

Persistent soil seed banks in *Phacelia secunda* (Hydrophyllaceae): experimental detection of variation along an altitudinal gradient in the Andes of central Chile (33° S)

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Summary

1 It is unclear whether soil seed banks in alpine environments are a result of selection for extended seed dormancy, of ideal conditions for seed preservation in the soil, or a combination of both.

2 The nature of the soil seed bank was investigated in the perennial herb *Phacelia secunda* (Hydrophyllaceae) through reciprocal burial experiments using seeds obtained from populations growing at 1600, 2200, 2900 and 3400 m a.s.l. in the mediterranean Andes of central Chile. At the four elevations, six replicates of 50 seeds each, from each of the four elevational sources, were buried at 5 cm depth in mesh envelopes, placed in wire cages to protect against predation. Seeds were retrieved 1, 2 and 3 years after burial, and numbers of ungerminated seeds, and of those that remained viable, were determined.

3 At all elevations of seed burial, increasing proportions of seeds remained ungerminated, and proportionately more of the ungerminated seeds remained viable, as elevation of source of seed increased. For seed from low elevation, more seeds remained viable in the soil at the higher burial sites. However, for the seeds from higher elevation sources, seeds remaining viable were similar in number at all sites for seed burial. Half-lives of seed buried at the source elevation, calculated from the log-logistic distribution, increased with elevation, and ranged from 188 days at 1600 m to 354 days at 3400 m.

4 The results suggest that the propensity to form a persistent seed bank in *P. secunda* increases with elevation. Seeds from the highest elevations had the longest persistence, and this was largely unaffected by soil preservation conditions. Seeds from lower elevations survived for less time, and this was modifiable by preservation conditions. These results suggest that both selective effects and soil conditions may be involved in soil seed bank expression in the alpine environment.

Key-words: alpine environments, elevational gradient, persistent seed bank, *Phacelia secunda*

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Introduction

Numerous studies have reported the presence of viable seeds in the soil in arctic and alpine habitats (see McGraw & Vavrek 1989 and references therein, Ebersole 1989; Chambers *et al.* 1990; Chambers 1993; Diemer & Prock 1993; Ingersoll & Wilson 1993; Onipchenko *et al.* 1998; Arroyo *et al.* 1999), but most studies have been limited to describing the composition and magnitude

of the seed bank, without making clear discrimination between its transient and persistent components. There is however, good evidence for the formation of persistent seed banks by several species characteristics of high elevations in the mediterranean Andes of central Chile (Arroyo *et al.* 1999), as well as the Venezuelan paramo (Guariguata & Azocar 1988).

A number of factors predict that persistent seed banks will be favoured by selection in alpine habitats (Cavieres 1999). For instance, seed dormancy and the formation of a persistent seed bank should be

advantageous in temporally and spatially unpredictable habitats (Cohen 1966; Grime 1979; Venable & Brown 1988). Alpine habitats periodically experience unseasonably cold summers (Bliss 1985) in addition to the strong interannual variation in the length of growing season on account of yearly differences in the amount of winter snow. Nine years of climatic data (1982–90) taken at 3650 m at Niwot Ridge, Colorado, showed that winter precipitation varied by as much as 1.5 times between years, while an estimator of temperature (total annual thawing-degree days) varied by as much as 1.6 times (Walker *et al.* 1994). Unseasonably cold years and/or short growing seasons can produce strong reductions in seed output (Kudo 1991), while also decreasing seed germination and seedling establishment (Bliss 1985; Galen & Stanton 1991; Stanton & Galen 1997). A persistent seed bank in alpine habitats may therefore permit species to cue their germination to more favourable years (Cavieres 1999). Seasonal freeze/thaw activity disrupts the soil of arctic and alpine habitats extensively (Johnson & Billings 1962; Fox 1981), and it has been demonstrated that such disturbance, in exposing the deeper soil layer, can produce relatively fertile conditions (Chambers *et al.* 1990). Such disturbed sites therefore often offer better environments for seed germination and seedling establishment (Chapin & Chapin 1980; McGraw & Shaver 1982; McGraw & Vavrek 1989; Chambers *et al.* 1990), and a persistent seed bank might permit alpine species to cue their germination to the advent of favourable sites, increasing the probability of successful seedling establishment.

