthly intervals for three years, at four years, and then biennially. The number of seeds remaining within each bag was counted. Seeds were placed on wet filter paper in a Petri dish and incubated at 15°C in the dark. After two weeks, germinated seeds were counted. Remaining seeds were chipped with a scalpel and incubated once more to determine viability. Any developmental abnormalities were noted. The seeds missing from the bags at harvest were counted as lost from the seed bank, but it was not possible to accurately determine their fate. At the outset, a sample of the seed used at each study site was stored in a refrigerator at 5–10°C. A sub-sample of 100 seeds was drawn at each sampling date, and germinability and viability were determined.

Data analysis

Data analysis using strictly parametric continuous-time survival models (e.g., Kalbfleisch & Prentice 1980) or their non-parametric alternatives (Rees & Long 1993) was rejected for two reasons. Firstly, choice of a baseline model was uncertain due to unknown patterns of age-specific recruitment from the seed bank (Rees & Long 1993) and likely changes in the instantaneous risk of mortality over time. Secondly, and more importantly, seeds buried together in bags were not able to act independently of each other, an important assumption in the use of such models. Instead, we treated bags of seed as independent sampling units, and modelled the natural logarithm of the proportion of surviving seeds p as a linear function of time using linear regression analysis. To provide a partial justification of our choice of transformation it should be noted that under an exponential survival model, the proportion of survivors to t, p_t, is given by $\eta_t = e^{-rt}$, hence $\log_e p_t$ is a linear function of time.

Under this approach, irregular changes in instantaneous risk of mortality are incorporated in the random error term of the model. The influence of duration and depth of burial and influence of site on the decay rate r was tested using standard ANOVA methods. In addition, systematic time trends were modelled using quadratic and cubic effects. The validity of the model was assessed by examining residuals and quantile plots.

Using the linear model, the estimated time required for the seed bank to reach a 10% threshold probability of survival is given by

$$t = \left(\frac{1}{\beta_1 + \beta_3 \text{.depth}} \right) \times \log_e \left(\frac{0.1}{e^{(\mu + \beta_2 \text{.depth})}} \right) \qquad (1)$$

where β_1 is the days effect, β_2 is the depth effect, and β_3 is the days by depth interaction.

RESULTS

Comparison of sites

Vegetation cover was similar at all three sites. The silt loam soils at Lincoln and Totara Flat were similar in texture but differed from the coarse volcanic soil at the Auckland site. Seasonal temperature patterns were broadly similar at Lincoln and Totara Flat, but the Auckland site was much warmer than the southern sites. For example, mean annual soil temperature at 10 cm depth was 10.4°C and 10.8°C at Lincoln and Reefton, respectively, but 14.9°C at Auckland (Table 1). Rainfall at Totara Flat was much higher than at Lincoln and less seasonal, and rainfall at Auckland was in between the other two sites (Table 1).

Seed viability and germinability

Seed viability was high. The viability of seed stored in the laboratory during the 10-year period exceeded 99%, and, therefore, seed survival was not age specific over that period. For this study, seed survival was assumed to be not age specific. Over the same period, all but one or two seeds recovered from the soil germinated when first incubated or after physical scarification. The data are not presented, but the proportion of recovered seeds that germinated without scarification varied greatly both within and between sampling occasions.

Survival of seeds in the soil

Bags settled in the soil after burial and were not necessarily recovered from the same depth at which they were buried. Final depth was considered a better measure of the position of the seeds than initial depth. For this reason, depth was treated as a continuous variable in the analysis. Analysis of variance showed no significant sub-plot effect, which indicated that there was no systematic difference in survival of seeds across the plots. Data from each depth were therefore pooled at each study site (Fig. 1).

