

Soil seed banks and plant community assembly following disturbance by fire and logging in interior Douglas-fir forests of south-central British Columbia

Kaeli E. Stark, André Arsenault, and Gary E. Bradfield

Abstract: Relationships between soil seed banks and aboveground understory vegetation were examined in dry Douglas-fir (*Pseudotsuga menziesii* (Beissn.) Franco) forests near Kamloops, British Columbia, to compare the effects of different disturbance types (low and high severity fires and non-salvage logging), and to evaluate how seed banks contribute to post-disturbance vegetation establishment. Sites were selected to represent disturbances at 1, 5, and 10 years prior to sampling, and data were analyzed using nonparametric univariate and multivariate statistical techniques. Seed density and species composition of seed banks did not differ significantly among the 1 year disturbed sites; however, the rooted frequencies of seed-origin plants in the establishing vegetation decreased in the order: lightly burned > severely burned > logged. Seed dispersal within the first year following fire is believed to be an important recovery mechanism on burned sites. Low frequencies of seed-derived plants, particularly conifer seedlings, on logged sites pose concerns for the initial recovery of vegetation following logging; nonetheless, the lack of significant differences in understory species composition between sites burned 5 years prior to sampling and sites logged 10 years prior to sampling, and their corresponding undisturbed sites, suggests that vegetation recovery can occur relatively quickly. Rooted frequencies of plants establishing naturally in burned areas were similar to those in undisturbed areas, which suggests that post-fire erosion control seeding using agronomic species may not be necessary in these forests.

Key words: disturbance, fire, logging, multi-response permutation procedures, nonmetric multidimensional scaling, forest soil seed bank.

Résumé : Afin de comparer les effets de différents types de perturbation (coupe de récupération à la suite d'un feu de faible ou forte intensité et autres), et afin d'évaluer comment les banques de graines contribuent au retour de la végétation après les perturbations, les auteurs ont examiné les relations qui existent entre les banques de graines et la végétation de sous-bois, dans des forêts de sapin Douglas (*Pseudotsuga menziessi* (Beissn.) Franco), près de Kamloops, C.-B. Ils ont sélectionné des sites afin de représenter des perturbations survenues 1, 5 et 10 ans avant l'échantillonnage, et ils ont analysé les données à l'aide des techniques statistiques univariées et multivariées non paramétriques. La densité des graines et la composition en espèces des banques de graines ne diffèrent pas significativement, sur les sites perturbés depuis 1 an; cependant, les fréquences d'enracinement, chez les plants venant de semences dans la végétation en cours d'établissement, diminuent selon l'ordre : faiblement brûlé > sévèrement brûlé > récolté. On croit que la dispersion des graines au cours de l'année suivant le feu serait un important mécanisme de reprise sur les sites brûlés. Les faibles fréquences de plants dérivés de semences, en particulier de conifères, sur les sites récoltés, soulève des préoccupations quant au retour de la végétation après la coupe; cependant, l'absence de différences significatives dans la composition en espèces de sous-bois, entre les sites brûlés depuis 5 ans et coupés depuis 10 ans, et les sites correspondants non perturbés, suggère que le retour de la végétation s'effectue relativement vite. Les similitudes des fréquences d'enracinement des plants s'installant naturellement sur les sites brûlés avec ceux des endroits non perturbés, suggèrent que l'ensemencement d'espèces agronomiques, pour contrôler l'érosion, ne serait pas nécessaire dans ces forêts.

Mots clés : perturbation, feu, récolte, procédures de permutation multi-réponses, échelle multidimensionnelle non métrique, banque de semences de sols forestiers.

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Introduction

Plant species often exhibit particular life history strategies that have enabled them to persist under the natural disturbance regimes of their native habitats. For example, in fire-prone forest ecosystems, successful strategies include the production of thick, insulative bark or belowground regenerative structures, germination from seeds stored in a buried seed bank or in serotinous cones, and recolonization via

seed dispersal from adjacent, unburned forest stands (Rowe 1983; Agee 1993). Ecosystem management approaches to logging that attempt to emulate natural disturbance regimes have been adopted by forest managers in hopes that exploiting successful regeneration strategies will minimize the negative effects of logging on biodiversity and ecosystem integrity (Duchesne 1994). Although this “have your cake and eat it too” argument is enticing, the underlying assumption that forest harvesting can actually mimic natural disturbance regimes has been called into question (Whittle et al. 1997).

Studies have shown that the contribution of the seed bank to post-disturbance plant communities is species-specific, system-dependent, highly variable and, thus, often unpredictable (Beatty 1991; Yearsley 1993; Hyatt 1999; Lee 2004). Variability in the relative success of different modes of persistence or regeneration following different types and severities of disturbance further complicates our understanding of post-disturbance plant community assembly. The importance of the assemblage of species present immediately following disturbance in determining the subsequent course of succession was recognized by Egler (1954); however, the roles of various persistence mechanisms, which can influence the early stages of regeneration, remain poorly understood for most forest ecosystems (Whittle et al. 1997).

In this study, we use a retrospective approach to quantitatively compare the relative effects of fire and logging on the structure and composition of seed bank and understory species assemblages in dry Douglas-fir forests of south-central British Columbia. Both types of disturbance occur widely throughout the region, and there is considerable silvicultural interest in determining how closely vegetation responses to logging resemble those to fire. At present there is insufficient information to distinguish between “transient” and “persistent” seed-banking strategies (sensu Thompson and Grime 1979) for most species of the study area forests; hence, in this paper, the term “seed bank” refers to the collection of species that germinated from soil samples in greenhouse germination trials, regardless of individual seed longevity and potential to persist in the soil.

The objectives of our study were to (i) conduct a detailed comparison of the responses of soil seed banks and establishing understory vegetation to disturbance by low severity fire, high severity fire, and logging (non-salvage) within the first post-disturbance growing season, (ii) assess the importance of seed (including both that stored in the seed bank throughout disturbance, and that which disperses to a site soon after disturbance) for initial post-disturbance vegetation recovery, and (iii) determine the relationship between seed bank and aboveground understory vegetation 5 and 10 years after fire and logging.

