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Buried propagules in an old-growth forest and their response to experimental disturbances

CHERYL A. INGERSOLL

AND

MARK V. WILSON

Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902, U.S.A.

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Soil blocks collected from an old-growth *Pseudotsuga menziesii* forest were subjected to three types of disturbances (shade removal, surface burning, and soil churning) in a factorial experiment. Most emergents (88%) were vegetative sprouts. Total emergence and emergence of vegetative sprouts were significantly higher in the undisturbed (control) treatment than in any other treatment. As intensity of disturbance (measured by the number of disturbance factors applied) increased, the number of emergents declined. Exposure to sun caused a significant decline in emergence of each of the six most abundant species; the effects of burning and churning varied by species. Burning decreased the emergence of species with shallow regenerating structures. None of the experimental treatments significantly affected seedling emergence. Density of emergents (both seedlings and vegetative sprouts) was higher under greenhouse condition (411.7/m^2) than in the experimental treatments (94.6/m^2), indicating that greenhouse emergence is more suitable for quantifying the buried propagule bank.

Key words: seed bank, propagules, old-growth forest, disturbance, fire.

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Des blocs de sol d'une vieille forêt de *Pseudotsuga menziesii* ont été soumis, dans une expérience factorielle, à trois types de perturbations (réduction d'ombrage, brûlage superficiel et brassage du sol). La plupart des émergents (88%) étaient des rejets végétatifs. L'émergence totale et l'émergence des rejets végétatifs ont été significativement plus élevées dans les blocs non perturbées (témoins) que dans tout autre bloc ayant subi un traitement. À mesure que l'intensité de perturbation (mesurée par le nombre de facteurs de perturbation appliqués) augmentait, le nombre d'émergents diminuait. L'exposition au soleil a provoqué un déclin significatif d'émergence chez chacune des six espèces les plus abondantes, alors que les effets de brûlage et de brassage variaient selon les espèces. Le brûlage a diminué l'émergence des espèces ayant des structures de régénération peu profondes. L'émergence des semis n'a été affectée par aucun des traitements expérimentaux. La densité des émergents (tant des semis que des rejets végétatifs) a été plus élevée en serre (411,7/m^2) que dans le cas des traitements expérimentaux (94,6/m^2), indiquant que l'émergence obtenue en serre est plus appropriée pour quantifier la banque des propagules enfouis dans le sol.

Mots clés : banque de graines propagules, vieille forêt, perturbation, feu.

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Introduction

Recent reviews (e.g., Bazzaz 1983; Pickett and White 1985; Pickett et al. 1987) proposed that patterns of early revegetation after disturbance can be predicted from an understanding of the interaction between (*i*) propagule availability before disturbance, (*ii*) disturbance characteristics (including the type, intensity, timing, and frequency), and (*iii*) morphological and physiological characteristics of plant species that influence their response to disturbance. Most studies of propagule availability focused on seed banks and on seed dispersal, but vegetative regeneration after disturbance is common in many species and may make a major contribution to the postdisturbance community (Ahlgren 1960; Lyon and Stickney 1976; Flinn and Wein 1977, 1988; Archibold 1979; Malanson and O'Leary 1982; Franklin et al. 1985; Halpern 1988). Most studies of species response to disturbance used natural, uncontrolled disturbances, making inferences about the effects of the components of disturbance difficult. The goal of this study was to examine both vegetative and seed sources of revegetation in the face of experimental disturbances. The specific objectives were (*i*) to assess the relative contributions of seeds and vegetative sprouts to the total soil propagule bank of an old-growth coniferous forest, (*ii*) to compare seed germination and vegetative sprouting of individual species following three types of experimental disturbances (canopy removal, surface burning, and soil churning), and (*iii*) to compare an estimate of the buried propagule bank derived from emergence under greenhouse conditions with that from intact soil blocks subjected to different experimental treatments.

Methods

The study was conducted in greenhouses and outdoors at Oregon State University, Corvallis, OR, using soil samples collected from an old-growth stand located in the H.J. Andrews Experimental Forest, 150 km southeast of Corvallis, OR. The H.J. Andrews lies in the Western Cascades physiographic province, and Corvallis lies in the Willamette Valley physiographic province (Franklin and Dyrness 1973). The climate of both areas is maritime, with mild, wet winters and warm, dry summers. Corvallis, at about 60 m elevation, has slightly warmer winters than does the H.J. Andrews (January mean temperatures of 4.1 and 2.3°C, respectively), while summers are comparable (July mean temperatures of 19.1 and 20.6°C, respectively). Annual precipitation in Corvallis averages 894 mm (Pacific Northwest River Basins Commission 1969) compared with 2300 mm at the H.J. Andrews (Rothacher et al. 1967).