An alternative explanation for the presence of persistent seed banks in the alpine environment proposes that conditions will favour seed remaining in a viable state in the soil, without any effect on selection for seed longevity. In cold climates the diversity of both seed predators and pathogenic fungi is low (McGraw & Vavrek 1989), and low temperatures are also associated with low embryonic metabolic rates and slow consumption of seed reserves, favouring greater seed longevity (Villiers 1973; Murdoch & Ellis 1992). Persistent seeds banks in alpine environments may therefore simply reflect ideal conditions for seed preservation.

We used studies along an elevational gradient to elucidate the relative importance of factors responsible for the presence of persistent seed banks in an alpine environment. Factors leading to selection for dormancy (e.g. disturbances associated with freezing and thawing, and fluctuations in growing season length) become more pronounced with increasing elevation, while conditions for seed preservation also improve (Cavieres 1999). If the formation of a persistent seed bank is due to seed dormancy, being a selected life history trait in the alpine zone, then seeds produced by plants at higher elevations should show similar levels of persistence regardless of the elevation (and hence variation in soil conditions) at which they are subsequently buried. If the persistent seed bank simply reflects soil storage conditions, then seeds produced by high elevation

populations should be less persistent when they are experimentally buried at lower elevations, where soil conditions are less favourable for seed preservation. Conversely, lower elevation populations would be expected to show lower seed persistence *in situ*, but this should increase when seeds are experimentally buried at higher elevations. The perennial herb *Phacelia secunda* J.F. Gmel. (Hydrophyllaceae) occurs over a wide elevational range in the alpine zone of central Chile, allowing us to perform reciprocal burial experiments using seeds from populations at four elevations.

Methods

STUDY SPECIES

In central Chile, the perennial herb *Phacelia secunda* grows from close to sea level to the upper vegetation limit in the Andes (3400 m a.s.l.) and inhabits coastal, mediterranean-type montane forest and alpine communities. *P. secunda* forms rosettes and reproduces by seeds (2–3 mm in length and 1 mm in width) which are dispersed passively from a dry capsule (Cavieres *et al.* 1999). The species forms seed banks that vary in density from 20 m⁻² at 1600 m to 190 m⁻² at 3400 m (Cavieres & Arroyo 1999a).

STUDY SITES

Field work was conducted in the central Chilean Andes (Lat. 33°S), at Santuario de la Naturaleza Yerba Loca and at Valle Nevado, located 50 km and 80 km east of Santiago, respectively, at elevations ranging from 1600 to 3400 m a.s.l. (Fig. 1). Central Chile is characterized by a mediterranean-type climate (Di Castri & Hajek 1976), with high interannual variability in precipitation (Aceituno 1990). In the study area, above treeline, precipitation mainly occurs in the form of winter snow, with mean annual precipitation of 472 mm at 2400 m, but varying as much as 278 mm in 1990 to 678 mm in 1991 (L. Cavieres, unpublished data). At the lower site (1600 m, below the treeline), snow persists for 0–3 months, whereas at the highest site (3400 m), snow persists for 3–5 months. At 1600 m, the mean annual temperature is 12.7 °C compared with approximately 6.5 °C at 2600 m and 3 °C at 3150 m (Cavieres & Arroyo 1999b).

SEED SOURCES

Seeds were obtained from populations of *P. secunda* located immediately below the treeline and from above the treeline to the upper vegetation limit. Source populations were located on south-facing slopes either in the Río Molina valley or above the Valle Nevado ski complex.

