

Full Length Research Paper

Persistent soil seed banks along altitudinal gradients in the Qilian Mountains in China and their significance for conservation management

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Accepted 31 January, 2011

The qualitative and quantitative parameters of persistent soil seed bank, including species composition, seed density, vertical distribution and the relationship of soil seed bank and vegetation, were assessed along an altitudinal gradient in seven communities in shady slope, sunny slope and summit plain of Qilian Mountains. The highest density of soil seed bank of 3946 seeds m⁻² was found in grassland in summit plain, and lowest of 225 seeds m⁻² in the dwarf scrub grassland in shady slope, while the highest numbers of species of 21 species in per sampled area of 962 cm² was found in grassland in sunny slope and lowest of 5 species in per sampled area of 962 cm² in scrub land in shady slope. Of the species 18% were annuals and 73% perennial herbs, only 1 shrub of *Salix gilashanica* was recorded. Considerably more seeds were concentrated in the upper layer (0 to 5 cm), and seed density declined by 71.10% in the lower layer (5 to 10 cm). There was a tendency for the soil seed bank to decrease in density with increasing elevation in both shady slope and sunny slope, although this pattern is complicated by the occurrence of different plant communities and species at different altitudes. Sorensen similarity index between soil seed bank and vegetation of the seven habitats was very low, and *Picea crassifolia* was absent in the soil seed bank despite being a prominent component of the surface vegetation at woodlands; thus, *P. crassifolia* has no persistent seed bank. It will be important to maintain the existing vegetation in the future management.

Key words: Soil seed bank, seed density, altitudinal gradients, slopes, conservation.

INTRODUCTION

The soil seed bank is defined as the mature viable seeds stock existing in the soil surface, or buried in the soil, duff or litter, in a determinate moment and place (Walck et al., 2005; Martins and Engel, 2007). The soil seed bank plays an important role in the composition of different plant communities and thus in their conservation (Grubb, 1977; Leck et al., 1989; Wisheu and Keddy, 1991). Seed bank composition can be used to predict the initial composition of post-recruitment vegetation and yield information on the species composition of previous and new vegetation,

the relative abundance of recently recruited species and the potential distribution of each species (Major and Pyott, 1966; Donelan and Thompson, 1980; Welling et al., 1988). Besides, it represents a store of evolutionary memory (Harper, 1977). Thus, knowledge of the seed bank and an understanding of the population dynamics of buried viable seeds is of practical importance in agriculture, forestry and conservation (Onaindia and Amezaga, 2000). The capacity to form persistent seed banks allows species to survive episodes of disturbance and destruction (Thompson, 2000). Many species have this capacity and many do not (Thompson et al., 1997). An understanding of persistent seed banks is the key to many aspects of practical management for agriculture and conservation, and to effective conservation of rare

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species and diverse ecosystems (Keddy and Reznicek, 1982; Bertiller and Aloia, 1997; Jalili et al., 2003).

Recently, studies in alpine site have revealed appreciable soil seed banks in many different habitats. For example, deciduous forest (Jankowska-Blaszczuk and Grubb, 1997; Augusto et al., 2001; Onaindia and Amezaga, 2000), Mediterranean shrubland (Valbuena and Trabaud, 2001), hay meadow (Bekker et al., 2000), lowland grass heath (Pakeman and Marshall, 1997), lowland heath (Mitchell et al., 1998), subalpine (Ingersoll and Wilson, 1993; Zabinski et al., 2000) and alpine (Cavieres and Arroyo, 2001; Chambers, 1993; Diemer and Prock, 1993) communities, and arctic tundra (Ebersole, 1989; Molau and Larsson, 2000). Although seed banks may be a potential source of regeneration in some of these fragile montane communities, Miller and Cummins (2003) found that, montane seed banks was so species poor that any resultant vegetation is unlikely to resemble the original community. The prospects for recovery were poor in montane sites and it is clearly preferable to minimise or avoid damage to the vegetation. However, most of these investigations of soil seed banks have been centred on single vegetation types in particular habitats, comparisons amongst an array of vegetation types within a single defined geographical area are seldom made.

Therefore, this paper focuses on the soil seed banks associated with a range of vegetation and habitats in the northern slopes of Qilian Mountains along with the altitude, from grassland to woodland and to scrubland, from shady slope to sunny slope and to summit plain. Thus, the aims of the paper were:

- (1) To evaluate the qualitative and quantitative parameters (species composition, seed density, vertical distribution and the relationship of soil seed bank and vegetation) of soil seed banks in different habitats;
- (2) To elucidate the density of soil seed banks along an elevational gradient in mountain environment;
- (3) To analyze the role of mountain soil seed banks in ecological implications.

MATERIALS AND METHODS

Site description

The study was carried out in Pailugou catchment in the northern slope of Qilian Mountains, near Zhangye city, Gansu Province, in northwest China (latitude 38°31' to 38°34'N and longitude 100°17' to 100°18'E) (Figure 1). The annual average temperature declines from 0.7 °C to -5.4 °C and mean annual precipitation increases from 433.6 to 690.26 mm with an increasing elevation from 2600 to 3800 m. Owing to the steep temperature and precipitation gradient, vegetation displayed a mosaic of patches of grasslands, shrublands and forests. Soil sampling was centred on and around seven habitats in shady slope, sunny slope and summit plain. Sunny slope and summit plain are in the same hill, and the shady slope was opposite to them about 1 km long. They were in the same catchment. The habitats of shady slope contain grassland,

woodland, scrubland and dwarf scrub grassland, while sunny slope is occupied by grassland and scrub grassland, and the summit plain is grassland.

Vegetation survey

In the center of each stand of each site, the size of vegetation sampling unit used was 600 m² (20 × 30 m) for woodland and 5 replicates of 100 m² (10 × 10 m) for scrubland and 5 replicates of 1 m² (1 × 1 m) for grassland. From this vegetation survey, seven major habitats and 27 plant communities have been recognized (Table 1). For each sample plot, the vegetation surveys were made in July 2005. Species that could not be identified in the field were brought to the laboratory for complete identification.