The forest stand was located at approximately 800 m elevation in the *Tsuga heterophylla* zone and was classified as a *Tsuga hetero-*

phylla / Rhododendron macrophyllum / Berberis nervosa community (Dyrness et al. 1974). The overstory was dominated by *Pseudotsuga menziesii*,[1] *Tsuga heterophylla*, and *Thuja plicata*, and the oldest trees were approximately 500 years old. Understory vegetation consisted of shrubs and low-growing herbs, principally *R. macrophyllum*, *Linnaea borealis*, and *Rubus ursinus*. Other species abundant in the understory included *Acer circinatum*, *Viola sempervirens*, *B. nervosa*, *Coptis laciniata*, *Chimaphila umbellata*, and *Vaccinium* spp.

We removed blocks of soil on April 26 and 27, 1985, shortly after snowmelt and before any sprouting or germination occurred. At an arbitrary location near the center of the stand, we removed 360 blocks, 12.5 × 12.5 × 10 cm deep, for a total area sampled of 5.8 m^2. Each block was removed intact with a specially constructed scoop and placed immediately in a plastic pot to minimize exposure of buried seeds to light. We avoided large shrubs, logs, and stones, and where necessary, cut rhizomes at the edges of blocks. We clipped vegetation to the soil surface in each pot.

Treatments

We selected 320 of the 360 intact soil blocks at random, then randomly assigned each to one of eight treatments in a 2 × 2 × 2 factorial design. The three experimental factors consisted of the following:

(1) Sun vs. shade. We placed the pots either in full sun or under an awning of wood lattice and colored polythane (Dennison Mfg. Co., Framingham, MA.) approximating the average intensity and typical spectrum reaching the understory of an old-growth *P. menziesii* forest (Atzet and Waring 1970).

(2) Burned vs. unburned. In the burn manipulation, we spread dry litter (collected from the site) on the surface of each pot, ignited it with a propane torch, and allowed it to burn continuously for about 30 s. Trials of the burning technique with replicate soil blocks in pots showed that temperatures at 2.5 cm below the soil surface reached approximately 55°C. This fire intensity was sufficient to consume all surface litter and char the mineral soil, and it is comparable to temperatures recorded by Wright and Bailey (1982) during a springtime prescribed burn in a Douglas-fir forest.

(3) Churned vs. intact. In the churn manipulation, we thoroughly mixed the soil in each pot with a trowel to break up clods and mix layers. Pots that were burned and churned were burned first.

We intended these manipulations to stimulate three types of disturbances occurring in old-growth forests: (*i*) removal of canopy shading resulting from crown fires or clear-cut logging; (*ii*) high soil temperatures and consumption of litter occurring in forest fires or slash burns; and (*iii*) soil churning resulting from tree falls or soil movement during logging. Thus, one of the factorial treatments (shade–intact–unburned) corresponded to undisturbed old-growth forest; the other seven treatments incorporated either one, two, or all three types of disturbance. The experimental design was completely random, except for the shade vs. sun treatments, which were blocked.

Each of the 40 soil blocks not used in the factorial experiment was removed from its pot and spread over a 50:50 mixture of sterilized sand and vermiculite in a 25 × 25 cm flat. We kept the flats in the Oregon State University greenhouses and conducted the experimental study outdoors adjacent to the greenhouses. We watered the flats and pots as needed to keep them moist, although the pots in the sun treatment dried more rapidly than those in the shade or in the greenhouse, and occasionally became dry between waterings. To assess contamination of samples by local seeds we placed pots or flats of sterilized potting soil at both locations. The only species emerging in these contamination test pots or flats were common greenhouse weeds (e.g., *Euphorbia supina*) not found in the study area (Franklin and Dyrness 1971); these species were omitted from the analysis.