Population 1 was below the treeline at 1600 m a.s.l. The vegetation here is montane sclerophyllous woodland dominated by 5–10 m individuals of *Kageneckia*

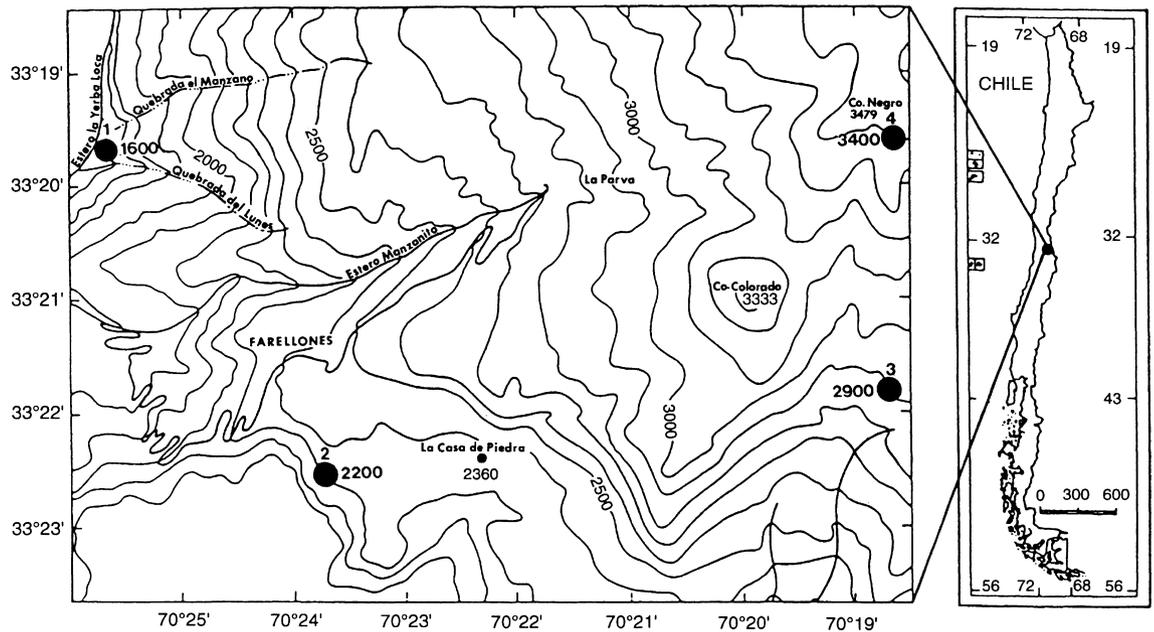


Fig. 1 Map showing the location of altitudes (●) where seed collection and burial were carried out.

angustifolia D. Don (Rosaceae), with a discontinuous shrub layer interspersed with a rich flora of annual and perennial herbs. *Phacelia secunda* populations, which are found in the intertree spaces, are composed of individual plants with small rosettes each bearing one or two large inflorescences (Cavieres 2000).

Population 2 was located at 2200 m a.s.l. in the sub-Andean scrub belt (2100–2500 m) dominated by low shrubs as *Chuquiraga oppositifolia* D. Don (Compositae) and *Berberis empetrifolia* Lam. (Cavieres *et al.* 2000). *Phacelia secunda* is found in the open spaces between shrubs.

Population 3 was located at 2900 m a.s.l. in the lower Andean belt (2600–3100 m) which is dominated by cushion plants such as *Laretia acaulis* (Cav.) Gill. *et Hook.* (Umbelliferae) and *Anarthrophyllum gayanum* (A. Gray) Jacks. (Papilionaceae) (Cavieres *et al.* 2000), with *P. secunda* as one of the most abundant perennial herbs.

Population 4 was at 3400 m a.s.l. in the high Andean belt dominated by the cushion species *Azorella madreporica* Clos. (Umbelliferae) and the perennial herb *Nassauvia pyramidalis* Meyen (Asteraceae). Vegetation is low and sparse, and many species of perennial herbs are interspersed with the dominants. *Phacelia secunda* is found on finer and often reworked soil in scattered dense patches, which are composed of large, compact rosettes with more than 10 inflorescences per individual (Cavieres 2000).

