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Vegetation development on pumice at Mount St. Helens, USA

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Abstract

This study explores early vegetation development on pumice at Mount St. Helens. We monitored species annually in a grid of 200 contiguous 100-m^2 plots between 1989 and 1999. Of interest were how vegetation changed and if it became more homogeneous over time. Species richness and cover increased annually. Diversity (H') stabilized by 1996 and began to decline as long-lived stress-tolerant species such as *Agrostis pallens, Carex mertensii* and *Penstemon cardwellii* began to dominate. Protected sites had more species and higher cover than did exposed ones. Plots next to relict vegetation had more species and cover than did distant plots. The vegetation initially was dominated by species with good dispersal, but subsequently those with poor dispersal became dominant. We compared species expansion patterns to a model based on random colonization. The results implied that populations with poor dispersal derived from a few colonists that then produced seeds for local expansion. Detrended correspondence analysis showed a pronounced shift in species composition. This analysis also showed that species composition was becoming more homogeneous over time. However, significant heterogeneity remained and some plots are diverging from others. As yet, this vegetation is not developing towards a regional vegetation type. Rather, an unusual community with *Agrostis* spp., *Carex* spp., *Penstemon cardwellii, Lupinus lepidus, Anaphalis margaritacea* and *Salix commutata* has developed. The accumulation phase of primary succession is nearly complete. The next phase, in which vertical structure develops as *Salix* and conifers mature, has scarcely begun. It should be marked by the invasion of forest understory species and loss of subalpine meadow species. Assembly rules based on biotic interactions may then become evident.

Introduction

The eruption of Mount St. Helens has provided the opportunity to examine many aspects of early vegetation development. These include patterns of population expansion, the development of homogeneity and the effects of surviving vegetation on surrounding primary successional areas. Invasion patterns are often described, but mechanisms of community development are not well known. Colonization of new substrates is spatially variable (van der Walk 1992) and the factors that control population expansion are poorly understood. The mechanisms of community formation have been studied intensively on Mount St. Helens since 1980 (del Moral and Bliss 1993). We know that vegetation of isolated sites on Mount St. Helens has not migrated along broad fronts from adjacent vegetation (del Moral 1998) as it does where intact vegetation is next to a new surface (Borgegärd 1990; Allen et al. 1991). Initially, colonization occurs by random long-distance dispersal. Subsequently, vegetation may develop by expansion from these nascent foci (Salonen et al. 1992; Blundon et al. 1993), but there is little direct evidence that this is so.

Heterogeneity measures the internal variation of a community. Convergence occurs when a plant community comes to resemble a more mature local community. While these two concepts are linked, convergence can occur without reduced heterogeneity. Conversely, a community can become homogeneous without convergence. In secondary succession, vegetation often converges on a mature community, in part because the pre-disturbance “signal” can channel development (Christensen and Peet 1984; Inouye and

Tilman 1995). Convergence in primary succession is less certain. The sequence effects and random dispersal that dominate early primary succession result in highly variable vegetation. Factors such as competition and herbivory (Fagan and Bishop 2000) may constrain community composition, but history or chance can create multiple stable states (Samuels and Drake 1997). It is still early to determine if successional vegetation is converging to a local stable community.

Early vegetation developing on primary surfaces is heterogeneous due to random dispersal and scattered favorable microsites. Heterogeneity must decline (Myster and Pickett 1990, 1994), if only by expansion of the initial colonists. Environmental constraints and other species can restrict species distributions and reduce spatial heterogeneity (del Moral 1999b), though environmental heterogeneity can maintain heterogeneous vegetation. Heterogeneity declined on lahars (del Moral 1998) in ways suggesting the importance of landscape factors. Adjacent vegetation can accelerate succession and can result in heterogeneity declines (Dlugosch and del Moral 1999). Isolated sites on Mount St. Helens supported few founders (Wood and del Moral 1987) and received little seed input (Wood and del Moral 2000).

It is unclear to what degree intrinsic habitat variation persists to limit the development of homogeneous vegetation. Primary successional sites on Mount St. Helens have not stabilized (del Moral 2000) as they continue to add species and cover. Some pioneer species are declining in abundance, but these declines appear unrelated to interference from other species.

Communities assemble in three phases: dispersal, environmental selection and internal dynamics (Belyea and Lancaster 1999). Dispersal is spatially dependent and stochastic, while subsequent vegetation development can lead to greater homogeneity. Internal dynamics may involve competition, herbivory, allelopathy or mycorrhizae. Here we explore expansion patterns and developing homogeneity during the first two phases of assembly and the effects of relict vegetation on succession of an isolated, stressful volcanic habitat. The study of changes before the development of internal dynamics will improve the understanding of succession. We ask how early establishment occurs and how subsequent vegetation development unfolds.

Methods

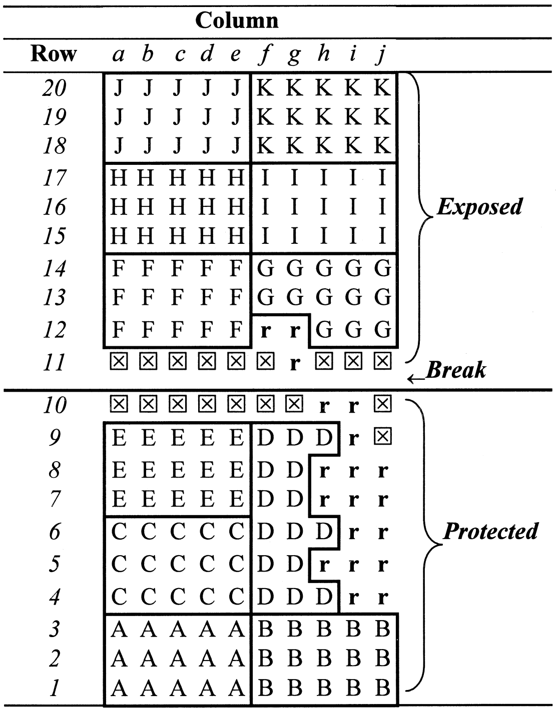
Study site

Mount St. Helens experienced a massive lateral eruption in May of 1980. North and east of the crater, primary succession was initiated on new land formed of pyroclastic materials (del Moral and Bliss 1993). Pumice, frothy rock composed primarily of silica and aluminum oxides, was ejected during the first four main eruptions to form the Pumice Plain. These events provided a unique chance to examine vegetation development (del Moral et al. 1995). We followed this vegetation since its inception (Wood and del Moral 2000). Populations of potential colonists were distant, yet vegetation survived on some north-facing slopes and in gullies (Fuller 1999).

Bakker et al. (1996) demonstrated that permanent plot studies provide information about community development, eliminate concerns associated with chronosequences and help to distinguish directional change from secular variation. The present study demonstrates that they also permit insights into the mechanisms of vegetation development. Each year between 1989 and 1999, we monitored vegetation on pumice on a grid of 200 100-m^2 plots arrayed in 20 rows of 10 plots each. This 2-ha site is 4.5 km northeast of the crater, between 1225 and 1250 m elevation a.s.l. (Lat. 46°13′59″ N, Long. 122°9′34″ W). The lower portion of the grid sloped gently upwards for 50 to 60 m. The slope increased for 30 to 40 m, and then again became gradual. We pivoted the upper half of the grid at a corner to avoid erosion features. The maximum separation between rows 10 and 11 was 8 m. We divided the grid into three portions. Pumice dominated the surfaces except where a gully dissects the grid to reveal original surfaces and surviving (relict, "r", Figure 1) vegetation on 19 plots. The ten lower rows (84 "protected" plots) experience reduced wind, insolation and drought stress. Erosion is slight and more fine material has remained in place. The ten upper rows (97 "exposed" plots) are stressful due to wind and direct insolation, which both increase drought stress. Erosion has removed most fine soil material from the surface.