At 1- to 2-week intervals from April through July 1985, we counted and identified to species all emerging sprouts and seedlings. Emergents that we could not identify by species were drawn and described, and when possible, grown to maturity for identification. We classified an emergent as a seedling if it bore cotyledons, or as a vegetative sprout if it was connected to a rhizome, corm, or other plant part capable of vegetative sprouting. When we terminated the study, we sifted through the soil to confirm assignment of stems to seedling and sprout categories and to determine whether neighboring stems connected to form a single individual.

[1]Taxonomy and nomenclature follow Hitchcock and Cronquist (1973).

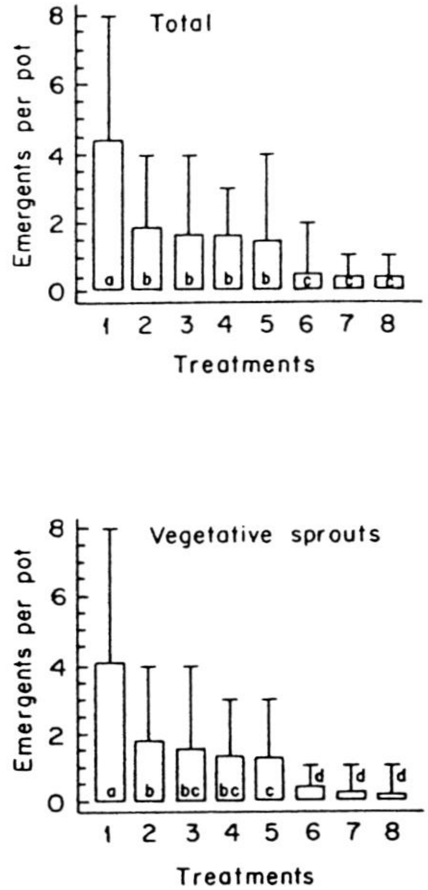

FIG. 1. Effect of experimental treatments on total emergence and emergence of vegetative sprouts. Treatments were ranked on the basis of disturbance intensity: treatment 1 was undisturbed (shade–intact–unburned); treatments 2 (shade–intact–burned), 3 (shade–churned–unburned), and 4 (sun–intact–unburned) had a single disturbance factor; treatments 5 (shade–churned–burned), 6 (sun–intact–burned), and 7 (sun–churned–unburned) had two disturbance factors; and treatment 8 (sun–churned–burned) was the most intensely disturbed. Bars show mean and 90th percentile of emergence. Means with the same letter did not differ significantly at the 0.05 level (Fisher's protected LSD test of ranked data).

Statistical analysis

We applied a rank transformation (Conover 1980) to each data set and performed all analyses on the ranked data. We analyzed the effects of the experimental treatments on total emergence, emergence of seedlings and sprouts, and emergence of the seven most abundant species by three-factor analyses of variance. Fisher's protected LSD test (FPLSD, 96% level) was used to identify treatments that had significant effects on emergence.

Results

Greenhouse study

A total of 265 individuals from 24 species emerged in the greenhouse treatment, of which 195 (74%) were vegetative sprouts and 70 were seedlings (Table 1). Four understory herb and shrub species regenerated nearly exclusively by vegetative