Seeds were collected from at least 50 individuals per population at the dispersal stage during summer 1995 (January to March, depending on site elevation) and stored in paper bags in cool dry laboratory conditions until the following autumn. However, few or no populations between 2100 and 2500 m produced seeds in

1995, and experiments were therefore repeated in 1996. Immediately before the burial experiments were started, 50 seeds from each of the four seed sources were scored for viability with tetrazolium chloride (Moore 1973). Seeds were cut lengthwise and placed in a 0.5% aqueous solution of tetrazolium chloride in the dark for 24 h. We considered seeds with embryos staining completely red to be viable. Viability was close to 100% in all populations.

SEED BURIAL EXPERIMENTS

Many studies have evaluated longevity by monitoring the viability of seeds recovered at various time after artificial burial (e.g. Roberts 1986; Guariguata & Azocar 1988; Zhang & Maun 1994). This protocol would not, however, distinguish between true longevity and seed persistence, which is merely the product of favourable soil conditions for storage. We therefore used a system of reciprocal burials, where seeds collected from all four elevational sites were buried at each elevation at the same time and under the same conditions. As far as we are aware, this is the first time that such a procedure has been used in an alpine habitat, allowing control of the effect of soil conditions in promoting persistence of viable seeds.

Six replicate burial points were randomly selected at each elevation in April 1995 and again in 1996. Three cages (one for each year of retrieval) were placed 5 cm below the soil surface at each of the burial points. The cages were made of 0.5-cm wire mesh to protect the seeds from potential predators, and contained plastic mesh envelopes (one per population, including that from the elevation as the burial), each containing 50 seeds. There were therefore three envelopes per cage in 1995 and four in 1996, to produce all possible combinations of seed sources and burial elevation.

RETRIEVAL OF BURIED SEEDS

One cage was exhumed 1, 2 or 3 years after burial (six replicates per elevation per date). Seeds buried in April 1995 were exhumed in April 1996, 1997 and 1998, while those buried in 1996 were exhumed in 1997, 1998 and 1999.

The exhumed material was transported to the laboratory where a binocular microscope was used to assess how many ungerminated but physically intact seeds remained. After testing with TTC, the number of recovered intact viable seeds was expressed as a percentage of the initial number of buried seed to provide a measure of the 'potential' seed bank (Zhang & Maun 1994).

DATA ANALYSES

The percentage of ungerminated seeds and percentage viability of the remaining ungerminated seeds were analysed with two-way ANOVA using elevational origin of seed and elevation of burial as independent factors. Percentage values were arcsine-transformed prior to analysis (Steel & Torrie 1988).

To assess loss of viability of seeds over time (and hence depletion of the potential soil seed bank), we applied the log logistic survival distribution to our data. Rees & Long (1993) demonstrated that this model provides an accurate description of seedling recruitment (seed bank decay) processes in many species. We used the continuous distribution model: $N_t = N_0 / (1 + (kt)^b)$, where N_t = mean number of viable seeds at time t (in days), N_0 = mean initial number of viable seeds, and k and b are constants. For comparative purposes we estimated the longevity of the seed bank by calculating the half-life (the time, in days, taken for half of a cohort of seeds in the seed bank to die) of buried seeds according to the equation $t_{1/2} = 1/k$.

Results

Elevation of burial site, elevation of seed source and duration of burial had significant effects on both the percentage of ungerminated seeds and their viability (Table 1). The year in which seed were collected and buried had no significant effects (Table 1).

SEEDS FROM LOWER ELEVATIONS

As little as 1 year after burial, only a low proportion (< 20%) of the seeds from 1600 m remained ungerminated (Fig. 2a,b) at any elevation, and there were no significant differences between burial elevations (Table 2). Viability of these ungerminated seeds ranged from 10% to 60% (Fig. 3a,b), and was significantly higher with increasing elevation of burial site (Table 3). After 2 years of burial at 1600 m, there were no ungerminated 1600 m source seeds while fewer than 10% of these seeds remained at other elevations (Fig. 2c,d); and their viability ranged from 7% to 40% (Fig. 3c,d). By this storage, elevation of burial site significantly affected the percentage of ungerminated seed, but not its viability (Tables 2 and 3). No ungerminated seeds from 1600 m source remained after 3 years at any site (Fig. 2e,f). In seeds from 2200 m, only available in 1996, both germination and viability showed similar patterns for 1600-m seed from 1996 (see Figs 2b,d,f and 3b,d,f).