Vegetation structure

We characterized the grid annually using total and mean richness (species per plot), mean cover index and diversity (H'), calculated with PC-ORD (McCune



	Column										
Row	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	
20	J	J	J	J	J	K	K	K	K	K	
19	J	J	J	J	J	K	K	K	K	K	
18	J	J	J	J	J	K	K	K	K	K	
17	H	H	H	H	H	I	I	I	I	I	
16	H	H	H	H	H	I	I	I	I	I	***Exposed***
15	H	H	H	H	H	I	I	I	I	I	
14	F	F	F	F	F	G	G	G	G	G	
13	F	F	F	F	F	G	G	G	G	G	
12	F	F	F	F	F	**r**	**r**	G	G	G	
11	☒	☒	☒	☒	☒	☒	**r**	☒	☒	☒	***Break***
10	☒	☒	☒	☒	☒	☒	☒	**r**	**r**	☒	
9	E	E	E	E	E	D	D	D	**r**	☒	
8	E	E	E	E	E	D	D	**r**	**r**	**r**	
7	E	E	E	E	E	D	D	**r**	**r**	**r**	
6	C	C	C	C	C	D	D	D	**r**	**r**	***Protected***
5	C	C	C	C	C	D	D	**r**	**r**	**r**	
4	C	C	C	C	C	D	D	D	**r**	**r**	
3	A	A	A	A	A	B	B	B	B	B	
2	A	A	A	A	A	B	B	B	B	B	
1	A	A	A	A	A	B	B	B	B	B	

Figure 1. Grid map. Plots selected to form groups for DCA are shown by capital letters (e.g. A, B, etc.). **r** = relict sites in a gully that were excluded from analysis; ☒ are pumice plots excluded from DCA. Rows 1 to 10 are in the more protected portion of the grid, while rows 11 to 20 are in the more exposed portion of the grid. (The map is arrayed as it would appear to an investigator looking uphill.)

and Mefford 1997). One of us (RdM) estimated cover visually each year with this index: 1 = one to five plants; 2 = six to 20 plants; 3 = > 20 plants *or* 0.25 to 0.5% cover; 4 = > 0.5% to 1% cover; 5 = > 1% to 2% cover; 6 = > 2% to 4% cover; 7 = > 4% to 8%; 8 = > 8% to 16%; 9 = > 16% to 32% and 10 = > 32% (Wood and del Moral 1988). The index sacrifices precision for generality and provides reliable estimates of between plot and between year differences. We compared means using Bonferroni comparisons after any significant one-way ANOVA. We compared subsets of the data within years using t-tests (Analytical Software 1994).

We used these data to study species changes over time with ANOVA and to compare their performances in protected and exposed plots using a t-test. We used index values in detrended correspondence analysis (DCA), classifications and similarity studies (see below). For analyses of relict effects and dispersal, cover percentages of each species were estimated by back transforming index scores: scores of 1 and 2 were converted typical species size when first encountered (Wood and del Moral 1988): Index 1 = 0.06% for small species, 0.09% for intermediate species and 0.12% for large species. Index 2 = 0.08, 0.12 and 0.15%, respectively. We transformed higher scores to the mid-point of their range.

In order to focus on trends rather than seasonal fluctuations, we selected data from years at three-year intervals, plus the most recent year for most analyses. This provided five data sets for comparisons of individual species changes, species expansion, species dispersal, directional vegetation change and similarity. We used the 1999 data to analyze the effects of relicts on surrounding vegetation.

Vascular plant nomenclature follows Titus et al. (1998). Mosses were identified using Vitt et al. (1988). Where no confusion might arise, we use only the genus name.

Species expansion

We explored species expansion patterns with distribution maps we created from data collected in 1989, 1992, 1995 and 1998. This provided sufficient time between samples for changes to be observed. We excluded initially very common species and rare species. For each species in each study year, a ratio of the number of clusters (consisting of occupied contiguous plots) to all occupied plots was calculated. Two plots were "contiguous" if they shared a border. If no occupied plot had an occupied neighbor, the ratio was 1.0. If all occupied plots were in one cluster, the ratio approaches 0.005.

In order to evaluate the observed patterns with respect to the null hypothesis of random colonization from distant populations, a simulation model was developed. For each species, each successive sample years were compared. Input data were the species distribution in a given year (with an empty grid used as the basis for predicting 1989 patterns) and N, the number of newly colonized plots determined from the net increase in the next comparison year. N quadrats were filled randomly, excluding relict and occupied plots. The number of clusters and the ratio of clusters to occupied plots were calculated as above. We repeated the simulation 100 times for each species in each comparison. The mean ratio and its standard deviation were calculated to compare to the observed ratio using a t-test. Simulation distributions were tested for normality using the D'Agostino-Pearson test (Zar 1996).

We classified species by their dispersal ability using the system applied to lahars (del Moral 1998). The five dispersal categories were condensed into poor (the three less able categories), moderate and good dispersers. The dispersal category of most species is shown in Table 2. Other species were poor dispersers except for *Vaccinium membranaceum* Dougl. Ex. Torr. (moderate), *Hieracium gracile* Hook. (good) and ferns (good). The percent cover values for species in each category in each year were summed and the relative scores calculated.

Effects of relict sites

We divided the pumice plots into the 17 next to relict plots (Figure 1) and 164 not touching ("distant") relict plots. A subset of 120 distant plots whose *Lupinus lepidus* cover was less than index 7 was distinguished from the 44 distant plots with dense *Lupinus* cover. We excluded dense *Lupinus* plots because this species is not associated with relict plots and its inclusion could mask real effects. We made the comparisons with the 1999 data to provide the greatest opportunity for cover differentials to develop.

Analyses of heterogeneity

We used three methods to examine heterogeneity. Percent similarity (PS) is a widely used and simple metric that measures floristic similarity. We calculated the percent similarity (which ranges from 0 to 100%) among plots or clusters using this formula:

$$PS_{ij} = 200 \sum_{k=1}^{n} \min(X_{ik}, X_{jk}) / \sum_{k=1}^{n} (X_{ik} + X_{jk})$$

where i and j are two samples, there are n species, X is the cover index and *min* is the lower of the two index values (Kovach 1998). We calculated the mean PS of plots within groups (see below) and among protected and exposed plots of the grid in the five representative years.

Cluster analyses described overall vegetation structure. We used the 1999 data as a template to explore similarity changes within floristic groups. A cluster analysis of 181 pumice plots with minimum variance and squared Euclidean distance of index scores (Kovach 1998) produced 12 well-defined groups (I to XII). This method partitions continuous data well (Kent and Coker 1992). A second cluster analysis, using the farthest neighbor (complete linkage) method with percent similarity, used the data from each of the five years. After the initial fusion, subsequent fusions are based on the minimum distance between the most distant members of a group. This method is robust in relatively homogeneous data and avoids chaining. Eight similarity classes were established *a priori* and the number of fusions (nodes) within each class was determined for each year. This provides a way to evaluate changed in heterogeneity during the study.

Indirect ordination (DCA)

Indirect gradient analyses efficiently summarize complex data and finds trends (Lockwood 1997; del Moral 2000). We used DCA (Hill and Gauch 1980) after down-weighing rare species (frequency < 20%). Axes were rescaled with 26 segments for detrending (McCune and Mefford 1997). In each of the five study years, we divided the grid into eleven composite groups (A to K, Figure 1). Groups A to E were more protected while groups F to K were more exposed. Rows 10 and 11 were excluded to emphasize any distinction between the two portions of the grid. All clusters had 15 plots except G (n = 13) from which relict plots were excluded. We used the mean cover index score of each species in this analysis. We tested for time trends in DCA scores by ANOVA followed by Bonferroni comparisons. We also compared the mean DCA-1 and DCA-2 scores of protected with exposed groups. Finally, we compared the mean PS of groups in each year by ANOVA.

Results

Vegetation structure

Vegetation has developed remarkably since 1989 (Table 1). Total grid richness and of all subsets increased, as did the mean richness. The mean cover index (sum of the index scores) increased annually overall (from 6.5 to 45.0 units) and in all subsets. Mean H' peaked in 1996 and has since declined steadily on pumice. A similar peak occurred in 1993 on relict plots.

