Mature forest seed banks of three habitat types in central Idaho

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Soils were sampled in two 5-cm layers under mature forests in *Pseudotsuga menziesii/Physocarpus malvaceus*, *Abies grandis/Acer glabrum*, and *Abies grandis/Vaccinium globulare* habitat types in central Idaho. Seed content of sampled soils was determined using a wet sieve seed extraction process followed by greenhouse germination tests. Viable seeds representing more than 80 different species were recorded, with viable seed densities averaging 1065 ± 727/m² and ranging as high as 4116/m². Most viable seeds (67%) were found in the top 0- to 5-cm soil layer. *Ceanothus velutinus*, *Physocarpus malvaceus*, and *Carex* spp. accounted for nearly 50% of all viable seeds encountered. Buried seed constancies are presented to compare buried seed occurrence by habitat type.

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Le sol de deux couches, chacune d'une épaisseur de 5 cm sous des forêts complètement développées de l'Idaho central dans les types d'habitats suivants : *Pseudotsuga menziesii/Physocarpus malvaceus*, *Abies grandis/Acer glabrum*, et *Abies grandis/Vaccinium globulare* a été échantillonné. Le contenu séminal des sols échantillonnés a été déterminé par une méthode d'extraction humide des graines à l'aide de tamis, suivi de tests de germination en serres. Des graines viables représentant plus de 80 espèces différentes ont été répertoriées; la densité de graines viables était en moyenne 1065 ± 727/m² et atteignait même 4116/m². La plupart des graines viables (67%) se retrouvaient dans la couche de terre supérieure (0–5 cm). Les *Ceanothus velutinus*, *Physocarpus malvaceus* et *Carex* spp. représentaient presque 50% de toutes les graines viables obtenues. Les constances des graines enfouies sont présentées dans le but de comparer la présence des graines enfouies par types d'habitats.
[Traduit par la revue]

Introduction

Plant species that are seemingly rare or absent in mature forest stands may become established and quickly dominate the initial vegetation following timber harvest, fire, or other major forest disturbances. One important source contributing to revegetation following disturbance is the forest seed bank (Archibold 1979; Moore and Wein 1977; Strickler and Edgerton 1976; Kellman 1970; Olmsted and Curtis 1947). Buried viable seeds, some of which have remained dormant in the soils for many years, can germinate in response to changes in light, soil temperatures, or other factors following site disturbance (Wesson and Wareing 1969; Barton 1961) and produce an abundant new flora.

The existence of dormant buried seeds and their ability to remain viable for long periods of time have been recognized for many years. Results of a buried seed longevity experiment initiated by W. J. Beal of the Michigan Agricultural College in 1879 show that seeds of some species can remain viable in the soil for at least 100 years (Kivilaan and Bandurski 1981). Recent studies calling attention to the important role of seed banks in forest soils report seed-bank densities ranging from zero under subarctic forests (Johnson 1975) to as high as 14 463 seeds/m² under one eastern Washington ponderosa pine stand (Pratt et al. 1984). Tables reviewing previous studies of temperate forest seed banks have been presented by Pratt et al. (1984) and Roberts (1981).

A lack of knowledge about forest seed banks in central Idaho has hampered efforts to predict natural vegetation response following disturbance (Steele and Geier-Hayes 1982, 1983, 1985). The following study was initiated to characterize central Idaho forest seed banks in terms of species, seed densities, and depth distribution. An additional objective was to identify specific buried seed distribution patterns that might be useful in predicting buried seed occurrence.

Study area and field methods

Field sampling for this study took place on the Payette and Boise National Forests in west central Idaho (center at 116° N, 44° W). The study focused on three major timber-producing habitat types of the area: *Pseudotsuga menziesii/Physocarpus malvaceus* (Psme/Phma), *Abies grandis/Acer glabrum* (Abgr/Acgl), and *Abies grandis/Vaccinium globulare* (Abgr/Vagl) (Steele et al. 1981).