SEEDS FROM HIGHER ELEVATIONS

After 1 year of burial, the proportions of ungerminated 2900-m and 3400-m source seeds were relatively high (Fig. 2a,b), but significantly lower when buried at higher elevation (Table 2). Viability of ungerminated seeds was consistently high (> 80%) (Fig. 3a,b), but was not significantly affected by elevation of burial site, except for 3400-m source seed in 1996 (Table 3).

Table 1 Results of MANOVAS performed to determine the effects of the altitude of burial, elevation of seed source, year of collection and burial, and duration of burial on the percentage of ungerminated seeds (a) and percentage of viability of ungerminated seeds (b) of *Phacelia secunda* collected and buried at different elevations during 1995 and 1996 in the Andes of central Chile (33°S)

Source	Sum of squares	d.f.	Mean square	F-ratio	P
Duration of burial	109713.2	2	54856.6	2248.9	0.000
Year	2.0	1	2.0	0.1	0.773
Site of burial	273.8	3	91.3	3.7	0.011
Seed source	21279.6	2	10639.8	436.2	0.000
Error	8342.2	342	24.4		

(b) Percentage viability of ungerminated seeds					
Source	Sum of squares	d.f.	Mean square	F-ratio	P
Duration of burial	13685.9	2	6842.5	23.7	0.000
Year	436.1	1	436.1	1.5	0.317
Site of burial	14873.1	3	4957.7	17.1	0.000
Seed source	113447.4	2	56723.7	196.2	0.000
Error	98884.3	342	289.1		

