

Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation

Charles B. Halpern, Shelley A. Evans, and Sarah Nielson

Abstract: During early stand development, coniferous forests of the coastal Pacific Northwest commonly pass through a period of dense shade and intense competition during which the abundance and diversity of understory plants decline dramatically. In young, managed forests, silvicultural thinning has been proposed to enhance the structural and floristic diversity of the understory. Although germination of buried seeds is likely to be stimulated by thinning, we know little about the composition of the soil seed bank in these forests. We used the greenhouse emergence method to assess the potential contribution of the seed bank to understory reinitiation in 40- to 60-year-old, closed-canopy forests on the Olympic Peninsula, Washington. Seed banks were well developed (610–7009 germinants/m²), containing 46 native and exotic species representing a diversity of life forms. However, many common forest understory species were absent; only 11 species were typical understory plants and these comprised <10% of all germinants. In contrast, 30% of all species and 50% of all germinants were exotic, ruderal forbs. Wind-dispersed annuals and perennials dominated litter samples, whereas ruderal forbs and graminoids with limited dispersal dominated soil samples. Our results suggest that silvicultural thinning will enhance the establishment of ruderal, exotic species but will contribute little to the regeneration from buried seed of the vast majority of forest understory plants.

Key words: canopy closure, forest understory, seed germination, soil seed bank, succession, understory reinitiation.

Résumé : Au premières étapes du développement de la station, les forêts conifériennes de la région côtière du Pacific Northwest passent généralement à travers une période d'ombrage opaque et d'intense compétition, période au cours de laquelle l'abondance et la diversité des espèces du sous-bois diminuent brusquement. Dans les jeunes forêts aménagées, l'éclaircie sylvicole a été proposée pour promouvoir la diversité structurelle et floristique du sous-bois. Bien que la germination des graines enfouies soit vraisemblablement stimulée par l'éclaircie, peu de choses sont connues sur la composition de la banque de graines dans le sol de ces forêts. Les auteurs ont utilisé la méthode d'émergence en serre pour évaluer la contribution potentielle de la banque de graines à la réinstallation des sous-étages, dans des forêts à canopée fermée, âgées de 40–60 ans, de la péninsule Olympic dans l'état de Washington. Les banques de graines sont bien nanties (610–7009 germes par m²), contenant 46 espèces indigènes et exotiques représentant une diversité de formes biologiques. Cependant, plusieurs espèces communes des sous-étages forestiers sont absentes; seulement 11 espèces sont typiques des sous-étages forestiers et elles comprennent moins de 10% des germes. Au contraire, 30% de toutes les espèces et 50% des germes sont des herbes rudérales non-graminéennes et exotiques. Les espèces annuelles et pérennes dispersées par le vent dominant dans les échantillons de litière, alors que les herbacées graminéennes et non-graminéennes rudérales à dispersion limitée dominant dans les échantillons de sol. Ces résultats suggèrent que l'éclaircie sylvicole encouragerait l'établissement d'espèces rudérales exotiques, mais contribuerait faiblement à la régénération des graines enfouies de la grande majorité des espèces de plantes du sous-bois.

Mots clés : fermeture de la canopée, sous-bois, germination des graines, banque de graine édaphique, succession, réinstallation du sous-bois.

[Traduit par la Rédaction]

Introduction

Early in stand development, coniferous forests of the coastal Pacific Northwest commonly pass through a period

of dense shade and intense tree competition during which the abundance and diversity of understory plants are greatly reduced (Alaback 1982; Oliver and Larson 1990). Subsequently, as stem densities decline because of natural mortality and tree canopies increase in height and openness, understory communities are reinitiated. The closed-canopy, or stem-exclusion, stage of stand development (sensu Oliver and Larson 1990) represents a critical juncture in the successional development of the forest understory. Canopy closure may result in the local extinction of some forest species and thus shape longer term patterns of understory composition and diversity. Despite the significance of this period for

Received December 18, 1998.

C.B. Halpern,¹ S.A. Evans, and S. Nielson. Division of Ecosystem Sciences, College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

¹Author to whom all correspondence should be addressed.
e-mail: chalpern@u.washington.edu

understory development, little research has been devoted to the mechanisms by which plant species persist through canopy closure or reestablish once growing conditions improve.

In this study we examined the potential contribution of the soil seed bank to the reinitiation of forest understories in low-elevation forests of the Olympic Peninsula, Washington. Here, the effects of canopy closure can be particularly dramatic because in this very wet and productive climate, tree densities and light attenuation are often extreme in young, regenerating stands. Using the greenhouse emergence method, we assessed the floristic composition, abundance, and diversity of viable seeds in the soil and litter of 40- to 60-year-old, closed-canopy forests. We posed the following four questions: First, which species are present in the seed bank and how do they vary in frequency of occurrence and relative abundance? Second, what are the relative contributions to the seed bank of species representing contrasting habitat preferences, biogeographic origins, and life forms? Specifically, how do species density and diversity compare among (i) forest understory versus ruderal, open site species, (ii) native versus exotic species, and (iii) major plant life forms (e.g., grasses, sedges and rushes, forbs, shrubs, trees)? Third, do the density, diversity, and composition of germinants from the litter layer (the more recent and transient pool of seeds) differ from those of the mineral soil (the older and more persistent pool)? Fourth, how does seed bank composition vary within and among spatially distinct blocks of forest of comparable age, plant association, and management history?

The few investigations of soil seed banks in forests of the Pacific Northwest have been largely restricted to older stands or recently clearcut sites (Kellman 1970, 1974; Ingersoll and Wilson 1989; Clark 1991; Harmon and Franklin 1995). These studies indicate that to a large degree, species of the forest understory are greatly under-represented in the belowground community of viable seeds (as suggested for coniferous forests in general by Archibold 1989). However, with few comparable studies in young, closed-canopy forests of the Pacific Northwest (but see McGee and Feller 1993), we had little basis for evaluating the potential contribution of the seed bank to understory reinitiation. Furthermore, we are aware of no published studies of soil seed banks in any forest type within the Olympic Peninsula region.

The potential for the seed bank to contribute to understory reinitiation has particular relevance for vast areas of lowland forest in the Pacific Northwest. More than half a century of clearcut logging and intensive forestry have produced a landscape dominated by relatively young, even-aged, closed-canopy forests. Concern over large-scale loss of biological diversity from these systems has spurred recent interest in silvicultural approaches to enhance the structural complexity and biological diversity of the understory (DeBell et al. 1997; Tappeiner et al. 1997). However, attempts to stimulate or accelerate understory development through silvicultural manipulation (e.g., thinning) requires an understanding of the sources and potential responses of plant propagules to such manipulations. Germination of buried viable seeds is likely to be stimulated by the abrupt increases in light produced by thinning. To what degree this promotes desirable

species (e.g., shade-tolerant, native forest herbs or shrubs) or encourages the germination of ruderal or exotic species depends, in part, on the composition of the seed bank.

Methods

Study sites

Soil and litter samples for this study were collected from three permanent plots at each of three locations (blocks). These plots comprise a subset of the experimental units of the Olympic Habitat Development Study (C. A. Harrington and A. B. Carey, unpublished study plan), a more comprehensive study of variable-intensity thinning and manipulation of coarse woody debris. The southernmost block, Bait, is on the western margin of the Olympic Range near the Queets River (190–230 m elevation; T24N R10½W S14); two of the three plots lie adjacent to each other and the third lies 1 km to the northeast. The two remaining blocks, Fresca and Clavicle, are on the northern margin of the Olympic Range in the Soleduck River drainage. Fresca lies on the Soleduck floodplain (150 m elevation; T29N R12W S5); all three plots about one another. Clavicle lies 5 km to the east of Fresca (430–520 m; T29N R12W S2 and 11); its three plots are separated by ca. 1 km. All of the study plots lie within the *Picea sitchensis* and *Tsuga heterophylla* forest zones (Franklin and Dyrness 1973). Slopes are gentle and soils are silty loams (Bait and Clavicle) or gravelly, sandy loams (Fresca) (Table 1). The climate is maritime with uniformly cool, wet growing conditions. Mean July and January temperatures are 15–17 and 4°C, respectively (Henderson et al. 1989). Precipitation is very high (annual totals of 300 cm or more) and is concentrated between October and April (Henderson et al. 1989).

Each plot supported young, coniferous forest that originated after clear-cut logging ca. 40–60 years prior to sampling. All were planted and precommercially thinned, although dates of these activities varied within and among blocks (Table 1). At the time of sampling, all were dense, closed-canopy forests dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* (Bait) or *Tsuga heterophylla* and *Picea sitchensis* (Fresca and Clavicle) (Table 1). Total understory, vascular plant cover was low (range of 17–21% among blocks; Table 2). The most abundant species were the herbs *Oxalis oregana*, *Maianthemum dilatatum*, and *Disporum smithii*, the ferns *Polystichum munitum* and *Blechnum spicant*, and the shrub *Vaccinium parvifolium* (Table 2). Ground cover of moss averaged 32–81% (Table 2) and mean litter depth varied from 3.3 to 7.5 cm (Table 1).