Seed bank study

Soil for sampling the seed bank was collected in July 2005 from an area of 50 m² at the center of a representative and homogeneous area of each of the 27 plant communities. Within each community, five sampling points were randomly selected within this 50 m² and five soil cores (diameter 7 cm, depth 10 cm) were collected from each. Thus, 962 cm² of soil surface were sampled within each community. Each core was then subdivided into an upper (0 to 5 cm) and a lower (5 to 10 cm) layer. Surface litter and cryptogams were included with the upper soil core. The samples were stored in the dark for 2 weeks at 5°C. The soil cores were sieved through an 8 mm mesh to remove stones and twigs, then the soil from the 25 replicate cores for each layer from each community was combined and five subsamples were spread out to a depth about 10 mm in two trays (diameter 24 cm) of sand. Thus, a total of 540 trays were used: 5 subsamples × 2 trays × 5 depths × 27 plant communities. For each vegetation type 9616 cm³ of soil was used, 4808 cm³ from each of the two layers. The trays were placed in a greenhouse and watered regularly. As seedlings germinated, they were identified and removed. The soil was disturbed after the first flush of germination and recording lasted for one year. Ceasing only when no new germination had been recorded for 6 weeks. The seedling counts were converted to numbers of seeds m². The characteristics of the seeds were summarized using descriptive statistical techniques. The effects of layer and altitude on density of soil seed banks were analyzed using two-way ANOVAs in the treatments. Differences among means were assessed using Tukey's studentized range test. The degree of similarity between vegetation and soil seed bank in each habitat was assessed using Sorensen's qualitative index (Magurran, 1988).

RESULTS

Qualitative and quantitative parameters of soil seed bank

Arguably, the most important feature of the results is the low density of seeds in all communities, for samples being collected in July, well after the period of early summer seedling emergence but before most current year's seeds were shed. From a total of 540 trays, 5397 seedlings (upper layer, 4187; lower layer, 1210) from 56 species germinated in the soil samples (Tables 2 and 3). Of the species 18% were annals and 73% perennial herbs, only 1 shrub of *Salix gilashanica* was recorded, with only 1 seedling in sunny slope and 4 seedlings in

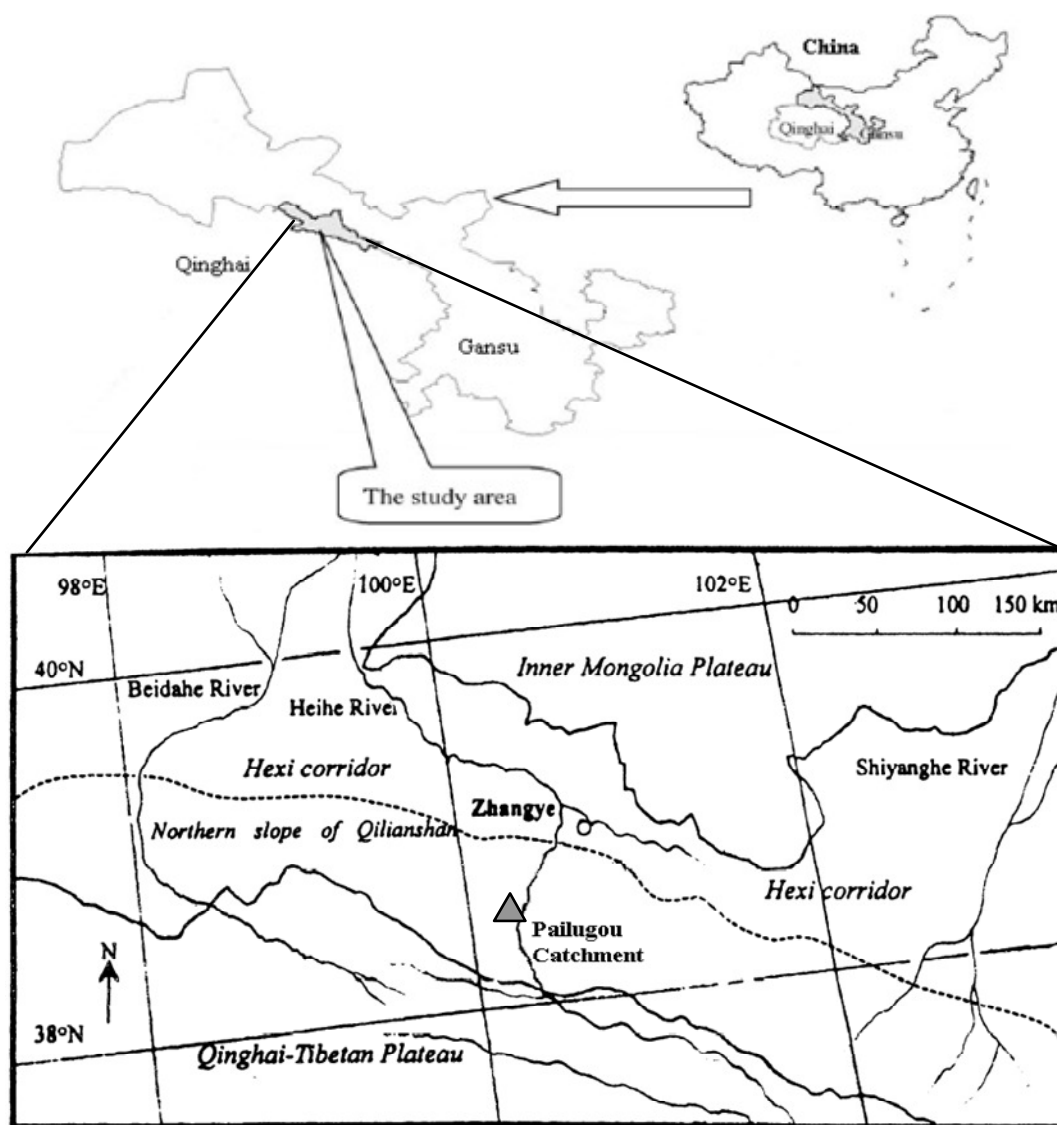


Figure 1. Location of study area in the northern slopes of Qilian Mountains in Northwest China. The gray triangle indicates the sample area.

shady slope. Statistically significant differences in density of the soil seed bank were detected between woodland and dwarf scrub grassland in shady slope and grassland and scrub grassland in sunny slope.

Highest density of soil seed bank was found in grassland of summit plain (3946 seeds m^{-2}), and lowest in the dwarf scrub grassland in shady slope (225 seeds m^{-2}), while the highest numbers of species was found in grassland in sunny slope (21 species in per sampled area of 962 cm^2) and lowest in scrub land in shady slope (5 species in per sampled area of 962 cm^2) (Figure 2). Species such as *Achnatherum inebrians*, *Allium cyaneum*, *Aneurolepidium dasystachys*, *Atriplex sibirica*, *Carex lanceolata*, *Herminium monorchis*, *Lancea tibetica*, *Medicago lupulina*, *Oxytropis melanocalyx*, *Plantago depressa*, *Polygonum viviparum*, *Potentilla bifurca*, *S.*

gilshanica, *Stellera chamaejasme* and so on were common both in vegetation and in the seed bank. However, 29 species including *Melica scabrosa*, *Setaria glauca*, *Setaria viridis*, *Chenopodium album*, were present in the soil seed bank but absent from the vegetation. Table 2 also includes a list of species abundant in the vegetation but unrecorded from the soil seed bank, which illustrated that these species lack persistent seed banks.