Materials and methods

Study area

This study was carried out in the Interior Douglas-fir (IDF) biogeoclimatic zone of south-central British Columbia near Kamloops (50°45'N, 120°20'W) (Fig. 1). Mean annual precipitation ranges from 300 to 850 mm, and the climate is characterized by warm, dry summers and cool winters with low to moderate snowfall (Lloyd et al. 1990). Soils are gen-

erally Orthic or Dark Gray Luvisols, and Eutric or Dystric Brunisols with a medium to rich nutrient regime. Humus forms are usually 2–5 cm thick Hemimors and Mormoders (Lloyd et al. 1990).

Study sites were located in two subzones of the IDF: the IDF_{xh} subzone (located at elevations between 400 and 1250 m) and the IDF_{dk} subzone (located between 600 and 1460 m in elevation) (Lloyd et al. 1990). The dominant canopy species in both subzones is Douglas-fir (*Pseudotsuga menziesii* (Beissn.) Franco), with ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) as a common associate on the drier IDF_{xh} sites and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) on the moister IDF_{dk} sites. Characteristic understory species in both subzones include prostrate shrubs such as *Arctostaphylos uva-ursi*, *Linnaea borealis*, and *Paxistima myrsinites*, and perennial herbs such as *Arnica cordifolia* and *Calamagrostis rubescens* (Lloyd et al. 1990).

Interior Douglas-fir forests are subject to a variety of disturbances including fire, wind-throw, insect outbreaks, livestock grazing, and logging (Huggard et al. 2005). The fire regime in the IDF forest zone is classified as mixed-severity, meaning that low, moderate, and high severity fires, often occurring in close spatial proximity, are common. The result is a structurally complex forest made up of patches of varying size, shape, and age (Arsenault and Klenner 2004).

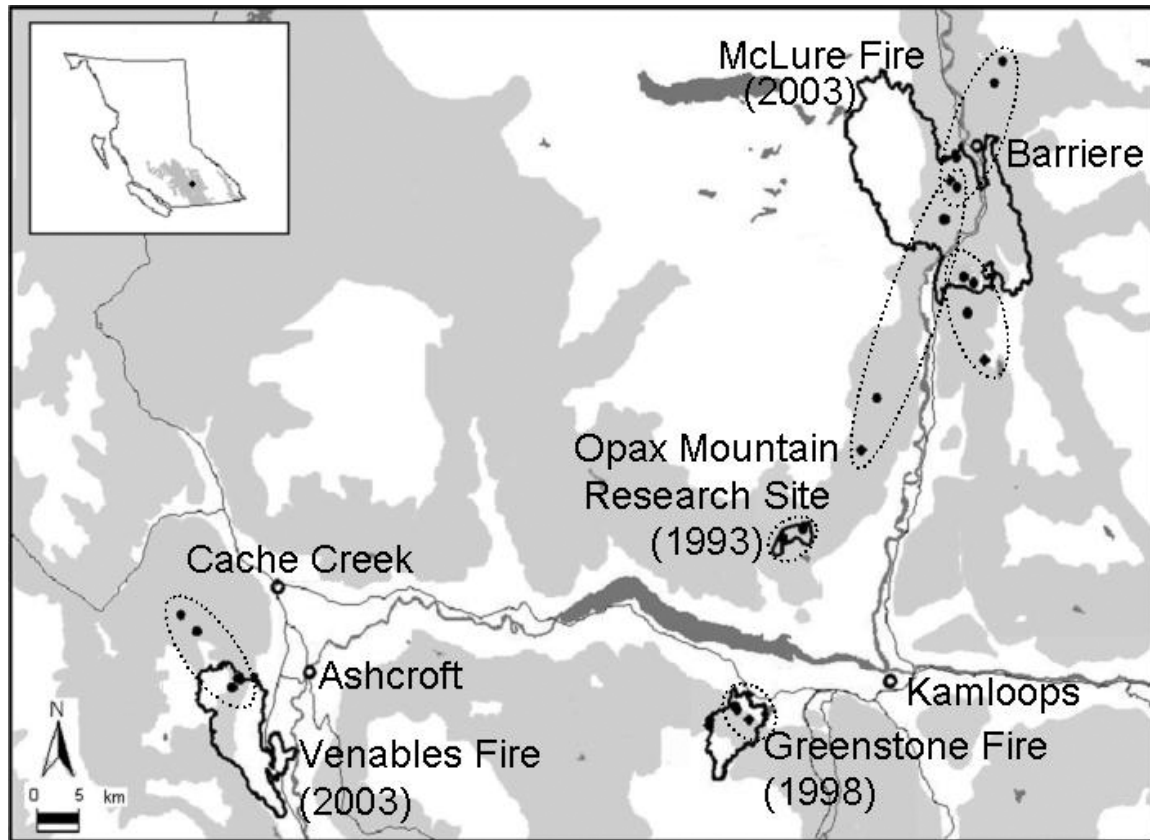
During July and August of 2003, wildfires burned more than 80 000 ha of forest throughout the interior of British Columbia. Within the study area, the mosaic nature of the post-fire landscape (i.e., stands of unburned, burned at varying severities, and recently unburned logged forests) presented an opportunity for a comparative evaluation of the patterns and mechanisms of vegetation response to different types and severities of disturbance.

Field sampling

Within the study area, 34 sites were selected to represent various combinations of type (fire, logging, undisturbed) and timing (within 1, 5, or 10 years) of disturbance. Apart from these selection criteria, sites were chosen in an unbiased fashion. Owing to the recent history of fire and logging throughout the study area, it was not possible to achieve a fully balanced sampling design with all disturbance types and time classes represented. Specifically, the 5 year sites (3 burned sites [B-5] and 3 adjacent unburned sites [UN-5]) related to a fire event in 1998, and the 10 year sites (6 clear-cut logged sites [CC-10] and 6 adjacent unlogged sites [UN-10]) related to logging activity in 1993. The 1 year sites were grouped into four clusters, with two fire severity classes (low severity burn [LB-1] and high severity burn [SB-1] relating to the 2003 wildfires), one clear-cut logging patch (CC-1), and one undisturbed site (UN-1) represented within each cluster for a total of 16 1 year sites (12 disturbed and 4 undisturbed) (Fig. 1).

Fire severity on the 1 year burned sites was determined using a post hoc classification scheme based on the extent of forest floor charring and resultant exposure of mineral soil (Ryan and Noste 1985). All burned sites were required to be relatively uniform in terms of disturbance to the soil over an area of at least 50 m × 50 m. On lightly burned sites (LB-1), the surface of the forest floor was scorched, and the

Fig. 1. Map of study area showing locations of clusters of sampling sites (ellipses) and disturbed areas (black outlines) within the IDF vegetation zone (grey). The extent of the IDF vegetation zone in British Columbia and the location of Kamloops are shown in the inset.