We compared richness between protected and exposed plots each year by a t-test. The protected plots always had more species and higher cover per plot than did exposed plots ($P < 0.001$). Moss cover in exposed plots began to develop strongly in 1998, which diminished cover differences between protected and

Table 1. Vegetation structure. Total Richness is the number of all species encountered in the sample; Mean Richness is the number of species per 100 m^2 plot; Mean Cover is the sum of a nonlinear index score for each species in each plot; H' is the mean Shannon information theory statistic (natural logarithm). Comparisons within a row were made by ANOVA followed by Bonferroni comparisons of means. Entries sharing the same superscript are not significantly different ($P < 0.05$).

	Year										
Attribute	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
The Entire Grid, n = 200 plots.											
Total Richness	35	36	41	50	51	51	52	52	52	54	55
Mean Richness	4.4^{a}	5.8^{b}	6.8^{b}	9.0^{c}	10.9^{d}	13.5^{e}	13.5^{ef}	13.9^{ef}	14.9^{fg}	16.0^{gh}	16.5^{h}
Mean Cover Index	6.5^{a}	9.2^{ab}	11.9^{bc}	14.8^{c}	19.1^{d}	25.0^{f}	27.7^{e}	24.6^{e}	33.4^{f}	39.4^{g}	45.0^{h}
Mean H′	1.26^{a}	1.57^{b}	1.67^{bc}	1.84^{cd}	2.02^{def}	2.19^{f}	2.20^{fg}	2.43^{g}	2.12^{ef}	2.05^{def}	1.94^{de}
All Pumice Plots, n = 181 plots.											
Total Richness	28	30	33	39	40	43	45	45	47	48	50
Mean Richness	4.3^{a}	5.7^{ab}	6.6^{b}	8.7^{c}	10.6^{d}	13.1^{e}	13.2^{e}	13.5^{ef}	14.6^{fg}	15.8^{gh}	16.3^{h}
Mean Cover Index	6.0^{a}	8.7^{ab}	10.6^{bc}	13.2^{c}	17.4^{d}	22.7^{ef}	25.2^{f}	21.8^{e}	31.2^{g}	37.6^{h}	43.5^{i}
Mean H′	1.28^{a}	1.57^{b}	1.70^{bc}	1.87^{cd}	2.05^{def}	2.23^{ef}	2.26^{fg}	2.50^{g}	2.17^{e}	2.07^{def}	1.95^{cde}
Pumice, Protected Grid, n = 84 plots.											
Total Richness	28	30	31	35	40	43	42	42	44	45	49
Mean Richness	5.0^{a}	6.7^{b}	8.0^{c}	10.4^{d}	12.3^{e}	13.9^{f}	14.8^{fg}	15.3^{gh}	16.2^{hi}	17.2^{ij}	17.8^{j}
Mean Cover Index	7.5^{a}	10.6^{ab}	13.1^{bc}	15.9^{c}	21.4^{d}	25.1^{de}	30.3^{f}	26.2^{ef}	37.2^{g}	42.8^{h}	48.3^{i}
Mean H′	1.42^{a}	1.70^{b}	1.83^{bc}	2.10^{de}	2.17^{ec}	2.35^{f}	2.38^{f}	2.48^{f}	2.14^{de}	2.04^{de}	1.96^{cd}
Pumice, Exposed Grid, n = 97 plots.											
Total Richness	22	23	23	29	33	32	32	33	37	37	37
Mean Richness	3.6^{a}	4.8^{ab}	5.4^{ab}	7.2^{c}	9.1^{d}	11.2^{e}	11.8^{e}	12.1^{ef}	13.2^{fg}	14.6^{gh}	14.9^{h}
Mean Cover Index	4.7^{a}	7.1^{a}	8.4^{ab}	11.0^{bc}	14.0^{c}	20.6^{d}	21.0^{d}	17.9^{d}	26.1^{e}	33.2^{f}	39.3^{g}
Mean H′	1.15^{a}	1.46^{ab}	1.59^{abc}	1.68^{bcd}	1.95^{cde}	2.12^{def}	2.15^{ef}	2.53^{f}	2.21^{ef}	2.10^{def}	1.94^{cde}
Relicts, n = 19 plots.											
Total Richness	22	23	25	31	33	37	36	39	38	40	40
Mean Richness	5.7^{a}	7.0^{a}	8.8^{ab}	12.1^{bc}	13.7^{cd}	16.8^{de}	16.9^{de}	17.4^{e}	17.4^{e}	17.8^{e}	18.5^{e}
Mean Cover Index	12.0^{a}	14.5^{ab}	25.0^{bc}	29.6^{c}	34.5^{c}	46.9^{d}	51.7^{d}	52.0^{d}	53.4^{d}	54.9^{d}	57.9^{d}
Mean H′	1.36^{a}	1.58^{ab}	1.34^{a}	1.52^{ab}	1.73^{ab}	1.86^{b}	1.64^{ab}	1.66^{ab}	1.63^{ab}	1.82^{b}	1.79^{b}

exposed sites. Forest understory shrubs such as *Rubus, Ribes* and *Sambucus* dominated the 19 relict plots, and *Epilobium angustifolium* and *Anaphalis* thrived in the old soil. Relict richness was similar to the protected pumice plots, but cover was higher. Strong dominance by a few woody species reduced mean H' in relict plots compared to pumice.

Table 2 compares mean cover index scores for 22 common taxa through time and between protected and exposed plots. Conifer cover has not increased. The few seedlings suffer high mortality. Cover of all other species increased significantly. Most are less abundant in exposed plots, though the pioneer *Anaphalis* has declined in protected sites and increased in exposed sites. Pioneers *E. angustifolium, Hieracium* and *Hypochaeris* are similar in both sets.

Expansion patterns

Wood and del Moral (1988) noted that pumice sustained few individuals in 1986. In 1989, we found 21 sufficiently rare species for this analysis. Wood and del Moral (2000) showed that *Anaphalis* (29%) and *Epilobium angustifolium* (32%) accounted for most of the seed rain on pumice during 1989 and 1990. It is not surprising that they were too common to include

Table 2. Development of common species on the primary surfaces of the protected (n = 84) and exposed grid (n = 97). Values are mean cover index scores. P = protected plots; E = exposed plots. P is significance of changes in a species, determined by one-way ANOVA (** = $P < 0.01$; *** = $P < 0.001$; n.s. = $P > 0.05$.) For each species, values in exposed rows marked by (^{a}) are significantly different from the value in the protected row ($P < 0.05$, by t-test).