The fitted models for the natural logarithm of the probability of survival of a seed at the three sites are:

Auckland

$$\log_e(p) = -0.9004 + (-0.0754*100\text{days}) + (0.0467*\text{depth}) + (0.0040*100\text{days}*\text{depth})$$

Totara Flat

$$\log_e(p) = -0.4687+(-0.0048*100\text{days}) + (0.0081*\text{depth}) + (-0.00010799*100\text{days}*\text{depth})$$

Lincoln

$$\log_e(p) = -0.1872+(-0.1234*100\text{days}) + (0.0057*\text{depth}) + (0.00629668*100\text{days}*\text{depth})$$

Within sites, time elapsed since burial was the strongest predictor of probability of survival (Auckland, $F_{1,56} = 14.74$, $P = 0.0003$; Totara Flat, $F_{1,56} = 28.08$, $P = 0.0001$; Lincoln, $F_{1,85} = 71.09$, $P = 0.0001$). Survival of seed increased significantly with depth at Auckland ($F_{1,56} = 12.33$, $P = 0.0009$) and Lincoln ($F_{1,85} = 38.00$, $P = 0.0001$) (Fig. 1). Bags buried 3 cm deep at Totara Flat sank soon after burial, and the mean depth from which bags were recovered was 7.2 cm. This may explain why there was no significant difference in survival with depth at this site ($F_{1,56} = 3.43$, $P = 0.07$). The interaction term (days by depth) was significant only at Lincoln, but it was incorporated into the model for each site.

Length of time required to exhaust the seed bank at different depths at the three sites was estimated by substitution into Equation 1. No seeds were buried at depths less than 3 cm, and only at Lincoln were seeds buried at a depth greater than 10 cm. Extrapolation of the model beyond these soil depths is problematic. However, the data clearly show that the seed buried high in the soil profile disappeared rapidly at Auckland and Lincoln. The model predicted decline in the seed bank in the top 5 cm of the soil profile to 10% of its original level within approximately 5.6–8.1 years at Auckland, and 5.0–6.4 years at Lincoln (Table 2). Deeply buried seed survived longer. Assuming that the model holds beyond the 10-year term of this study, it predicts 99% decline in the seed bank within 20 years at Auckland and Lincoln. In contrast, the model predicts that decline in the seed bank at Totara Flat to 10% of its original level will take over 90 years. This estimate involves extrapolation far beyond the data used to construct the model and may not be accurate. However, it is clear that decline in the seed bank is gradual (Fig. 1) and the seed bank is long-lived.

The predicted change in seed survival with depth 10 years after burial was calculated by substituting

Table 2 Predicted time (yr) required to reach 10% and 1% of the original *U. europaeus* seed bank at four soil depths at Lincoln, Auckland, and Totara Flat.

Depth	Lincoln		Auckland		Totara Flat	
cm	10%	1%	10%	1%	10%	1%
1	5.0	10.4	5.6	14.5	102.0	230.0
3	5.6	11.6	6.7	16.7	99.0	221.0
5	6.4	13.3	8.1	19.6	95.0	213.0
10	9.4	19.3	14.6	32.7	88.0	195.0