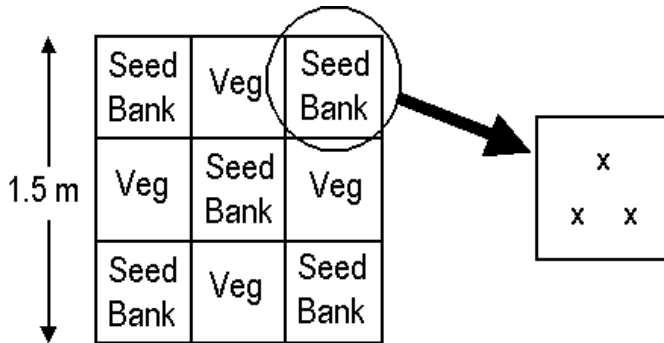
majority of trees were alive with varying degrees of scorching on the bole. On severely burned sites (SB-1), the forest floor was completely consumed with mineral soil exposed and only the charred boles of fire-killed trees remaining standing. The 1 year logged areas (CC-1) had not been recently burned and were harvested in the winter of 2003–2004, creating canopy openings of at least 1.5 ha. Immediately following logging, sites were mechanically prepared for planting by exposing mineral soil either in pits (ca. 0.5 m × 0.5 m × 0.5 m, and 5 m apart) or in trenches (ca. 0.5 m deep, and 4–5 m apart). Time since the last stand-replacing disturbance (estimated using cores taken from the largest standing trees) exceeded 100 years for all sites. Non-stand-replacing disturbances such as occasional wind-throw and livestock grazing also have affected stands throughout their development.

Sampling of soil seed banks on the 5 year burned and 10 year logged sites, as well as in adjacent undisturbed forest stands, was conducted during October 2003. At each site, three to nine soil samples, each ca. 10 cm × 10 cm × 10 cm, were collected from three sampling locations ca. 30 m apart. Sampling to greater depths was considered unnecessary, as the soil seed bank is believed to be concentrated near the soil surface (McGee and Feller 1993; Warr et al. 1993). Soil samples were stored between 0 and –2 °C (approximate soil temperature beneath a snow pack in the IDF; McLean 1967) from the time of collection until early January 2004 to simulate a winter stratification period known to break dormancy in many species (Baskin and Baskin 1998).

Sampling of soil seed banks on the 1 year sites in early May 2004 avoided the need for a simulated winter stratification period and allowed the possible inclusion of both late-summer and early-spring dispersing species in addition to those species with seeds already present in the soil when the disturbances occurred (i.e., both transient and persistent seed banks were sampled, *sensu* Thompson and Grime 1979). Sampling intensity was increased on the 1 year sites to permit a more detailed investigation of within-site variability (K.E. Stark, A. Arsenault, and G.E. Bradfield, manuscript in preparation). In this case, multiple soil samples were collected using an Oakfield soil corer from four 1.5 m × 1.5 m sampling grids located 10 m in each cardinal direction from a central point at each site. Three composite soil samples, each consisting of eight 2 cm (diameter) × 12 cm (depth) soil cores, were collected within each of the five “seed bank” quadrats of each sampling grid (Fig. 2). Any seeds that had already germinated at the sampling locations were recorded prior to soil removal, as they constituted part of the current year’s seed bank.

Vegetation sampling at all sites was conducted during late June and early July of 2004. At the 5 and 10 year sites, three 50 cm × 50 cm quadrats, each subdivided into 25 10 cm × 10 cm subplots, were used to record rooted frequencies of all understory vascular plant species adjacent to the respective seed bank sampling locations from the previous autumn. The intention of this sampling was not to characterize the entire aboveground plant community, but rather to assess the relationship between the seed bank and

Fig. 2. Sampling grid design used for collecting soil seed bank samples and vegetation data at the 1 year disturbed and undisturbed study sites (4 sampling grids per site). The sampling grid consisted of nine contiguous 50 cm × 50 cm quadrats, with the four vegetation quadrats further divided into 25 10 cm × 10 cm subplots for recording rooted frequencies of plant species. Three composite soil samples (indicated by “x”), each consisting of eight individual samples collected with an Oakfield soil corer, were taken from the five “seed bank” quadrats of each grid.



the vegetation in the immediate vicinity. Plants with prostrate growth forms (e.g., *Arctostaphylos uva-ursi*, *Linnaea borealis*, and *Paxistima myrsinites*) were recorded only in the subplots in which they were rooted. At the 1 year sites, rooted frequency data were recorded within the four 50 cm × 50 cm vegetation quadrats of each sampling grid (Fig. 2). Root versus seed origin of the plants establishing on the 1 year sites was determined by examination of representatives of each species; plants of seed origin were identified by the presence of cotyledons or a delicate, relatively undeveloped root system. In total, 1070 soil seed bank samples (960 samples from 1 year sites, 54 samples from 5 year sites, and 56 samples from 10 year sites) and 309 vegetation quadrats (256 quadrats from 1 year sites, 18 quadrats from 5 year sites, and 35 quadrats from 10 year sites) were collected to evaluate seed bank and vegetation responses to disturbance.

Greenhouse procedure

To allow for comparisons among samples of different size, soil volumes were measured prior to set-up in the greenhouse. The species composition and density of seeds germinating from the seed bank were determined using the seedling emergence method with the improvements suggested by Ter Heerdt et al. (1996). Specifically, each soil sample was wet-sieved to remove plant and rock material larger than the largest expected seed (4.0 mm sieve), and fine particulate matter smaller than the smallest expected seed (0.15 mm sieve). The soil samples were then spread in 0.5 cm thick layers over sterilized potting soil in 10 cm × 10 cm pots. Samples were exposed to a 16 h day-length regime (supplemented by artificial lighting when natural day lengths were less than 16 h), and seedlings were identified, enumerated, and removed as they emerged, or else transplanted and grown until identification was possible. Upon cessation of germination, soil samples were placed in cold storage at 0 °C to –2 °C (McLean 1967) for 8 weeks and

then returned to the greenhouse to stimulate further germination. In total, samples were monitored in the greenhouse for a cumulative time period of 18 weeks, after which the numbers of ungerminated seeds were expected to be low. The germination studies were carried out at greenhouse facilities at Thompson Rivers University (Kamloops) and at the University of British Columbia (Vancouver).