In general, Sorensen similarity index between seed bank and vegetation of the seven habitats was very low, which were 0.22, 0.33, 0.23, 0.29, 0.3, 0.27 and 0.4 respectively, although the vegetation and seed bank were more similar for woodland in shady slope and for grassland in summit plain than for other vegetations (Figure 3). Seed density differed significantly among

Table 1. The major habitats of the area.

Habitat types (communities number)	Altitudinal range (m)	Slopes	Species number in vegetation	Description
1 Grassland (4)	2700-2850	Shady	66	Occurs on gentle slopes, and main species are <i>Iris lacteal</i> , <i>Pedicularis kansuensis</i>
2 Woodland (4)	2850-3100	Shady slope	34	The moss is 2.5 to 6 cm, and main species are <i>Picea crassifolia</i> , <i>Polygonum viviparum</i>
3 Scrublands (5)	3100-3500	Shady slope	41	Occurs on the steep hillsides, and main scrubs are <i>Rhododendron przewalskii</i> , <i>Potentilla fruticosa</i> , <i>Caragana jubata</i>
4 Dwarf scrub grassland (3)	3500-3800	Shady slope	30	Near the summit of the shady slope, main species are <i>Potentilla fruticosa</i> , <i>Caragana rosea</i>
5 Grassland (3)	2600-2700	Sunny slope	30	Occurs immediately above the valley bottoms, and main species are <i>Medicago hispida</i> , <i>Oxytropis melanocalyx</i>
6 Scrub grassland (5)	2700-2950	Sunny slope	38	Occurs on the steep hillsides, and main scrubs are <i>Potentilla fruticosa</i> , <i>Caragana korshinskii</i>
7 Grassland (3)	2870-3005	Summit plain	26	The slope is slight, and main species are <i>Polygonum viviparum</i> , <i>Achnatherum inebrians</i> , <i>Iris lacteal</i>

were concentrated in the upper layer (0-5 cm), and seed density declined by 71.10% in lower layer 5-10 cm (Table 4).

Density along an altitudinal gradient

There was a tendency for the soil seed bank to decrease in density with increasing elevation in both shady slope and sunny slope, although this pattern is complicated by the occurrence of different plant communities and species at different altitudes (Figure 4). However, in the summit plain, the highest density of soil seed bank was in the highest altitude of 3005 m for the slope of the summit plain is slight. The density of soil

seed bank (y) at various elevations both in shady slope and in sunny slope could be described by a quadratic function of elevation (x):

Shady slope: $y = 22.494x^2 - 594.28x + 4460.2$ ($R^2 = 0.5934$, $p = 0.0059$).

Sunny slope: $y = 45.29x^2 - 723.75x + 4612.9$ ($R^2 = 0.8315$, $p = 0.0117$) (Figure 4).

DISCUSSION

Qualitative and quantitative parameters of soil seed bank

In our paper, the highest density of soil seed bank

was found in grassland of summit plain (3946 seeds m^{-2}), and lowest in the dwarf scrub grassland in shady slope (225 seeds m^{-2}), which was different with many surveys for example, a recent review of 70 studies of persistent seed banks revealed only seven recorded densities of greater than 10^4 seeds m^{-2} , this figure was exceeded in all 7 habits in our paper (Baskin and Baskin, 1998). However, our paper was also well within the range of densities found in many studies. For instance, Fenner (1985) cited 10^3 to 10^6 of seeds per m^2 as typical values for grassland; montane sites contained only a few hundred of seeds m^{-2} , comparable with many estimates from arctic tundra (Roach, 1983;

Table 2. The representation of species in the soil seed bank and the vegetation.

Name of species	Family	Life form	Soil seed bank	Vegetation
<i>Achnatherum inebrians</i>	Gramineae	Perennial	6,7	6,7
<i>Adonis coerulea</i>	Ranunculaceae	Perennial	1,2,5	Absent
<i>Allium cyaneum</i>	Liliaceae	Perennial	5,6	5,6
<i>Aneurolepidium dasystachys</i>	Gramineae	Perennial	1,5,6,7	1,2,4,5,6,7
<i>Aquilegia viridiflora</i>	Ranunculaceae	Perennial	5	Absent
<i>Artemisia annua</i>	Compositae	Annual	2	1
<i>Aster flaccidus</i>	Compositae	Perennial	4,6,7	Absent
<i>Astragalus monadelphus</i>	Leguminosae	Perennial	5,6	Absent
<i>Atriplex sibirica</i>	Chenopodiaceae	Annual	5	5,6
<i>Capsella bursa-pastoris</i>	Cruciferae	Annual or biennial	1	Absent
<i>Carex lanceolata</i>	Gramineae	Perennial	1,2,3,4,5,6,7	1,2,3,4,5,6,7
<i>Cerastium arvense</i>	Caryophyllaceae	Perennial	3	1,3,4,7
<i>Chenopodium album</i>	Chenopodiaceae	Annual	6	Absent
<i>Cremanthodium lineare</i>	Compositae	Perennial	1,5,6,7	Absent
<i>Crepis crocea</i>	Compositae	Perennial	5	Absent
<i>Equisetum ramosissimum</i>	Equisetaceae	Perennial	1,2	Absent
<i>Eragrostis cilianensis</i>	Gramineae	Annual	5	Absent
<i>Eragrostis minor</i>	Gramineae	Annual	2,5,6,7	1,2,3,4,7
<i>Euphorbia micractina</i>	Euphorbiaceae	Perennial	2	3,4,5
<i>Gentiana przewalskii</i>	Chntianaceae	Perennial	1,3,5,6	3,4
<i>Halerpestes cymbalaria</i>	Ranunculaceae	Perennial	6	Absent
<i>Herminium monorchis</i>	Orchidaceae	Perennial	1,5,6,7	6,7
<i>Iris potaninii</i>	Iridaceae	Perennial	4	5,7
<i>Ixeris chinensis</i>	Compositae	Perennial	5	Absent
<i>Ixeris denticulata</i>	Compositae	Biennial	1,2,5,6,7	Absent
<i>Lancea tibetica</i>	Scrophulariaceae	Perennial	1,2,5,6,7	1,2,3,4,6
<i>Leontopodioides</i>	Compositae	Perennial	1	1,3,4,5,6
<i>Limonium aureum</i>	Plumbaginaceae	Perennial	1,2	Absent
<i>Limonium bicolor</i>	Plumbaginaceae	Perennial	1,5	Absent
<i>Meconopsis integrifolia</i>	Papaveraceae	Perennial	4	Absent
<i>Medicago hispida</i>	Leguminosae	Perennial	5	1,3,5,6,7
<i>Medicago lupulina</i>	Leguminosae	Annual or biennial	1,4	1,2,3,4,6,7
<i>Melica scabrosa</i>	Gramineae	Perennial	1,2,3,4,5,6,7	Absent
<i>Oxytropis glabra</i>	Leguminosae	Perennial	1,2,5,6	Absent
<i>Oxytropis melanocalyx</i>	Leguminosae	Perennial	1,2,6,7	1,2,3,4,5,6,7
<i>Plantago depressa</i>	Plantaginaceae	Perennial	1,2,5,7	1,4,5,7
<i>Poa sphondylodes</i>	Gramineae	Perennial	1,5,7	1,2,3,4,5,6,7
<i>Polygonatum kansuense</i>	Liliaceae	Perennial	1,3	Absent
<i>Polygonum viviparum</i>	Polygonaceae	Perennial	1,2,3,4,7	1,2,3,4,7
<i>Portulaca oleracea</i>	Portulacaceae	Annual	1,2,3,5,7	Absent
<i>Potentilla anserina</i>	Rosaceae	Perennial	6	1
<i>Potentilla bifurca</i>	Rosaceae	Perennial	1,3,5,6,7	1,5,7
<i>Potentilla chinensis</i>	Rosaceae	Perennial	1	1,2,4,5,6,7
<i>Potentilla multifida</i>	Rosaceae	Perennial	1,3,4,5,6,7	1,2
<i>Primula tangutica</i>	Primulaceae	Perennial	2	Absent
<i>Salix gilashanica</i>	Salicaceae	Shrub	2,3,4,6	1,2,3
<i>Salsola rutheanica</i>	Chenopodiaceae	Annual	4,6	Absent
<i>Sanicula chinensis</i>	Umbelliferae	Perennial	2,3,4	Absent
<i>Saussurea superba</i>	Compositae	Perennial	4	1,2,3,4,7
<i>Saxifraga atrata</i>	Saxifragaceae	Perennial	2	Absent
<i>Setaria glauca</i>	Gramineae	Annual	6	Absent