Field sampling

Soil and litter samples were collected between 25 April and 3 May 1995. Fourteen paired soil and litter samples were removed from each of the nine plots, yielding a total of 126 paired samples. Samples were collected adjacent to 14 centrally located, permanent grid points in each plot, from within a total sample area of 280 m² (the full grid system at each plot contained 8 × 12 points spaced 20 m apart). At each of these 14 points, three paired subsamples of litter and soil were collected from random locations 1 m apart. Woody material (twigs, cones, branches) and moss on the ground surface were discarded, and the litter layer (O horizon) circumscribed by a bulb planter (surface area of 27.3 cm²) was collected and bagged. Mineral soil to a depth of 10 cm was extracted with the bulb planter and placed in a separate bag. The three subsamples representing each layer were then combined; each litter or soil sample thus represents a total surface area of 81.9 cm². Although the volume of litter samples varied with the depth of the forest floor, the volume of soil (819 cm³/sample) remained relatively constant. Cores with noticeable amounts of stone or wood were rejected and replaced with more acceptable samples. Additional data

Table 1. Physical site characteristics, forest stand characteristics, and management histories of the study plots within each block.

Block and plot No.	Elevation (m)	Aspect	Slope (%)	Soil texture ^a	Litter depth (cm) ^b	Major tree species ^c	Basal area (m ² /ha)	Density (no./ha)	Plant association ^d	Years since harvest ^e	Years since planting ^f
Bait											
1	230	W	5-35	SIL	3.3	Psmc, Tshe	65	850	Pomu-Oxor, Gash-Oxor	44	42
2	190	E	5-35	SIL	5.1	Tshe, Psmc	70	1574	Pomu-Oxor, Gash-Oxor	41	37
3	210	N	5-35	SIL	4.9	Tshe, Psmc	49	840	Pomu-Oxor, Gash-Oxor	41	37
Fresca											
1	150	Flat	0	GSL	4.6	Tshe, Pisi	73	498	Pomu-Oxor	55-60	—
2	150	Flat	0	GSL	4.4	Tshe, Pisi	66	509	Pomu-Oxor	55-60	—
3	150	Flat	0	GSL	7.5	Tshe, Pisi	73	775	Pomu-Oxor	55-60	—
Clavicle											
1	490	W	5-35	SIL	4.7	Pisi, Tshe	72	590	Pomu-Oxor	60	—
2	520	S	10-35	SIL	5.2	Tshe, Pisi	98	1327	Pomu-Oxor	60	—
3	430	S	5-35	SIL	6.0	Tshe, Pisi	81	1010	Pomu-Oxor	60	—

^aSIL, silty loam; GSL, gravelly sandy loam (C.A. Harrington and A.B. Carey, unpublished data).

^bLitter depth represents the average of 42 subsamples per plot.

^cPsmc, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Pisi, *Picea sitchensis*. Tree species are listed in descending order of basal area.

^dPlant associations according to Henderson et al. (1989): Pomu, *Polystichum munitum*; Oxor, *Oxalis oregana*; Gash, *Gauthieria shallon*.

^ePrecise dates of harvest are unknown for Fresca.

^fDates of planting are unknown for Fresca and Clavicle.

were collected at each grid point and averaged to describe physical site conditions and vegetation at each plot or block (Tables 1 and 2).

Greenhouse methods

Soil and litter samples were processed within 1 or 2 days of collection. Each of the 126 pairs of samples was randomly assigned to a position in one of two rows along each of two, 32-m long, plastic-lined greenhouse benches. Standard germination flats were lined with plastic trays to create paired sections (26 cm per side) into which a 2-cm deep layer of pumice was placed; paired litter and soil samples were then assigned to the two halves of each flat in alternating fashion along each greenhouse bench. Litter samples were mixed with standard potting soil to yield the same volume as the mineral soil samples. Both sets of samples were then spread in a ca. 2-cm layer over the pumice.

Several strategies were used to control for contaminants. First, because several fern and *Equisetum* species can be common greenhouse weeds, we considered only Angiosperm taxa in this study. Second, to reduce aerial deposition of wind-dispersed seeds, greenhouse benches were covered with white Remay cloth supported by a PVC frame. Finally, to account for possible contaminants in the potting soil or pumice, seven additional flats containing only potting soil on pumice were spaced evenly among the field samples on each bench, providing a total of 28 control samples for the study.

Samples were watered from below by regularly flooding the plastic-lined benches. Natural lighting was supplemented with 1000-W metal halide lamps to provide a 16-h photoperiod. Greenhouse temperatures ranged from a minimum of 13°C (May) to a maximum of 35°C (July).

Data on germinants were collected twice weekly between mid-May 1995 and early March 1996. Each germinant was marked with a colored toothpick, recorded by date of appearance, and assigned a code representing a distinguishable morphological form. Germinants were removed from the flats as they were identified to species. Seedling mortality was also recorded and included in the final tallies. Germinants representing unidentified, morphological types (primarily graminoids) were transplanted to stimulate flowering to aid in identification. The experiment was concluded in early March 1996 allowing ca. 9 months for germination. Nomenclature follows Hitchcock and Cronquist (1973).

Data manipulation and analysis

To characterize the distribution and abundance of germinant species, we calculated the frequency of occurrence (percentage of sample points) and mean germinant density (number of germinants per 81.9-cm² sample) for each taxon within each block. To compare the abundance and diversity of species with different habitat preferences, biogeographic origins, and physiognomic characteristics, all taxa were classified in three ways: (i) as forest understory species (those typical of mature forests of the region) or open site species (those common to disturbed sites or agricultural fields but rare in mature forests of the region); (ii) as native or exotic species; and (iii) by life form (grass, sedge or rush, forb, shrub, or tree). Germinant frequency of occurrence, density, and species richness were then calculated for each group. To compare the contributions of the more recent, transient pool of seeds with the older, more persistent store, species frequency, density, and richness were estimated separately for litter and soil samples. Richness was estimated at three spatial scales: sample, plot (representing 14 samples), and block (representing 42 samples).

To test for differences in the density or richness of germinants between litter and soil layers or between pairs of plant groups, paired *t* tests (Sokal and Rohlf 1981) were conducted on block-level germinant densities and two measures of richness: mean number of species per sample (within each block) and total number

Table 2. Frequency of occurrence and mean cover (± 1 SE) of understory species in the aboveground vegetation in each study block.

Growth form and species	Bait		Fresca		Clavicle	
	% Freq.	% Cov. (SE)	% Freq.	% Cov. (SE)	% Freq.	% Cov. (SE)
Mosses						
All mosses	100	32 (3)	100	81 (3)	100	54 (5)
Graminoids						
Grass sp.			2	Tr (Tr)		
<i>Luzula parviflora</i>	10	Tr (Tr)	10	Tr (Tr)		
Forbs and sub-shrubs						
<i>Dicentra formosa</i>			2	Tr (Tr)	1	Tr (Tr)
<i>Disporum smithii</i>	2	Tr (Tr)	38	Tr (Tr)	31	Tr (Tr)
<i>Galium triflorum</i>	2	Tr (Tr)				
<i>Lactuca muralis</i>	5	Tr (Tr)				
<i>Linnaea borealis</i>			5	Tr (Tr)		
<i>Listera</i> spp.	2	Tr (Tr)	19	Tr (Tr)	7	Tr (Tr)
<i>Maianthemum dilatatum</i>	7	Tr (Tr)	88	6 (1)	33	1 (Tr)
<i>Montia sibirica</i>	19	Tr (Tr)				
<i>Oxalis oregana</i>	29	8 (3)	48	6 (2)	86	16 (3)
<i>Pyrola</i> sp.			2	Tr (Tr)		
<i>Rubus lasiococcus</i>	2	Tr (Tr)				
<i>Tiarella trifoliata</i>	7	Tr (Tr)	5	Tr (Tr)		
<i>Trientalis latifolia</i>			7	Tr (Tr)	2	Tr (Tr)
<i>Trillium ovatum</i>	7	Tr (Tr)	12	Tr (Tr)	10	Tr (Tr)
<i>Viola sempervirens</i>			19	Tr (Tr)		
Ferns and fern allies						
<i>Athyrium filix-femina</i>	19	Tr (Tr)	10	Tr (Tr)	5	Tr (Tr)
<i>Blechnum spicant</i>	33	1 (Tr)	50	3 (1)	2	Tr (Tr)
<i>Lycopodium</i> sp.			2	Tr (Tr)		
<i>Polystichum munitum</i>	43	4 (1)	26	2 (1)	17	Tr (Tr)
<i>Pteridium aquilinum</i>			26	Tr (Tr)	5	Tr (Tr)
Shrubs						
<i>Acer circinatum</i>			2	Tr (Tr)		
<i>Gaultheria shallon</i>	10	Tr (Tr)	26	1 (1)		
<i>Menziesia ferruginea</i>	2	Tr (Tr)	7	Tr (Tr)		
<i>Rubus parviflorus</i>			7	Tr (Tr)		
<i>Rubus spectabilis</i>	2	Tr (Tr)	12	Tr (Tr)		
<i>Rubus ursinus</i>	10	Tr (Tr)				
<i>Vaccinium parvifolium</i>	48	1 (Tr)	55	1 (Tr)	45	1 (Tr)
<i>Vaccinium membranaceum</i>					2	Tr (Tr)
Understory trees						
<i>Rhamnus purshiana</i>	24	Tr (Tr)	50	Tr (Tr)		
<i>Thuja plicata</i>	2	Tr (Tr)				
<i>Tsuga heterophylla</i>	2	Tr (Tr)	5	Tr (Tr)	10	Tr (Tr)