Species	Dispersal	P/E	1989	1992	1995	1998	1999	P
Abies spp.	Poor	P	0.05	0.11	0.13	0.31	0.18	n.s.
		E	0.00	0.01^a	0.04	0.07	0.05	n.s.
Agrostis pallens Trim.	Poor	P	0.07	0.49	1.63	1.71	1.51	***
		E	0.04	0.34	0.91^a	1.78	1.57	***
Agrostis scabra Willd.	Poor	P	0.01	0.23	1.21	3.38	3.89	***
		E	0.00	0.20	1.41	3.63	4.75^a	***
Anaphalis margaritacea (L.) B. & H.	Good	P	2.30	2.36	2.96	2.30	3.89	n.s.
		E	1.54^a	2.16	3.36^a	3.05^a	2.55^a	***
Carex microptera MacKenzie	Poor	P	0.26	0.48	0.99	1.14	1.40	***
		E	0.08^a	0.12^a	0.38^a	0.67^a	0.97^a	***
Carex mertensii Prescott ex Bong.	Poor	P	1.10	1.51	3.36	3.70	3.75	***
		E	0.81^a	0.68^a	2.11^a	2.81^a	3.10^a	***
Carex pachystachya Cham. ex Steud	Poor	P	0.17	0.54	1.91	1.10	1.45	***
		E	0.01^a	0.50	0.84^a	0.74^a	1.15^a	***
Epilobium anagallidifolium Lam.	Good	P	0.08	0.34	0.49	0.52	0.43	**
		E	0.07	0.05^a	0.26^a	0.41	0.41	***
Epilobium angustifolium L.	Good	P	1.06	1.31	1.57	1.91	1.62	***
		E	0.86	1.20	1.49	1.85	1.43	***
Hieracium albiflorum Hook.	Good	P	0.59	0.99	1.23	1.04	1.07	***
		E	0.42^a	0.95	1.13	1.21	1.22	***
Hypochaeris radicata L.	Good	P	0.29	1.38	1.63	1.04	1.35	***
		E	0.32	1.32	1.38^a	1.41^a	1.53	***
Juncus mertensianus Bong.	Poor	P	0.06	0.21	0.30	1.06	1.19	***
		E	0.01^a	0.01^a	0.11^a	0.28^a	0.32^a	***
Juncus parryi Engelm.	Moder	P	0.06	0.14	0.42	0.89	0.89	***
		E	0.01^a	0.14	0.36	0.72^a	0.70^a	***
Luetkea pectinata (Pursh.) Kuntzel	Poor	P	0.14	0.33	0.54	1.22	0.95	***
		E	0.08	0.19	0.41	0.85^a	1.09	***
Lupinus lepidus Dougl.	Poor	P	0.23	1.37	2.26	3.44	6.31	***
		E	0.18	0.68^a	1.41^a	2.00^a	3.84^a	***
Luzula parviflora (Ehrh.) Desv.	Poor	P	0.07	0.25	0.83	1.50	1.05	***
		E	0.01^a	0.05^a	0.29^a	0.37^a	0.43^a	***
Penstemon cardwellii J. T. Howell	Poor	P	0.25	0.65	2.85	4.55	3.67	***
		E	0.13	0.46^a	2.27^a	3.67^a	3.43	***
Pseudotsuga menziesii (Mirb.) Franco	Poor	P	0.13	0.14	0.20	0.32	0.35	n.s.
		E	0.05	0.03^a	0.09	0.14	0.16	n.s.
Salix commutata Bebb.	Good	P	0.08	0.37	1.12	2.61	3.06	***
		E	0.00^a	0.09^a	0.70^a	1.92*	2.33*	***
Saxifraga ferruginea Graham	Moder	P	0.26	1.77	2.26	3.59	2.77	***
		E	0.06^a	0.53^a	0.96^a	1.72^a	1.23^a	***
Polytrichum spp.	Poor	P	0.00	0.03	0.26	1.97	2.12	***
		E	0.00	0.03	0.13^a	1.56^a	1.94	***
Racomitrium canescens (Itwdw.) Brid.	Poor	P	0.00	0.08	0.36	2.15	2.24	***
		E	0.00	0.08	0.19^a	1.20^a	1.30^a	***

here. However, *Hieracium albiflorum* and *Hypochaeris* also had measurable seed rains, but were sparse in 1989. Species such as *Agrostis pallens, Carex mertensii, Hieracium albiflorum, Hypochaeris, Lupi-*

Table 3. Expansion of species on the grid. Observed (OB) values are ratios of the number of groups to the number of occurrences in 181 primary plots. SIM is the mean ratio simulated on the basis of random invasions. Ratios range from < 0.01 when all occurrences are in contiguous plots to 1.0 when no plots are contiguous. The 1989 simulation is based on a previously empty grid. SIM was compared to OB via a t-test ([a] = P < 0.05; [b] = P < 0.01; [c] = P < 0.001). Significant differences are shown in bold.

Species	1989	1989	1992	1992	1995	1995	1998	1998
	SIM	OB	SIM	OB	SIM	OB	SIM	OB
Abies spp.	0.98[1]	1.0	0.92[1]	0.89	N/A[3]	0.67	0.75	0.73
Agrostis pallens	0.91[1]	0.80	0.37	0.38	N/A[2]	0.04	N/A[2]	<0.01
Agros scabra	—	—	0.69	**0.54**[a]	N/A[2]	0.03	N/A[2]	<0.01
Carex microptera	—	—	0.52	**0.24**[c]	0.20	0.16	N/A[2]	0.09
Carex mertensii	0.15	**0.09**[a]	N/A[2]	<0.01	N/A[2]	<0.01	N/A[2]	<0.01
Carex pachystachya	0.76	**0.38**[c]	0.21	0.14	N/A[2]	0.02	N/A[2]	0.02
Epilobium anagallidifolium	0.90	1.0	0.72	**0.40**[c]	0.35	**0.20**[b]	0.21	0.18
Hieracium albiflorum	0.26	**0.15**[b]	N/A[2]	<0.01	N/A[2]	<0.01	N/A[2]	<0.01
Hypochaeris radicata	0.52	**0.39**[a]	N/A[2]	<0.01	N/A[2]	<0.01	N/A[2]	<0.01
Juncus mertensianus	0.95[1]	1.0	0.83	**0.47**[c]	0.54	0.54	0.38	**0.29**[a]
Juncus parryi	0.95[1]	1.0	0.75	0.67	0.42	**0.30**[a]	0.18	0.23
Luetkea pectinata	0.83	0.88	0.70	**0.57**[a]	0.53	0.48	0.33	**0.23**[b]
Lupinus lepidus	0.73	**0.34**[c]	N/A[2]	0.08	N/A[2]	<0.01	N/A[2]	<0.01
Luzula parviflora	0.96[1]	1.0	0.84	**0.58**[c]	0.45	**0.16**[c]	0.21	**0.14**[b]
Penstemon cardwellii	0.70	0.69	0.17	0.16	N/A[2]	<0.01	N/A[2]	<0.01
Poa secunda J. Presl.	0.97[1]	1.0	0.97[1]	1.0	0.90	**0.75**[a]	0.70	0.63
Pseudotsuga menziesii	0.86[1]	0.75	N/A[3]	0.50	0.58	0.55	0.55	0.63
Salix commutata	0.96[1]	1.0	0.69	**0.50**[b]	0.18	0.15	N/A[2]	0.05
Saxifraga ferruginea	0.82	**0.60**[b]	0.20	**0.11**[b]	N/A[2]	0.05	N/A[2]	0.02
Polytrichum ssp.	—	—	—	—	0.84	**0.65**[a]	0.22	0.19
Racomitrium canescens	—	—	0.89	0.88	0.60	0.52	N/A[2]	0.07

[1] Simulation distribution failed the D'Agostino-Pearson normality test (Zar 1996)

[2] Frequency exceeded 100 plots so simulations were not conducted.

[3] Turnover led to lower frequency in subsequent year making simulation impossible.

nus and *Penstemon* each expanded from a few sites to form a single cluster by 1998; species such as *Carex microptera, Epilobium anagallidifolium, Juncus mertensianus, J. parryi, Luetkea, Luzula, Poa, Salix, Saxifraga* and the mosses developed more slowly. The ratio of cluster number to frequency always declined, though in theory the ratio could increase because random invasions could form more, isolated, clusters.

The simulation model provided a conservative test of which of these patterns resulted from random invasion rather than expansion from local seed sources (Table 3). Except for *Abies* spp. and *Pseudotsuga menziesii*, frequency always increased between years and turnover (at the 100-m^2 scale) was very low. Simulation distributions were skewed if species occupied < 15 plots, invalidating t-tests. In any case, the observed ratios of infrequent species were usually similar to the random simulations, suggesting that rare species continue to invade from a distance, or that establishment is rare. Once species occupy more than 100 plots, the expected cluster ratio was so low as to render detection of departures from random impossible.

Most species with intermediate frequencies had a significantly lower cluster ratio than would be expected by random dispersal (Table 3). Several species with no significant difference were those for which random dispersal was expected because they have yet to reproduce on the grid. *Agrostis pallens* and *Penstemon*, each with moderate dispersal ability, did not have significantly lower ratios. However, other species with good dispersal did demonstrate significant clustering. These included *Hieracium albiflorum* and *Hypochaeris*, species not spatially restricted on the grid. *Salix commutata* has yet to produce seeds here, yet it demonstrated significant clustering, perhaps because it is restricted from some plots.