Field sampling began in late May 1982 and continued through that August. A reconnaissance of the study area was made to locate stands of mature harvestable-age timber with minimal evidence of recent disturbance of any type. Forty-eight stands (16 on each of the three habitat types studied) were selected for sampling and a 375-m² circular plot was established on a representative area within each of the 48 stands. A plant species list with corresponding Braun–Blanquet cover classes (Mueller-Dombois and Ellenberg 1974) was compiled for each 375-m² sample plot so that comparisons could be made between buried seeds and existing vegetation. The age of the dominant overstory tree class was determined and information on elevation, slope, aspect, and depth of litter layer was collected for each plot.

Twenty soil sample points were located systematically at 7.3 and 10.9 m along transects running north, south, east, and west of the plot center and at 3.6, 7.3, and 10.9 m along transects running northeast, southwest, northwest, and southeast of the plot center. After removing loose twigs, leaves, and needles, soil samples were collected to a depth of 10 cm in two 5-cm layers by using a bulb planter of 5.5 cm diameter. The 20 soil samples from each 5-cm layer were pooled for the entire 375-m² plot, resulting in one 0- to 5-cm soil sample and one 5-to 10-cm soil sample for each of the 48 stands studied. The top 5-cm sample generally contained compacted litter along with organic soil layers, while the lower 5-cm sample was predominantly mineral soil. The soil area sampled was 475 cm² in each stand, 0.76 m² per habitat type. Sampled soils were kept at about 2°C until they could be examined.

Laboratory methods

The seed content of sampled soils was determined using a wet sieve

TABLE 1. Seed-bank species, buried seed numbers, seed depth distribution in two 5-cm layers, and maximum viable seed densities encountered for each species, pooled for three forest habitat types

	Total viable seeds	Seed depth distribution (% of total viable seeds) 0–5 cm	5–10 cm	Maximum density/m²
Shrubs				
Berberis repens	13	77	23	168
*Ceanothus (sanguineus + velutinus)**	611	58	42	1155
Cornus stolonifera	1	100	0	21
Holodiscus discolor	3	67	33	21
Pachistima myrsinites	1	100	0	21
Philadelphus lewisii	4	100	0	21
Physocarpus malvaceus	344	78	22	1092
**Prunus (emarginata + virginiana)*	24	54	46	189
Ribes irriguum	1	0	100	21
**Ribes (lacustre + viscosissimum)*	91	81	19	567
Rubus parviflorus	35	91	9	189
Sambucus (cerulea + racemosa)	24	58	42	210
Vaccinium globulare	24	100	0	210
Perennial forbs				
Achillea millefolium	2	50	50	21
Agastache urticifolia	5	100	0	63
Antennaria luzuloides	6	67	33	42
Arabis spp.	6	50	50	63
Arenaria macrophylla	15	87	13	84
Arnica cordifolia	4	25	75	42
Astragalus canadensis	8	50	50	63
Circaea alpina	1	0	100	21
Cirsium arvense (alien)	11	100	0	84
Fragaria vesca	19	95	5	84
Fragaria virginiana	2	50	50	42
Galium triflorum	23	87	13	126
Geranium viscosissimum	9	56	44	189
Geum macrophyllum	2	100	0	21
Heuchera grossulariifolia	33	6	94	376
Hieracium albiflorum	1	100	0	21
Hydrophyllum capitatum	16	81	19	294
Iliamna rivularis	90	29	71	1470
Lathyrus nevadensis	8	88	12	63
Mitella stauropetala	25	92	8	252
Penstemon wilcoxii	52	23	77	273
Penstemon spp.	5	60	40	21
Phacelia spp.	18	72	28	63
Polemonium pulcherrimum	65	85	15	1197
Potentilla glandulosa	116	62	38	840
Silene menziesii	2	100	0	42
Taraxacum officinale (alien)	2	100	0	21
Thermopsis montana	9	67	33	168
Trillium ovatum	8	88	12	147
Typha latifolia	5	40	60	42
Urtica dioica	8	88	12	105
Viola glabella	8	38	62	147
Viola orbiculata	13	77	23	84
Annual–biennial forbs				
Aster sp.	1	100	0	21
Cirsium vulgare (alien)	38	87	13	210
Collinsia parviflora	111	68	32	588
Cryptantha spp.	2	100	0	21
Descurainia richardsonii	17	29	71	126
Erigeron annuus	1	100	0	21
Galium aparine	2	50	50	21
Lactuca serriola (alien)	14	100	0	63
Melilotus alba (alien)	1	0	100	21
Montia perfoliata	95	65	35	903
Nemophila parviflora	4	100	0	42