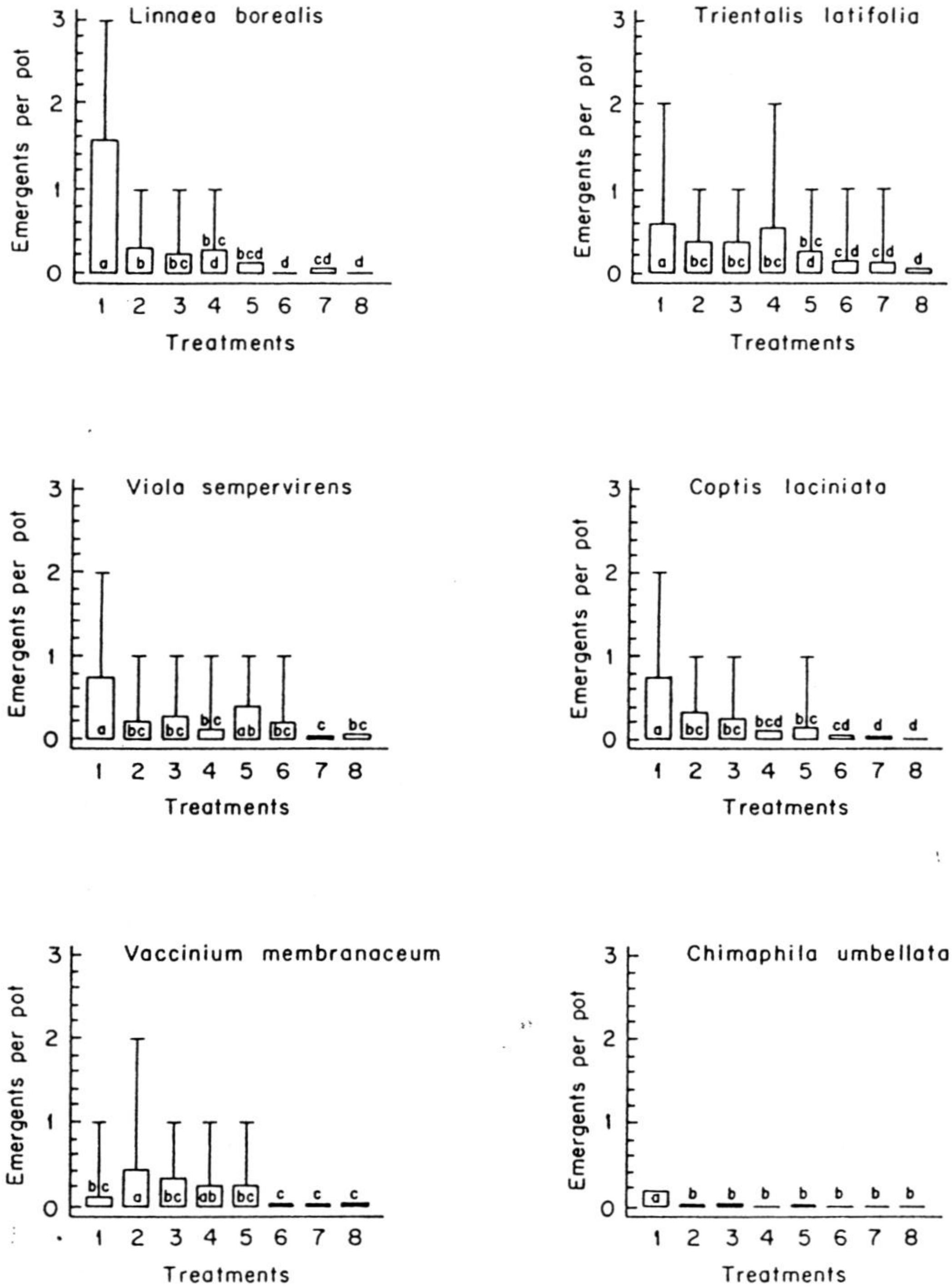

FIG. 2. Effect of experimental treatments on emergence of the six most abundant species. Fisher's protected LSD test was performed on rank-transformed number of individuals. Treatments are ranked on the basis of disturbance intensity (see Fig. 1 for details).

sprouting (*L. borealis*, *Vaccinium membranaceum*, *Trientalis latifolia*, and *C. laciniata*), constituting over 60% of the total emergence. *Epilobium watsonii* and *Senecio sylvaticus* were the only abundant species regenerating from seeds. All species regenerated exclusively by either seeds or vegetative sprouts, except *V. sempervirens*, which regenerated mostly from vegetative parts with a few emergents from seeds.

Experimental treatments

A total of 488 individuals representing 24 species emerged in the 320 experimental soil blocks. Of these, 431 (88%) were vegetative sprouts (Table 2). Each of the disturbance factors (sun, burning, and churning) caused a highly significant reduction ($P < 0.01$) in total emergence and emergence of vegetative sprouts (Table 3). The sun manipulation caused a highly significant reduction ($P < 0.01$) in emergence of six of the seven most abundant species (Table 3). *Linnaea borealis* and *C. laciniata* emergence was also significantly reduced by the burning and churning manipulations, and emergence of *V. membranaceum* was reduced by churning (Table 3). *Senecio sylvaticus*, the only abundant species to regenerate from seeds, was not significantly affected by any experimental

TABLE 1. Number of individuals emerging from soil spread in flats and held in the greenhouse