Data analysis

Because of strong departures from normality in the seed bank and vegetation frequency data (e.g., positive skewness and unequal variances among disturbance classes), nonparametric methods of analysis were employed. Univariate tests for differences among the 1 year disturbance types in seed density and species richness of the seed bank, and for differences in establishing vegetation frequency (total rooted frequency for all plants, as well as separate total frequencies for seed-origin and root-origin plants) were run using Kruskal–Wallis and Mann–Whitney *U* tests (Zar 1999). All univariate comparisons were run using SYSTAT version 10 with sites as replicates.

Multivariate relationships among the seed bank and vegetation species assemblages on the 1, 5, and 10 year sites were examined using nonmetric multidimensional scaling (NMS) and multiresponse permutation procedures (MRPP). Several runs of NMS using the Sørensen distance metric and random starting configurations were performed, followed by Monte Carlo tests to determine the statistical validity of the final configurations (i.e., whether the axes extracted by NMS were stronger than those expected by chance). MRPP was used to test for seed bank – vegetation differences within disturbance classes. MRPP was also used to test for pair-wise differences in overall species composition of the seed bank and vegetation species assemblages between disturbance classes. When significant differences ($p < 0.05$) were found, indicator species analysis (ISA; Dufrière and Legendre 1997) was used to identify species that were both faithful (i.e., always present in a group) and exclusive (i.e., never present in other groups) to particular groups (McCune et al. 2002). All multivariate analyses were performed using PC-ORD version 4.0 (McCune and Mefford 1999).

Results

General characteristics of seed bank and aboveground vegetation

Seventy-four vascular plant taxa (represented by 2489 seedlings) emerged from seed bank samples in greenhouse germination trials over all disturbance classes (Appendix A). Thirty (40%) of these taxa did not occur in the vegetation. The five most frequent taxa in the seed bank, and the percentage of quadrats in which they occurred, were *Epilobium ciliatum* (38%), *Epilobium angustifolium* (28%), *Cirsium vulgare* (16%), *Poa* sp. (16%), and *Carex* sp. (9%). Eighty-seven taxa were recorded in the vegetation adjacent to the seed bank sampling locations (Appendix A). Of the 117 taxa encountered in this study (seed bank and vegetation combined), 17 (15%) were not native to North America. Eleven of these exotic species were restricted to the seed

bank, while the remainder occurred in both the seed bank and the vegetation (Appendix A).

Univariate comparisons of seed bank and vegetation on 1 year sites

Seed banks on the 1 year disturbed sites contained both fewer seeds and fewer species than those on neighbouring undisturbed sites (Fig. 3). A median density of 470 seeds/m² was recorded on undisturbed sites, whereas median densities on disturbed sites were 80 seeds/m² (logged), 174 seeds/m² (lightly burned), and 83 seeds/m² (severely burned). None of the differences in seed density between pairs of disturbed sites was significant ($p > 0.05$). Similarly, the median species richness (i.e., the number of species counted in the 60 seed bank samples on each site) was significantly greater on undisturbed sites (17 species) compared with disturbed sites (5 species for logged, 8 species for lightly burned, 4.5 species for severely burned). Unlike seed density, median species richness differed significantly between lightly burned and severely burned sites ($p < 0.05$). *Epilobium angustifolium* and *Populus tremuloides*, two species with reportedly short seed longevities and dispersal times between late summer and early spring (Granström 1987; US Forest Service 2005), and therefore assumed to be recent arrivals, were 4–10 times more frequent in seed banks on burned than logged sites (Appendix A).

Total vegetation frequency, defined as the percentage of 10 cm × 10 cm subplots occupied by seed- and root-origin plants (combined), was highest on lightly burned and undisturbed sites (Fig. 4). High frequencies of seed-origin plants were responsible for the high total vegetation frequency on lightly burned sites, although considerable among-site variability (indicated by longer boxes in Fig. 4) was evident. Plants of seed origin, including three species assumed to have colonized burned areas after disturbance (*Pinus contorta*, *Populus tremuloides*, and *Pseudotsuga menziesii*; US Forest Service 2005), occurred with higher frequencies on burned sites than logged sites (Fig. 4); in contrast, frequencies of root origin plants did not differ among disturbance types (Fig. 4). Total vegetation frequencies were low (median <25%) on both the logged and severely burned sites 1 year after disturbance.

Multivariate comparisons of seed bank and aboveground vegetation

A graphical summary of intersite relationships derived from NMS ordination of the seed bank and vegetation species composition data is shown in Fig. 5. The first NMS axis (24% of variation explained) separated sites into their seed bank and vegetation components. Substantial variation was evident among replicate sites of most disturbance classes along the first axis. The third NMS axis (29% of variation explained) separated the 1, 5, and 10 year post-disturbance treatments; however, separation of corresponding undisturbed sites along this axis suggests a possible relationship with larger scale site characteristics (e.g., climate and (or) soil) that was unrelated to recent disturbance history. For the 1 year group, the lightly burned sites appeared relatively similar in both seed bank and vegetation species composition compared with the severely