TABLE 1 (*concluded*)

	Total viable seeds	Seed depth distribution (% of total viable seeds) 0–5 cm	5–10 cm	Maximum density/m²
Polygonaceae†	16	56	44	63
Tonella floribunda	10	70	30	210
Verbascum thapsus (alien)	16	94	6	126
Graminoids				
Agrostis scabra	3	100	0	42
Bromus vulgaris	3	67	33	21
Carex concinnoides	14	29	71	147
Carex geyeri	121	74	26	756
Carex rossii	144	72	28	273
Carex spp.	13	77	23	—
Festuca occidentalis	3	33	67	42
Luzula campestre	1	0	100	21
Phleum pratense (alien)	2	100	0	21
Poa compressa	1	0	100	21

*Difficulty in distinguishing some buried seeds to species made it necessary to combine species of *Ceanothus, Prunus, Ribes,* and *Sambucus*.

†Includes *Polygonum aviculare, P. douglasii, P. sawatchense,* and *Rumex acetosella* (alien).

seed extraction process in conjunction with a greenhouse germination test. Soil samples were first washed through a series of sieves (4, 2, 1, and 0.5 mm) to clean soil from seeds and to reduce the samples to particle-size fractions convenient for inspection for seeds. After drying, soil fractions were examined with a dissecting microscope and seeds were extracted, identified, and recorded. Viability of extracted seeds was determined by cutting or breaking open each seed. A seed filled with an apparently healthy embryo (endosperm) was counted as viable.

Soil samples that had been examined for seeds were subsequently placed in the greenhouse, where germinating seedlings revealed additional seed bank elements missed during the seed extraction process. Sampled soils were spread in an even 1- to 2-cm layer over a 4-cm base of packaged potting mix in greenhouse flats. A thin layer of shredded sphagnum was added as a mulch to reduce surface drying. Seed-bank flats were randomly distributed on greenhouse benches with control flats (potting mix only) interspersed at regular intervals. A light shade cloth was installed above the flats to reduce insolation and moderate temperatures. As seedlings emerged and were identified, they were recorded and removed from flats, so that their presence would not influence other potential germinants. Soils were stirred periodically over the course of the greenhouse study. Greenhouse temperatures averaged 22 during the day and 14°C at night. The greenhouse testing began on May 12, 1983, and was terminated on January 18, 1984.

Buried seed counted by the combined seed extraction and greenhouse germination processes is thought to represent all but a very small fraction of the seed bank.

Results and discussion

The mean age of the 48 stands studied was 101 years. Psme/Phma stands averaged 88 (55–172), Abgr/Acgl stands averaged 102 (64–220), and Abgr/Vagl stands averaged 113 years (62–180). Elevation, slope, and aspect varied but fell well within parameters used to describe each of the three habitat types in "Forest habitat types of central Idaho" (Steele et al. 1981). The average depth of the litter layer was 6 under Psme/Phma stands, 5.4 under Abgr/Acgl stands, and 4.3 cm under Abgr/Vagl stands.

Seed-bank species

Over 80 different species were found as viable seeds in seed banks of the three mature forest habitat types studied (Table 1). Seed-bank elements include 17 different shrub species, 36 species of perennial forbs, 13 species of annual–biennial forbs, and 12 species of graminoids. Species that were especially common, occurring as buried seeds on at least 50% of the sites studied, include *Ceanothus velutinus, Physocarpus malvaceus, Ribes* spp. (*R. lacustre* and *R. viscossimum*), *Rubus parviflorus, Sambucus* spp. (*S. cerulea* and *S. racemosa*), *Potentilla glandulosa*, and *Carex rossii*.[1] Seed and plant vouchers have been deposited in the Research Herbarium (IDF) of the Idaho Forest, Wildlife and Range Experiment Station.