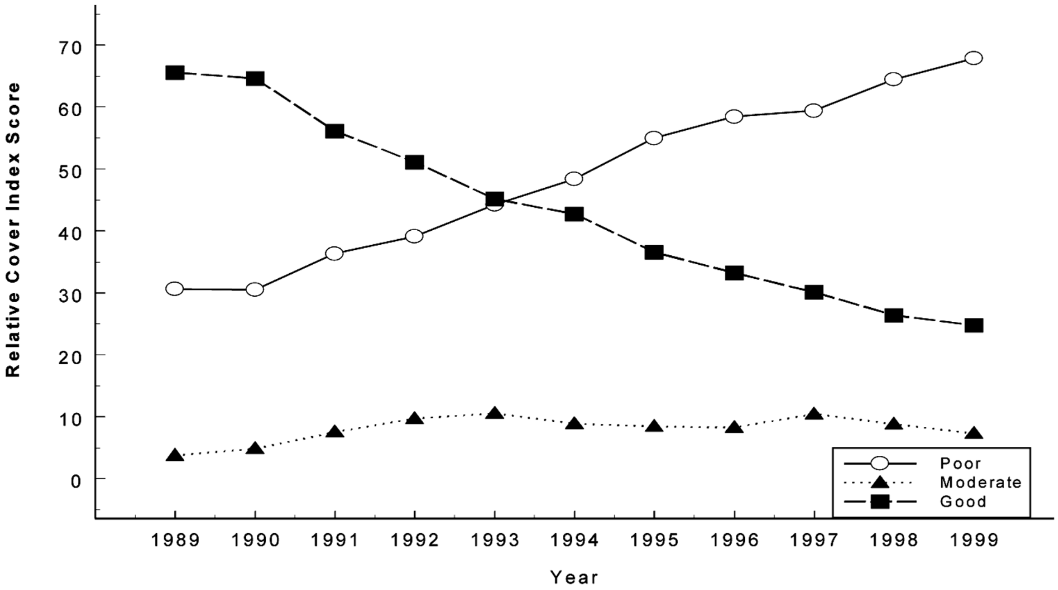


Figure 2. Relative cover of poor, moderate and good dispersers calculated from cover index scores.

Analysis of invasion by dispersal ability confirmed that early dominants were primarily those with good dispersal (Figure 2). In 1989, over 65% of cover was from the eight good dispersers. By 1999, relative cover of the 21 poor dispersers increased to 68%. Absolute cover of poor dispersers increased from 2 to 27 cover units, while the four moderate dispersers increased from 0.2 to 3.3 cover units and good dispersers increased only from 3.8 to 9.8 cover units.

Analysis of heterogeneity changes

We explored changing vegetation heterogeneity in three ways. PS evaluates heterogeneity directly. By geographically clustering plots, we investigated an intermediate spatial scale to determine if parts of the grid are becoming more or less similar as revealed by DCA. Cluster analyses investigated whether community structure was becoming homogeneous.

We calculated mean PS within protected and exposed pumice for each year to explore large-scale heterogeneity changes (Table 4). Similarity among protected pumice plots peaked in 1995 at 69.4%, then declined slightly due to large increases in *L. lepidus* in 1998 and 1999. Bonferroni comparisons showed that each year differed from all others. A similar pattern occurred among exposed plots, which became more similar through 1998, then declined. PS was always higher in protected plots than in exposed ones. This analysis showed a widespread reduction in heterogeneity, with the pattern delayed in the more exposed upper plots.

Table 4. Percent Similarity, 1989–1999, on protected and exposed portions of the grid. Each value within a row is significantly different from all others (Bonferroni comparison of means, $P < 0.05$). Percent similarity values in each column are significantly different by t-test ($^a = P < 0.05$; $^c = P < 0.0001$).

	Year				
Habitat	1989	1992	1995	1998	1999
Protected[1]	48.3	55.5	69.4	67.5	66.4
(s.d.)	(18.3)	(13.4)	(7.4)	(7.2)	(7.8)
Exposed[1]	46.8^a	48.2^c	61.8^c	65.2^c	63.0^c
(s.d.)	(18.6)	(18.2)	(11.2)	(9.1)	(8.7)

[1] One-way ANOVA significant $P < 0.0001$

We grouped pumice plots into 11 spatial groups (Figure 1) and analyzed them by DCA to focus on trends at a larger scale. The eigenvalue of DCA-1 was 4.3 times greater (0.165) than that of DCA-2 (0.036) and represented 43.7% of the variation. Each of the groups (A to K) shifted downward along DCA-1 (Figure 3). Bonferroni comparisons of means indicated that DCA-1 scores declined significantly in each year (Table 5). Standard deviations of DCA-1 scores were low in 1989 due to low cover and richness, but jumped dramatically. Thereafter, there was a decline. Changes in mean similarity also implied that overall homogeneity increased. Mean PS among the groups increased from 67.5% in 1989, through 69.4%, 76.1%, and 78.4%, and to 80.2% in 1999 (ANOVA,

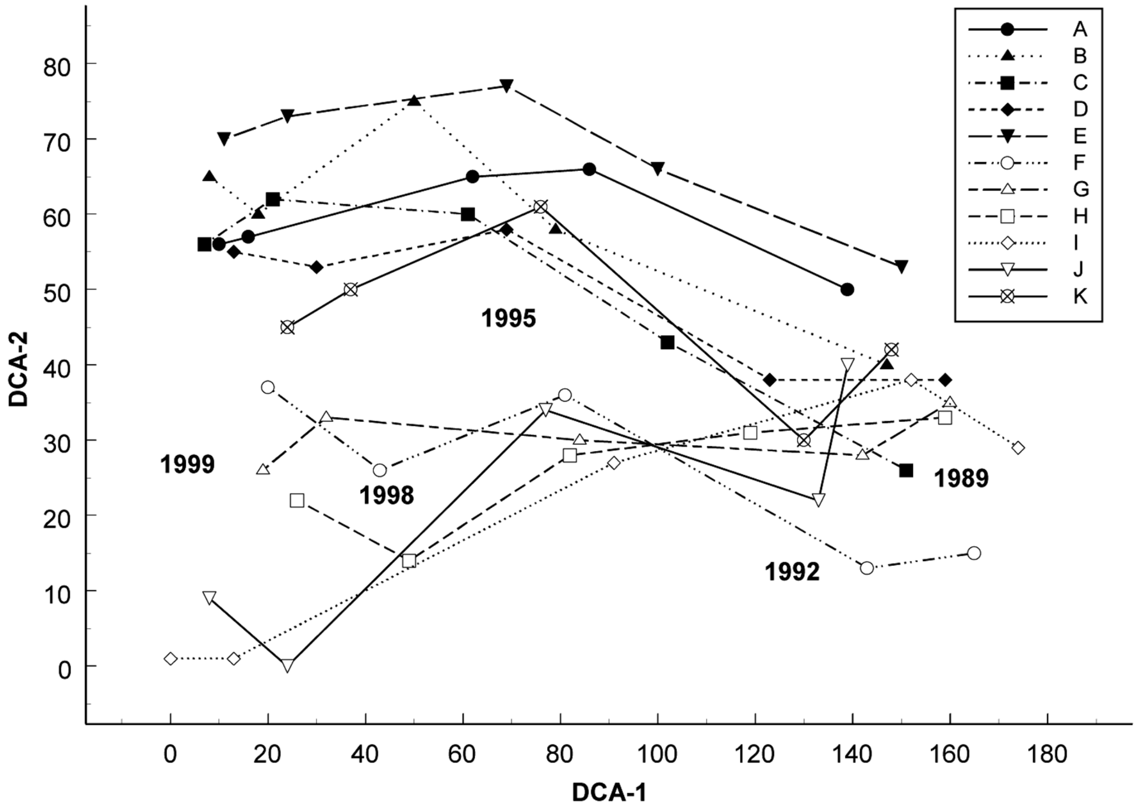


Figure 3. Detrended correspondence analysis of 11 composite groups on the grid. Lines connect the same plots in successive years.

Table 5. Change in percent similarity and mean DCA scores in eleven composite plots on pumice. DCA means were compared by ANOVA; significant patterns were tested by Bonferroni comparisons, P <0.05. Differences between protected and exposed plots were determined by t-test (* = P < 0.01).