Note: Frequency (Freq.) is the percentage of subplots within a block in which a species was observed ($n = 42$). Plant cover (Cov.) was estimated within circular subplots of 2-m radius at each seed bank sample point. Six cover classes were used (0–1, 2–5, 6–25, 26–50, 51–75, and 76–100%) and mean cover values were calculated from the midpoints of these classes. Tr, trace (<0.5).

of species per block ($n = 3$ for all tests). SYSTAT® 6.0 (SPSS Inc. 1996) was used for t tests.

Detrended correspondence analysis (DCA; Hill 1979; Gauch 1980) was used to explore the compositional variation in germinant pools within and among forest blocks. We ordinated 18 samples representing the average species composition (mean germinant densities) of soil or litter samples in each of the nine study plots. Default settings of the program DECORANA (Hill 1979) were implemented. In addition to this ordination analysis, we calculated matrices of within- and between-block compositional similarity (i.e., similarity of plots within and between blocks, respectively) using Sørensen's community coefficient (Sørensen 1948 cited in

Mueller-Dombois and Ellenberg 1974). Sørensen's index is a ratio of the number of species found in common to the average number of species in two samples and is expressed as follows:

$$[1] \quad S_{ij} = \frac{100c}{0.5(a + b)}$$

where c is the number of species common to samples i and j and a and b are the total numbers of species found in samples i and j , respectively.

Table 3. Frequency of occurrence and mean density (number per sample) (± 1 SE) of germinant taxa in litter and soil samples from the three study blocks.

Life form and species	Species classification ^a		Bait					
			Litter			Soil		
			Habitat	Origin	Freq.	Den.	(SE)	Freq.
Grasses								
<i>Agrostis alba</i>	O	E				2.4	0.02	(0.02)
<i>Agrostis scabra</i>	O	N	4.8	0.07	(0.05)	9.5	0.19	(0.11)
<i>Deschampsia elongata</i>	O	N	2.4	0.02	(0.02)	4.8	0.21	(0.15)
<i>Festuca occidentalis</i>	F	N						
Sedges / rushes								
<i>Carex aquatilis</i>	O	N						
<i>Carex deweyana</i>	O	N	4.8	0.05	(0.03)			
<i>Carex hendersonii</i>	O	N	2.4	0.02	(0.02)	7.1	0.93	(0.75)
<i>Carex laeviculmis</i>	O	N	9.5	0.30	(0.18)	11.9	0.50	(0.38)
<i>Carex rossii</i>	O	N						
<i>Carex</i> sp.	O	N	2.4	0.02	(0.02)	7.1	0.14	(0.10)
<i>Juncus acuminatus</i>	O	N						
<i>Juncus effusus</i>	O	N	50.0	2.95	(0.77)	57.1	12.05	(3.66)
<i>Juncus ensifolius</i>	O	N	2.4	0.02	(0.02)			
<i>Luzula campestris</i>	O	N				4.8	0.05	(0.03)
<i>Luzula parviflora</i>	F	N				7.1	0.07	(0.04)
<i>Luzula</i> spp.	—	N						
Forbs								
<i>Anaphalis margaritacea</i>	O	N	4.8	0.05	(0.03)	2.4	0.02	(0.02)
<i>Arabidopsis thaliana</i>	O	E	23.8	0.38	(0.16)			
<i>Chrysanthemum leucanthemum</i>	O	E						
<i>Cirsium vulgare</i>	O	E						
<i>Digitalis purpurea</i>	O	E				2.4	0.02	(0.02)
<i>Epilobium watsonii</i>	O	N	19.0	0.19	(0.06)	7.1	0.10	(0.06)
<i>Erechtites minima</i>	O	E	40.5	0.76	(0.19)	7.1	0.10	(0.06)
<i>Galium</i> sp.	O	N						
<i>Gnaphalium purpureum</i>	O	N				2.4	0.02	(0.02)
<i>Hypericum perforatum</i>	O	E						
<i>Lactuca muralis</i>	O	E						
<i>Lactuca serriola</i>	O	E						
<i>Mimulus primuloides</i>	O	N				2.4	0.02	(0.02)
<i>Montia sibirica</i>	F	N				7.1	0.10	(0.06)
<i>Oxalis oregana</i>	F	N						
<i>Rumex acetosella</i>	O	E				2.4	0.02	(0.02)
<i>Senecio sylvaticus</i>	O	E	38.1	0.52	(0.12)	11.9	0.17	(0.08)
<i>Sonchus asper</i>	O	E						
<i>Solidago canadensis</i>	O	N						
<i>Spergularia rubra</i>	O	E				2.4	0.02	(0.02)
<i>Stachys cooleyae</i>	O	N						
<i>Tolmiea menziesii</i>	F	N						
Shrubs / Trees								
<i>Gaultheria shallon</i>	F	N	4.8	0.07	(0.05)	31.0	0.57	(0.16)
<i>Menziesia ferruginea</i>	F	N				9.5	0.29	(0.18)
<i>Rubus laciniatus</i>	O	E				7.1	0.07	(0.04)
<i>Rubus leucodermis</i>	O	N						
<i>Rubus spectabilis</i>	F	N	16.7	0.17	(0.06)	31.0	0.55	(0.19)
<i>Rubus ursinus</i>	F	N						
<i>Rubus</i> spp.	—	—	2.4	0.02	(0.02)	7.1	0.07	(0.04)
<i>Sambucus racemosa</i>	F	N	2.4	0.02	(0.02)	7.1	0.07	(0.04)
<i>Spiraea</i> sp.	O	N						
<i>Vaccinium parvifolium</i>	F	N	2.4	0.02	(0.02)	4.8	0.05	(0.03)
<i>Alnus rubra</i>	—	N	7.1	0.10	(0.06)	2.4	0.10	(0.10)

Fresca						Clavicle					
Litter			Soil			Litter			Soil		
Freq.	Den.	(SE)	Freq.	Den.	(SE)	Freq.	Den.	(SE)	Freq.	Den.	(SE)
Grasses											
						4.8	0.07	(0.05)	9.5	0.41	(0.21)
			2.4	0.02	(0.02)						
			4.8	0.05	(0.03)	4.8	0.05	(0.03)	2.4	0.02	(0.02)
			2.4	0.02	(0.02)						
Sedges / rushes											
2.4	0.02	(0.02)							2.4	0.02	(0.02)
11.9	0.14	(0.06)	26.2	0.33	(0.10)	2.4	0.02	(0.02)	14.3	0.19	(0.08)
			7.1	0.10	(0.06)				2.4	0.02	(0.02)
2.4	0.02	(0.02)	2.4	0.05	(0.05)				2.4	0.02	(0.02)
2.4	0.02	(0.02)							2.4	0.05	(0.05)
21.4	0.24	(0.08)	45.2	0.98	(0.25)	2.4	0.05	(0.05)	28.6	0.60	(0.20)
4.8	0.12	(0.10)	33.3	0.95	(0.30)	9.5	0.17	(0.09)	33.3	0.95	(0.31)
			4.8	0.05	(0.03)	2.4	0.02	(0.02)	2.4	0.02	(0.02)
Forbs											
			16.7	0.21	(0.08)	2.4	0.02	(0.02)	19.0	0.21	(0.07)
4.8	0.33	(0.24)				16.7	0.43	(0.20)			
2.4	0.02	(0.02)									
4.8	0.05	(0.03)	2.4	0.02	(0.02)	2.4	0.02	(0.02)			
16.7	1.69	(0.96)	23.8	5.38	(2.79)	16.7	1.10	(0.58)	21.4	15.88	(12.95)
26.2	0.41	(0.12)	4.8	0.07	(0.05)	21.4	0.21	(0.06)	2.4	0.02	(0.02)
16.7	0.19	(0.07)									
2.4	0.02	(0.02)									
			2.4	0.10	(0.10)						
7.1	0.07	(0.04)									
2.4	0.02	(0.02)	2.4	0.02	(0.02)	2.4	0.02	(0.02)			
									4.8	0.05	(0.03)
2.4	0.05	(0.05)							2.4	0.02	(0.02)
			2.4	0.02	(0.02)						
42.9	0.64	(0.14)	7.1	0.07	(0.04)	26.2	0.45	(0.14)	11.9	0.12	(0.05)
2.4	0.02	(0.02)									
2.4	0.02	(0.02)									
						2.4	0.05	(0.05)	2.4	0.29	(0.29)
			2.4	0.02	(0.02)	2.4	0.02	(0.02)	2.4	0.07	(0.07)
Shrubs / Trees											
2.4	0.02	(0.02)	2.4	0.02	(0.02)				4.8	0.05	(0.03)
									2.4	0.02	(0.02)
2.4	0.02	(0.02)	14.3	0.17	(0.07)				28.6	0.38	(0.12)
						4.8	0.05	(0.03)	2.4	0.02	(0.02)
			2.4	0.02	(0.02)				4.8	0.05	(0.03)
2.4	0.07	(0.07)	9.5	0.12	(0.06)	7.1	0.10	(0.06)	42.9	0.91	(0.28)
						2.4	0.02	(0.02)			
									2.4	0.02	(0.02)
2.4	0.02	(0.02)	2.4	0.02	(0.02)	4.8	0.05	(0.03)	2.4	0.02	(0.02)