Three genera accounted for 50% of all viable seeds encountered in soils sampled for this study. The genus *Ceanothus* (predominantly *C. velutinus*) contributed 25%, *Physocarpus malvaceus* contributed 14%, and species of *Carex* (predominantly *C. rossii* and *C. geyeri*) made up an additional 11% of the total viable seed count.

In all cases, where *Physocarpus malvaceus* was found in the seed bank, the species was also present in the plot or immediately adjacent vegetation, providing a current on-site seed source. *Ceanothus* spp., on the other hand, were present in the vegetation on only 5% of the mature forest plots where *Ceanothus* seeds were found in the soil. *Ceanothus* seeds have no obvious means of long-distance dispersal. It is, therefore, reasonable to assume that *Ceanothus* seeds encountered under mature forest stands were deposited years earlier when successional conditions favored their growth and reproduction. It has been inferred from fresh stump ring counts that some seeds of *C. velutinus* may retain their viability in forest seed banks for more than 500 years (Zavitkovski and Newton 1968).

Seeds of seven species of coniferous trees were extracted from the soil samples. The conifers, however, contribute little to the seed bank. Of 2038 coniferous seeds recorded, only 1, a Douglas-fir seed, was counted as viable. Coniferous species for which only nonviable seeds were found include *Abies grandis, A. lasiocarpa, Larix occidentalis, Picea engelmannii, Pinus contorta*, and *P. ponderosa*. This low coniferous seed viability is consistent with findings of previous studies dealing

[1]Plant nomenclature follows Hitchcock and Cronquist (1973).

TABLE 2. Percent constancy of viable buried seed by habitat type

	Habitat type		
	Psme/Phma $n=16$	Abgr/Acgl $n=16$	Abgr/Vagl $n=16$
Shrubs			
Berberis repens	0	6	19
Ceanothus (*sanguineus* + *velutinus*)	75	94	75
Cornus stolonifera	0	0	6
Holodiscus discolor	19	0	0
Pachistima myrsinites	0	0	6
Philadelphus lewisii	19	0	6
Physocarpus malvaceus	100	38	0
Prunus (*emarginata* + *virginiana*)*	25	38	13
Ribes irriguum	6	0	0
Ribes (*lacustre* + *viscosissimum*)*	6	75	69
Rubus parviflorus	13	44	25
Sambucus (*cerulea* + *racemosa*)*	25	31	31
Vaccinium globulare	6	31	25
Perennial forbs			
Achillea millefolium	6	6	0
Agastache urticifolia	13	6	6
Antennaria luzuloides	13	13	6
Arabis spp.	19	6	0
Arenaria macrophylla	13	25	13
Arnica cordifolia	6	13	0
Astragalus canadensis	0	13	6
Circaea alpina	0	6	0
Cirsium arvense (alien)	13	19	6
Fragaria vesca	6	50	19
Fragaria virginiana	6	0	0
Galium triflorum	13	38	6
Geranium viscosissimum	0	6	0
Geum macrophyllum	6	0	6
Heuchera grossulariifolia	19	19	0
Hieracium albiflorum	0	6	0
Hydrophyllum capitatum	19	0	0
Iliamna rivularis	0	19	6
Lathyrus nevadensis	19	6	6
Mitella stauropetala	0	31	13
Penstemon wilcoxii	31	31	25
Penstemon spp.	13	6	6
Phacelia spp.	25	25	19
Polemonium pulcherrimum	0	6	13
Potentilla glandulosa	38	38	44
Silene menziesii	0	6	0
Taraxacum officinale (alien)	6	6	0
Thermopsis montana	0	13	0
Trillium ovatum	6	0	6
Typha latifolia	6	0	19
Urtica dioica	13	6	6
Viola glabella	0	13	0
Viola orbiculata	0	13	25
Annual–biennial forbs			
Aster sp.	0	6	0
Cirsium vulgare (alien)	31	38	38
Collinsia parviflora	69	25	19
Cryptantha spp.	0	6	13
Descurainia richardsonii	19	13	0
Erigeron annuus	0	6	0
Galium aparine	6	0	6
Lactuca serriola (alien)	25	25	13
Melilotus alba (alien)	6	0	0
Montia perfoliata	44	0	0
Nemophila parviflora	13	6	0
Polygonaceae†	25	0	25
Tonella floribunda	6	0	0