	Years					
Attribute	1989	1992	1995	1998	1999	ANOVA
Percent Similarity	67.5	69.4	76.1	78.4	80.2	P < 0.0001
DCA-1 score	153.6^{a}	118.7^{b}	72.8^{c}	27.9^{d}	13.3*e*	P < 0.0001
DCA-1 s.d.	[10.6]	[24.0]	[12.0]	[11.4]	[8.0]	
DCA-2 score	36.4	39.4	50.4	39.0	40.2	n.s.
DCA-2 s.d.	[10.8]	[17.5]	[19.4]	[25.6]	[23.0]	
DCA-1, protected	149.2^{a}	98.0^{b}	62.2^{c}	21.5^{d}	9.8^{d}	P < 0.0001
DCA-1, exposed	157.3^{a}	136.0^{b*}	81.7^{c*}	33.0^{d}	16.2^{d}	P < 0.0001
DCA-2, protected	41.4	54.2	67.4	61.0	60.4	n.s.
DCA-2, exposed	32.3	26.5*	30.8*	24.0*	23.7*	n.s.

P < 0.0001). Increasing similarity is due to declines in the relative importance of pioneers (*Anaphalis, Hieracium* spp., *Epilobium* spp. and *Hypochaeris*) and increases in persistent species (*Penstemon, Racomitrium, Polytrichum* spp., *Carex paysonis, Salix, Juncus mertensianus* and *Agrostis* spp.).

Figure 3 implies that the protected plots (Groups A to E) differ from the exposed plots in both dimensions. We compared DCA scores of protected plots to

Table 6. Percent Similarity, 1989–1999, within 12 clusters defined by species composition in 1999. Values with the same superscript fall within the same homogeneous group (Bonferroni comparisons of means after ANOVA, $P < 0.05$). N is the number of plots in the group.

Group	N	Dominants, ordered by cover[1]	1989	1992	1995	1998	1999
I	17	*Agsc, Saco, Peca, Came*	49.0^{a}	60.0^{a}	67.6^{b}	69.8^{b}	68.8^{b}
II	18	*Agsc, Peca, Raca, Came, Lule*	48.4^{a}	47.2^{a}	61.4^{b}	66.0^{c}	69.6^{c}
III	28	*Agsc, Peca, Lule, Came, Anma*	48.2^{a}	51.9^{b}	59.4^{c}	65.4^{d}	65.1^{d}
IV	9	*Lule, Agsc, Came, Anma, Epan*	37.4^{a}	56.4^{b}	68.0^{c}	67.9^{c}	66.9^{c}
V	13	*Lule, Agsc, Peca, Came, Anma*	50.0^{a}	57.3^{b}	65.8^{c}	65.8^{c}	72.6^{d}
VI	13	*Lule, Agsc, Peca, Saco, Came, Lupe*	37.3^{a}	56.4^{b}	68.6^{c}	69.1^{c}	73.9^{d}
VII	17	*Lule, Came, Peca, Agsc, Saco, Safe*	43.7^{a}	55.5^{b}	68.3^{c}	67.9^{c}	73.7^{d}
VIII	22	*Lule, Posp, Agsc, Peca, Came, Saco*	35.6^{a}	58.3^{b}	63.8^{c}	71.0^{d}	70.1^{d}
IX	13	*Lule, Agsc, Posp, Peca, Came*	46.6^{a}	52.4^{b}	67.1^{c}	69.4^{c}	71.8^{c}
X	7	*Lule, Posp, Agsc, Came, Saci*	45.4^{a}	67.3^{b}	69.9^{b}	74.3^{c}	74.5^{c}
XI	12	*Lule, Agsc, Peca, Saco, Safe*	59.4^{a}	63.5^{b}	75.1^{c}	74.5^{c}	80.9^{d}
XII	13	*Lule, Came, Agsc, Saco, Raca*	44.6^{a}	63.8^{b}	69.2^{b}	69.5^{b}	69.4^{b}

[1] Code: *Agsc* = *Agrostis scabra*; *Anma* = *Anaphalis margaritacea*; *Lule* = *Lupinus lepidus*; *Came* = *Carex mertensii*; *Safe* = *Saxifraga ferruginea*; *Saco* = *Salix commutata*; *Peca* = *Penstemon cardwellii*; *Posp* = *Polytrichum* sp.; *Raca* = *Racomitrium canescens*; *Epan* = *Epilobium angustifolium*

Table 7. Development of plant community structure. Values are the number of fusions in the similarity class of an agglomerative clustering conducted using Percent Similarity and Farthest Neighbor clustering. (Large number of fusions at high similarities in 1989 due to low species richness).

Year	Similarity Class (Percent)							
	0	1–20	20.1–40	40.1–50	50.1–65	65.1–80	80.1–90	>90
1989	6	4	27	6	27	62	21	27
1992	2	2	12	14	34	77	34	4
1995	0	1	4	9	26	79	60	1
1998	0	0	4	6	25	87	57	1
1999	0	0	4	6	31	85	52	2

those of the exposed plots using t-tests (Table 5). Scores of exposed plots were always higher than protected sites in DCA-1; thus, changes develop more slowly in exposed plots. DCA-2 scores did not change significantly, though the trends in protected and exposed plots were in opposite directions. Exposed plots differed significantly from protected plots along DCA-2 in each year except 1989.

The five protected groups became homogeneous (Figure 3). Groups I and J developed close similarities based on *Lupinus, Racomitrium* and *Polytrichum* ssp. and diverged from the other groups. The mosses appear to have developed where erosion has removed fine material, leaving a coarse surface to protect establishing mosses. These initially barren plots now have substantial cover and lower DCA-1 scores than the protected groups (Figure 3).

We describe the 12 floristic groups determined with the 1999 data in (Table 6). Similarity of each increased from 1989 to 1998 (ANOVA, $P < 0.05$). Some groups became more homogeneous than others. Within-group similarity was stabilized by 1995 in Groups I, IV and XII, and were similar in 1998 and 1999 in Groups III, VIII, IX and X, but continues to increase in the remaining five groups. This suggests that further change should occur in some groups.

Farthest-neighbor classification with PS showed moderate homogeneity (Table 7). In 1989, there were plots in each previously determined similarity class. The large number of fusions in high similarity classes in 1989 resulted from many plots with low richness. As vegetation developed, no plot was less than 20% similar to another, and two linkages occurred above 90%. Fusion levels stabilized in the 65 to 80% range, though the recent pulse of *Lupinus* cover lowered fusion levels. Even in 1999, ten fusions occurred below 50% similarity, suggesting significant, persistent heterogeneity on the grid.

Table 8. Effect of refugia on surrounding plots. Richness is the mean number of species per plot; Cover Index is the mean total cover index per plot; Cover Percent is the total index converted to absolute cover on a per-species basis; and H' is the Shannon information statistic. Adjacent = plots next to relicts; Distant = all plots not next to relicts; Distant less *Lupinus* = distant plots excluding plots with *Lupinus* having an index of 7 or more. *N* is the number of plots in the sample. Comparisons of each attribute are to the adjacent plots. Superscripts indicate significant differences (t-test: ^{a} = $P < 0.05$; ^{c} = $P < 0.001$).

	Attributes			
Habitat, *N*	Richness	Cover Index	Cover Percent	H'
Adjacent, 17	17.8	46.2	6.71	2.14
Distant, 164	16.1^a	43.2	7.88^a	1.94
Distant less dense *Lupinus*, 120	15.3^c	37.0^c	4.20^c	2.11

Effects of relict habitats

Relict plots measurably impacted adjacent barrens (Table 8). Refugia had little *Lupinus* cover (mean cover = 0.1%, mean index = 1.7). Adjacent plots (n = 17) had more species than either distant plots (164) or distant plots with low *Lupinus* cover (n = 120). The latter group had 2.5 fewer species per plot than the plots adjacent to relict sites. All distant plots had a lower cover index than adjacent plots, despite the abundance of *Lupinus* in 1999. Those distant plots lacking dense *Lupinus* had a significantly lower cover index than adjacent plots. Distant plots without dense *Lupinus* had lower cover percent than did plots next to refugia, while distant plots with dense *Lupinus* had much higher cover percent than did the plots adjacent to refugia.

