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Seedling establishment patterns on the Pumice Plain, Mount St. Helens, Washington

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Abstract. We examined the factors that control seedling establishment on barren substrates on the pyroclastic flows from Mount St. Helens. From June to September in 1993, we monitored seedling and microhabitat changes in 240 20 cm × 20 cm quadrats on the Pumice Plain. Seedlings emerged in 104 quadrats (43.3 %). The most abundant species were *Anaphalis margaritacea*, *Hypochaeris radicata*, *Lupinus lepidus* and *Epilobium angustifolium*. Measured site characteristics included topography, particle size distribution, ground surface movements, soil water content, organic matter, pH, and presence or absence of dead lupines. Quadrats with seedlings had higher cover of dead lupines, higher amount of rock and gravel substrate, and a greater cover of rills. More seedlings emerged where eroded material accumulated. Compared to coarse-textured surfaces, silt surfaces had higher organic matter, held more water, and showed higher pH. However, seedlings became established more frequently on coarse-textured surfaces. In greenhouse experiments, a higher percentage of *Hypochaeris* seeds germinated on silt than on sand or gravel. The germination of *Anaphalis* and *Epilobium* did not differ with soil texture, but was higher at higher moisture levels. Seedling colonization is more dependent on ground surface microtopography, particle size, and ground movement than on the chemical status of these volcanic deposits.

Keywords: Ground surface movement; Microhabitat; Safe site; Seed germination; Soil texture; Tephra; USA.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

Seedling establishment is crucial to the development of spatial pattern during the early stages of primary succession (e.g. Bornkamm 1981; Tsuyuzaki 1991; del Moral & Wood 1993). The role of safe-sites, which can be uncommon and patchy in distribution (del Moral & Bliss 1993), must be considered in order to understand how seedling germination and growth are controlled (Grubb 1977; Pickett & White 1985; Watkins & Wilson 1992). Features of surface topography have major effects on seedling establishment in habitats as diverse as abandoned fields, chalk grasslands, and forest floors (Harper 1977; White 1979; Silvertown & Dickie 1980; Collins 1989).

The eruption of Mount St. Helens in 1980 created a landscape with low nutrient availability, frequent drought, varied microtopography and frequent surface movement and erosion. Ground surface instability can supersede soil nutrient status as a barrier to seedling survival in these harsh environments (Tsuyuzaki 1994; Tsuyuzaki & del Moral 1994; del Moral et al. 1995). This suggests that texture and ground surface movements may determine plant establishment patterns. In addition, safe-sites for seed germination are not necessarily suitable sites for plant growth (del Moral & Bliss 1993; Tsuyuzaki 1996). Therefore, we tested these two hypotheses: (1) ground surface movement and surface texture determine seedling establishment patterns; and (2) germination and seedling growth rate are influenced by surface texture as well as water and nutrient deficiencies. To test these hypotheses, we monitored seedling establishment patterns, correlated these with environmental factors, and conducted greenhouse germination and growth studies.

Material and Methods

Study site

The most recent eruption on Mount St. Helens began on May 18, 1980. Before the eruption, vegetation was dominated by conifers such as *Abies* spp., *Pseudotsuga menziesii* and *Pinus contorta* and a variety of subalpine meadow species including *Lupinus lepidus*, *Penstemon cardwellii* and *Luetkea pectinata*. The eruption destroyed the summit and subsequently created a new landscape devoid of vegetation (Foxworthy & Hill 1982). With few, localized, exceptions, vegetation disappeared from the summit and north flank of the volcano (Chapin & Bliss 1989; del Moral & Wood 1993).

The Pumice Plain study site, located on the north side of the mountain at an elevation of 1200 m, received the brunt of the blast, including thick accumulations of pyroclastic material and pumice, which destroyed all vegetation (del Moral & Bliss 1993). By 1993, many gullies had formed in the erosive tephra substrate. The Pumice Plain was, and remains, isolated from major sources of plant colonists. Invasion has been dominated by wind-dispersed species such as *Anaphalis margaritacea, Hypochaeris radicata, Epilobium angustifolium* and *Hieracium albiflorum* (del Moral 1993). *Lupinus lepidus* (lupine) often developed dense patches of short lived individuals (< 6 yr). Invasion and growth of other species are facilitated on the edges of these patches (Morris & Wood 1989).

Survey design

In mid-June 1993, before seedlings emerged, 240 20 cm × 20 cm plots were randomly established on the Pumice Plain. Seedling survival and soil movements were monitored at 10 to 20 day intervals. All seedlings were marked with toothpicks soon after their emergence, and their survival was monitored through September. The distance from each plot to the nearest previously-fruiting individual was also measured. In 1993, the snow-free period was from mid-June to mid-October. Cover and fruiting of the overwintering individuals of each species were evaluated by monitoring 48 1 m × 1 m plots in the general vicinity of the 240 seedling plots. Length and width on each seedling leaf were measured and used to calculate cover, assuming that each seedling leaf was elliptical. Plot cover percent was calculated as:

$$\frac{\sum_{i}^{n} \text{cover}_i}{\text{plot size}} \times 100(\%) \qquad (1)$$

where n = number of seedlings in a plot.