Species	Total	Sprouts	Seedlings	% of total	No./m²	SE
Linnaea borealis	80	79	1	30.0	124.1	17.4
Epilobium watsonii	33		33	12.5	51.2	9.7
Vaccinium membranaceum	30	30		11.3	46.5	12.7
Trientalis latifolia	28	28		10.6	43.4	13.7
Coptis laciniata	26	26		9.8	40.3	10.3
Viola sempervirens	23	19	4	8.6	35.7	10.4
Senecio sylvaticus	10		10	3.8	15.5	4.8
Goodyera oblongifolia	4	4		1.5	6.2	3.7
Chimaphila umbellata	4	4		1.5	6.2	3.0
Hieraceum albiflorum	2	2		0.8	3.1	3.1
Chimaphila menziesii	1	1		0.4	1.6	3.1
Cornus canadensis	1		1	0.4	1.6	1.6
Erichtites hieracifolia	1		1	0.4	1.6	1.6
Erigeron sp.	1		1	0.4	1.6	1.6
Viola sp.	1		1	0.4	1.6	1.6
Unknown (9 species)	20	2	18	7.6	31.0	—
Total	265	195	70	100.0	411.2	34.3

NOTE: A total of 24 species emerged. n = 40 flats, each containing 1560 cm³ of soil.

manipulation. The burned vs. unburned × churned vs. intact interaction (Table 4) significantly affected total emergence and emergence of sprouts and seedlings. All interactions significantly affected emergence of *L. borealis*, and the sun vs. shade × burned vs. unburned and the three-way interactions significantly affected *V. membranaceum* emergence.

Significantly more vegetative sprouts emerged in the undisturbed (shade–intact–unburned) treatment (Fig. 1) than in any other treatment (FPLSD, $P < 0.05$, df = 312). Five of the seven most abundant species (*V. sempervirens, C. laciniata, T. latifolia, C. umbellata*, and *L. borealis*), all primarily vegetative sprouters, also emerged most abundantly in the undisturbed (shade–intact–unburned) treatment (Fig. 2). Emergence of *V. membranaceum* was greatest in the shade–intact–burned treatment. Sun treatments that were also churned and (or) burned showed significantly lower total emergence (FPLSD, $P < 0.05$, df = 312) than the other treatments (Fig. 1). Sun–intact–unburned, shade–churned–unburned, and shade–churned–burned treatments produced intermediate rates of emergence. There was a clear decrease (FPLSD, $P < 0.05$) in total emergence and emergence of vegetative sprouts from the least to the most disturbed treatments (Fig. 1). Seedling emergence was low overall, and treatment differences were not significant ($P > 0.05$; Table 3).

Sprouting individuals dominated seedlings in all but the most intensely disturbed (sun–churned–burned) treatment, which produced the fewest emergents (Table 2). *Epilobium watsonii* did not emerge in any experimental treatment, despite its abundance in the greenhouse treatment (Table 1). Only three tree seedlings (all *T. heterophylla*) emerged in the experimental treatments.

Discussion

Comparison of methods assessing the propagule bank

The method most frequently used to estimate the total buried seed bank is monitoring emergence from field soil samples in a uniform environment, usually in a greenhouse (e.g., Oosting and Humphreys 1940; Kellman 1970; Strickler and Edgerton 1976; Whipple 1978). This method is likely to underestimate the total seed bank, since the seeds of some species may fail to germinate under greenhouse conditions (van der Valk and Davis 1978). Exposing soil samples to a variety of environmental conditions that may break seed dormancy or provide favorable conditions for sprouting can increase emergence in some species and result in a more accurate estimate of the buried propagule bank (e.g., see Pratt et al. 1984). In our study, the density of emergents was higher in the unmanipulated greenhouse treatment (411.2 individuals/m²) than in the experimental treatments (94.6 individuals/m²), and no experimental treatment significantly increased emergence over that in the greenhouse in any of the 34 species (t-test, $P > 0.05$). The greater emergence in the greenhouse may be attributed to spreading the soil over a wider surface area in the greenhouse flats than in the experimental pots and to greater soil moisture.

Effects of experimental disturbances

Some differences between our experimental manipulations and actual clear-cutting and burning disturbances were inevitable. Removal of soil blocks from their surrounding forest soil altered the environment experienced by seeds and vegetative parts and probably increased fluctuations in temperature and soil moisture. Thus, even the undisturbed (shade–intact–unburned) treatment experienced some disturbance that was not directly assessed. Likewise, soil temperatures in pots during our burning treatments were not as high as those in many slashburns. Nevertheless, the range of conditions produced by our treatments was sufficient to produce significant effects on emergence.