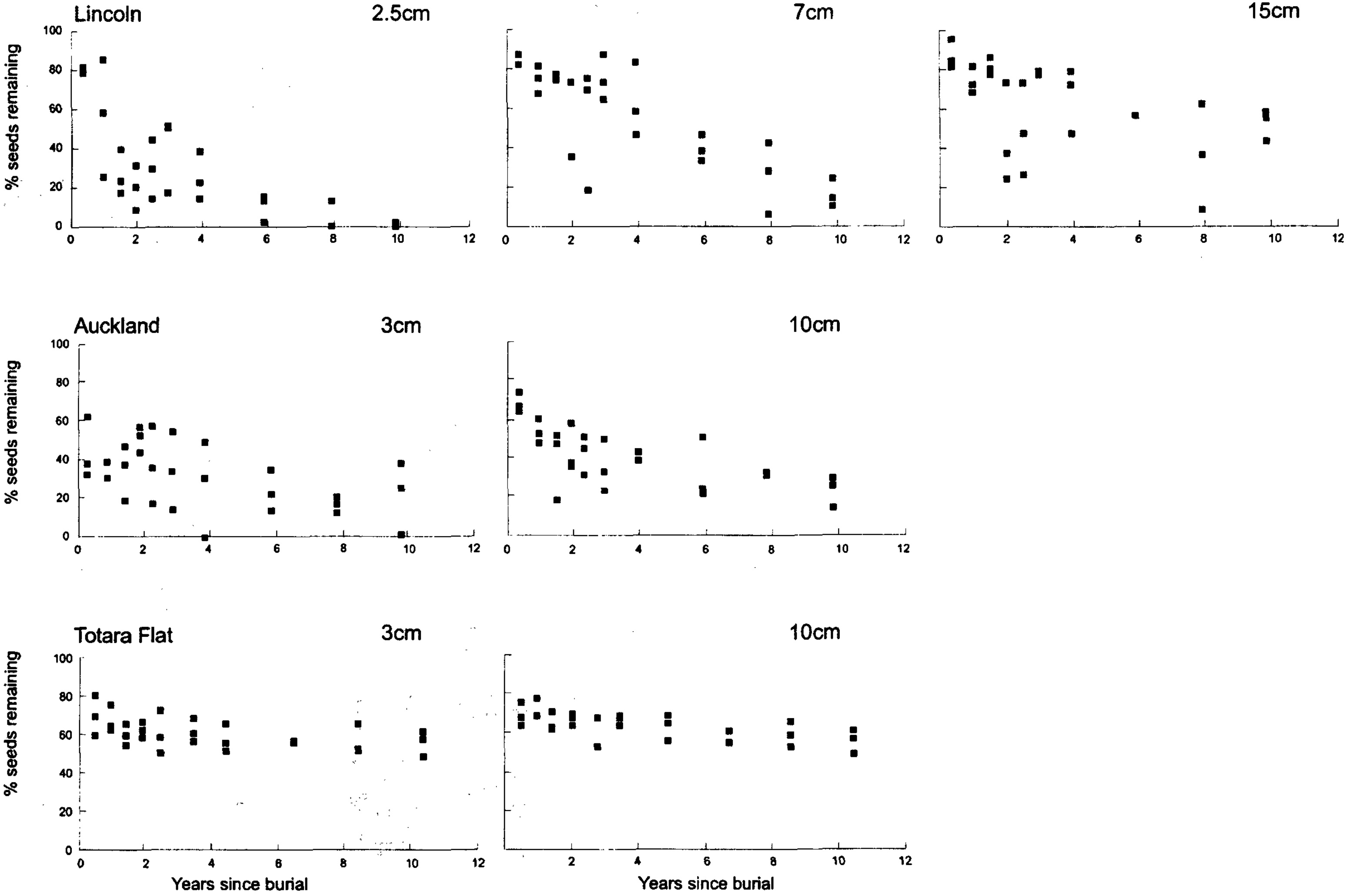
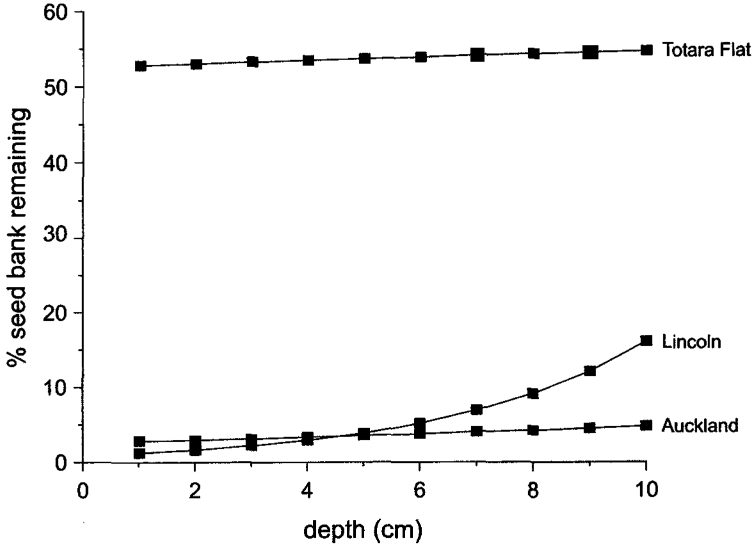


Fig. 1 Log$_e$ (n+1) of seeds remaining in bags buried at different depths at three sites over 10 years.

Fig. 2 Percentage of seed predicted to remain in the *U. europaeus* seed bank at different depths at three sites after 10 years.



depths into Equations 2–4 (Fig. 2). Our analysis suggests that seeds last longer when buried deeper ($P < 0.0001$), but the rate of change with depth is small. This effect is unlikely to be of ecological significance for seed buried less than 8 cm below the surface.