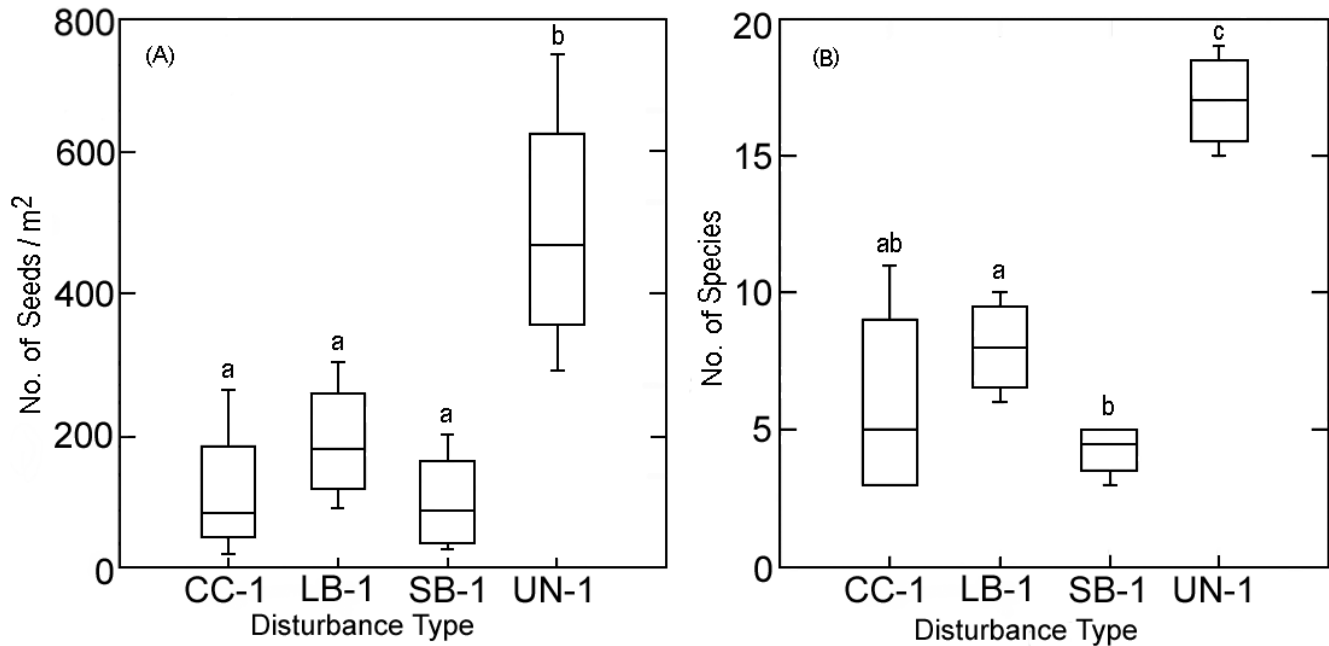
burned and logged sites, which showed greater between-site variation. Whereas the 1 year lightly burned seed bank appeared relatively similar to the undisturbed seed bank, the opposite trend was observed in the vegetation where the lightly burned sites were positioned farther than the severely burned and logged sites from the undisturbed vegetation. For both the 5 and 10 year groups, no clear differences were evident between disturbed and undisturbed sites.

The seed bank – vegetation relationships illustrated in the NMS ordination were generally supported by the MRPP comparisons (Table 1). Seed bank species assemblages were significantly different from the vegetation ($p < 0.05$) for all except the 1 year severely burned and the 5 year undisturbed groups; however, the nonsignificant result was marginal for the 5 year undisturbed sites ($p = 0.056$), and it appeared to be related to a single site showing strong seed bank – vegetation similarity in the 1 year severely burned group (Fig. 5). Indicator species associated with the differences in species composition between seed bank and vegetation on undisturbed sites included *Epilobium angustifolium*, *Epilobium ciliatum*, and *Carex* sp. for the seed bank, and *Arnica cordifolia*, *Goodyera oblongifolia*, and *Rosa* spp. for the vegetation (ISA: $p < 0.05$ for all species listed).

In contrast to the seed bank – vegetation comparisons within disturbance classes, fewer significant comparisons among disturbance classes were noted using either the seed bank or vegetation data (Table 1). For the 1 year group, the seed banks on severely burned and logged sites differed from those on undisturbed sites ($p < 0.05$), but differences among disturbed sites were nonsignificant (although the nonsignificance was marginal ($p = 0.057$) for the 1 year logged – lightly burned comparison; Table 1). Notably absent from the seed banks of the 1 year disturbed sites were *Galium triflorum*, *Rubus parviflorus*, and *Viola* sp., each of which occurred in >10% of undisturbed seed bank samples (Appendix A).

As with the seed bank comparisons, significant differences in species composition of the vegetation were detected only among some of the 1 year treatments (Table 1). The significant differences between the 1 year burned (both low and high severities) and undisturbed sites were associated with higher frequencies of *Epilobium angustifolium* and *Pseudotsuga menziesii* seedlings on burned sites, and higher frequencies of *Calamagrostis rubescens* on undisturbed sites (ISA: for all species listed $p < 0.05$). The difference between the 1 year logged and lightly burned sites, noted as marginally nonsignificant for the seed bank comparisons, was strongly significant ($p = 0.013$) for the vegetation comparisons. Despite the lack of significant difference in understory species composition for the 1 year logged – undisturbed comparison ($p = 0.089$), total species frequency was significantly lower on the logged sites (Fig. 4). Similarly, despite the lack of significant differences in understory species composition (and seed bank composition) for the 5 and 10 year disturbed – undisturbed comparisons (Table 1), some species (e.g., *Epilobium angustifolium*, *Fragaria virginiana*, and *Spiraea betulifolia*) were notably more frequent on disturbed than undisturbed sites (Appendix A).

Fig. 3. Box plots showing seed density (A) and seed bank species richness (B) on the 1 year disturbed and undisturbed sites (disturbance classes are defined in Table 1). Different letters above the bars denote significant differences based on Mann–Whitney comparisons among disturbance classes ($p < 0.05$).



Discussion

Seed bank and vegetation responses 1 year after disturbance

The complex responses of soil seed banks and understory vegetation within the first year following logging non-salvage and fire resist easy generalization. Although seed banks on logged and burned sites did not differ in total seed density or species richness, significantly lower frequencies of seed origin plants were observed on logged sites. For example, the three main colonizing tree species, *Pinus contorta*, *Populus tremuloides*, and *Pseudotsuga menziesii*, all occurred with lower frequencies on logged sites than on burned sites. It is possible that these species did not disperse within logged areas as readily as they did within burned areas (e.g., Turner et al. 1994; Timoney and Peterson 1996; Hughes and Bechtel 1997) or that they were present in logged areas but substrate conditions were not conducive to germination and survival (Zasada et al. 1983). In addition, seeds may have been buried too deeply by post-logging site preparation treatments to break dormancy and germinate in the field, whereas they were detected in the greenhouse germination trials (Baskin and Baskin 1998).

The general lack of difference between lightly burned and severely burned sites in several features (e.g., seed density, frequency of root-derived plants, and overall species composition of seed bank and vegetation) is likely associated with the shallow forest floor depths of Interior Douglas-fir forests. Unlike boreal forests where forest floors can exceed 20–25 cm in depth (e.g., Dyrness and Norum 1983), the ca. 3 cm thick forest floors on the undisturbed IDF sites sampled here did not have much potential for differential responses to fire. Despite the general lack of difference between lightly burned and severely burned sites, more species were present in seed banks of the lightly burned sites.