Table 2. Contd.

<i>Setaria viridis</i>	Gramineae	Annual	2,5,6,7	Absent
<i>Solanum nigrum</i>	Solanaceae	Annual	6	Absent
<i>Stellera chamaejasme</i>	Thymelaeaceae	Perennial	6	1,4,5,6
<i>Thalictrum foetidum</i>	Ranunculaceae	Perennial	6	Absent
<i>Tibetan hullless barley</i>	Gramineae	Annual or biennial	5	Absent
<i>Anaphalis lactea</i>	Compositae	Perennial	Absent	1,2,3,7
<i>Caragana jubata</i>	Leguminosae	Scrub	Absent	2,3
<i>Caragana rosea</i>	Leguminosae	Scrub	Absent	4
<i>Iris potaninii</i>	Iridaceae	Perennial	Absent	5,7
<i>Picea crassifolia</i>	Pinaceae	Tree	Absent	2,3
<i>Potentilla glabra</i>	Rosaceae	Scrub	Absent	1,2,3,5,6
<i>Potentilla fruticosa</i>	Rosaceae	Scrub	Absent	1,3,4,5,6
<i>Potentilla parvifolia</i>	Rosaceae	Scrub	Absent	1,2,7
<i>Rhododendron przewalskii</i>	Ericaceae	Scrub	Absent	3,4
<i>Sabina przewalskii</i>	Cupressaceae	Tree	Absent	2,3
<i>Sophora alopecuroides</i>	Leguminosae	Semiscrub	Absent	1,5,6,7

Communities are abbreviated as follows: 1, Grassland; 2, Woodland; 3, Scrubland; 4, Dwarf scrub grassland; 5, Grassland; 6, Scrub grassland; 7, Grassland.

Table 3. Density of seeds in the soil seed bank (m^{-2}) in the seven habitats.

Habitat types	Seedling number in 0-5 cm	Seedling number in 5-10 cm	Seedling number in total	Seed density (seeds m^{-2})
1 Grassland	905	235	1140	2963.73±2118.21
2 Woodland	353	150	503	1307.68±316.26
3 Scrubland	453	165	618	1286.02±866.54
4 Dwarf scrub grassland	52	13	65	225.31±62.49
5 Grassland	828	132	960	3327.70±780.21
6 Scrub grassland	784	188	972	2020.89±510.71
7 Grassland	812	327	1139	3945.87±2440.79

Ebersole, 1989; Molau and Larsson, 2000). Ingersoll and Wilson (1993) studied a treeless high subalpine site on Mount Jefferson in Oregon, dominated by perennial herbs with presence of shrubs, reporting a persistent seed bank of 3112 seeds m^{-2} comprised of 12 of the 22 standing vegetation species. So the density will depend on the different habitats and sampling technique.

Of the species 18% were annals and 73% perennial herbs, only 1 shrub and no woody species, so annual and perennial herbs were more abundant than woody species, as found in most other studies (Lunt, 1997; Thompson et al., 1998). The seed bank was very different from the vegetation in species composition for all habitats. Similar trends had been reported by Roach (1983), Kalin et al. (1999) and Ingersoll and Wilson (1993). Woodland seed banks are nearly always sparse (Thompson, 2000; Lopez-Marino et al., 2000), and Jalili et al. (2003) found the grassland had low density, but seed densities beneath the scrub grasslands studied

here are exceptionally low. For many species, especially scrubs species present in the vegetation and not in the soil seed bank. *Picea crassifolia* was all absent despite being a prominent component of the surface vegetation at woodlands; thus, *P. crassifolia* has no persistent seed bank.

Density of seeds in relation to environment

The size of the soil seed bank appears to be affected by sampling time, altitude, slope, depth, plant communities, plant life form and soil environment parameters such as moisture, aeration, fertility or activity of soil micro-organisms. Soil seed banks vary seasonally in their size and content (Thompson and Grime, 1979). Our samples were collected in July, well after the period of early summer seedling emergence but before most current year's seeds were shed. They therefore represent mostly

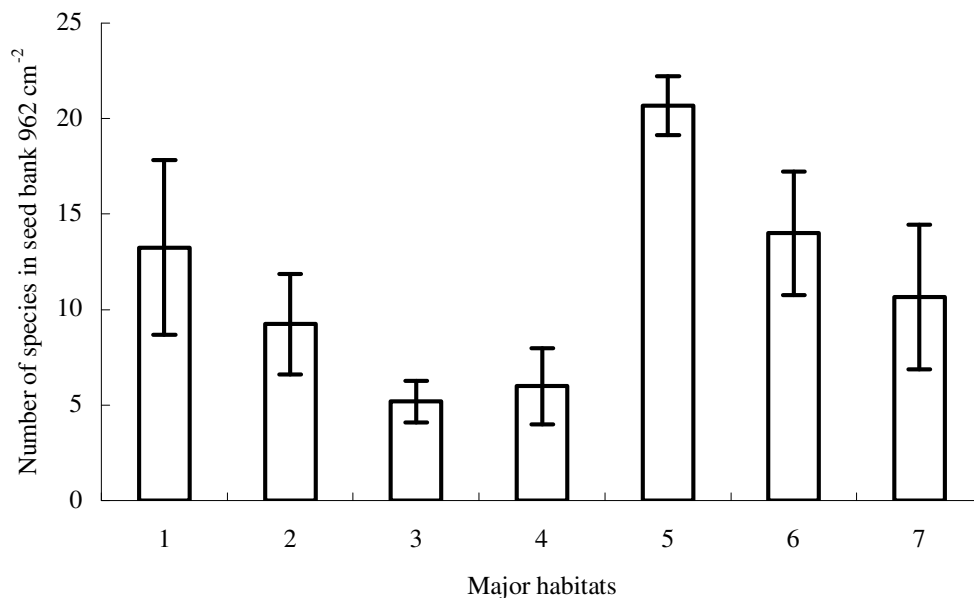


Figure 2. Number of species in seed bank per sampled area of 962 cm² in each major habitat. The number of x-axis represents the seven habitats.