TABLE 2 (*concluded*)

	Habitat type		
	Psme/Phma $n=16$	Abgr/Acgl $n=16$	Abgr/Vagl $n=16$
Verbascum thapsus (alien)	0	19	13
Graminoids			
Agrostis scabra	6	6	0
Bromus vulgaris	0	19	0
Carex concinnoides	0	0	19
Carex geyeri	88	19	25
Carex rossii	56	81	75
Carex spp.	25	38	25
Festuca occidentalis	0	13	0
Luzula campestre	0	6	0
Phleum pratense (alien)	0	6	6
Poa compressa	6	0	0

*Difficulty in distinguishing some buried seeds to species made it necessary to combine species of *Ceanothus, Prunus, Ribes,* and *Sambucus*.
†Includes *Polygonum aviculare, P. douglassii, P. sawatchense,* and *Rumex acetosella* (alien).

with conifer seeds on the forest floor (Isaac 1935; Frank and Safford 1970).

Viable seeds of eight alien species (Eurasian origins) were found in the sampled soils (Table 1). Although alien seeds accounted for only about 3% of the total seed bank, they were widespread, occurring under 54% of the 48 stands sampled.

Several plant species are notable for their apparent absence from the seed bank. Although *Amelanchier alnifolia, Rosa gymnocarpa,* and *Spiraea betulifolia* were present in the vegetation on at least 75% of the study plots, no seeds of these species were found in the soil.

Seed-bank densities

A total of 8514 seeds were extracted from the sampled soils. Of these, 2059 (23%) were filled seeds and thus considered viable. Greenhouse germinations revealed an additional 376 viable seeds through germinants, bringing the total viable seed count to 2434. This value represents an average viable buried seed density of 1065 $\pm$ 727/m^2 for the 48 forest stands sampled. Considering stands by habitat type, Psme/Phma sites averaged 1273 $\pm$ 647, Abgr/Acgl sites averaged 1154 $\pm$ 949, and Abgr/Vagl sites averaged 753 $\pm$ 405 viable seeds/m^2. Viable buried seed densities ranged from 189 on one Abgr/Vagl site to 4116/m^2 on one Abgr/Acgl site. Seed-bank densities encountered during this study fall well within the range of densities reported for previous studies of temperate forest seed banks (Pratt et al. 1984).

A list of maximum viable seed densities encountered, by species, is included in Table 1. These densities reflect the potential for individual species in the seed bank to enter succession after tree harvest. Although *Iliamna rivularis* was present in the seed bank on only 8% of the sites sampled, it had the highest seed density of any single species, with 1470 seeds/m^2 under one stand. Seeds of three other species, *Ceanothus velutinus, Physocarpus malvaceus,* and *Polemonium pulcherrimum,* also occurred in densities greater than 1000/m^2.

Seed depth distribution

Of 2434 viable seeds recorded during this study, 1620 (67%) were found in the top 0- to 5-cm layer and 813 (33%) were found in the lower 5- to 10-cm soil layer. Although seeds of 18 species were found only in the top 0- to 5-cm soil layer, most seed-bank species were represented to some degree in both layers (Table 1). Several species are notable for a high percentage of buried seeds found in the lower 5- to 10-cm soil layer; these include *Arnica cordifolia, Astragalus canadensis, Descurainia richardsonii, Heuchera grossulariifolia, Iliamna rivularis,* and *Penstemon wilcoxii*.

Predicting buried seed occurrence

Seed-bank species composition and seed densities varied greatly from site to site and consequently no clear buried seed distribution patterns emerged from study data. Constancies calculated to compare buried seed occurrence by habitat type (Table 2), however, reflect a probability of encountering a particular species in the seed bank on each of the three habitat types studied. As such, these constancy values can serve as a preliminary guide for predicting buried seed occurrence in the study area and can, therefore, aid in predicting secondary succession vegetation.

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