Slope angle was measured by a clinometer. Elevation difference within each plot was measured by a level. Three erosion pins were established upslope of each plot to measure ground surface movement. The length of pins appearing above the ground surface was measured and averaged (Yamamoto 1984). Positive and negative values represent the accumulation and removal of volcanic deposits, respectively. Cumulative ground surface movements and maximum accumulation and removal of ground surface were calculated from these measurements. The areas of gravel (2 - 20 mm in diameter), rock (> 20 mm), and dead lupine were estimated in each plot. Two 200 g substrate samples were collected on the edge of each plot. Rocks (> 2 cm) were excluded. Percent water content was determined gravimetrically. Samples were weighed, dried at 80 °C for 72 hr, and reweighed. Loss on ignition was measured by ignition at 700 °C for 8 hr in a muffle furnace. pH was measured directly with a glass electrode in a 1:1 soil paste. Each sample was sieved into silt (< 0.05 mm), sand (0.05 - 2.00 mm) and gravel (> 2.00 mm), and these fractions were weighed.

Germination and growth patterns in the greenhouse

Anaphalis, Hypochaeris and *Epilobium* were used in germination trials to determine the most favorable particle sizes and moisture levels for seed germination and for growth. Volcanic deposits were collected from the Pumice Plain, and were sorted by sieving. Nine treatments were prepared for the germination tests. We used all combinations of volcanic deposit particle sizes (silt, sand and gravel) with water depth (2 cm dry = shallow, 6 cm = medium and 10 cm = deep). For each treatment, three replicate pots were used. Each 15 cm × 15 cm pot contained 100 seeds of one species. Pots were observed daily for the first one month and at 2 -3 day intervals thereafter, continuing until germination stopped. During the germination test, water depth was adjusted at two to four day intervals. Except for the first three seedlings in each pot, all seedlings were gently removed. When seed germination ceased for all the species, the surviving seedlings were harvested. Seedling shoot height, root length, above-and below-ground biomass were measured. The ratio of above-ground biomass (T) to below-ground biomass (R) (hereafter T/R ratio) was calculated.

Data analysis

One-way analysis of variance (ANOVA) was conducted to determine differences in 17 environmental factors measured between plots with and without seedlings (Zar 1984). Two-way ANOVA explored seedling germination and growth differences due to water depth and soil texture for each species in the greenhouse experiments. A correlation coefficient matrix was obtained for environmental factors (Zar 1984). Detrended Canonical Correspondence Analysis (DCCA) was applied using only those factors that differed significantly between quadrats with and those without seedlings to assess environment-species correlations (ter Braak 1987). DCCA were performed independently with seedling density and with cover, with the same environmental factors. Statistical validity of resulting environmental axes were evaluated by an unrestricted Monte Carlo permutation test (ter Braak 1988).

Results

Established vegetation

Nine vascular plant species were observed in the 48 1 m × 1 m quadrats; three of them are common and attain some cover, *Anaphalis margaritacea* up to 23 %:

Anaphalis margaritacea	60 % frequency	2.0 % mean cover
Lupinus lepidus	46 %	2.0 %
Hypochaeris radicata	35 %	0.5 %
Epilobium angustifolium	17 %	
Salix commutata	8 %	
Penstemon cardwellii	8 %	
Agrostis diegoensis	6 %	
Hieracium albiflorum	4 %	
Cirsium arvense	2 %.	

Moss cover was < 0.1 % in each plot (frequency = 3 %). Plot cover averaged 5.2 % and did not exceed 25 %. The cover of dead lupine averaged 1.2 %.

For all the species found as seedlings, individuals that were well-developed and produced seeds occurred in or adjacent to these plots. Except for *Lupinus* and *Agrostis*, all species produced wind-dispersed seeds that can travel long-distance. However, most seedlings in our study emerged before the adult plants dispersed seeds. Those results suggested that most seedlings were derived from the soil seed bank buried in previous years. Immigration by long distance dispersal remains possible for the wind-dispersed species, but not likely.