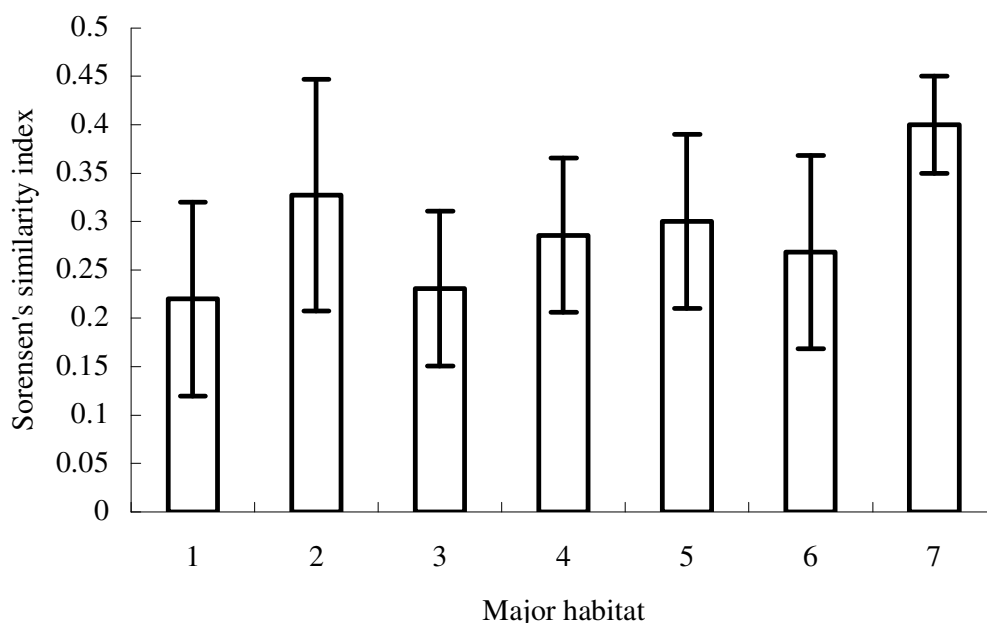


Figure 3. Sorensen's similarity index comparing the species composition of the vegetation and the soil seed bank. The number of x-axis represents the seven habitats.

species with persistent seed banks, as discussed by Thompson et al. (1997), and the seasonal minimum density for each community (Miller and Cummins, 2003).

Alpine habitats periodically experience unseasonable 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 (Bliss, 1956). Unseasonably, cold years and short

growing seasons can produce strong reductions in seed output (Kudo, 1991; Thompson, 1978), while also decreasing seed germination and seedling establishment (Bliss, 1985; Galen and Stanton, 1991; Stanton and Galen, 1997). A persistent seed bank in alpine habitats may therefore permit species to cure their germination to more favorable years (Cavieres, 1999). The size of a soil seed bank is controlled primarily both by the numbers of

Table 4. Density of soil seed banks in upper layer (0 to 5 cm) and lower layer (5 to 10 cm) at each altitude.

Slopes	Altitude (m)	0-5 cm (density±SE)	5-10 cm (density±SE)	d.f.	F	p
Shady slope	2700	4194.28±143.29	1005.24±12.59	1	29.49	<0.001
	2750	3587.68±133.94	554.62±30.61	1	29.24	<0.001
	2800	1282.55±74.89	762.60±40.36	1	2.24	0.16
	2850	343.20±15.54	124.79±9.56	1	14.33	0.001
	2900	1455.87±38.91	218.38±10.34	1	94.48	<0.0001
	2950	509.55±15.85	499.16±30.54	1	0.009	0.92
	3000	644.74±39.76	436.76±26.31	1	1.90	0.18
	3050	1060.71±62.55	405.56±46.36	1	7.08	0.02
	3100	1681.18±44.42	606.61±114.03	1	6.94	0.04
	3200	1403.87±67.06	311.97±13.43	1	22.94	0.003
	3300	121.32±9.96	69.33±8.49	1	1.42	0.28
	3400	294.64±26.00	294.64±9.96	1	0	1
	3500	1213.22±59.13	433.29±23.06	1	13.59	0.01
	3600	259.98±13.09	34.66±6.00	1	22.04	0.003
	3700	138.65±14.71	34.66±6.00	1	3.86	0.1
3800	138.65±14.71	69.33±8.49	1	1.5	0.27	
Sunny slope	2600	3150.92±51.19	831.93±38.60	1	130.83	<0.0001
	2650	3171.72±83.95	363.97±17.84	1	107.03	<0.0001
	2700	2287.79±55.46	176.78±13.02	1	137.31	<0.0001
	2750	1861.43±139.21	218.38±15.85	1	13.75	<0.002
	2800	2183.80±75.28	658.61±19.36	1	23.10	<0.001
	2850	1438.54±70.35	485.29±10.74	1	10.77	<0.01
	2900	1161.23±45.29	311.97±6.58	1	20.66	0.001
	2950	1507.86±35.87	277.31±16.98	1	57.68	<0.0001
Summit plain	2870	2738.42±60.52	225.31±7.83	1	101.77	<0.0001
	2950	953.25±43.83	1195.89±63.34	1	0.60	0.46
	3005	4748.91±252.14	1975.82±68.35	1	6.76	<0.03

seeds produced at the site and secondarily by the fate of these seeds after dispersal. Number of buried germinable heather seeds did indeed decline with increasing altitude (Miller and Cummins, 1987). The fact that this decline is disproportionately much less than the altitudinal decrease in seed production was attributed to increasing seed longevity in cold soils at high altitude. Seed bank density and species numbers decreased in the present study with increasing elevation both in shady slope and sunny slope. However, seeds survive longer in montane soils (Miller and Cummins, 1987), thus impairing the relationship between seed bank size and altitude. Pakeman et al. (1999) failed to detect any altitudinal influence on buried seed densities amongst geographically and altitudinally diverse heathland sites.