It is possible that soil samples collected from less-disturbed areas on the unevenly scorched forest floors of lightly burned sites contained seeds of some species that were absent from the seed banks of severely burned sites, but that these species were not present in high enough numbers to influence the comparisons of overall seed bank species composition or seed density.

Many of the species that were abundant in the seed banks of severely burned sites had dispersal and germination capabilities that allowed them to recruit successfully in the vegetation following fire (e.g., small, easily-dispersed seeds and a preference for mineral soil as a germination substrate; Zasada et al. 1983). Because of the dominance of these species in both the seed bank and establishing plant communities, there were no differences between seed bank and vegetation species composition on severely burned sites. In contrast, on lightly burned sites, the vigorous sprouting of root-derived species such as *Arnica cordifolia*, *Calamagrostis rubescens*, and *Spiraea betulifolia* (in addition to the post-fire success of seed-derived species) contributed to the observed significant differences between seed bank and vegetation. The weak correspondence between seed bank and vegetation observed on the 1 year logged sites was associated with low numbers of seed bank germinants in the field.

Longer term seed bank and vegetation responses

In addition to the overall differences in species composition between adjacent seed bank and understory vegetation within sites, the proportion of seed bank species present in the vegetation as seedlings or mature plants declined with time since disturbance (64% on 1 year disturbed sites (all disturbance types combined), 44% on 5 year burned sites, 42% on 10 year logged sites, and 32% on undisturbed sites). The greater representation of seed bank species in the vege-

Fig. 4. Box plots showing variation in modes of regeneration in the field (i.e., seed vs. root origin) for the 1 year disturbed and undisturbed sites (disturbance classes are defined in Table 1). Box lengths denote variation among replicate sites in percentage of total subplots occupied by plants of either seed or root origin (400 subplots sampled per site). Also shown are total vegetation frequencies (seed and root origin combined). Letters beside bars denote results from Mann–Whitney comparisons among disturbance types within the three separate regeneration categories (different letters denote $p < 0.05$).

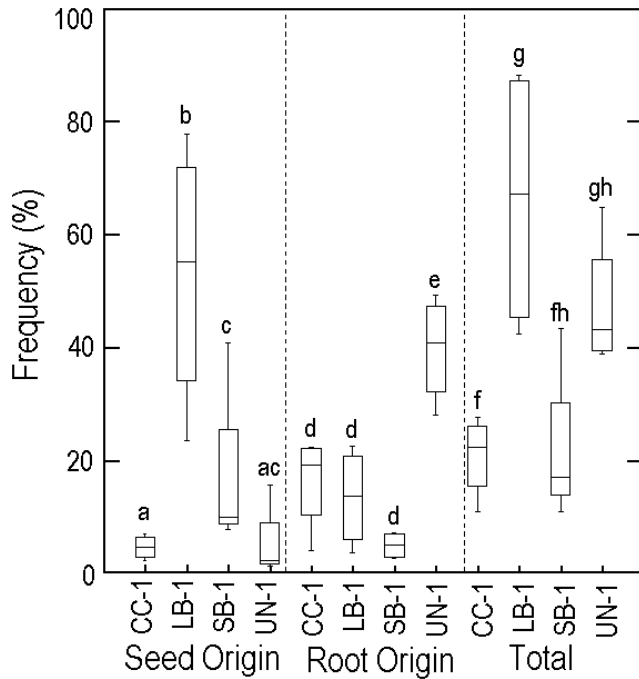


Fig. 5. NMS ordination of vegetation (veg) and seed bank (sb) species assemblages on the 1, 5, and 10 year disturbed (CC-1, LB-1, SB-1, B-5, CC-10) and corresponding undisturbed (UN-1, UN-5, UN-10) sites. Disturbance classes are defined in Table 1.

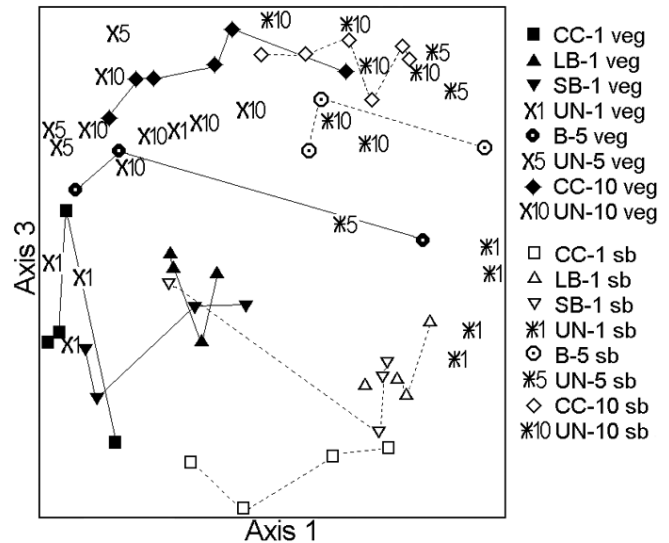


Table 1. Summary of MRPP results (p values) for pair-wise comparisons within and between disturbance classes using species frequency data from seed bank and vegetation quadrats.

Disturbance class ^a	Seed bank – vegetation	Seed bank			Vegetation		
		UN	LB-1	SB-1	UN	LB-1	SB-1
UN-1	0.007	—	—	—	—	—	—
LB-1	0.011	0.070	—	—	0.014	—	—
SB-1	0.104	0.010	0.459	—	0.011	0.159	—
CC-1	0.011	0.042	0.057	0.861	0.089	0.013	0.078
UN-5	0.056	—	—	—	—	—	—
B-5	0.023	0.197	—	—	0.590	—	—
UN-10	0.000	—	—	—	—	—	—
CC-10	0.001	0.108	—	—	0.136	—	—

Note: Seed bank – vegetation comparisons were made within the disturbance classes listed at left. Comparisons in the seed bank and vegetation groups (middle and right portions of the table) are between disturbance classes listed in corresponding rows and columns. Significant p values ($p < 0.05$) are shown in bold.

^aCC, clear-cut logging; LB, low severity fire; SB, high severity fire; B, fire of unknown severity; UN, undisturbed; numbers indicate 1, 5, or 10 years after disturbance.

tation of 1 year sites could be the result of disturbance-related changes to light and temperature regimes at the soil surface for species persisting in situ throughout disturbance (Kramer and Johnson 1987), or the availability of suitable microsites for the germination and recruitment of species arriving within the first year after disturbance (Zasada et al. 1983).