DISCUSSION

Measuring seed bank dynamics

Past studies of seed banks have almost always used a log-linear decay curve to depict the survival of seed in the soil, implying that the probability of a seed dying does not vary with the age of the seed (Harper 1977). Lonsdale (1988) suggested that the common use of log-linear survivorship curves may simply reflect the inability of other models to adequately describe a data set and that other non-linear curves would probably be more realistic. Rees & Long (1993) explored this further by fitting four alternative survivorship models to data on seedling recruitment over time in 145 plant species sown as seed. They found that most seed banks did not decay in an exponential fashion and other patterns of recruitment were more common. On the other hand, the age-specific recruitment rate (Rees & Long 1993) was constant over time in 28% of the species they examined, suggesting that for some species, at least, the exponential model is appropriate to describe the survival of seeds in seed banks.

In our analysis, we found no evidence that the decay rate changed systematically with time, but that it was strongly affected by location and depth of burial. Seeds were subjected to fluctuating light and temperature regimes between exhumation and analysis. This may have broken dormancy in some seeds and obscured any age-dependent germination pattern. However, if the observed germination pattern occurs in the field, then the probability of germination of *U. europaeus* seeds from the seed bank is independent of age. The fact that seed stored in constant conditions displayed similar patterns of germination over 10 years lends support to the conclusion that germination and survival were not age-dependent in this study.

The absence of any apparent change in the decay rate over time does not mean there was no such effect, but, rather, if such an effect was present, it was small relative to the overall variation in the data. This is clear from the plots of survival versus time; the dominant features are the steady decline with time and a large scatter about the linear trend line at some of the sites. In germination tests on the seeds of 42 plant species recovered from the soil, Burnside et al. (1996) showed that non-viable (essentially dead) seed persisted in the seed bank for long periods, the rate of mortality was age-specific, and that the strength of this characteristic varied from species to species. By contrast, over 99% of the seeds stored in constant conditions or recovered from the soil during this study were viable. Observed seed mortality rate was constantly low over 10 years. Similar high levels of *U. europaeus* seed viability have been reported by Moss (1959) and Zabkiewicz & Gaskin (1978). This suggests that losses from the seed bank are best attributed to germination rather than to seed mortality. Very similar patterns of viability and germinability were observed in an *Acacia suaveolans* seed bank (Auld 1986) (a similar fire-adapted leguminous shrub) and in *Lupinus arboreus* (Maron & Simms 1997).

The recorded proportion of seed capable of germinating without scarification (data not presented) in both recovered and stored seed was highly variable. The incubation conditions employed may have allowed germination of a proportion of the seed that would normally remain dormant. Alternatively, this may be the true permeable fraction of the seed bank, in which case the probability of a seed germinating is constant with age; certainly it would be difficult to prove the contrary. If mortality of buried seed is low and constant and the rate of germination is constant, then the rate of loss from the seed bank is also constant. This would support the conclusion that *U. europaeus* seed survival in the seed bank is adequately described by a linear function.

Factors affecting the longevity of *U. europaeus* seed in the soil

The major predictor of seed survival in the soil was elapsed time since burial. At Auckland and Lincoln, the model predicted depletion in the seed bank in the top 5 cm of the soil profile within 20 years, although this conclusion extrapolates beyond the data. Moss (1959) found no seed in the upper layers of fields in which gorse had not grown for 28 years. This suggests rapid decline n the seed bank, as suggested by the model. There is a generally accepted view that *U. europaeus* has a long-lived seed bank (Moss 1959, 1960; Zabkiewicz & Gaskin 1978), but this may be overstated, at least for some sites.