Table 3. (concluded).

Life form and species	Species classification ^a		Bait					
			Litter			Soil		
			Habitat	Origin	Freq.	Den.	(SE)	Freq.
Unknown taxa	—	—	4.8	0.05	(0.03)	7.1	0.24	(0.14)
Unknown Gramineae	—	—	7.1	0.10	(0.06)	11.9	0.24	(0.11)
Unknown graminoids	—	—	11.9	0.14	(0.06)	2.4	0.02	(0.02)
<i>Erechtites minima</i> or <i>Senecio sylvaticus</i>	O	E	9.5	0.09	(0.05)	14.3	0.17	(0.07)
Other unknown taxa	—	—	92.9	6.17	(0.88)	90.5	17.19	(4.02)
Total germinants	—	—						

Note: Frequency (Freq.) is the percentage of sample points within a block in which a species was observed ($n = 42$). Den., mean density.
^aF, forest understory species; O, open site species; N, native; E, exotic.

Table 4. Results of paired t tests ($n = 3$) comparing the density and richness of germinants representing litter (L) versus soil (S) samples, open site (O) versus forest (F) species, and native (N) versus exotic (E) species (see also Table 3 and Figs. 2–4).

Comparison	No. of germinants per sample	P value	
		Richness per sample	Richness per block
Litter vs. soil samples			
All taxa	0.106	0.243	0.580
Open site taxa	0.119	0.478	1.000
Forest understory taxa	0.043* (S)	0.035* (S)	0.122
Native taxa	0.211	0.031* (S)	0.257
Exotic taxa	0.387	0.047* (L)	0.802
Open site vs. forest understory taxa			
Pooled litter and soil	0.032* (O)	0.062	0.026* (O)
Litter	0.046* (O)	0.039* (O)	0.010** (O)
Soil	0.058	0.199	0.039* (O)
Native vs. exotic taxa			
Pooled litter and soil	0.998	0.006**(N)	0.019* (N)
Litter	0.848	0.840	0.046* (N)
Soil	0.978	0.009**(N)	0.043* (N)

Note: Where differences are statistically significant, letters indicate the layer or species group with the greater density or richness. P values are not adjusted for multiple comparisons. *, $P \leq 0.05$; **, $P \leq 0.01$.

Results

Floristics

A total of 2602 germinants representing 19 families, 34 genera, and 46 species emerged from the 126 paired soil and litter samples (Table 3). Families with the greatest number of species included the Compositae (10), Cyperaceae (5), Juncaceae (5), Rosaceae (5), and Gramineae (4). The most diverse genera were *Carex* (5 species), *Rubus* (4), and *Juncus* (3). Of the total pool of germinants, 126 (4.8%) could not be identified to species, although most of these were distinguishable at higher taxonomic levels (Table 3).

Composition and density of contaminants

Relatively few contaminants emerged from the control flats: a total of 11 germinants were found in 9 of the 28 controls (0.32/sample). Field samples, however, contained an average of 10.32 germinants/sample. Of the five species that emerged in the controls, three were common in field samples (*Arabidopsis thaliana*, *Epilobium watsonii*, and *Juncus effusus*) and two were rare (*Lactuca serriola* and *Spiraea* sp.) (Table 3). Given these very low densities of contaminants, field sample densities were not adjusted prior to anal-

ysis. Although the few germinants of *Lactuca serriola* and *Spiraea* in our field samples may be contaminants, they are fairly common plants near our study sites and were thus retained in subsequent analyses.

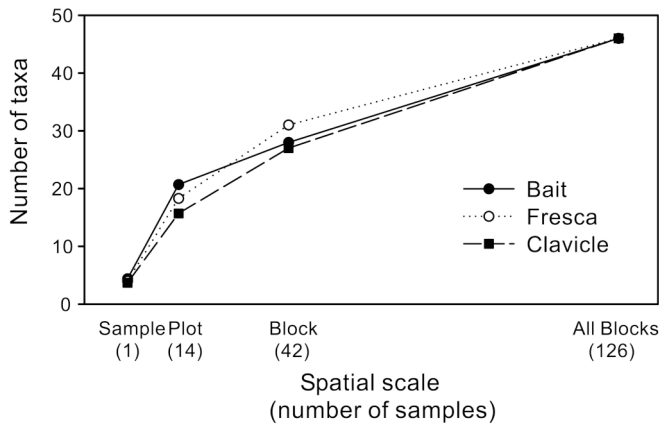
Frequency, density, and diversity of germinants

Nearly all of the field samples produced germinants. Seedlings emerged from 122 of 126 sample points (99% of pooled litter and soil samples) and from equal proportions (87 and 88%) of the individual litter and soil samples. Within individual blocks, germinants emerged from 74 to 95% of litter samples and from 86 to 90% of soil samples (Table 3). Within plots, the frequency of occurrence of germinants was more variable for litter (range of 57–100%) than for soil samples (range of 79–100%).

The density of germinants varied greatly at all spatial scales. Individual pooled samples (representing 81.9 cm² of litter and soil) contained from as few as 0 to as many as 583 germinants (0–71,184 per m²). Plots averaged 5.0–57.4 germinants/sample (610–7009/m²) and blocks averaged 13.5–25.0/sample (1648–3052/m²). More than three times as many germinants emerged from soil as from litter samples, but this difference was not statistically significant (Table 4).

Fresca						Clavicle					
Litter			Soil			Litter			Soil		
Freq.	Den.	(SE)	Freq.	Den.	(SE)	Freq.	Den.	(SE)	Freq.	Den.	(SE)
Unknown taxa											
2.4	0.02	(0.02)				11.9	0.21	(0.13)	16.7	1.17	(0.72)
2.4	0.02	(0.02)	4.8	0.05	(0.03)				2.4	0.02	(0.02)
7.1	0.10	(0.06)	7.1	0.07	(0.04)						
7.1	0.07	(0.04)	4.8	0.05	(0.03)	4.8	0.07	(0.05)	9.5	0.10	(0.05)
95.2	4.48	(0.99)	88.1	9.02	(2.86)	73.8	3.21	(0.74)	85.7	21.74	(13.32)

Fig. 1. Species accumulation curves for pooled litter and soil samples in each block. Values in parentheses are the number of sample points.



Each of the three blocks contained similar numbers of germinant species at most spatial scales examined (Fig. 1). Individual pooled samples contained 21–25% of the species within a plot, plots contained 58–74% of the species within a block, and blocks contained 59–67% of the total pool of 46 species. Litter and soil samples yielded species-accumulation curves of similar shape and magnitude (not shown); similar numbers of species were found in litter and soil samples at most spatial scales (Table 4).

Forest understory versus open site species

Open site species were much more abundant in the seed bank than were forest species. Among pooled litter and soil samples, both the mean density and species richness per block of open site taxa were significantly greater than those of forest understory species (Figs. 2B, 2D; Table 4). Species richness per sample showed a similar, but nonsignificant trend (Fig. 2C; Table 4). Forest understory taxa had greater density and richness in the soil than in the litter samples (Fig. 2; Table 4), whereas open site taxa showed more even distributions between soil and litter (Figs. 2B–2D; Table 4).

Native versus exotic species

Both native and exotic species were well represented in the seed bank. Germinant densities for both groups were highly variable among blocks (Fig. 3B), but the richness of native species was generally greater than that of exotics

Fig. 2. Various measures of the abundance and diversity of open site versus forest understory taxa in litter and soil samples. (A) Frequency of occurrence. (B) Mean germinant density (number per sample). (C) Mean number of taxa per sample. (D) Total number of taxa per block. The stacked bars to the left of the vertical line represent pooled litter and soil samples.