The negative effects of exposure to sun on emergence of all the understory species most likely resulted from drier soil conditions, but may also reflect the intolerance of some understory species to high light levels (Raven 1989). The observed variation in species response to burning can be partly attributed to differences in the depth of regenerating structures (McLean 1969; Flinn and Wein 1977; Flinn and Pringle 1983). Burning significantly reduced emergence of *L. borealis* and *C. laciniata*, the species with the shallowest regenerative buds, which would likely be killed by low-intensity fires. Burning did not

TABLE 2. Number of sprouts and seedlings emerging in soil blocks subjected to eight experimental treatments

	Treatment									
Species	ShIU	ShIB	ShCU	SIU	ShCB	SIB	SCU	SCB	Total	No./m^2
Vegetative sprouts										
Linnaea borealis	63	12	9	11	5		2		102	19.8
Trientalis latifolia	23	15	15	21	10	6	5	2	97	18.8
Viola sempervirens	30	8	11	5	16	8	1	3	82	15.9
Coptis laciniata	30	13	10	4	6	2	1		66	12.8
Vaccinium membranaceum	5	18	13	10	10	1	1	2	60	11.6
Chimaphila umbellata	7	1	2		1				11	2.1
Goodyera oblongifolia	3				1				4	0.8
Tiarella trifoliata	2		1						3	0.6
Acer circinatum			1						1	0.2
Viola sp.		1							1	0.2
Unknown (2 species)	1		1	1					3	0.6
Sprouts total	164	69	63	54	49	15	10	7	431	83.5
Seedlings										
Senecio sylvaticus	2	3		2	1		1	1	10	1.9
Cornus canadensis				2	1		1	2	6	1.2
Viola sempervirens	3					1			4	0.8
Tsuga heterophylla	1		1	1					3	0.6
Acer circinatum		1			1				2	0.4
Circaea alpina						1			1	0.2
Coptis laciniata		1							1	0.2
Epilobium watsonii						1			1	0.2
Hypochaeris radicata								1	1	0.2
Rubus ursinus		1							1	0.2
Tiarella trifoliata	1								1	0.2
Trientalis latifolia					1				1	0.2
Unknown (5 species)	5	1	2	5	3	3	2	5	21	5.1
Seedlings total	12	6	3	10	7	6	4	9	57	11.0
Grand total	176	75	66	64	56	21	14	16	488	94.6

NOTE: The treatments consisted of zero to three manipulations of the following three experimental factors: Sh, shade, vs. S, sun; I, intact, vs. C, churned; U, unburned, vs. B, burned. n = 40 intact blocks, each containing 1560 cm^3 of soil, per treatment.

TABLE 3. Analysis of variance (F-values) of disturbance effects on total emergence, vegetative sprout emergence, seedling emergence, and emergence of the seven most abundant species

	Sun vs. shade	Burn vs. unburned	Churn vs. intact
Total emergence	86.5 − **	20.6 − **	37.9 − **
Vegetative sprouts	108.7 − **	23.6 − **	40.8 − **
Seedlings	0.1 +	0.4 +	1.6 −
Linnaea borealis	67.1 − **	38.4 − **	42.7 − **
Vaccinium membranaceum	9.2 − **	0.0 +	4.5 − *
Coptis laciniata	24.7 − **	4.5 − *	8.0 − **
Viola sempervirens	11.1 − **	0.5 −	3.5 −
Trientalis latifolia	8.2 − **	3.5 −	3.8 −
Chimaphila umbellata	8.4 − **	2.1 −	0.5 −
Senecio sylvaticus	0.4 −	0.0	1.6 −

NOTE: n = 40 intact blocks, each containing 1560 cm^3 of soil, per treatment. + and − indicate the direction of effect of the first factor. *, $0.01 < P < 0.05$; **, $P < 0.01$.

reduce emergence of *T. latifolia*, whose deeply buried rhizomes would be insulated from high temperatures.

The vertical distribution of propagules can also alter the effects of churning on emergence. If buried propagules are concentrated near the soil surface, soil mixing will result in net downward movement from the surface region favorable for emergence. Emergence of vegetative sprouts did show a highly significant decline because of churning (Table 3), largely owing to decreased emergence of the shallow-rhizomatous *L. borealis* and *C. laciniata*.