Environmental conditions

Aspect among the quadrats ranged from 0° to 170°. Maximum elevation difference within a plot was related to the slope gradient and ranged from 0 mm to 70 mm. Total ground surface movement ranged from + 6.5 mm to – 5.3 mm, and averaged +0.4 mm (Table 1). Maximum accumulation of deposits was + 4.3 mm and maximum removal of deposits was 4.3 mm. The area covered by rocks changed little during the survey, indicating that large volcanic materials did not move during the snow-free period. Therefore, measured surface movements resulted primarily from movement of fine-particles. Rills were observed in most plots. Mean rock cover varied greatly with a maximum of 80 %. Gravel occupied 21 % of the surface. Soil texture was dominated by silt, but soil texture also varied greatly. For example, the silt fraction ranged from 30 % to 99 %, and the gravel fraction ranged from 0.1 % to 58 %. The sand fraction was generally low. Loss on ignition of volcanic deposits was always < 1.2 % (Table 1), indicating that organic matter was very low even 13 yr after the eruption. The water content of volcanic deposits was less than 32 %. The pH varied from 4.3 to 5.9.

Correlation among environmental variables suggested that fine-textured surfaces tended to contain more organic matter and hold more water (Table 2). Area of rock and gravel, soil pH, soil water content, and soil organic matter were highly significantly correlated, indicating that substrates with higher organic matter, relatively-neutral pH, and high water content were generally silts. We therefore hypothesized that seedling growth would be best on silt if nutrients strongly affected growth. However, this hypothesis was not supported, as described below. The cover of dead lupines did not show significant relationships with soil organic matter, water, or pH. There were no significant relationships among other environmental factors, other than a weak relationship between dead lupines and elevation difference.

Seedling emergence and distribution patterns

We found 399 seedlings of seven species in 104 of the 240 quadrats. Mean seedling density was 41.6/m^2. 51 % of total seedlings belonged to *Anaphalis margaritacea* (see further Table 4 below).

All common species began to germinate soon after the snowmelt, i.e. mid-June (Fig. 1). The germination periods of *Hypochaeris* and *Lupinus* were short, from mid-June to mid-July. In contrast, *Anaphalis* germinated from mid-June to mid-August. Infrequent species, e.g. *Penstemon*, *Hieracium*, and *Agrostis*, germinated from early July to mid-August. Total seedling mortality from late June to September was 29 %. Of the three common

Table 1. Mean characteristics of microhabitats with or without seedlings. One-way ANOVA was conducted to confirm any differences. Col. 1: Plots with seedlings (+); Col. 2: Plots without seedlings (–); Col. 3: All plots (Σ); Col. 4: *F*-value; * = significantly different at $P < 0.01$; others not significantly different.

Plot characteristics		+	–	Σ	*F*
Number of microhabitats surveyed		104	136	240	
Percentage area of	rill	58.6	38.2	47.0	10.20 *
	rock	5.3	3.3	4.2	1.59
	gravel	22.1	20.6	21.2	0.37
	rock and gravel	27.4	23.9	25.4	4.16 *
Percentage weight of	silt	65.2	65.9	65.6	0.15
	sand	17.8	17.6	17.7	0.10
	gravel	17.0	16.5	16.7	0.09
Aspect		72.7	79.2	76.4	1.15
Elevation difference within plot (mm)[1]		20.0	16.6	18.1	4.27 *
Movement of volcanic deposits (mm)[1]		0.7	0.2	0.4	5.86 *
Max. accumulation of volc. dep. (mm)[1]		1.0	0.8	0.9	2.15
Max. removal of volc. dep. (mm)		0.6	0.6	0.6	0.54
Water content (%)		13.7	13.5	13.6	0.08
pH		5.02	5.02	5.02	0.04
Organic matter[2] (%)		0.56	0.53	0.54	0.73
Percentage cover of dead lupine		7.4	1.4	4.0	13.62 *
Percentage cover of live plants		14.8	12.3	13.4	0.85

[1] During measurement period; [2] Evaluated by loss on ignition.

Table 2. Correlation coefficients among environmental factors that showed significant differences between quadrats with and without seedlings or physically related to plant growth. **: significant at $P < 0.001$; *: $P < 0.01$; others not significant. $n = 240$.

Factor	Area of rock and gravel	Elevation difference	Surface movements	Water content	pH	Organic matter	Area of dead lupine
Rill	–0.132	+0.126	+0.067	+0.000	–0.023	–0.044	–0.003
Area of rock and gravel	–	+0.105	–0.050	–0.451**	–0.299**	–0.412**	+0.058
Elevation difference	–	–	–0.007	–0.119	+0.100	–0.061	+0.222*
Surface movements	–	–	–	+0.080	+0.147	+0.158	+0.048
Water content	–	–	–	–	+0.500**	+0.719**	–0.099
pH	–	–	–	–	–	+0.380**	–0.037
Organic matter	–	–	–	–	–	–	+0.044

species, the mortality of *Anaphalis* was the highest, 37.9 %. Most seedlings died from mid-July to early-September. Morphological observation of leaves that were withered suggested that most seedlings were killed by drought. *Hypochaeris* and *Lupinus* showed less than 20 % mortality. *Epilobium* and *Penstemon*, suffered 37.5 % and 50.0 % mortality, respectively, but the low number of seedlings makes any conclusions speculative.