In contrast to the seed bank – vegetation differences

within-sites, the lack of differences in either seed bank or understory species assemblages on the 5 year burned and 10 year logged sites with those on corresponding undisturbed sites, suggests that ongoing seed dispersal processes may have eliminated any initial post-disturbance differences (i.e., those observed among some of the 1 year disturbed sites). These results suggest that a convergence in the vegetation of disturbed and undisturbed sites may occur rela-

tively quickly; however, greater sampling intensity on the 5 and 10 year sites is needed to fully support this interpretation.

Egler (1954) proposed that the majority of species that would eventually develop on a site were present immediately following disturbance, and that changes in the post-disturbance community were simply the result of shifts in dominance of different species groups over time. Even though there were no significant differences in understory species composition between the 5 year burned and 10 year logged sites and corresponding undisturbed sites, some disturbance-tolerant, early-successional species occurred with higher frequency on the disturbed sites (e.g., *Epilobium angustifolium*, *Taraxacum officinale*, and *Verbascum thapsus*). A number of shade-tolerant, later-successional species occurred on the 10 year logged sites, but with higher frequency on the corresponding undisturbed sites (e.g., *Goodyera oblongifolia*, *Thalictrum occidentale*, and *Viola canadensis*). Barring further disturbance, it is expected that the disturbance-tolerant species will decline in frequency and the shade-tolerant species will increase in frequency as canopy closure progresses.

Management implications

The possibility that disturbance by fire or logging improves conditions for the germination and spread of exotic species is an important forest management consideration. Seed banks can function as reservoirs that hold species on a site between disturbances, and concern arises when growing conditions suitable for undesirable, weedy species contained in the seed bank are promoted by disturbance (Warr et al. 1993; Qi and Scarratt 1998). In this study, 17 exotic species were found in soil seed banks, but only 6 of these were recorded during vegetation sampling. Three of these species (*Cirsium vulgare*, *Lactuca serriola*, and *Taraxacum officinale*) were found in both disturbed and undisturbed vegetation, indicating that some weedy exotics, particularly those with small, wind-dispersed seeds, are able to both disperse and recruit into mature, intact forest vegetation.

Broadcast seeding of nonnative grass species is often carried out in burned areas for erosion control in British Columbia and in the western United States, but the effectiveness of this practice for controlling post-fire erosion has been questioned (e.g., Robichaud et al. 2000). The extent to which natural vegetation recovery took place on lightly burned and severely burned sites (i.e., total rooted frequency on 1 year burned sites did not differ from that on undisturbed sites) suggests that broadcast seeding might not be necessary following fire in this system (Curran et al. 2006). At the very least, these results, combined with those from other studies raising concerns about the potentially negative environmental consequences of post-wildfire grass-seeding (Beschta et al. 2004; Beyers 2004), suggest that this practice should be implemented only after careful consideration.

Following fire, natural regeneration of conifer species was scattered but significantly more frequent than following logging. The infrequency of conifer seeds on logged sites one year after disturbance suggests that conifer regeneration will be dependent on the success of planted seedlings (Simard et al. 1998). Continued monitoring of vegetation, including

sites affected by post-wildfire management interventions (i.e., salvage harvesting and grass-seeding), is needed to better understand the longer-term dynamics of disturbance responses in Interior Douglas-fir forests.

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Appendix A

Appendix A appears on the following pages.

Table A1. List of taxa recorded during seed bank and vegetation sampling of the 1, 5, and 10 year disturbed (LB-1, SB-1, CC-1, B-5, CC-10) and corresponding undisturbed (UN-1, UN-5, UN-10) sites; disturbance classes are defined in Table 1. Values shown are percentages of 50 cm × 50 cm quadrats in which taxa occurred within each treatment (total number of quadrats are given in parentheses).

Species	Seed bank								Vegetation							
	UN-1 (80)	LB-1 (80)	SB-1 (80)	CC-1 (80)	UN-5 (27)	B-5 (27)	UN-10 (28)	CC-10 (28)	UN-1 (64)	LB-1 (64)	SB-1 (64)	CC-1 (64)	UN-5 (9)	B-5 (9)	UN-10 (17)	CC-10 (18)
<i>Achillea millefolium</i>							14	8	3	9					12	39
<i>Agropyron</i> sp.										3						
<i>Agropyron spicatum</i>									3	8				11	6	
<i>Allium cernuum</i>							3		16	28	3		22		18	17
<i>Alnus incana</i>					44		6									
<i>Alnus viridis</i>								22								
<i>Amelanchier alnifolia</i>									5			3				
<i>Anethum graveolens*</i>				2												
<i>Antennaria</i> sp.	10	3	2	2		7	25	25		13		2	11	33	41	28
<i>Aquilegia formosa</i>	2											2				
<i>Arabis holboellii</i>	12	7			7		3	11	8	11					12	22
<i>Aralia nudicaulis</i>									5			13				
<i>Arctostaphylos uva-ursi</i>									13	2	5	3			18	33
<i>Arnica cordifolia</i>							12		33	27	25	20	11	11	76	50
<i>Aster conspicuus</i>									6	2		2				
<i>Aster foliaceus</i>									2							
<i>Aster</i> sp.		3	2				6		2	2		2		44	24	28
<i>Astragalus miser</i>									13	2	3				29	17
<i>Balsamorhiza sagittata</i>											3					
<i>Betula papyrifera</i>	48	3		3						3	5					
Brassicaceae					4	11										
<i>Bromus</i> sp.												2				
<i>Calamagrostis rubescens</i>					4	4	10	34	73	48	42	53	67	56	76	94
<i>Campanula rotundifolia</i>					4			6								6
<i>Carex</i> sp.	15	2	7	5	41		48	14	20	17	27	9	11	33	24	50
Caryophyllaceae														22		
<i>Castilleja</i> sp.																17
<i>Cerastium fontanum*</i>	5			2	7	4	18	28		2						
<i>Chenopodium album*</i>								6								
<i>Chimaphila umbellata</i>									25			11				
<i>Cirsium vulgare*</i>		8		8	56	44	6	6		4	2	2			6	
<i>Clematis occidentalis</i>									2							
<i>Clintonia uniflora</i>									8			6				
<i>Collinsia parviflora</i>	8	5			11		15	6	8	22	9		11		12	
<i>Collomia linearis</i>					7		6	7							12	17
<i>Conyza canadensis*</i>	2															
<i>Cornus canadensis</i>									16			17			6	
<i>Cornus stolonifera</i>									3	11		3				

Table A1 (continued).