It seems likely that the harshness of environment at higher altitudes, and heavy grazing, would reduce seed production and encourage reliance on vegetative reproduction. For the grassland in our paper, the density in summit plain was highest, and the density in sunny slope was lower than that in shady slope, which can be

attributed to the degree of slope, because the summit plain only has a slight slope less than 5°, the degree of grassland in shady slope is about 15°, and sunny slope is steep with a degree of slope about 45°; which would have been consistent with Jalili et al. (2003), who found that there were more seeds in the soil in the scrubby grassland where the intensity of grazing was high, compared with steep grassland with only moderate grazing.

Soil transport within the mounds may also be responsible for the different proportion of seeds present in the upper (0 to 5 cm) and the lower layer (5 to 10 cm). Seed density and diversity usually declines significantly below 5 cm (Jalili et al., 2003; Bakker et al., 1996; Kitajima and Tilman, 1996; Leck, 1989; Nicolson and Keddy, 1983; Dostál, 2005; Roberts, 1981) and several previous studies of podzolic soils (Putwain and Gillham, 1990; Legg et al., 1992) have shown that, more than 90% of the seed bank is concentrated in the top 40 mm of the profile, the number of seeds germinating from the lower (5 to 10 cm layer) was very low. This pattern was also

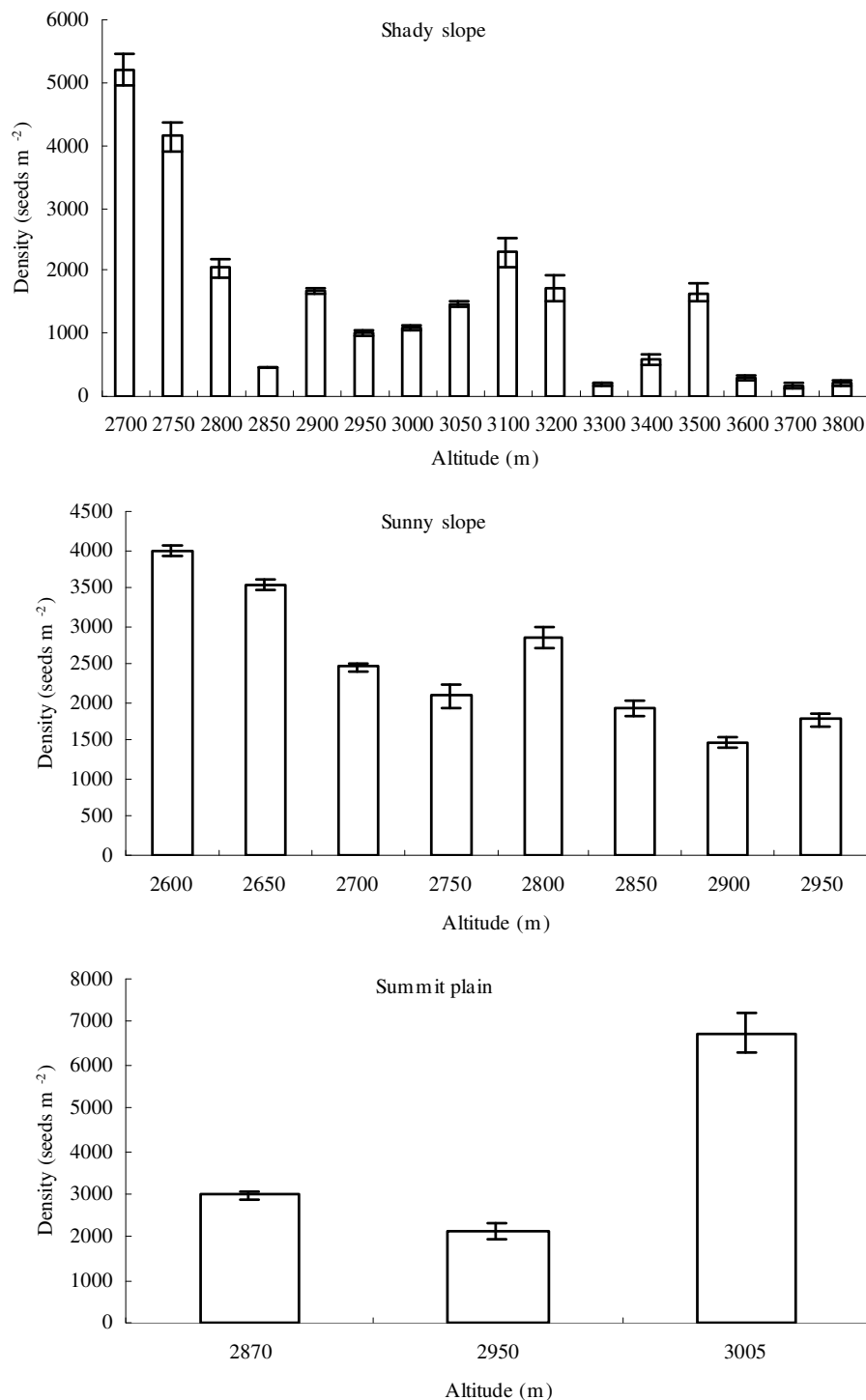


Figure 4. The density of soil seed bank along an altitude gradient in sunny slope, shady slope and summit plain.

found in the soil of our paper, seed density declined by 70% in the lower layer 5 to 10 cm. However, there have been insignificant differences in some communities, for they have low densities in total at those altitudes. Different habitats, plant life forms and soil environment also influence the size of soil seed bank. The seven

major habitats, including an array of vegetation types from grassland to woodland and to scrubland, where soil environment parameters were different such as moisture, aeration, fertility or activity of soil micro-organisms as discussed by Cavers and Benoit (1989), Parker et al. (1989), Bekker et al. (1998) and Qaderi et al. (2002),

which influence seed survival and germination in the soil, had different densities of soil seed bank.

Ecological implication

Soil seed banks are important components of vegetation dynamics affecting both ecosystem resistance and resilience (Pugnaire and Lázaro, 2000). What might be the role of seed banks in the natural recolonisation of ground bared by disturbance? The seed banks in most submontane soils are therefore, a potentially important seed reservoir, particularly where extensive severe disturbance of the vegetation prevents fresh seed dispersal. Information on buried germinable seed populations can be of practical value because of their influence on the nature and rate of plant succession, that follows from the perturbation of established vegetation whether by long-term climatic change or by direct human interference.

In the woodland, deep shade species once lost from a site and not having a buried seed bank, may well be slow to return and in the absence of adjoining areas containing reservoirs of the original flora, some species may not return at all (Rackham, 1975; Brown and Oosterhuis, 1981). However, this view can also be extended to the native tree species like *P. crassifolia*, as they usually lack seed banks. Once lost from an area might take centuries to return, if ever, as has been reported before for woodlands (Onaindia and Amezaga, 2000; Rackham, 1975; Brown and Oosterhuis, 1981; Demel and Granstrom, 1995; Amezaga and Onaindia, 1997; Buckley et al., 1997). If large areas are clear felled, re-establishment may be difficult (Frank and Safford, 1970). A similar idea has been reported for grasslands, where their restoration cannot depend on recruitment from the seed bank, as some of the species are not present in the vegetation (Bekker et al., 1997).