The distance from the nearest previously-fruited plants to these plots varied from 0 to 30 m. The relationship between distance from the nearest previously-fruiting individuals to the quadrats and number of seedlings in the quadrats was not significant for any species except *Lupinus* (Table 3). *Lupinus*, which produces heavy seeds dispersed explosively and by water, showed a positive relationships between seedlings and adults. This pattern suggests that plants with limited dispersal range require adjacent seed sources to establish.

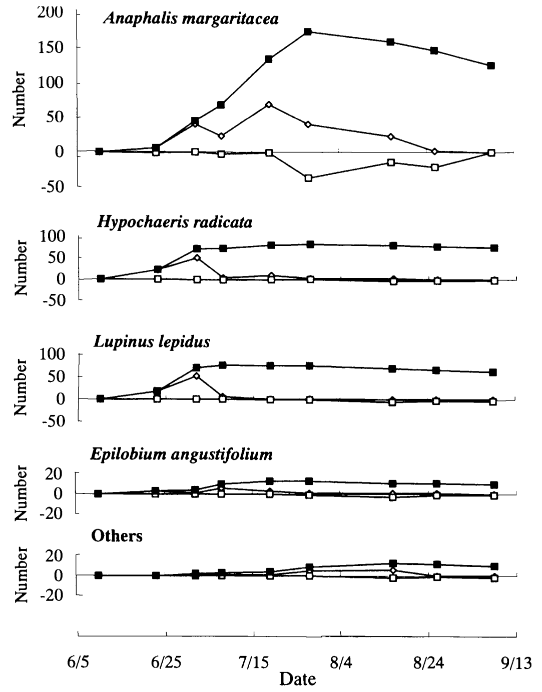

Fig. 1. Seasonal fluctuation of seedling emergence, death and total numbers of dominant species. ◊ = number of newly-emerged seedlings; □ = number of dead seedlings; ■ = total number of seedlings.

Determinants of seedling establishment and growth

The quadrats with seedlings had five times more dead lupine cover than did quadrats lacking seedlings. These quadrats also had more rocks, gravel and rills (Table 1). Silt accumulated to a greater depth in seedling plots and total ground surface movements were three times higher than in non-seedling quadrats. No significant differences between seedling quadrats and non-seedling quadrats were detected in organic matter, pH, water content, aspect, or area of living lupines.

Seedling sizes, expressed as number of leaves and leaf area, differed significantly among species (Table 4). *Lupinus* produced seedlings that were over 5 × larger than any other species. Therefore, DCCA analyses using density may show different results from those using cover. Independent DCCA were conducted separately for each parameter using the five variables that differed significantly between those quadrats with and without seedlings. The density-environment correlations were 0.61 ($P < 0.05$) on the first axis and an insignificant 0.35 for the

Table 3. Linear relationship between distance from the nearest fruiting individual and number of seedlings. $y = ax + b(r)$; y is number of seedlings; x is distance from the nearest fruiting individual; a and b are constant; r is regression coefficient. $n = 240$. *: significant at $P < 0.001$; others not significant.

Species	a	b	r	Dispersal	Seed weight (mg)
Lupinus lepidus	– 0.02	+0.51	– 0.241 *	G	4.87 ± 0.25^{a}
Anaphalis margaritacea	– 0.09	+1.03	– 0.069	W	0.071 ± 0.006
Hypochaeris radicata	– 0.02	+0.45	– 0.041	W	0.727 ± 0.080
Epilobium angustifolium	+0.01	–0.03	+0.135	W	0.106 ± 0.007
Penstemon cardwellii	+0.00	+0.00	+0.09	G	0.465 ± 0.024^{a}
Hieracium albiflorum	+0.00	+0.03	– 0.08	W	0.300 ± 0.003^{a}
Agrostis diegoensis	+0.00	+0.00	+0.04	G	0.140 ± 0.015^{a}

[a]: data from Wood (1987).

Table 4. Maximum sizes of annual seedlings, expressed as number of leaves and leaf area for each species during the surveyed period in the field. Each value is mean ± standard deviation. One-way ANOVA established that the sizes of seedlings differed among species ($P < 0.001$) when *Agrostis diegoensis* was excluded from the calculations.

Species	Number of seedlings	Number of leaves	Area (cm^2)
Anaphalis margaritacea	203	3.00 ± 0.53	0.35 ± 0.33
Lupinus lepidus	77	8.83 ± 4.27	15.00 ± 11.82
Hypochaeris radicata	88	3.71 ± 1.85	2.97 ± 1.49
Epilobium angustifolium	16	5.63 ± 1.06	1.43 ± 1.02
Penstemon cardwellii	10	3.90 ± 0.16	0.34 ± 0.16
Hieracium albiflorum	4	2.75 ± 0.75	0.17 ± 0.05
Agrostis diegoensis	1	3.00	0.13
F-value		28.53	22.08

second axis (Table 5). Monte Carlo permutations indicated that the environmental relationship to density was weak, but significant ($P < 0.05$). The first axis was related to the area of dead lupine and to ground surface movement (Fig. 2), suggesting that these two factors are related to seedling germination. The second axis was related to rock and gravel area. In contrast, there was no significant relationship between plant cover and environment.