Discussion

This study revealed substantial development of early successional vegetation on pumice. Vegetation structure continues to develop, but more slowly than in early years. For several years after the eruption, no plants were found on pumice (Wood and del Moral 1988), despite a measurable seed rain (Wood and del Moral 2000). Some colonists were observed by 1985, always in favorable microsites (del Moral and Wood 1993; del Moral 1993b). As pumice decomposed to eliminate safe-sites (Titus and del Moral 1998) and surfaces stabilized, *Lupinus* improved soil through nitrogen fixation (Halvorson and Smith 1995) and soil organic matter increased through dry deposition (Edwards and Sugg 1993; Sugg and Edwards 1998). As a result, mosses began to colonize widely only after 1992. Species such as *Penstemon* and *Luetkea* continue to expand from vegetatively initial establishment sites and populations of *Carex mertensii*, *Agrostis scabra*, *Lupinus* and *Saxifraga* have expanded greatly due to locally-produced seeds. The pool of available species for barrens is relatively small. del Moral and Wood (1988b) noted that the flora of Mount St. Helens before the eruption was smaller than surrounding volcanoes. Titus et al. (1998) listed 151 upland native species on the Pumice Plain barrens. Of these, 27 are widespread on the barrens and 22 are common, but not present throughout the area. The grid contains 26 of the widespread species and 15 common ones. The missing common species are from moist habitats and wetland edges. It is unlikely that more than a few additional native species will establish on the grid until *Salix* or conifers begin to alter the environment.

Mean richness continues to increase, now almost entirely by the spread of existing species. Cover continues to increase. The *Lupinus* expansion suggests that facilitation will increase productivity since nitrogen, produced symbiotically, eventually becomes available to other species (del Moral 1993a; Halvorson and Smith 1995). Competition cannot be demonstrated without experiments, but declining H' implies that dominance hierarchies are developing. Species with spreading root systems (e.g., *Carex mertensii*) or prostrate stems (e.g., *Penstemon*) will probably exclude some species. This intensifying interaction phase should produce better correlations between species and environment (del Moral 1999a) and greater predictability.

Species accumulation and spread characterized the first 20 years of primary succession. When a third dimension of vegetation develops, biomass accumulation should intensify and new species should invade (Debussche and Lepart 1992). These will be dominated by bird-dispersed species and mesophytes restricted to favorable microsites, refugia or wetlands (Titus et al. 1999).

The early seed rain during species accumulation was almost exclusively composed of wind-dispersed species such as *Anaphalis*, *Epilobium* spp., *Hieracium* spp. and *Salix* spp. (Wood and del Moral 2000). Input of species now common was extremely low before local seed production. Therefore, even a single plant setting seed on the grid must have produced many more local seeds than could be introduced from long distances.

Most species established in favorable microsites, set seed and contributed directly to further population growth. Initially sparse populations developed in several ways. *Anaphalis* and *E. angustifolium* colonized rapidly and were widely distributed by 1989. *Anaphalis* routinely sets seed on the grid and contributed strongly to early local recruitment. In contrast, *Epilobium* rarely flowers under these conditions of limited nutrients and seedlings are recruited from refugia or long distances. Woody species (e.g., *Salix* and conifers) invading pumice require many years to mature, so their colonization must be from long-distance dispersal. Population expansion of the other species resulted primarily from locally produced seeds and led to population clustering, as shown by the simulation. Species that produce many seeds with moderately good seed dispersal and tolerance for harsh conditions formed a single group of contiguous plots by 1998 (e.g., *Agrostis* spp., *Carex mertensii*, *Hieracium*, *Lupinus* and *Penstemon*). Species with either less efficient dispersal (e.g., *Carex pachystachya*, *Juncus parryi*, *Luetkea* and *Poa*) or less tolerance for pumice (e.g., *Carex microptera*, *Juncus mertensianus*, *Luzula*, *Polytrichum* ssp. and *Racomitrium*) have not yet fully colonized the grid. That relative dominance changes among dispersal types suggested that poorly dispersed species grew better than did good dispersers.

Most primary successional situations are initially very heterogeneous due to stochastic immigration and few safe-sites (Chesson and Case 1986). As vegetation matures, it normally becomes more homogeneous unless further disturbance precludes homogeneity. However, the presence of environmental gradients, resource variation or the sporadic occurrence of woody plants (Sterling et al. 1984; Debussche and Lepart 1992) can also limit homogeneity.

The PS among the 11 spatially determined vegetation groups increased significantly (from 67.5% to 80.2%). This suggests a trend towards one local vegetation type at the scale of the composite plots used (0.15 ha). However, while protected plots appear to be very similar, (Figure 3), exposed plots have developed differently. The 11 spatially determined groups continue to change directionally in DCA, with no indication that they have equilibrated or that the grid has become uniform. Some exposed groups have increased their differences from the protected groups. The rate of change may accelerate when conifers and willows become dominant because they will reduce habitat variation.

Heterogeneity also decreased on the scale of individual plots, but may have stabilized. This is shown by the overall PS in both the exposed and protected pumice (Table 4) and by farthest-neighbor classifications (Table 6). These results support the conclusions of DCA that while overall heterogeneity was reduced, environmental variation sustains persistent differences. The last four clusters to merge in 1999 were found in protected sites, moderately exposed sites, exposed sites with high *Lupinus* and exposed sites with little *Lupinus*. It is unlikely that these floristic differences will be reduced further, at least until trees or tall shrubs dominate. Therefore, this is evidence for parallel or even divergent succession (Samuels and Drake 1997) based on initially random dispersal followed by environmental filters in different microhabitats. While the several analyses indicate increasing similarity, differences have persisted. The mean similarity among the stressful plots is always lower than that of the more protected lower grid.

While vegetative heterogeneity has decreased, the vegetation does not appear to be converging towards an external "target" found elsewhere. This combination of dominant species, a variable mixture of *Agrostis* spp., *Carex mertensii*, *Penstemon*, *Lupinus* and *Salix*, does not occur in this region. Lockwood (1997) emphasized that "natural" communities are often only one of several possible results of past events and that input order can strongly affect successional trajectories. Since the Pumice Plains was formed by a regionally unique set of events, it should not be surprising that novel communities have developed or that each may persist indefinitely in subtly different habitats within a small area.

Vegetation may become homogeneous while still undergoing change if there is directional turnover (del Moral 2000) or a sequence of species becomes dominant. On pumice, there has been little turnover and no dominant has been replaced completely by a competitively superior dominant. However, directional composition change has occurred (Figure 3), and will continue. There is ample room for some species (e.g., *Agrostis pallens*, *Carex paysonis*, *Juncus mertensianus*, *J. parryi*, *Luetkea*, *Polytrichum* and *Saxifraga*) to continue expansion, even though roots fill proportionately more soil volume than stems cover the surface.

Landscape ecology theory states that the vegetation of a newly created site will be strongly influenced by the surroundings (Borgegärd 1990; Larson and Bliss 1998; Fuller 1999; Wiegleb and Felinks 2000). Relict sites on the Pumice Plain had two effects on adjacent pumice. First, the soil of these sites was relatively rich and the sites open, so they were readily colonized. Typical invading species were much denser in relict sites than in typical pumice. For example, in 1999, the mean index value of *Anaphalis* on pumice was 2.2, while in relicts it was 5.4; *Epilobium angustifolium* on pumice averaged 1.53, while in relicts it averaged 7.3. Similar contrasts occurred for other invaders such as *Hypochaeris*, *Saxifraga* and *Salix*. These invaders dispersed many seeds to adjacent pumice. Second, biomass from relict species was exported to physically ameliorate adjacent plots. The present study demonstrates that mature vegetation has a subtle role on surrounding vegetation, even though relict species themselves do not invade barren sites. Excluding *Lupinus*, plots immediately adjacent to relicts had more species and were more densely vegetated than distant plots lacking dense *Lupinus* populations. This result supports the conclusion of Fuller (1999) that relicts are nurseries for pumice species and accelerate amelioration of their immediate neighborhood.