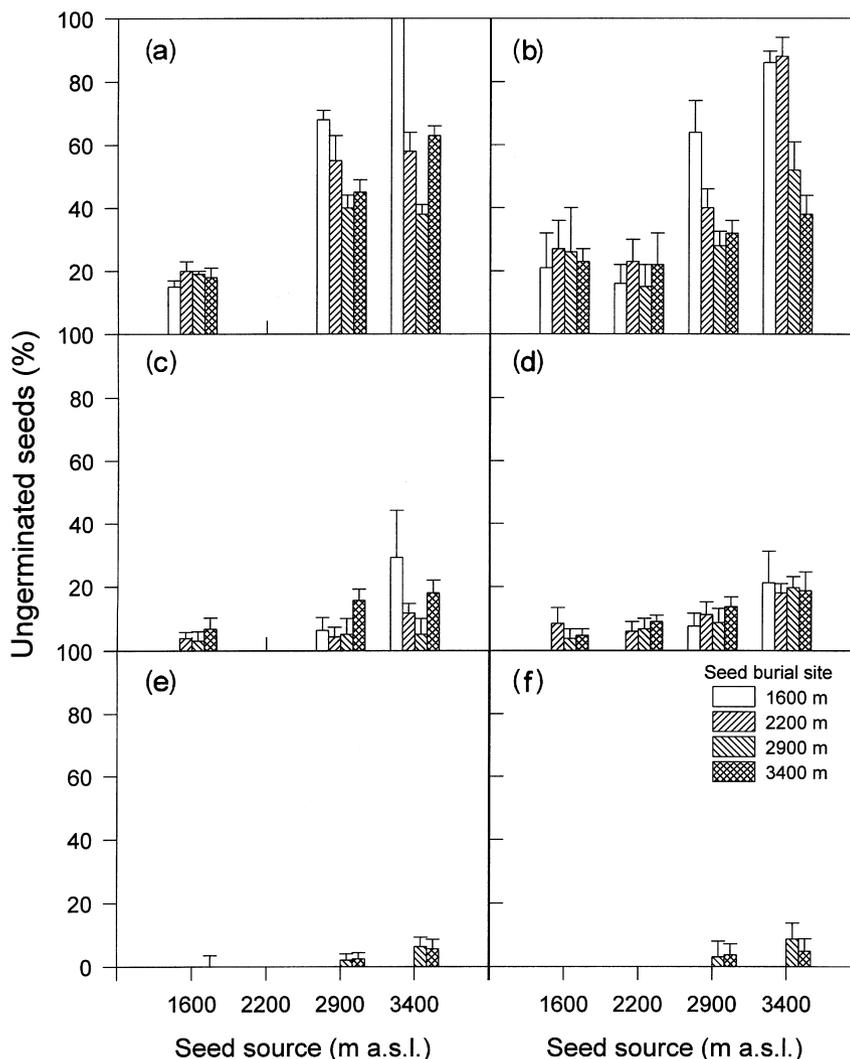


Fig. 2 Persistence of seed collected and buried at different elevations. Percentage of seeds remaining ungerminated for seed buried in 1995 for 1, 2 and 3 years (a, c, e, respectively); seed buried in 1996 for 1, 2 and 3 years (b, d, f, respectively).

Table 2 *F*-values from ANOVAS performed to determine the effects of the altitude of burial site on the percentage of ungerminated seeds of *Phacelia secunda*. Seed were collected and buried at different elevations during 1995 and 1996. Seed remained buried for 1 to 3 years. **P* < 0.01

Seed source (m a.s.l.)	After 1 years		After 2 years		After 3 years
	Seed buried in 1995 (<i>F</i> _{3,20})	Seed buried in 1996 (<i>F</i> _{3,20})	Seed buried in 1995 (<i>F</i> _{3,20})	Seed buried in 1996 (<i>F</i> _{3,20})	Seed buried in 1995 (<i>F</i> _{3,20})
1600	3.0	0.2	8.9*	9.0*	–
2200	–	0.7	–	19.0*	–
2900	18.4*	16.6*	4.7	1.6	2.9
3400	296.6*	39.8*	1.0	0.1	20.2*

Fewer seeds remained ungerminated after 2 years (Fig. 2c,d), but there were no significant differences between burial elevations (Table 2). Viability of ungerminated seeds was now > 50% (Fig. 3c,d), with no significant effect of elevation. After 3 years, ungerminated seeds were found only in higher elevations, and even then, only < 5% remained ungerminated (Fig. 2e,f). Viability of ungerminated seeds after 3 years was > 28%

(Fig. 3e,f), with no significant effect of burial elevations (Table 3).

LONGEVITY OF BURIED SEEDS

The log logistic distribution for decline of viability through time explained more than 99% of variation in all cases (results not shown). Half-lives of buried