Seedling germination and growth patterns under greenhouse conditions

The seeds of *Hypochaeris* and *Epilobium* started to germinate within four days of planting in volcanic material, and *Anaphalis* began to germinate after eight days. The first two species completed germination within 45 days, while the latter required 70 days for complete germination. These germination patterns were similar to the field observations (Fig. 1).

Table 5. Eigenvalues and intra-set correlations of standardized environmental variables with the first two DCCA axes evaluated by density and by cover. Sums of all unconstrained eigenvalues were 3.496 and 8.008 and sums of all canonical eigenvalues 0.276 and 0.773 for density and cover DCCA, respectively.

	Density		Cover	
Axis	I	II	I	II
Eigen values	0.17	0.04	0.35	0.04
Lengths of gradient	0.69	0.27	0.71	0.50
Species-environment correlations	0.61	0.35	0.77	0.50
Cumulative percentage variance				
of species data	4.9	5.9	10.6	11.7
of species-environment relation	59.7	83.5	57.4	95.8
Inter-set correlations of environmental variables				
Percentage area of dead lupine	–0.465	+0.052	–0.684	+0.358
Percentage area of rock and gravel	+0.272	–0.329	–0.056	+0.246
Percentage of rill inside	–0.190	+0.104	–0.247	+0.161
Topography difference	–0.257	–0.046	–0.376	+0.253
Surface ground movements	–0.463	+0.047	–0.551	+0.343

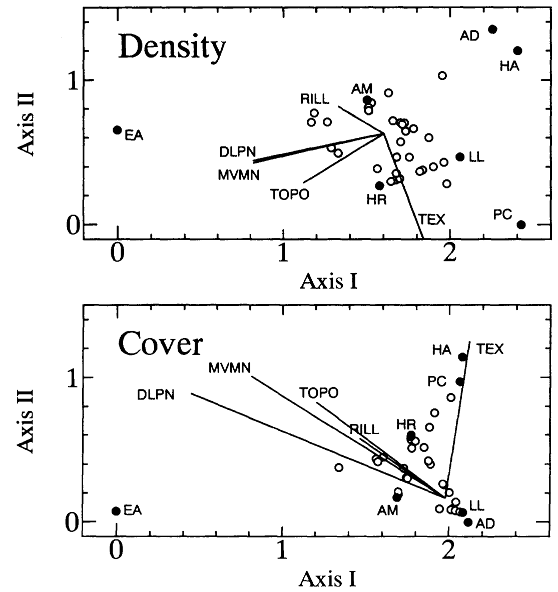

Fig. 2. DCCA diagram on the first two axes evaluated by seedling density and cover. Environmental factors: DLPN, percentage area of dead lupine; TEX, percentage area of rock and gravel; RILL, percentage of rill inside; TOPO, topography difference; MVMN, surface ground movements. Species: AD, *Agrostis diegoensis*; AM, *Anaphalis margaritacea*; EA, *Epilobium angustifolium*; HA, *Hieracium albiflorum*; HR, *Hypochaeris radicata*; LL, *Lupinus lepidus*; PC; *Penstemon cardwellii*. ○ = plot score on the first two axes; ● = species score on the first two axes.

More than 88 % of *Hypochaeris* seeds germinated on silt but < 77 % germinated on gravel at any water depth (Table 6). *Hypochaeris* had its lowest germination percentage on gravel. Water depth significantly affected germination rates of *Anaphalis* and *Epilobium*, but seedbed texture did not influence germination. Interactions between texture and water depth with respect to germination were not observed for any species.

In all species, above-ground biomass increased significantly with increasing water depth (Table 6). There were no clear effects of seedbed texture on above-ground biomass. Below-ground biomass of *Hypochaeris* and *Anaphalis* was low on silt surface at all water depths. Although below-ground biomass was the lowest on silt surface with shallow water depth for *Epilobium*, this pattern did not occur when water depth was medium or deep. T/R ratio of all species decreased significantly both with an increase in particle size and with water depth. This was due primarily to a decrease in below-ground biomass. Interactions between seedbed texture and water depth were also observed on T/R ratio for the *Anaphalis* and *Epilobium*.

Table 6. Mean germination percentage and biomass of *Hypochaeris radicata*, *Anaphalis margaritacea* and *Epilobium angustifolium* along the gradient of particle sizes and water depths in a greenhouse experiment. Two-way ANOVA is conducted to confirm those differences (*F*-value). ** = significant at $P < 0.01$; * = $P < 0.05$; others non-significant; - not measured.