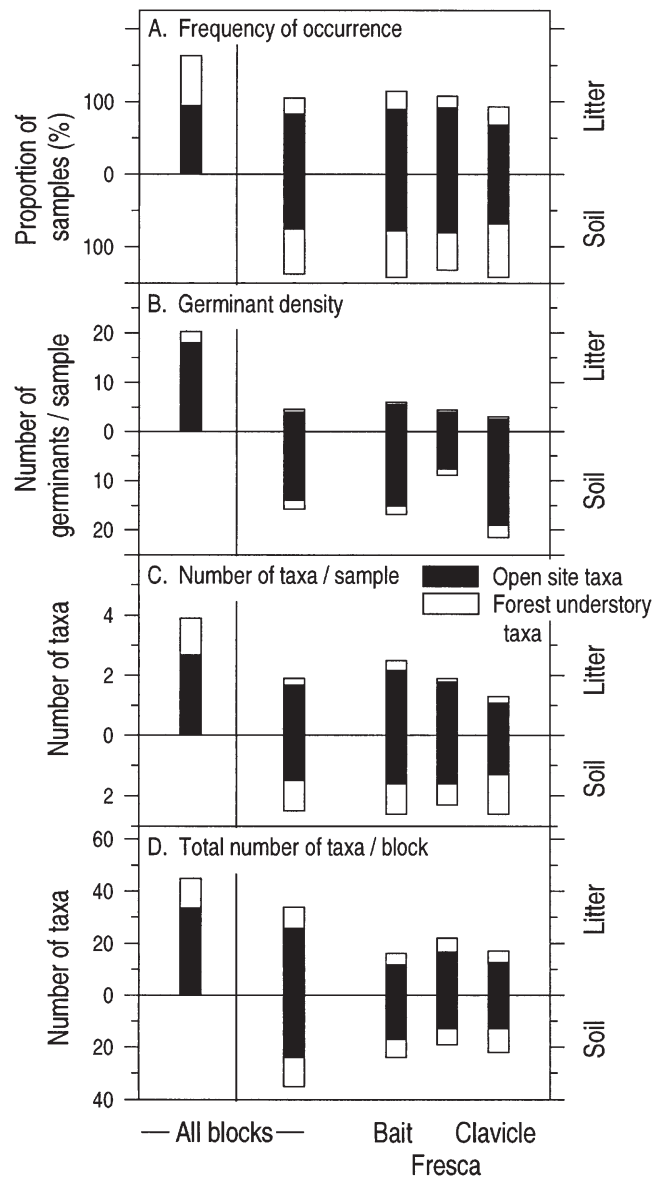
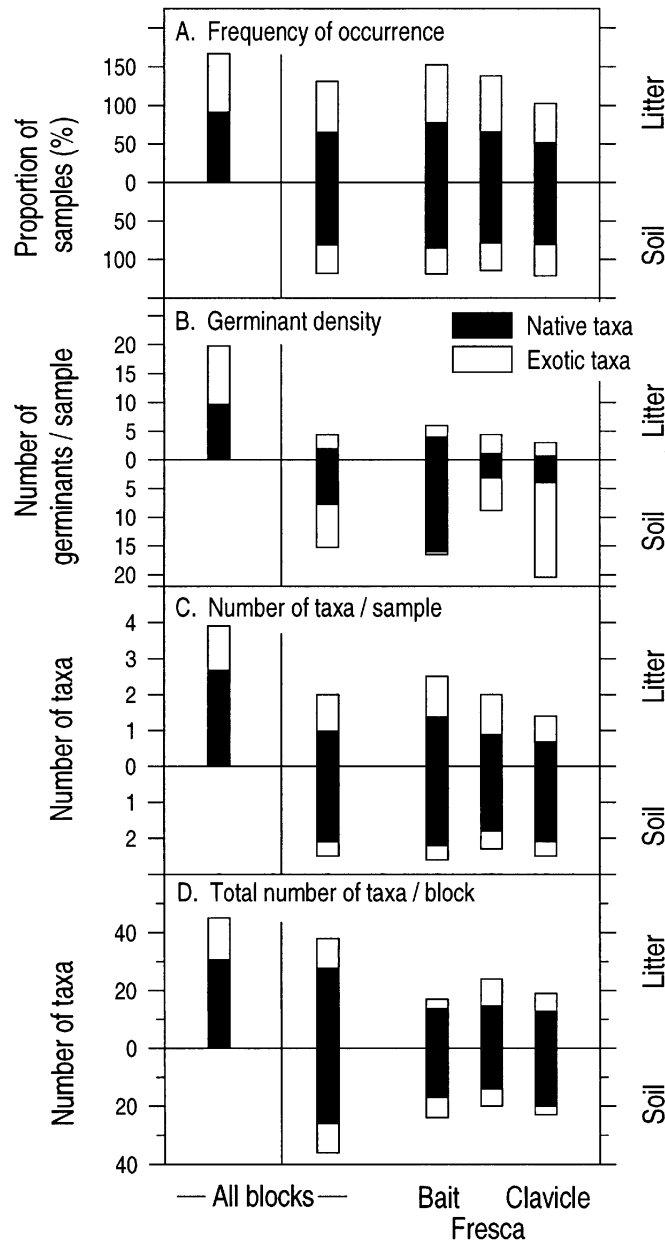


Fig. 3. Various measures of the abundance and diversity of native versus exotic taxa in litter and soil samples. (A) Frequency of occurrence. (B) Mean germinant density (number per sample). (C) Mean number of taxa per sample. (D) Total number of taxa per block. The stacked bars to the left of the vertical line represent pooled litter and soil samples.

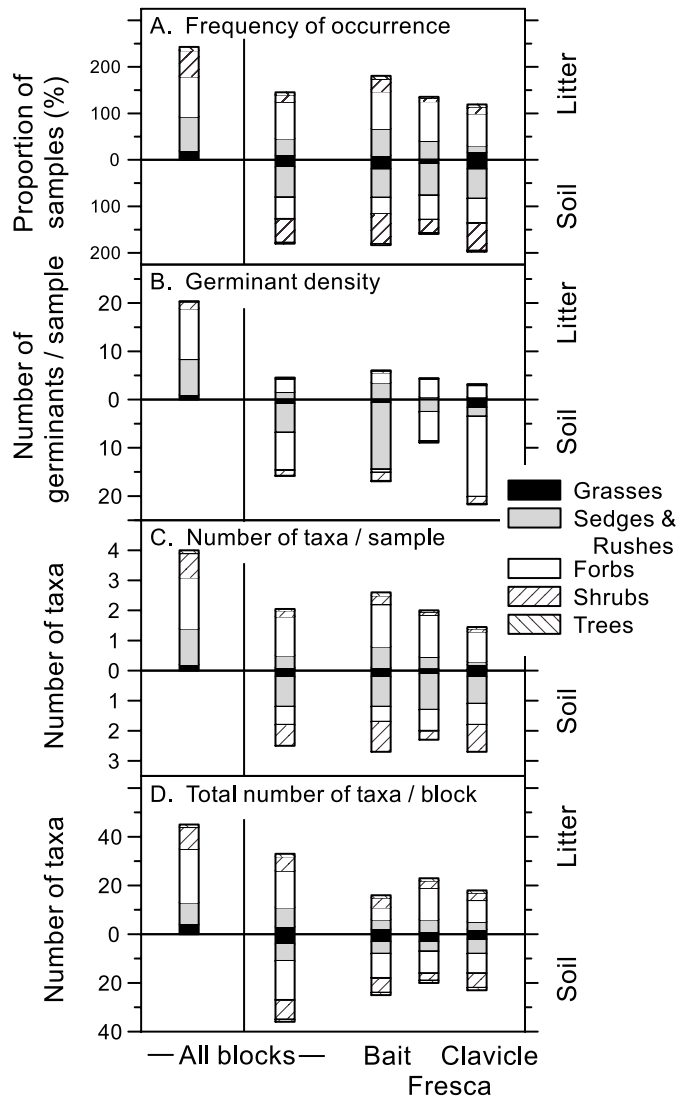


(Figs. 3C, 3D; Table 4). Native taxa tended to be more diverse in soil than in litter samples, and exotics more diverse in litter than in soil samples, although these patterns varied with spatial scale (Figs. 3C, 3D; Table 4).

Life-form spectra

The relative density of germinants representing each life form varied markedly among blocks (Fig. 4B). In particular, Bait was dominated by rushes (e.g., *Juncus effusus*) and Clavicle by forbs (e.g., *Digitalis purpurea*). In contrast, the relative richness of species within each life form was comparable among blocks (Figs. 4C, 4D). Species richness

Fig. 4. Various measures of the abundance and diversity of major life forms in litter and soil samples. (A) Frequency of occurrence. (B) Mean germinant density (number per sample). (C) Mean number of taxa per sample. (D) Total number of taxa per block. The stacked bars to the left of the vertical line represent pooled litter and soil samples.