Even if successful establishment could be achieved, montane persistent soil seed banks are so species-poor that, any resultant vegetation is unlikely to resemble the original community. Importing seed-rich topsoil from elsewhere, as suggested by Putwain et al. (1982) for lowland heaths, or harvesting and sowing wild seeds would be doubtfully cost effective in the mountains. In any case, both procedures may introduce poorly adapted genotypes (Grant and Hunter, 1962; Cavieres and Arroyo, 2001). Although, seed banks may be a potential source of regeneration in some of these fragile mountain communities, it is clearly preferable to minimize or avoid damage to the vegetation.

Future management should also take into account the fact that, the majority of the species, especially *P. crassifolia*, in Qilian mountains do not have a persistent seed bank, and therefore it is essential that they are maintained in the flora. For the woods of *P. crassifolia* functions as the water sources to maintain ecological

environments in Heihe river basin. Management plans should attempt to maintain a balance between nature and human activities and to ensure the maintenance of the species diversity. It will be important to maintain the existing vegetation in the future management.

In summary, our research assessed species composition, seed density, vertical distribution and the relationship of soil seed bank and vegetation, along an altitudinal gradient in seven communities in shady slope, sunny slope and summit plain of Qilian Mountains. Of the species 18% were annuals and 73% perennial herbs, only 1 shrub was recorded. There was a tendency for the soil seed bank to decrease in density with increasing elevation in both shady slope and sunny slope. *P. crassifolia* was absent in the soil seed bank despite being prominent component of the surface vegetation at woodlands; thus, *P. crassifolia* has no persistent seed bank. It will be important to maintain the existing vegetation in the future management.

ACKNOWLEDGEMENTS

This research was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences (KZCX2-YW-442) and Key Laboratory of Yellow River Sediment Research of the Ministry of Water Resources foundation (2010007) and China Postdoctoral Science Foundation funded project (20090460421). We are grateful to Professor Wenzhi Zhao, who provided us with the facilities and assistance to conduct the experiment at Chinese Ecosystem Network Research Linze Inland River Basin Comprehensive Research Station.

REFERENCES

- Amezaga I, Onaindia M (1997). The effect of evergreen and deciduous coniferous plantations on the field layer and seed bank of native woodlands. *Ecography*, 20: 308-318.
- Augusto L, Dupouey JL, Picard JF, Ranger J (2001). Potential contribution of the seed bank in coniferous plantations to the restoration of native deciduous forest vegetation. *Acta Oecol.*, 22: 87-98.
- Bakker JP, Bakker ES, Rosén E, Verwij GL (1996). Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *J. Veg. Sci.*, 7: 165-176.
- Baskin CC, Baskin JM (1998). *Seeds: Ecology, biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego.
- Bekker RM, Geurt LV, Bakker JP, Fresco LFM (2000). Soil seed bank dynamics in hayfield succession. *J. Ecol.*, 88: 594-607.
- Bekker RM, Knevel IC, Tallowin JBR, Troost EML, Bakker JP (1998). Soil nutrient input effects on seed longevity: a burial experiment with fen-meadow species. *Funct. Ecol.*, 12: 673-682.
- Bekker RM, Verweij GL, Reine JP, Schneider S (1997). Soil seed banks in European grasslands: does land use affect regeneration perspectives? *J. Appl. Ecol.*, 34: 1293-1310.
- Bertiller MB, Aloia DA (1997). Seed bank strategies in Patagonian semi-arid grasslands in relation to their management and conservation. *Biodivers. Conserv.*, 16: 639-650.
- Bliss LC (1956). A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecol. Monogr.*, 26: 303-337.