Species	Water depth	Shallow (dry)			Medium (moist)			Deep (wet)			*F*–value		
	Soil texture	Silt	Sand	Gravel	Silt	Sand	Gravel	Silt	Sand	Gravel	Texture	Water	Interaction
Anaphalis margaritacea	Germination (%)	64.7	70.3	46.0	91.1	91.1	85.3	92.1	91.1	88.1	0.79	14.05	0.36
	Above-ground biomass (mg)	5.0	14.7	25.7	41.8	25.7	25.1	31.6	24.7	35.3	0.04	11.42 **	5.29 *
	Height (mm)	5.9	11.1	11.9	13.6	13.2	13.4	13.7	13.0	15.1	1.31	7.78 *	2.69
	Below-ground biomass (mg)	0.9	5.2	4.4	6.8	4.4	8.0	4.4	5.3	9.3	8.55 *	8.86 **	3.83
	Root length (mm)	35.0	61.2	93.1	46.6	52.9	93.7	54.0	52.1	96.9	78.00 **	0.63	2.00
	T/R ratio	6.5	5.8	3.5	6.6	5.8	3.5	7.5	4.9	3.7	6.74 *	12.54 **	12.41 **
Hypochaeris radicata	Germination (%)	88.6	86.0	64.7	88.7	91.0	77.7	92.8	92.0	76.7	12.90 **	1.47	1.69
	Above-ground biomass (mg)	96.5	93.8	19.8	80.1	90.1	118.9	78.8	111.3	155.1	1.25	11.24 **	13.19 **
	Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-
	Below-ground biomass (mg)	37.0	40.0	17.4	13.4	31.8	56.5	18.0	37.0	49.4	14.52 **	0.48	16.08 **
	Root length (mm)	87.0	109.8	95.1	85.2	134.5	202.9	84.3	157.7	164.5	36.52 **	16.58 **	9.15 **
	T/R ratio	3.6	2.6	1.3	5.9	3.1	2.3	4.5	3.0	3.4	26.40 **	8.54 *	3.31
Epilobium angustifolium	Germination (%)	32.0	39.3	41.4	72.0	71.3	62.0	87.3	75.3	62.0	0.40	7.5 *	0.49
	Above-ground biomass (mg)	9.3	12.3	22.3	26.9	14.1	24.2	41.4	34.4	28.3	0.94	9.98**	1.90
	Height (mm)	4.2	3.4	3.0	4.4	3.6	5.9	8.1	6.8	9.5	4.57	44.44 **	2.30
	Below-ground biomass (mg)	1.3	4.5	12.6	6.9	6.7	12.9	14.5	15.9	12.9	4.54	11.32 **	2.81
	Root length (mm)	26.1	45.7	43.6	31.8	51.5	80.0	73.0	90.8	102.8	11.57 **	29.93 *	1.20
	T/R ratio	8.1	4.4	1.7	4.2	2.3	2.0	2.9	2.2	2.1	28.57 **	16.88 **	7.91 *

Discussion

Seed dispersal

Distance from seed sources is an important factor for colonization of a barren area (Tsuyuzaki 1989; del Moral 1993). The low probability of a seed arriving at any site strongly affects early successional processes (del Moral & Wood 1988). On Mount St. Helens, colonization patterns are more influenced by the available biota than by substrate characteristics (Dale 1989). Six years after the eruption, most seedlings invading high elevation lahars on Mount St. Helens occurred within 3 m of a conspecific adult and the boundaries between the lahar and intact vegetation was sharp (Wood & del Moral 1987). Most invasion of our study area was by wind dispersed species found in isolated patches. Only *Lupinus* required a proximate seed source and it was found in dense clusters. These observations suggest that, for wind-dispersed species, seed sources were sufficiently close to provide enough seeds to colonize barren areas after 13 yr. Low seedling density may be related to stressful conditions (del Moral & Bliss 1993). Most species found began to germinate before local seed production in this season, so a soil seed bank has developed since the surfaces have stabilized.

Seed germination and seedling establishment

Drought often inhibits seed germination in habitats such as prairies, tundra, and volcanoes (Loucks et al. 1985; Chapin & Bliss 1989; Chapin 1993). On Mount St. Helens, drought restricts seedling emergence and increases mortality (Wood & del Moral 1987; Wood & Morris 1990). Rainfall patterns strongly influence seedling mortality (del Moral & Wood 1988; Chapin & Bliss 1989). Greenhouse studies showed that there were no interactions between water depth and seedbed texture for germination of the species studied. This suggests that surface texture affects seed germination independently from drought. The importance of the two factors varied with species. Seed germination of *Anaphalis* and *Epilobium* was restricted by water deficits more than *Hypochaeris*.