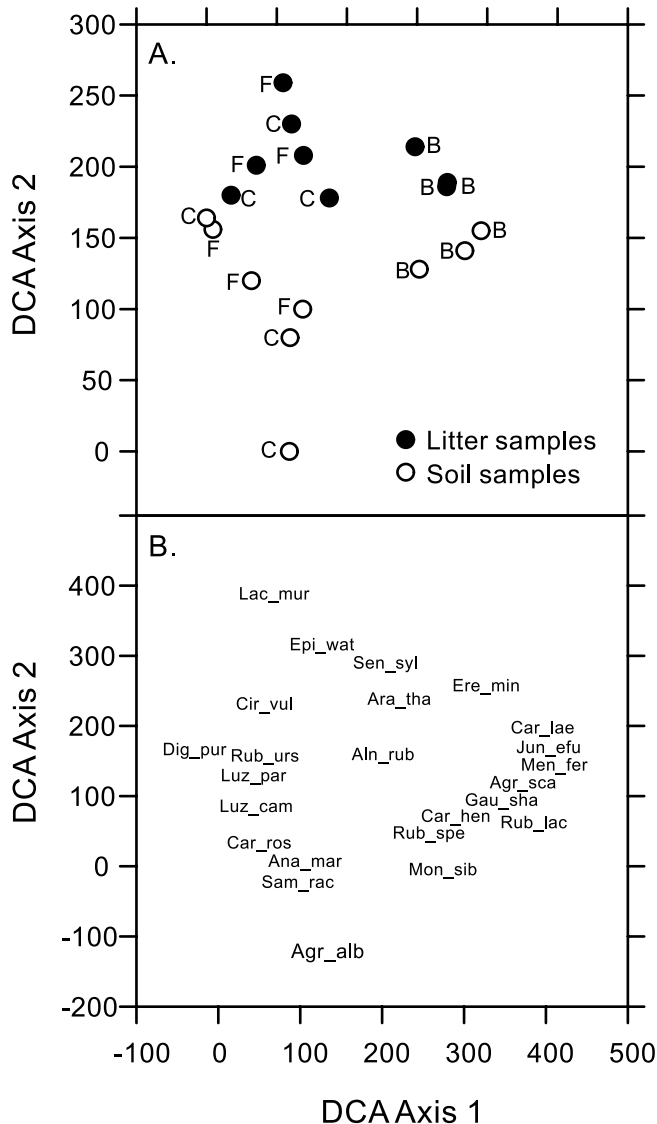


within life forms ranked as follows: forbs > sedges and rushes > shrubs > grasses > trees. Within individual samples, forbs tended to be more diverse in litter than in soil, but shrubs, sedges and rushes were more diverse in soil. At the block level, however, life-form richness in litter and soil were comparable (Figs. 4C, 4D).

Species composition: differences among layers and geographic locations

Detrended correspondence analysis of germinant density revealed strong compositional gradients associated with sample layer (litter versus soil) and geographic location (blocks). Litter and soil samples were distinct in composition (Fig. 5A). Litter was dominated by wind-dispersed, early seral forbs (e.g., *Epilobium watsonii*, *Senecio sylvaticus*, and *Erechtites minima*) and other short-lived annuals

Fig. 5. Detrended correspondence analysis ordination of 18 samples representing the average density of germinants for each plot-by-layer (i.e., soil or litter) combination. (A) Sample ordination with blocks. B, Bait; F, Fresca; C, Clavicle. (B) Species ordination illustrating only those species present in $\geq 5\%$ of the samples in at least one block. Species codes correspond to the first three letters of the genus and species name (see Table 3 for full binomials).



and biennials characteristic of disturbed sites (e.g., *Arabis thaliana*) (Fig. 5B; Table 3). Soil samples supported species with a broader diversity of dispersal strategies and life forms; they were also distinct from litter samples in containing most of the forest shrubs (e.g., *Gaultheria shallon*, *Rubus spectabilis*, and *Sambucus racemosa*) (Fig. 5B; Table 3). DCA results, which reflect both species presence and relative density, suggest greater similarity in species composition among litter samples than among soil samples (Fig. 5A). However, Sørensen's community coefficient, which reflects species co-occurrence alone, suggests that soil samples were floristically more similar than were litter samples (Table 5).

Table 5. Percent similarity (Sørensen's community coefficient) of germinant species composition within and between study blocks.

Comparison ^a	Pooled litter and soil samples	Litter samples	Soil samples
Within blocks (3)			
Bait	75	64	65
Fresca	59	47	64
Clavicle	56	36	51
Mean within blocks	63	49	60
Between blocks (9)			
Bait–Fresca	53	41	52
Bait–Clavicle	54	29	52
Fresca–Clavicle	58	38	61
Mean between blocks	55	36	55

Note: Values are the means of all possible pairwise comparisons among plots.

^aValues in parentheses are the numbers of pairwise comparisons of plots within or between blocks.

Similarity of species composition within blocks was greater than that between blocks (Fig. 5A; Table 5). Plots from the southernmost Bait block were homogenous and distinctive in composition compared with plots at Fresca and Clavicle (Fig. 5A; Table 5). Bait supported a unique assemblage of open site graminoids (*Juncus effusus*, *Carex laeviculmis*, and *Agrostis scabra*) and forest shrubs (*Menziesia ferruginea* and *Gaultheria shallon*) (Fig. 5B; Table 3). In contrast, there was significant overlap in species composition among plots at Fresca and Clavicle (Fig. 5A). In total, 13 species were common to all blocks, 14 were common to two blocks, and 19 were unique to a single block (7 in Bait, 8 in Fresca, and 4 in Clavicle; Table 3).

Discussion

Density and diversity of buried viable seeds

The seedling emergence method is the most feasible and commonly used technique for quantifying the potential of the seed bank to contribute to the aboveground vegetation; however, it is well recognized that it may underestimate the true density and diversity of buried viable seeds (Brown 1992). Although individual species may require particular environmental conditions or treatments (e.g., fire) to break dormancy, these requirements are likely to be diverse and in many instances unknown. As a consequence, experimental manipulations of the germination regime are problematic in community-level studies of seed banks (but see Ingersoll and Wilson 1989; McGee and Feller 1993). Despite these limitations, our emergence results illustrate that young, closed-canopy forests on the Olympic Peninsula support a well-developed and diverse community of buried seeds. Germinant densities (610–7009/m² among plots) were generally greater than those reported for older forests in the Pacific Northwest region (e.g., 109–1061/m²; Kellman 1970, 1974; Ingersoll and Wilson 1989; Harmon and Franklin 1995; Parendes 1997; the latter two studies sampled to a depth of 5 cm, compared with all others and the current study that sampled to a depth of 10 cm). Densities were comparable to those observed in slightly younger (30- to 40-year-old) coniferous forests adjacent to transmission line rights-of-way in southwestern British Columbia (1631–3462/m², but these

included ferns; McGee and Feller 1993). Quantitative comparisons of seed-bank richness are more difficult to make because such estimates are sensitive to the number, spatial distribution, and area encompassed by samples (e.g., Magurran 1988). Qualitatively, however, our results suggest that the richness of the seed bank in these forests is equivalent to, or greater than, that found in mature and old-growth forests of the Pacific Northwest region (cf. Kellman 1970, 1974; Ingersoll and Wilson 1989; Harmon and Franklin 1995; Parendes 1997). It is likely that the maximal viable seed density and diversity occur early in succession (e.g., Kellman 1974) long before the forest canopy closes, at a time when understory plant cover and species diversity are also greatest (e.g., Halpern and Franklin 1990; Halpern and Spies 1995) and flowering and fruit production are abundant. Gradual declines in seed density and diversity during succession probably reflect the combination of reduced seed production within and inputs to closed-canopy forests, as well as persistent loss of viable seeds to decay, predation, and germination (Leck et al. 1989).

We found high spatial variability in germinant density both for individual species and for the community as a whole (0–71,184 seeds/m² among all samples), which is apparently common (Major and Pyott 1966; Bigwood and Inouye 1988; Leck et al. 1989) and may reflect the patchy distributions of parent plants, local patterns of seed dispersal, and (or) variation in disturbance intensity, microtopography, or environment. Despite this high variability in density, however, 99% of our sample points yielded one or more germinants. Thus, buried viable seeds appear to be ubiquitous in these young forests, in stark contrast with the depauperate character of the aboveground vegetation (Table 2).