Burning reduced total emergence and emergence of vegetative sprouts to a greater degree in intact pots than in churned pots (Fig. 2), causing the significant interaction between the burning and churning factors (Table 4). Burning probably killed vegetative propagules in the upper soil layers; churning afterwards would have brought up reproductive structures from deeper layers, partially replenishing those killed by burning.

Relative contributions of seeds and vegetative propagules

Oliver (1981), Uhl and Jordan (1984), and Runkle (1985) proposed that mild disturbances favor initial revegetation by species that regenerate by sprouting and more intense disturbances favor regeneration from buried seeds. The most intense disturbances kill all buried propagules, forcing revegetation

TABLE 4. Analysis of variance (F-values) of factor interactions on total emergence, vegetative sprout emergence, seedling emergence, and emergence of the seven most abundant species

	Sun × burn	Sun × churn	Burn × churn	Sun × burn × churn
Total emergence	0.5 +	1.4 +	14.7 +**	0.1 +
Vegetative sprouts	0.7 +	0.9 +	9.6 +**	0.0 −
Seedlings	0.3 −	0.4 +	8.1 +**	0.1 +
Linnaea borealis	12.7 +**	27.6 +**	22.4 +**	11.9 −**
Vaccinium membranaceum	4.5 −*	0.0 −	0.1 −	8.8 +**
Coptis laciniata	1.3 +	1.4 +	1.1 +	0.5 −
Viola sempervirens	1.2 +	0.1 +	2.6 +	1.8 −
Trientalis latifolia	0.3 −	0.3 −	0.1 −	0.3 +
Chimaphila umbellata	2.1 +	0.5 +	0.5 +	0.5 −
Senecio sylvaticus	1.6 −	1.6 +	0.4 −	0.4 +

NOTE: n = 40 intact blocks, each containing 1560 cm^3, per treatment. + and − indicate the direction of effect of the first factor. *, $0.01 < P < 0.05$; **, $P < 0.01$.

from dispersed seeds. Although Leege and Hickey (1971) reported abundant sprouting of coniferous forest understory species following fire, understory species in the western Cascade Range that typically regenerate vegetatively are most abundant on sites that are unburned after logging; burned sites are typically dominated by species establishing primarily from seeds (Dyrness 1973; Halpern 1988, 1989). Our experimental results match this pattern, i.e., seedling emergence was relatively greater when disturbances reduced the emergence of vegetative sprouts.

Our estimate of the soil seed bank density for our study site is low (109/m^2), even in comparison with most other coniferous forests (Oosting and Humphreys 1940; Livingston and Allessio 1968; Johnson 1975; Thompson 1978; Pratt et al. 1984; Archibold 1989). The insignificant contribution of the canopy dominants (*T. heterophylla, P. menziesii*, and *T. plicata*) does match the pattern found in other coniferous forests (Oosting and Humphreys 1940; Livingston and Allessio 1968). Emergence of vegetative sprouts (303/m^2) was considerably higher than seedling emergence, attesting to the potential importance of asexual regenerative structures in initial revegetation following disturbance in this stand. The density of vegetative propagules is an underestimate, since the size of the soil samples precluded removal of species with large root crowns (e.g., *R. macrophyllum*). At 500 years, this stand was much older than other forest sites for which seed bank densities have been estimated (Pratt et al. 1984), and we suggest that the buried seed bank on this site had declined through time. The accumulation of buried seeds may have selective advantage only in habitats subjected to a high rate and intensity of disturbance (providing gaps for seedling establishment) or where vegetation productivity is high enough to support a large crop of seeds (Thompson 1978). Neither condition was met in our forest stand; as the forest canopy closed, opportunities for seedling establishment probably became rarer as light and nutrient availability were reduced (Grime 1979). A scarcity of favorable conditions for seedling establishment is probably typical of the forests like our study site, with long intervals between fires (Teensma 1987) and rapid growth of understory individuals in single-tree gaps (Spies and Franklin 1989). The decline in resource availability with successional age common in North American conifer forests limits understory productivity (Sprugel 1985) and probably seed production. Thus, seed input is less and mortality (through decay, predation, and germination) depletes the buried seed bank. Vegetative regenerative structures will then be more likely than seeds to provide a stable source of propagules.

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