Ulex europaeus seed bank dynamics varied greatly from site to site, which emphasises that seed bank dynamics must be interpreted carefully and within the context of past and present biotic and abiotic factors acting on them (Louda 1989; Hails et al. 1997). Our study was not designed to identify the cause of that variation, but there are two possible explanations. Differences in survivorship patterns may reflect the innate dormancy characteristics typical of the plant populations from which the seed was obtained. However, between-site seed bank survivorship also appeared to be strongly related to climate. Seed buried at Totara Flat lasted longer at all depths than at the other sites. Temperature (particularly diurnal fluctuations in temperature) is the most important factor that regulates breakdown in seed hardness (Baskin & Baskin 1989), and Ivens (1978) considered increased temperature fluctuations to be the major factor promoting *U. europaeus* seedling establishment. However, in this case temperature alone does not explain differences in seed bank dynamics between the sites, because Lincoln and Totara Flat had similar soil temperature profiles. These sites also had similar soil types, ground cover, and site management, but the rainfall at Totara Flat was much higher than at Lincoln or Auckland (Table 1). Seeds can be rendered permeable by alternate wetting and drying at high temperature (Baskin & Baskin 1989). It is unlikely that the upper layers of soil at Totara Flat ever dried out, whereas Lincoln is subject to summer drought. Auckland is also much drier in the summer. This may explain the difference in seed survival between sites.

Results suggest that there is little difference in the proportion of the seed bank surviving after 10 years anywhere in the top 10 cm of the soil profile. There may be deeply buried seeds that have significantly longer life expectancy than seeds in the upper profile. These seeds are unlikely to contribute to the population dynamics of *U. europaeus* in the short term because only a small proportion of the seed bank occurs at these depths, and because seedlings cannot successfully establish from deeper than 5 cm (R. L. Hill & A. H. Gourlay unpubl. data). However, this component of the seed bank enables the population to respond to massive soil disturbances such as cultivation or erosion. It is important to note that the model cannot take into account the effects of either seed predation or vertical transport of seed, which were prevented by placing the seeds in bags.

Implications for management and biological control of *U. europaeus*

Populations of 10 000 gorse seeds m^{-2} have been recorded in the soil (Moss 1959), and this has led to a long-held perception that land on which *U. europaeus* has grown is prone to re-invasion almost indefinitely. As a result, land managers often tolerate low-level infestations on the assumption that further seed production will not add significantly to the potential problem. Similarly, Auld (1986) concluded that once a sizeable seed bank of *Acacia suaveolans* had established, annual recruitment of seed to the seed bank was of minor importance. Where seed behaves as it did at Totara Flat, this may be true. However, where seed decline is rapid, as it was in Auckland and Lincoln, the annual input of seed from even a low density of plants could rejuvenate a seed bank that would otherwise decline rapidly. In this case, constant removal of isolated bushes will reduce the susceptibility of land to reinvasion in the long term. It is interesting to note that *U. europaeus* is not strongly invasive on the Canterbury Plains, where the Lincoln site was situated, but any disturbance of the soil near Totara Flat leads to germination of seedlings at a high density. This difference may reflect the behaviour of their seed banks.

A key element in the biological control programme against *U. europaeus* in New Zealand has been the introduction of seed-feeding insects as biological control agents. Seed predation can influence not only the characteristics of the seed bank but also the plant dynamics of such fugitive species as *U. europaeus*, at least in some places (Louda 1989). The aim is to reduce fecundity to such an extent that recruitment becomes seed-limited (Crawley 1990). However, this will work in the short term only if soil seed banks are rapidly depleted. For weeds like *U. europaeus* that have a long-lived seed bank, reducing the annual seed crop to a level where the seed bank declines incrementally (Parker & Kelly 1989) is a long-term strategy. Two insects have been introduced to New Zealand to reduce the seed production of *U. europaeus*. Gorse seed weevil, *Apion ulicis*, which was introduced from Europe and released in 1931, destroys approximately 30% of the annual seed production (Cowley 1983). Gorse pod moth, *Cydia succedana*, which was released in 1992 (Harman et al. 1996), has established, and unpublished data indicate that the two insects together may reduce annual recruitment to the seed bank by 90% in some places (T. R. Partridge pers. comm.). The results presented here suggest that these two agents may reduce the soil seed bank in some places more quickly than previously thought. Where a seed bank already exists, but declines as quickly as it did in two of the sites, the ability of seed-feeding insects to reduce the size of the seed bank may be apparent within 10 years. Conversely, reducing seed fall in some areas will have no measurable impact on the seed bank in the foreseeable future.

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