Species	Seed bank								Vegetation							
	UN-1 (80)	LB-1 (80)	SB-1 (80)	CC-1 (80)	UN-5 (27)	B-5 (27)	UN-10 (28)	CC-10 (28)	UN-1 (64)	LB-1 (64)	SB-1 (64)	CC-1 (64)	UN-5 (9)	B-5 (9)	UN-10 (17)	CC-10 (18)
<i>Descurainia sophia</i> *					7											
<i>Disporum hookeri</i>									6							
<i>Elymus glaucus</i>															18	6
<i>Elymus repens</i> *							24	6								
<i>Epilobium angustifolium</i>	8	13	17	2	15	52	66	54	3	77	47	30		44	6	22
<i>Epilobium ciliatum</i>	17	7	5	5	44	78	72	78		9	2	2				
<i>Epilobium</i> sp.						11	6	7								
<i>Equisetum sylvaticum</i>																6
<i>Erigeron flagellaris</i>					7	4			2	2						
<i>Festuca ovina</i>							6	11								
<i>Festuca</i> sp.												2				
<i>Filago arvensis</i> *	3															
<i>Fragaria vesca</i>	10			3	4		2	17	14	2						
<i>Fragaria virginiana</i>	2						2		6	3					47	78
<i>Galium boreale</i>									2			2				
<i>Galium triflorum</i>	15						6		11						12	
<i>Geum macrophyllum</i>					4		6	6								6
<i>Goodyera oblongifolia</i>									17	2			11	11	24	6
<i>Hieracium albiflorum</i>									5				11	11	24	44
<i>Hieracium umbellatum</i>	2															
<i>Juncus bufonius</i>	3												11			
<i>Lactuca serriola</i> *					4	4							11	22		6
<i>Lathyrus nevadensis</i>									14		2					
<i>Lathyrus ochroleucus</i>	2								3							
<i>Lathyrus</i> sp.															24	17
<i>Linnaea borealis</i>				2					52	6		28			12	11
<i>Mahonia aquifolium</i>									16	2		6			18	11
<i>Medicago lupulina</i> *					19											
<i>Medicago sativa</i> *												13				
<i>Mitella nuda</i>		5			11	4										
<i>Orthilia secunda</i>									19			8			12	11
<i>Oryzopsis pungens</i>								2								
<i>Osmorhiza chilensis</i>									13			8		11	35	
<i>Paxistima myrsinites</i>	8								34	5	6	28			12	22
<i>Pedicularis bracteosa</i>									2							
<i>Picea</i> sp.	2						12	6		2						
<i>Pinus contorta</i>								11	5	16	20					
<i>Plantago major</i>	2			2	7	4	6									
<i>Poa compressa</i>						56		11								
<i>Poa secunda</i>								6								
<i>Poa</i> sp.	40	8	2		44	33	12	36	8							

Table A1 (continued).

Species	Seed bank								Vegetation							
	UN-1 (80)	LB-1 (80)	SB-1 (80)	CC-1 (80)	UN-5 (27)	B-5 (27)	UN-10 (28)	CC-10 (28)	UN-1 (64)	LB-1 (64)	SB-1 (64)	CC-1 (64)	UN-5 (9)	B-5 (9)	UN-10 (17)	CC-10 (18)
<i>Polygonum convolvulus</i> *								6								
<i>Polygonum douglasii</i>							3	6		6	6				6	11
<i>Populus tremuloides</i>	12	20	18	2					45	20	5			11	6	6
<i>Potentilla arguta</i>					11			6								
<i>Potentilla diversifolia</i>	2															
<i>Potentilla norvegica</i>							18	17								
<i>Pseudotsuga menziesii</i>		3				2	12	6	11	48	8	5	22	56	12	
<i>Ranunculus</i> sp.									2			2				
<i>Ranunculus uncinatus</i>							6									
<i>Ribes lacustre</i>	3															
<i>Rosa acicularis</i>										16	2	8		11	18	17
<i>Rosa gymnocarpa</i>												3				
<i>Rosa nutkana</i>												3				
<i>Rosa woodsii</i>									14			3				
<i>Rubus idaeus</i>	5			2												6
<i>Rubus parviflorus</i>	10								6						6	
<i>Rubus</i> sp.	2								17	8						
<i>Sagina apetala</i> *				2												
<i>Salix</i> spp.	3	2	5	2								2		22		
<i>Sedum lanceolatum</i>	12			3					6	2						
<i>Shepherdia canadensis</i>		2										3				
<i>Smilacina racemosa</i>									8			2			12	
<i>Sonchus arvensis</i> *	2						6									
<i>Sorbus</i> sp.															12	
<i>Spiraea betulifolia</i>			5	17		11	2	17	33	45	17	28		11	41	50
<i>Symphoricarpos albus</i>									9	5	11	2			18	22
<i>Taraxacum officinale</i> *	2				11	4	18		2	2				33	24	56
<i>Thalictrum occidentale</i>									5						18	6
<i>Tragopogon dubius</i>										2	2		11			
<i>Typha latifolia</i>	5	5		2												
<i>Vaccinium</i> sp.									2		2	16				17
<i>Verbascum thapsus</i> *	3				11	7		41								6
<i>Veronica beccabunga</i>					4											
<i>Veronica serpyllifolia</i> *								17								
<i>Vicia americana</i>		2					6	6			2				18	22
<i>Viola adunca</i>									2							
<i>Viola canadensis</i>						11	12								24	17
<i>Viola</i> sp.	10															
Unknown dicot	52	32	13	8	22		12	29	16	42	8	18	11	33	18	22
Unknown grass														11	24	28
Unknown monocot	23	8	2	10	4	4	3	5	6	13		8				

Table A1 (concluded).

Species	Seed bank								Vegetation							
	UN-1 (80)	LB-1 (80)	SB-1 (80)	CC-1 (80)	UN-5 (27)	B-5 (27)	UN-10 (28)	CC-10 (28)	UN-1 (64)	LB-1 (64)	SB-1 (64)	CC-1 (64)	UN-5 (9)	B-5 (9)	UN-10 (17)	CC-10 (18)
Unknown sprout										8					12	28

*Species not native to North America.