Safe sites for seedling emergence and development occurred primarily in rills and in areas with coarse particles on volcanic deposits (Yamamoto 1984; del Moral & Wood 1988) and other habitats (Harper 1977; Silvertown & Dickie 1980; Howe & Smallwood 1982; Collins 1989). Most seeds were captured in rills or among coarse particles on the volcano Usu after being moved by snowmelt (Yamamoto 1984). Cracks and irregular surface topography trap seeds of early successional species (Wood & del Moral 1988) and provided the best conditions for seed germination (Hamrick & Lee 1987). Similar patterns were also observed in the Alaskan tundra (Chambers et al. 1991). Since dead lupines also provided irregular topography, more seeds may be found in dead lupine mounds.

Surface ground instability is usually considered to have negative effects on plant survival (Pickett & White 1985; Meyer et al. 1992). However, this study demonstrates that mild ground surface movement can promote seedling density. Seeds are likely to move with slight movements of volcanic deposits and therefore find more suitable germination sites. Seeds germinated over a wide array of conditions, and subsequent slope instability may result in gradual habitat differentiation as the season progress. Surviving seedlings may occur in only a subset of the microsites in which seeds germinated.

Seedling growth

The pattern of seedling density fluctuation, differed from that of the cover fluctuation on Mount Usu, Japan (Tsuyuzaki 1989, 1994). Different environmental factors are expected to affect density and cover in different ways. For example, the distance from a colonizing source can affect plant density, while ground surface instability can affect cover (del Moral & Wood 1988; Tsuyuzaki & del Moral 1994). The DCCA analyses suggested that the five factors analyzed which affected seedling density influenced seedling cover but little. Thus the determinants of seedling growth are not always the same as those for seedling emergence (Tsuyuzaki 1996).

The physiological characteristics of plants, such as their abilities to use nutrient and water, promote establishment and development (Harper 1977; Silvertown 1982; Chapin & Bliss 1989). Nutrient additions had only a marginal effect on seedling survivorship in field experiments on Mount St. Helens (Wood & del Moral 1987), but nutrients did enhance growth when the particle size was homogeneous (del Moral & Clampitt 1985). There may be a conflicting set of effects on seedling growth. Fine particles had more organic matter, which implies enhanced nutrient levels. However, fine texture also strongly inhibited root growth. It appears that this effect is stronger than any nutrient effect, resulting in slower growth and higher seedling mortality in fine-textured soils than in coarse-textured ones. Near this study area, there is a region with a large number of small depressions with level centers. Natural sorting processes have resulted in the sides and edges of these depressions having coarse texture and the centers being dominated by fine textures. Near all seedlings have established on the sides and edges, while there are very few seedlings in the center (R. del Moral pers. obs.).

On volcanoes where the ground surface is unstable, root development greatly determines seedling survival and/or plant growth (Antos & Zobel 1985; Tsuyuzaki 1989; Tsuyuzaki & Titus 1996). Our greenhouse studies suggested that germination and growth were significantly influenced by water depth. In particular, aboveground biomass in each species decreased with reduced water. However, water depth had little influence on the below-ground biomass of *Hypochaeris* and root length of *Anaphalis*, suggesting that those two species produced well-developed underground organs even under water deficit. In addition, the texture of volcanic deposits affected the root and underground biomass when the water depth did not influence them. Below-ground systems are crucially important for seedling survival and growth on unstable environments such as volcanoes. Our results suggest that particle size of volcanic deposits significantly affects the growth pattern of seedlings and should be carefully considered in any stressful system.

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References

Antos, A.J. & Zobel, D.B. 1985. Plant form, developmental plasticity, and survival following burial by volcanic tephra. *Can. J. Bot.* 63: 2083-2090.

Bornkamm, R. 1981. Rates of change in vegetation during secondary succession. *Vegetatio* 47: 213-220.

→ Chambers, J.C., MacMahon, J.A. & Haefner, J.H. 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology* 72: 1668-1677.

→ Chapin, D.M. & Bliss, L.C. 1989. Seedling growth, physiology, and survivorship in a subalpine, volcanic environment. *Ecology* 70: 1325-1334.

Chapin III, F.S. 1993. Physiological controls over plant establishment in primary succession. In: Miles. J., Walton, D.W. (eds.) *Primary succession on land*, pp. 161-178. Blackwell Scientific Publications, London.

Collins, S.L. 1989. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. *Can. J. Bot.* 68: 790-797.