Habitat affinities, species' origins, and life-form spectra

The seed-bank communities in these young forests contain species with diverse habitat preferences, biogeographic origins, and life forms. Despite this diversity, ruderal species were consistently dominant, and species characteristic of the primary forest were relatively uncommon. Of a total of 46 taxa, only 11 were classified as forest species and these comprised fewer than 10% of all germinants. Two of the more abundant forest shrubs, *Sambucus racemosa* and *Rubus spectabilis*, could easily have been classified as open-site species: both are more commonly found during the early stages of forest succession or beneath fairly open forest canopies (Franklin and Dyness 1973; Tappeiner et al. 1991). Of the remaining forest taxa, four (*Oxalis oregana*, *Tolmiea menziesii*, *Rubus ursinus*, and *Vaccinium parvifolium*) had very low frequencies and densities. Only two species that are common in mature forests, *Gaultheria shallon* and *Luzula parviflora*, were also common in the seed bank. Previous studies indicate that *Gaultheria* is more likely to contribute to understory reinitiation via vegetative spread than by seedling recruitment and that germination may be limited on non-organic substrates (Sabhasri 1961; McGee and Feller 1993; Huffman et al. 1994). Notably absent from the germinant pool were a large number of forest herbs that exhibit peak development in old growth (e.g., various genera in the Liliaceae and Orchidaceae, as well as other families; Halpern and Spies 1995).

As was observed in other coniferous forests, the vast majority of germinants, both in numbers and diversity of spe-

cies, were ruderal herbs and graminoids (e.g., Kellman 1970, 1974; Archibold 1989). These included both wind-dispersed annuals (e.g., *Erechtites minima* and *Senecio sylvaticus*) and perennials (e.g., *Anaphalis margaritacea* and *Epilobium watsonii*), as well as open site species with more limited dispersal (*Arabidopsis thaliana*, *Carex hendersonii*, *C. laeviculmis*, *Digitalis purpurea*, and *Juncus effusus*). The prominence of this latter group likely reflects their abundance at an earlier stage in succession, following harvest 40–60 years previously. However, the wind-dispersed forbs probably reflect more recent deposition of seeds from off-site sources, as densities are much higher in litter than in soil samples (see below; Kellman 1974).

Nearly 30% of all species and 50% of all germinants were exotic forbs. Some of the more common species, such as *Digitalis purpurea*, *Erechtites minima*, and *Senecio sylvaticus*, establish dense but relatively short-lived populations following clear-cut logging (e.g., Halpern 1988, 1989; Schoonmaker and McKee 1988; DeFerrari and Naiman 1994; Stein 1995; Halpern et al. 1997). Others (e.g., *Agrostis alba*, *Arabidopsis thaliana*, *Hypericum perforatum*, *Lactuca muralis*, and *Rumex acetosella*) are ubiquitous weeds of agricultural fields, disturbed sites, and roadsides (Hitchcock and Cronquist 1973; Parendes 1997). As a group, exotics currently play a relatively minor or transient role in the early, post-harvest dynamics of these forests (DeFerrari and Naiman 1994; Halpern and Spies 1995; Stein 1995; Halpern et al. 1997). Nevertheless, there is growing concern about the introduction and spread of non-native species in the region and on the Olympic Peninsula in particular (DeFerrari and Naiman 1994; Buckingham et al. 1995). Widespread, silvicultural thinning of young, closed-canopy forests is likely to provide a second "temporal window" for the establishment of these species, stimulating germination from a seed bank produced earlier in succession. Of the full suite of exotics found in our study, only *Lactuca muralis* appears sufficiently tolerant of shade to invade or persist in mature forest stands (DeFerrari 1993; C. B. Halpern, personal observation); it was the only exotic present in the aboveground vegetation at our sites (Table 2).

Although forbs and (or) graminoids consistently dominated the seed bank in number, nearly all life forms were present at all sites. The relative diversity of species within each group was remarkably similar among blocks (Figs. 4C, 4D) despite distinct differences in floristic composition (see below). Tree species, however, were conspicuously absent. The lack of conifers (i.e., *Tsuga*, *Picea*, and *Pseudotsuga*) was not surprising, and is consistent with observations in other coniferous forests (e.g., Oosting and Humphreys 1940; Livingstone and Alessio 1968; Strickler and Edgerton 1976; Ingersoll and Wilson 1989; McGee and Feller 1993). Conifers typically exhibit high annual variation in seed production and only short-term viability (e.g., Archibold 1989). However, the paucity of *Alnus rubra* in our samples was unexpected: it is common in this heavily managed landscape and it has the potential to dominate the seed bank in older coastal forests of the region (e.g., Kellman 1970).

Litter and soil seed banks

Comparisons of the seed bank community in litter and soil samples offer insights into the local seed rain and the history

of vegetation change in these forests. The litter layer, which presumably supports the more recent and transient seed bank (Thompson and Grime 1979), was dominated by wind-dispersed, ruderal forbs, most of which were poorly represented in the soil layer. These included taxa with plumed achenes (e.g., *Senecio sylvaticus* and *Erechtites minima*) and comose seeds (e.g., *Epilobium watsonii*). Direct seed trap measurements have confirmed that these species are a common and often dominant component of the seed rain in this region (e.g., Kellman 1974; Harmon and Franklin 1995).

In contrast, soil samples yielded ruderal forbs and graminoids with comparatively limited dispersal ability (e.g., *Arabidopsis thaliana*, *Carex* spp., *Digitalis purpurea*, and *Luzula campestris*; but note the abundance of the wind-dispersed forb *Anaphalis margaritacea*). Soil samples also supported the limited pool of forest understory species (primarily fleshy-fruited forest shrubs such as *Gaultheria shallon*, *Rubus spectabilis*, and *Sambucus racemosa*). Seeds of both groups were likely to have been deposited at a time when these species were more abundant and (or) reproductive, i.e., following the harvests that initiated the current stands. Although seed longevity is unknown for the vast majority of these species, our results suggest that seeds of many ruderal and some forest species may remain viable for at least 40–60 years.

Compositional patterns among and within sites

Although one would predict greater similarity in seed-bank composition within than among spatially disjunct blocks of forest, our DCA results suggest that factors other than geographic location may exert important controls on the seed bank. Thus, whereas sample plots at Bait were floristically distinct and relatively homogenous (Fig. 5), those at Fresca and Clavicle showed considerable overlap in composition; in some instances, litter and soil samples were more similar between blocks than within them. It may be that local variation in environment, stand history, or spatial context (i.e., the composition of adjacent clearcuts or forests) are as important as larger scale gradients in species' distributions. Clearly, more extensive sampling is necessary to tease apart the influence of location, site history, and other factors.

Implications for forest management

Increasingly, attention is being devoted to the potential role of the soil seed bank in the re-creation or restoration of native plant communities (e.g., Van der Valk and Pederson 1989; Hutchings and Booth 1996; Davies and Waite 1998). Where native vegetation and disturbance regimes have been severely modified by human activity, however, possibilities for restoring native communities through the seed bank are greatly diminished. The desired species are either absent or rare, and the vast majority of viable seeds are of weedy taxa.

In the Pacific Northwest, restorative silvicultural approaches, including variable intensity thinning, have been proposed to enhance the structural complexity and diversity of species in young managed forests (e.g., DeBell et al. 1997; Tappeiner et al. 1997; Carey et al. 1999). It has been hypothesized that the soil seed bank may provide one source of propagules for recruitment of forest understory species. Our results suggest otherwise: silvicultural thinning will re-

sult in limited germination of forest species but will favor recruitment of early seral and often exotic species. Moreover, retrospective studies of understory response to thinning suggest that some of these species may be able to persist for decades following treatment (e.g., Bailey et al. 1998; Thomas et al. 1999). Our results also suggest that depending on the nature of the ground disturbance associated with thinning operations, different ruderal communities may develop: where litter remains intact, wind-dispersed annuals and perennials may dominate; where mineral soil is exposed, forbs and graminoids with limited potential for dispersal may dominate (see also McGee and Feller 1993; Rydgren and Hestmark 1996).

Given these results, it appears that post-thinning recruitment or expansion of forest understory herbs and shrubs will necessarily depend on one or more alternative mechanisms: clonal spread of surviving plants, sexual reproduction of surviving plants, or long-distance dispersal of seed. Results of a companion study in these same forests suggest, however, that only a limited number of species (*Maianthemum dilatatum* and *Oxalis oregana*, in particular) appear capable of rapid vegetative expansion once resource conditions improve and that the vast majority of species that survive canopy closure have limited potential for clonal spread (Lezberg et al. 1999). It is possible that sexual reproduction will contribute to local increases in population size, but to date, little research has been devoted to the reproductive ecology of understory herbs in these forests (but see Jules 1998). Dispersal from off site will be necessary for the large number of species that are currently absent from the forest understory. However, few woodland herbs are thought to possess mechanisms for long-distance transport (Bierzychudek 1982; Cain et al. 1998). Thus, successful reestablishment will likely reflect proximity to, and size of, source populations. Dispersal limitation may be particularly problematic in lowland forests of the Olympic Peninsula, where young, secondary forests dominate the landscape (Morrison 1990) and potential source populations may be distant or patchily distributed. Reintroduction of these species may be possible through artificial seeding or transplanting, but these approaches would not be practical on a larger scale. Moreover, if rotation lengths are too short, or silvicultural activities are too frequent, disturbance-sensitive species with limited dispersal may be eliminated locally from the understory (Busing et al. 1995; Halpern and Spies 1995). Given these constraints, it appears that in response to silvicultural thinning, the longer term dynamics of forest species will be determined, in large part, by initial survival and by local patterns of vegetative and sexual reproduction.