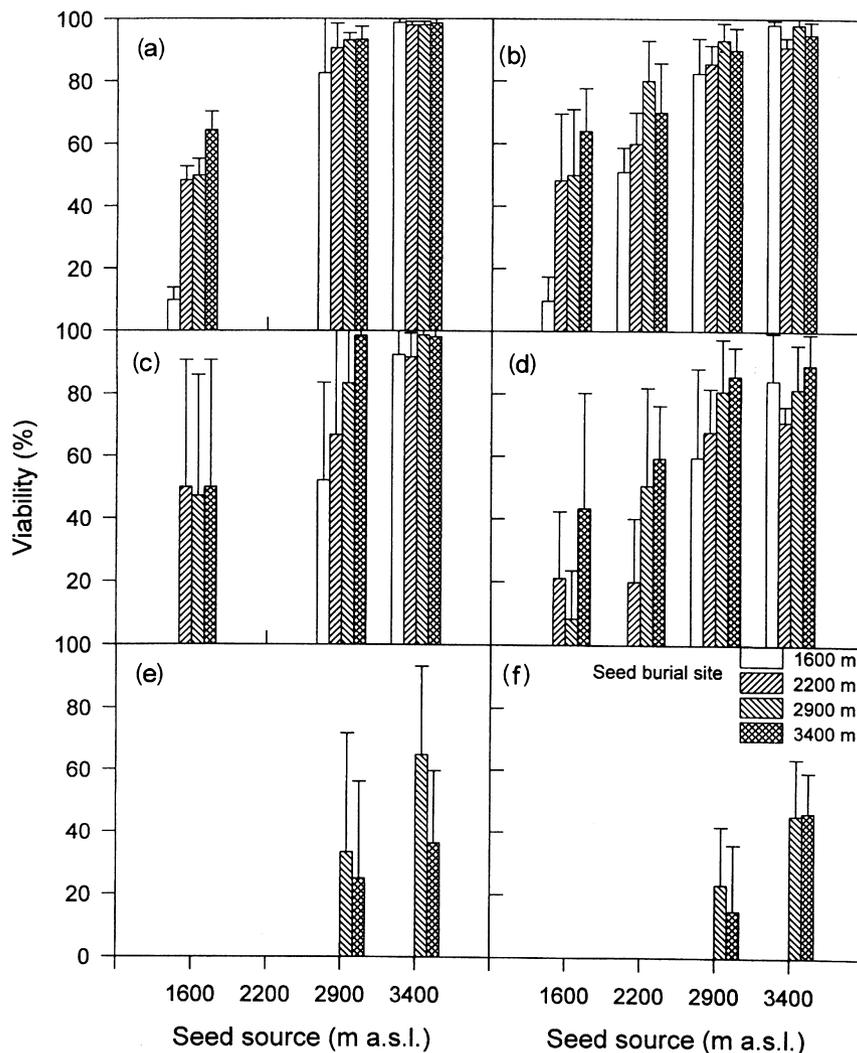


Fig. 3 Percentage viability of ungerminated seed collected and buried at different elevations. (a), (c) and (e): seed buried in 1995 for 1, 2 and 3 years, respectively. (b), (d) and (f): seed buried in 1996 for 1, 2 and 3 years, respectively.

Table 3 *F*-values from ANOVAS performed to determine the effects of the altitude of burial site on viability of the remaining ungerminated seeds of *Phacelia secunda*. Seed were collected and buried at different elevations during 1995 and 1996. Seed remained buried for 1 to 3 years. **P* < 0.01

Seed source (m a.s.l.)	After 1 years		After 2 years		After 3 years
	Seed buried in 1995 (<i>F</i> _{3,20})	Seed buried in 1996 (<i>F</i> _{3,20})	Seed buried in 1995 (<i>F</i> _{3,20})	Seed buried in 1996 (<i>F</i> _{3,20})	Seed buried in 1995 (<i>F</i> _{3,20})
1600	42.6*	4.6*	1.7	2.0	–
2200	–	2.9	–	5.2*	–
2900	0.3	1.6	2.9	1.4	1.6
3400	0.3	3.7*	0.2	1.1	1.0

seeds varied from 113 to 619 days, depending on seed source and elevation of site of burial (Table 4). Seeds collected from higher elevations (2900 m and 3400 m) showed a tendency to have shorter half-lives when buried at higher elevations (Table 4). In contrast, seeds from 1600 m showed a tendency for longer half-lives when buried at higher elevations (Table 4).

Specific half-lives calculated for seeds buried at the same elevation at which they were collected, and averaging the results of the 1995 and 1996 experiments (except for 2200-m source seed that was collected only in 1996), were: 188, 192, 269 and 354 days, for seeds collected at 1600, 2200, 2900 and 3400 m a.s.l., respectively.

Table 4 Half-lives (in days) calculated from the log logistic model for seed of *Phacelia secunda* collected and buried at different elevations during 1995 and 1996

Elevation of burial (m a.s.l.)	1995				1996			
	Seed source (m a.s.l.)				Seed source (m a.s.l.)			
	1600	2200	2900	3400	1600	2200	2900	3400
1600	113	–	395	619	198	215	378	486
2200	137	–	367	398	150	192	291	485
2900	168	–	297	446	228	128	241	371
3400	177	–	326	432	194	152	230	276

Discussion

Persistent seed banks, by definition (Thompson & Grime 1979), are those in which a fraction of the seeds of a species not only remain in the soil, but are also viable for at least 1 year after production. The formation of a persistent seed bank as a selected life history trait depends on innate or enforced dormancy.

In *Phacelia secunda*, very few seeds collected from lower elevations remained ungerminated and viable after 1 year of burial at any elevation, whereas few of those from higher elevations germinated, and most of those remaining (> 90%) were still viable. Even after 3 years, a considerable fraction of the seeds from the highest source remained ungerminated and viable. The trend for *P. secunda* seed dormancy to increase with elevation of seed source was apparent for collections from 2 years.