Dale, V.H. 1989. Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Can. J. Bot.* 67: 1434-1441.

del Moral, R. 1993. Mechanisms of primary succession on volcanoes: A view from Mount St Helens. In: Miles, J., Walton, D.W.H. (eds.) *Primary succession on land*, pp. 79-100.Blackwell Scientific Publications, London.

del Moral, R. & Bliss, L.C. 1993. Mechanisms of primary succession: Insights resulting from the eruption of Mount St. Helens. *Adv. Ecol. Res.* 24: 1-66.

del Moral, R. & Clampitt, C.A. 1985. Growth of native plant species on recent volcanic substrates from Mount St. Helens. *Am. Midl. Natur.* 114: 374-383.

del Moral, R. & Wood, D.M. 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio* 74: 11-27.

del Moral, R. & Wood, D.M. 1993. Early primary succession on a barren volcanic plain in Mount St. Helens, Washington. *Am. J. Bot.* 80: 981-991.

del Moral, R., Titus, J.H. & Cook, A.M. 1995. Early primary succession on Mount St. Helens, Washington, USA. *J. Veg. Sci.* 6: 107-120.

Foxworthy, B.L. & Hill, M. 1982. *Volcanic eruptions of 1980 at Mount St. Helens: the first 100 days.* U.S. Geological Survey Professional Paper 1249, U.S. Government Printing Office, Washington, DC.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Bot. Rev.* 52: 107-145.

Hamrick, J.L. & Lee, J.M. 1987. Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). *Am. J. Bot.* 74: 451-457.

Harper, J.L. 1977. *Population biology of plants.* Academic Press, London.

Hitchcock, C.L. & Cronquist, A. 1973. *Flora of the Pacific Northwest.* University of Washington Press, Seattle, WA.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.

Loucks, O.L., Plumb-Mentjes, M.L. & Rogers, D. 1985. Gap processes and large-scale disturbances in sand prairies. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of disturbance and patch dynamics*, pp. 71-83. Academic Press, San Diego, CA.

Meyer, S.E., Garcia-Moya, E. & Lagunes-Espinoza, L. 1992. Topographic and soil surface effects on a gypsophile plant community in central Mexico. *J. Veg. Sci.* 3: 429-438.

Morris, W.F. & Wood, D.M. 1989. The role of *Lupinus lepidus* in succession on Mount St. Helens: facilitation or inhibitory? *Ecology* 70: 697-703.

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, San Diego, CA.

Silvertown, J.W. 1982. *Introduction to plant population ecology.* Longman, New York, NY.

Silvertown, J.W. & Dickie, J.B. 1980. Seedling survivorship in natural populations of nine perennial chalk grassland plants. *New Phytol.* 88: 555-558.

ter Braak, C.J.F. 1987. Ordination. In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.) *Data analysis in community and landscape ecology*, pp. 91-173. Pudoc, Wageningen.

ter Braak, C.J.F. 1988. *Canoco - a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal component analysis and redundancy analysis.* TNO Institute of Applied Computer Science, Wageningen.

Tsuyuzaki, S. 1989. Analysis of revegetation dynamics in the volcano Usu, northern Japan, deforested by 1977-78 eruptions. *Am. J. Bot.* 76: 1468-1477.

Tsuyuzaki, S. 1991. Species turnover and diversity during early stages of vegetation recovery on the volcano Usu, northern Japan. *J. Veg. Sci.* 2: 301-306.

Tsuyuzaki, S. 1994. Fate of plants from buried seeds on volcano Usu, Japan, after the 1977-1978 eruptions. *Am. J. Bot.* 81: 395-399.

Tsuyuzaki, S. 1996. Species diversities analyzed by density and cover in an early volcanic succession. *Vegetatio* 122: 151-156.

Tsuyuzaki, S. & del Moral, R. 1994. Canonical correspondence analysis of early volcanic succession on Mount Usu, Japan. *Ecol. Res.* 9: 143-150.

Tsuyuzaki, S. & Titus, J.H. 1996. Vegetation development patterns in erosive areas on the Pumice Plains of Mount St Helens. *Am. Midl. Nat.* 135: 172-177.

Watkins, A.J. & Wilson, J.B. 1992. Fine-scale community structure of lawns. *J. Ecol.* 80: 15-24.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.

Wood, D.M. 1987. *Pattern and process in primary succession in high elevation habitats on Mount St. Helens.* Ph. D. Thesis, University of Washington, Seattle,WA.

Wood, D.M. & del Moral, R. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780-790.

Wood, D.M. & del Moral, R. 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. *Am. J. Bot.* 75: 1228-1237.

Wood, D.M. & del Moral, R. 1990. Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, Washington. *Am. J. Bot.* 77: 1411-1418.

Wood, D.M. & Morris, M.F. 1990. Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, Washington. *Am. J. Bot.* 77: 1411-1418.

Yamamoto, H. 1984. Erosion of the 1977-78 tephra layers on a slope of Usu Volcano, Hokkaido. *Trans. Jpn. Geomorphol. Union* 5: 111-124.

Zar, J.M. 1984. *Biostatistical analysis.* (2nd ed.) Prentice-Hall, Englewood Cliffs, NJ.

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