Acknowledgements

We thank Denise Liguori and Ann Lezberg for assistance with field sampling and greenhouse observations. We are extremely grateful to Doug Ewing, Department of Botany (University of Washington) for facilitating all aspects of our greenhouse work. Connie Harrington encouraged our participation in the Olympic Habitat Development Study and provided access to field sites and to background information on forest stand and site characteristics. Comments on earlier drafts of this manuscript were provided by Joseph Antos,

Ann Lezberg, Don McKenzie, Annette Olson, Mark Roberts, and two anonymous reviewers. Funding was provided by the USDA Forest Service, Pacific Northwest Research Station (PNW 94-0613).

References

- Alaback, P.A. 1982. Dynamics of understory biomass in Sitka spruce – western hemlock forests of southeast Alaska. *Ecology*, **63**: 1932–1948.
- Archibold, O.W. 1989. Seed banks and vegetation processes in coniferous forests. In *Ecology of soil seed banks*. Edited by M.A. Leck, V.T. Parker, and R.L. Simpson. Academic Press, Inc., San Diego, Calif. pp. 107–122.
- Bailey, J.D., Mayrsohn, C., Doucher, P.S., St. Pierre, E., and Tappeiner, J.C. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. *For. Ecol. Manage.* **112**: 289–302.
- Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytol.* **90**: 757–776.
- Bigwood, D.W., and Inouye, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology*, **69**: 497–507.
- Brown, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. *Can. J. Bot.* **70**: 1603–1612.
- Buckingham, N.M., Schreiner, E.G., Kaye, T.N., Burger, J.E., and Tisch, E.L. 1995. Flora of the Olympic Peninsula. Northwest Interpretive Association and the Washington Native Plant Society, Seattle, Wash.
- Busing, R.T., Halpern, C.B., and Spies, T.A. 1995. Ecology of Pacific Yew (*Taxus brevifolia*) in western Oregon and Washington. *Conserv. Biol.* **9**: 1199–1207.
- Cain, M.L., Damman, H., and Muir, A. 1998. Seed dispersal and the holocene migration of woodland herbs. *Ecol. Monogr.* **68**: 325–347.
- Carey, A.B., Thysell, D.R., and Brodie, A.W. 1999. The forest ecosystem study: background, rationale, implementation, baseline conditions, and silvicultural assessment. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-457.
- Clark, D.L. 1991. Factors determining species composition of post-disturbance vegetation following logging and burning of an old-growth Douglas-fir forest. M.Sc. thesis, Department of Botany, Oregon State University, Corvallis, Oreg.
- Davies, A., and Waite, S. 1998. The persistence of calcareous grassland species in the soil seed bank under developing and established scrub. *Plant Ecol.* **136**: 27–39.
- DeBell, D.S., Curtis, R.O., Harrington, C.A., and Tappeiner, J.C. 1997. Shaping stand development through silvicultural practices. In *Creating a forestry for the 21st century: the science of ecosystem management*. Edited by K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 141–149.
- DeFerrari, C.M. 1993. Exotic plant invasions across landscape patch types on the Olympic Peninsula. M.Sc. thesis, College of Forest Resources, University of Washington, Seattle, Wash.
- DeFerrari, C.M., and Naiman, R.J. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *J. Veg. Sci.* **5**: 247–258.
- Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- Gauch, H.G., Jr. 1980. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, U.K.
- Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology*, **69**: 1703–1715.
- Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology*, **70**: 704–720.
- Halpern, C.B., and Franklin, J.F. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. *J. Veg. Sci.* **1**: 475–482.
- Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.* **5**: 914–934.
- Halpern, C.B., Antos, J.A., Geyer, M.A., and Olson, A.M. 1997. Species replacement during early secondary succession: the abrupt decline of a winter annual. *Ecology*, **78**: 621–631.
- Harmon, J.M., and Franklin, J.F. 1995. Seed rain and seed bank of third- and fifth-order streams on the western slope of the Cascade Range. USDA For. Serv. Res. Pap. PNW-RP-480.
- Henderson, J.A., Peter, D.H., Leshner, R.D., and Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. USDA For. Serv. PNW Region, R6-ECOL-TP-001-88.
- Hill, M.O. 1979. DECORANA — a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, N.Y.
- Hitchcock, C.L., and Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Wash.
- Huffman, D.W., Tappeiner, J.C., II, and Zasada, J.C. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. *Can. J. Bot.* **72**: 39–51.
- Hutchings, M.J., and Booth, K.D. 1996. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *J. Appl. Ecol.* **33**: 1171–1181.
- Ingersoll, C.A., and Wilson, M.V. 1989. Buried propagules in an old-growth forest and their response to experimental disturbances. *Can. J. Bot.* **68**: 1156–1162.
- Jules, E.S. 1998. Habitat fragmentation and demographic change for a common plant: trillium in old-growth forest. *Ecology*, **79**: 1645–1656.
- Kellman, M. 1970. The viable seed content of some forest soil in coastal British Columbia. *Can. J. Bot.* **48**: 1383–1385.
- Kellman, M. 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. *J. Biogeogr.* **1**: 123–133.
- Leck, M.A., Parker, V.T., and Simpson, R.L. 1989. Ecology of soil seed banks. Academic Press, Inc., San Diego, Calif.
- Lezberg, A.L., Antos, J.A., and Halpern, C.B. 1999. Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. *Can. J. Bot.* **77**: 936–943.
- Livingstone, R.B., and Alessio, M.L. 1968. Buried viable seeds in successional field and forest stands, Harvard Forest, Massachusetts. *Bull. Torrey Bot. Club.* **95**: 58–69.
- Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, N.J.
- Major, J., and Pyott, W.T. 1966. Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio*, **13**: 253–282.
- McGee, A., and Feller, M.C. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. *Can. J. Bot.* **71**: 1574–1583.
- Morrison, P.H. 1990. Ancient forests on the Olympic National Forest: analysis from a historical and landscape perspective. The Wilderness Society, Washington, D.C.
- Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

- Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill Publishing Co., New York.
- Oosting, H.J., and Humphreys, M.E. 1940. Buried viable seeds in a successional series of old field and forest soils. *Bull. Torrey Bot. Club*, **67**: 253–273.
- Parendes, L.A. 1997. Spatial patterns of invasion by exotic plants in a forested landscape. Ph.D. thesis, Department of Geosciences, Oregon State University, Corvallis, Oreg.
- Rydgren, K., and Hestmark, G. 1996. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. *Can. J. Bot.* **75**: 121–128.
- Sabhasri, S. 1961. An ecological study of salal, *Gaultheria shallon* Pursh. Ph.D. thesis, College of Forest Resources, University of Washington, Seattle, Wash.
- Schoonmaker, P., and McKee, A. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* **34**: 960–979.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry*. W.H. Freeman, San Francisco, Calif.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Dan. Vidensk. Selsk. Biol. Skr.* (Copenhagen), **5**: 1–34.
- SPSS Inc. 1996. *Systat@ 6.0 for Windows®*. SPSS Inc., Chicago, Ill.
- Stein, W.I. 1995. Ten-year development of Douglas-fir and associated vegetation after different site preparation on Coast Range clearcuts. USDA For. Serv. Res. Pap. PNW-RP-473.
- Strickler, G.S., and Edgerton, P.J. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. *Ecology*, **57**: 801–807.
- Tappeiner, J.C., II, Zasada, J.C., Ryan, P., and Newton, M. 1991. Salmonberry clonal and population structure in Oregon forests: the basis for persistent cover. *Ecology*, **72**: 609–618.
- Tappeiner, J.C., Lavender, D., Walstaad, J., Curtis, R.O., and DeBell, D.S. 1997. Silvicultural systems and regeneration methods: current practices and new alternatives. *In* *Creating a forestry for the 21st century: the science of ecosystem management*. Edited by K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 151–164.
- Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., and Austin, K.A. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecol. Appl.* **9**: 864–879.
- Thompson, K., and Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* **67**: 893–921.
- Van der Valk, A.G., and Pederson, R.L. 1989. Seed banks and the management and restoration of natural vegetation. *In* *Ecology of soil seed banks*. Edited by M.A. Leck, V.T. Parker, and R.L. Simpson. Academic Press, Inc., San Diego, Calif. pp. 329–346.