Monitoring vegetation on this permanent 2-ha plot found that during accumulation, a diverse, open and variable vegetation developed. Early colonists were nearly all wind-dispersed species. Later arriving species were better adapted to stressful habitats on pumice (Wood and del Moral 1987), and the environment has selected for longer-lived, stress tolerant species. Existing populations are coalescing as soil fertility improves. This process is more rapid near relict and on more protected sites. Interactions among plants that might reveal assembly rules (*sensu* Belyea and Lancaster (1999)) remain subtle. The next phase, in which vertical structure develops and biotic interactions strengthen, is incipient. When existing *Salix* mature and conifers survive in significant numbers, species restricted to refuges or mesic sites will colonize and competitive interactions will intensify. Continued monitoring will permit a detailed examination of a successional transition driven by biotic interactions that are rarely observed directly.

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References

Analytical Software 1994. Statistix 4.1 User's Manual. Analytical Software, Tallahassee, FL.

Allen L.J.S., Allen E.J., Kunst C.R.G. and Sosebee R.E. 1991. A diffusion model for dispersal of *Opuntia imbricata* (cholla) on rangeland. Journal of Ecology 79: 1123–1135.

Bakker J.P., Olff H., Willems J.H. and Zobel M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics. Journal of Vegetation Science 7: 147–155.

Belyea L.R. and Lancaster J. 1999. Assembly rules within a contingent ecology. Oikos 86: 402–416.

Bishop J.G. and Schemske D.W. 1998. Variation in flowering phenology and its consequences for lupines colonizing Mount St. Helens. Ecology 79: 534–546.

Blundon D.J., MacIsaac D.A. and Dale M.R.T. 1993. Nucleation during primary succession in the Canadian Rockies. Canadian Journal of Botany 71: 1093–1096.

Borgegärd S.O. 1990. Vegetation development in abandoned gravel pits: effects of surrounding vegetation, substrate and regionally. Journal of Vegetation Science 1: 675–682.

Chesson P.L. and Case T.J. 1986. Overview: Nonequilibrium community theories: chance, variability, history and coexistence. In: Diamond J. and Case T.J. (eds), Community Ecology. Harper and Row, New York, pp. 229–239.

Christensen N.L. and Peet R.K. 1984. Convergence during secondary forest succession. Journal of Ecology 72: 25–36.

Debussche M. and Lepart J. 1992. Establishment of woody plants in Mediterranean old fields: opportunity in space and time. Landscape Ecology 6: 133–145.

del Moral R. 1993a. Mechanisms of primary succession on volcanoes: a view from Mount St. Helens. In: Miles J. and Walton D.H. (eds), Primary Succession on Land. Blackwell Scientific Publications, London, pp. 79–100.

del Moral R. 1993b. Understanding dynamics of early succession on Mount St. Helens. Journal of Vegetation Science 4: 223–234.

del Moral R. 1998. Early succession on lahars spawned by Mount St. Helens. American Journal of Botany 85: 820–828.

del Moral R. 1999a. Plant succession on pumice at Mount St. Helens, Washington. American Midland Naturalist 141: 101–114.

del Moral R. 2000. Succession and species turnover on Mount St. Helens, Washington. Acta Phytogeographica Suecica 85: 53–62.

del Moral R. 1999b. Predictability of primary successional wetlands on pumice, Mount St. Helens. Madroño 47: 177–186.

del Moral R. and Bliss L.C. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. Advances in Ecological Research 24: 1–66.

del Moral R., Titus J.H. and Cook A.M. 1995. Early primary succession on Mount St. Helens, Washington, USA. Journal of Vegetation Science 6: 107–120.

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

del Moral R. and Wood D.M. 1988b. The high elevation flora of Mount St. Helens. Madroño 35: 309–319.

del Moral R. and Wood D.M. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. American Journal of Botany 80: 981–992.

Dlugosch K. and del Moral R. 1999. Vegetational heterogeneity along elevational gradients. Northwest Science 73: 12–18.

Edwards J.S. and Sugg P. 1993. Arthropod fallout as a resource in the recolonization of Mount St. Helens. Ecology 74: 954–958.

Fagan W.F. and Bishop J.G. 2000. Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. American Naturalist 155: 238–251.

Fuller R.N. 1999. The Role of Refugia in Primary Succession on Mount St. Helens, Washington.

Halvorson J.J. and Smith J.L. 1995. Decomposition of lupine biomass by soil microorganisms in developing Mount St. Helens' pyroclastic soils. Soil Biology & Biochemistry 27: 983–992.

Hill M.O. and Gauch H.G. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47–58.

Inouye R.S. and Tilman D. 1995. Convergence and divergence of old-field vegetation after 11 year nitrogen addition. Ecology 76: 1872–1887.

Kent M. and Coker P. 1992. Vegetation Description and Analysis. Wiley & Sons, New York.

Kovach W.L. 1998. MVSP-a multivariate statistical package for Windows, version 3.1. Kovach Computing Services, Pentraeth, Wales, UK.

Larson D.R. and Bliss L.C. 1998. An analysis of structure of tree seedling populations on a lahar. Landscape Ecology 13: 307–322.

Lockwood J.L. 1997. An alternative to succession. Restoration & Management Notes 15: 45–50.

McCune B. and Mefford M.J. 1997. PC-ORD, multivariate analysis of ecological data, version 3.0. MjM Software Design, Gleneden Beach, OR, USA.

Moreno-Casasola P. and Vázquez G. 1999. The relationship between vegetation dynamics and water table in tropical dune slacks. Journal of Vegetation Science 10: 515–524.

Myster R.W. and Pickett S.T.A. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. American Midland Naturalist 124: 231–238.

Myster R.W. and Pickett S.T.A. 1994. A comparison of succession over 18 years in 10 contrasting old fields. Ecology 75: 387–392.

Salonen V., Penttinen A. and Sarkka A. 1992. Plant colonization of a bare peat surface: population changes and spatial patterns. Journal of Vegetation Science 3: 113–118.

Samuels C.L. and Drake J.A. 1997. Divergent perspectives on community convergence. Trends in Ecology & Evolution 12: 427–432.

Sterling A., Peco B., Casado M.A., Galiano E.F. and Pineda F.D. 1984. Influence of microtopography on floristic variation in the ecological succession in grassland. Oikos 42: 334–342.

Sugg P.M. and Edwards J.S. 1998. Pioneer aeolian community development on pyroclastic flows after the eruption of Mount St. Helens, Washington, USA. Arctic and Alpine Research 30: 400–407.

Titus J.H. and del Moral R. 1998. Seedling establishment in different microsites on Mount St. Helens, Washington, USA. Plant Ecology 134: 13–26.

Titus J.H., Moore S., Arnot M. and Titus P.J. 1998. Inventory of the vascular flora of the blast zone, Mount St. Helens, Washington. Madroño 45: 145–161.

Titus J.H., Titus P.J. and del Moral R. 1999. Wetland development in primary and secondary successional substrates fourteen years after the eruption of Mount St. Helens, Washington, USA. Northwest Science 73: 186–204.

van der Walk A.G. 1992. Establishment, colonization and persistence. In: Glenn-Lewin D.C., Peet R.K. and Veblen T.T. (eds), Plant Succession: Theory and Prediction. Chapman & Hall, London, pp. 60–102.

Vitt D.H., Marsh J.E. and Bovey R.B. 1988. Mosses, Lichens and Ferns of Northwest North America. University of Washington Press, Seattle.

Wiegleb G. and Felinks B. 2000. Predictability of primary succession in former lignite coal mining areas. Journal of Applied Vegetation Science 3 (in press).

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

Wood D.M. and del Moral R. 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. American Journal of Botany 75: 1228–1237.

Wood D.M. and del Moral R. 2000. Seed rain during early primary succession on Mount St. Helens, Washington. Madroño 47: 1–9.

Zar J.H. 1996. Biostatistical Analysis. 3rd edn. Prentice Hall, Upper Saddle River, NJ.