- Bliss LC (1985). Alpine. In: Billings WD, Mooney HA (eds) *Physiological Ecology of North American Plant Terrestrial Communities*. Chapman and Hall, New York, pp. 41-65.
- Brown AHF, Oosterhuis L (1981). The role of buried seeds in coppicewoods. *Biol. Conserv.*, 21: 19-38.
- Buckley GP, Howell R, Anderson MA (1997). Vegetation succession following ride edge management in lowland plantations and woods. 2. The seed bank resource. *Biol. Conserv.*, 82: 305-316.
- Cavers PB, Benoit DL (1989). Seed banks in arable land. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), *Ecology of Soil Seed Banks*. Academic Press, New York, pp. 309-328.
- Cavieres LA (1999). Bancos de semillas persistentes: modelos de germinación retardada de semillas y su aplicación en ambientes alpinos. *Revista Chilena de Historia Natural*, 72: 457-466.
- Cavieres LA, Arroyo MTK (2001). Persistent soil seed banks in *Phacelia secunda* (Hydrophyllaceae): experimental detection of variation along an altitudinal gradient in the Andes of central Chile (33°S). *J. Ecol.*, 89: 31-39.
- Chambers JC (1993). Seed and vegetation dynamics in an alpine herb field: effects of disturbance type. *Can. J. Bot.*, 71: 471-485.
- Demel T, Granstrom A (1995). Soil seed banks in dry Afromontane forests of Ethiopia. *J. Veg. Sci.*, 6: 777-786.
- Diemer M, Prock S (1993). Estimates of alpine seed bank size in two central European and one Scandinavian subarctic plant communities. *Arct. Alpine Res.*, 25: 194-200.
- Donelan M, Thompson K (1980). Distribution of buried viable seeds along a successional series. *Biol. Conserv.*, 17: 297-311.
- Dostál P (2005). Effect of three mound-building ant species on the formation of soil seed bank in mountain grassland. *Flora*, 200: 148-158.
- Ebersole JJ (1989). Role of the seed bank in providing colonizers on a tundra disturbance in Alaska. *Can. J. Bot.*, 67: 466-471.
- Fenner M (1985). *Seed Ecology*. Chapman and Hall, London.
- Frank RM, Safford LO (1970). Lack of viable seeds on the forest floor after clearcutting. *J. For.*, 68: 776-778.
- Galen C, Stanton ML (1991). Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *Am. J. Bot.*, 78: 978-988.
- Grant SA, Hunter RF (1962). Ecotypic differentiation of *Calluna vulgaris* (L.) in relation to altitude. *New Phytol.*, 61: 44-55.
- Gurbb PJ (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, 52: 107-145.
- Harper JL (1977). *Population Biology of Plant*. Academic Press, London.
- Ingersoll C, Wilson M (1993). Buried propagule bank of a high subalpine site: microsite variation and comparisons with aboveground vegetation. *Can. J. Bot.*, 71: 712-717.
- Jalili A, Hamzeh'ee B, Asri Y, Shirvany A, Yazdani S, Khoshnevis M, Zarrinkamar F, Ghahramani M, Safavi R, Shaw S, Hodgson JG, Thompson K, Akbarzadeh M, Pakparvar M (2003). Soil seed banks in the Arasbaran Protected Area of Iran and their significance for conservation management. *Biol. Conserv.*, 109: 425-431.
- Jankowska-Blaszczuk M, Grubb PJ (1997). Soil seed banks in primary and secondary deciduous forest in Białowieża, Poland. *Seed Sci. Res.*, 7: 281-292.
- Kalin Arroyo MT, Cavieres LA, Castor C, Humana AM (1999). Persistent soil seed bank and standing vegetation at a high alpine site in the central Chilean Andes. *Oecologia*, 119: 126-132.
- Keddy PA, Reznicek AA (1982). The role of seed banks in the persistence of Ontario's coastal plain flora. *Am. J. Bot.*, 69: 13-22.
- Kitajima K, Tilman D (1996). Seed banks and seedling establishment on an experimental productivity gradient. *Oikos*, 76: 381-391.
- Kudo G (1991). Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arct. Alpine Res.*, 23: 436-443.
- Leck MA (1989). Wetland seed bank. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), *Ecology of Soil Seed Banks*. Academic Press, San Diego, pp. 283-308.
- Leck MA, Parker YT, Simpson RL (1989). *Ecology of Soil Seed Banks*. Academic Press, New York.
- Legg CJ, Maltby E, Proctor MCF (1992). The ecology of severe moorland fire on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. *J. Ecol.*, 80: 737-752.
- Lopez-Marino A, Luis-Calabuig E, Fillat F, Bermudez F (2000). Floristic composition of established vegetation and the soil seed bank in pasture communities under different traditional management regimes. *Agr. Ecosyst. Environ.*, 78: 273-282.
- Lunt ID (1997). Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. *Plant Ecol.*, 130: 21-34.
- Magurran AE (1988). *Ecological Diversity and its Measurement*. Princeton University Press, New Jersey.
- Major J, Pyott WT (1966). Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio*, 13: 253-282.
- Martins AM, Engel VL (2007). Soil seed banks in tropical forest fragments with different disturbance histories in southeastern Brazil. *Ecol. Eng.*, 31: 165-174.
- Miller GR, Cummins RP (1987). Role of buried viable seed in the recolonization of disturbed ground by heather (*Calluna vulgaris* (L.) Hull) in the Cairngorm Mountains, Scotland. *Arct. Alpine Res.*, 19: 391-401.
- Miller GR, Cummins RP (2003). Soil seed banks of woodland, heathland, grassland, mire and montane communities, Cairngorm Mountains, Scotland. *Plant Ecol.*, 168: 255-266.
- Mitchell RJ, Marrs RH, Auld MHD (1998). A comparative study of the seedbanks of heathland and successional habitats in Dorset, Southern England. *J. Ecol.*, 86: 588-596.
- Molau U, Larsson EL (2000). Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Can. J. Bot.*, 78: 728-747.
- Nicoson A, Keddy PA (1983). The depth profile of a shoreline seed bank in Matchedash Lake, Ontario, Canada. *Can. J. Bot.*, 65: 2028-2035.
- Onaindia M, Amezága I (2000). Seasonal variation in the seed banks of native woodland and coniferous plantations in Northern Spain. *For. Ecol. Manage.*, 126: 163-172.
- Pakeman RJ, Cummins RP, Miller GR, Roy DB (1999). Potential climatic control of seedbank density. *Seed Sci. Res.*, 9: 101-110.
- Pakeman RJ, Marshall AG (1997). The seedbanks of the Breckland heaths and heath grasslands, eastern England, and their relationship to the vegetation and the effects of management. *J. Biogeogr.*, 24: 375-390.
- Parker VT, Simpson RL, Leck MA (1989). Pattern and process in the dynamics of seed banks. In: Leck MA, Parker VT, Simpson RL (eds), *Ecology of Soil Seed Banks*. Academic Press, New York, pp. 367-384.
- Pugnaire FI, Lázaro R (2000). Seed bank and understorey species composition in a semi-arid environment: the effect of shrub age and rainfall. *Ann. Bot.*, 86: 807-813.
- Putwain PD, Gillham DA (1990). The significance of the dormant viable seed bank in the restoration of heathlands. *Biol. Conserv.*, 52: 1-16.
- Putwain PD, Gillham DA, Holliday RJ (1982). Restoration of heather moorland and lowland heathland, with special reference to pipelines. *Environ. Conserv.*, 9: 225-235.
- Qaderi MM, Cavers PB, Bernards MA (2002). Seed bank dynamics of *Onopordum acanthium*: emergence patterns and chemical attributes. *J. Ecol.*, 90: 672-683.
- Rackham O (1975). *Harley Wood*. Cambridge and Isle of Elys' Trust Ltd., Cambridge.
- Roach DA (1983). Buried seed and standing vegetation in two adjacent tundra habitats, northern Alaska. *Oecologia*, 60: 359-364.
- Roberts HA (1981). Seed banks in soils. *Adv. Appl. Biol.*, 6: 1-55.
- Stanton ML, Galen C (1997). Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup, *Ranunculus odoneus*. *Am. Nat.*, 150: 143-177.
- Thompson K (1978). The occurrence of buried viable seeds in relation to environmental gradients. *J. Biogeogr.*, 5: 425-430.
- Thompson K (2000). The functional ecology of soil seed banks. In: Fenner M(ed) *Seeds: the Ecology of Regeneration in Plant Communities*, second ed. CAB International, Wallingford, pp. 215-235.
- Thompson K, Bakker JP, Bekker RM (1997). *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge.
- Thompson K, Bakker JP, Bekker RM, Hodgson JG (1998). Ecological correlates of seed persistence in soil in the NW European flora. *J.*

- Ecol., 86: 163-169.
- Thompson K, Grime JP (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.*, 67: 893-92.
- Valbuena L, Traub-Lidzbarski C (2001). Contribution of the soil seed bank to post-fire recovery of a heathland. *Plant Ecol.*, 152: 175-183.
- Walck JL, Baskin JM, Baskin CC, Hidayati SN (2005). Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. *Seed Sci. Res.*, 15: 189-196.
- Welling CH, Peterson RL, van der Valk AG (1988). Recruitment from the seed bank and the development of emerging zonation during a drawdown in a prairie wetland. *J. Ecol.*, 76: 483-496.
- Wisheu IC, Keddy PA (1991). Seed banks of a rare wetland plant community: distribution patterns and effects of human-induced disturbance. *J. Veg. Sci.*, 2: 181-188.
- Zabinski C, Wojtowicz T, Cole D (2000). The effects of recreation disturbance on subalpine seed banks in the Rocky Mountains of Montana. *Can. J. Bot.*, 78: 577-582.