The results of our reciprocal burial experiments are consistent with the hypothesis that selection has favoured greater seed persistence in the higher elevation populations of *P. secunda*. Although soil conditions do affect seed viability and longevity, soil conditions alone are insufficient to explain why seed are more persistent at the higher elevations. The significant increase in viability of the ungerminated seeds collected from the 1600-m source site with increasing elevation of the burial site is consistent with soil conditions at higher elevations allowing seeds to remain viable for longer periods. However at 3400 m, practically all 1600-m seeds germinated within 1 year compared with only 40% of the 3400-m seeds, indicating that some internal factor is involved in the large maintenance of the seed banks at higher elevations. More intriguingly, the absence of any decreasing viability of seeds when placed at 1600 m argues against the soil preservation hypothesis. Preliminary studies indicate that *P. secunda* seeds from higher elevation have a higher content of phenolic compounds (L. Cavieres, unpublished data). The well-known strong anti-fungal, bactericidal and anti-herpetic properties of such compounds (Hendry *et al.* 1994) might override the effect of soil properties at low elevations. Furthermore, it is well known that phenolic compounds are involved in seed dormancy (Baskin & Baskin 1998) and this is likely to contribute to the stronger innate dormancy of seeds from higher elevations.

The interpretation that there is selection for the propensity to form persistent seeds banks at higher elevations in *P. secunda*, would need to be modified if it were shown that high-elevation seeds of this species required a longer after-ripening period (cf. Barclay & Crawford 1984). Laboratory experiments, however, suggest that this is unlikely. Using the same seed sources as employed in this study, Cavieres & Arroyo (2000) demonstrated only minor effects of dry after-ripening, with no significant differences between seeds obtained from different elevations. In seeds dry stored for 4 months and then wet stratified at 4 °C for other 6 months, and germinated under standard lab conditions of light, humidity and temperature, higher germination from 1600-m sites than from 3400-m sites indicated a deeper level of seed dormancy at high elevation (Cavieres & Arroyo 2000). Moreover, in a time series experiment, it was shown that at least 3 months stratification is required for the initiation of germination of seeds from the 3400-m source, as opposed to 1 month for the 1600-m source seeds (Cavieres & Arroyo 2000). The unexpected absence of any germination in 3400-m source seeds when buried for 1 year at 1600 m may therefore be explained by the much shorter cold period at 1600 m being insufficient to break the deepest dormancy in the 3400-m seed.

Although it is well known that seeds of alpine species may remain viable for long periods in cold laboratory storage (Billings & Mooney 1968; Chambers 1989), few studies have addressed seed longevities in the natural habitat. According to the log logistic decay model of viability used here, mean longevity of the seed bank of *P. secunda* at 1600 m was 188 days, while at 3400 m it increased to 354 days. Using a negative exponential model, Miller & Cummins (1987) estimated a half-life for the seed bank of *Calluna vulgaris* in the subalpine zone of Scotland as *c.* 0.8 years, while in the alpine zone this increased to 5 years. Guariguata & Azocar (1988) similarly estimated that seeds of the giant tropical Andean rosette species, *Espeletia timotensis* have the potential to remain viable in the soil for 4–5 years. However, in another seed burial study, Spence (1990) showed that alpine *Chionochoa macra* does not have a persistent seed bank, and meaningful generalizations about the longevity of alpine seeds in the soil are clearly not yet possible.

There is significant variation in seed bank expression in *P. secunda* over a steep elevational gradient in which a linear distance of 10 km separates the extremes. In the case of *P. secunda*, genetic differentiation along such a gradient would be promoted by the lack of adaptations for long-distance seed dispersal (Cavieres *et al.* 1999), as well as non-overlapping flowering times and pollinator assemblages at the extremes of elevation (Arroyo *et al.* 1981, 1982). Nevertheless, the possibility that differences in propensity for seed bank formation in this species are a product of maternal effects (Roach & Wulff 1987) cannot be ruled out at this stage.

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