

PLANT SUCCESSION ON PUMICE AT MOUNT ST. HELENS, WASHINGTON

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ABSTRACT.—How vegetation develops from a source of potential species remains poorly understood. I explored whether colonizing species assemble randomly, or if local deterministic factors alter species establishment to create consistent vegetation patterns. Early primary successional vegetation in 111 small self-contained depressions (potholes) on Mount St. Helens was sampled. Mean richness was 8.8 species and mean cover was 2.6%. Mean percent similarity (PS) between potholes was 46%. A nearby grid of 100 contiguous 100 m² quadrats on a level barren plain was sampled for comparison. Barren quadrats had mean richness of 12.2 species, mean cover of 1.4% and mean PS of 63%. Pothole vegetation was much more variable than that of the barrens. Canonical correspondence analysis revealed a slight relationship between environmental factors and pothole vegetation. Species composition, cover and species rank orders were predicted extremely well by a stochastic model based on observed frequencies and random accumulation of species. These findings suggest that early colonization of isolated sites is stochastic, and that dispersal affects species composition more strongly than environmental factors or competitive interactions. Which species succeed at any particular site is poorly predictable, but once established, a local population can persist. As a result, there is often a poor correlation between species composition and environmental factors in mature vegetation.

INTRODUCTION

Community structure in mature vegetation is often assumed to result from deterministic links between plants and their environment. Many ecologists have recognized the importance of both historical and stochastic factors (*e.g.*, Gleason, 1926). However, the search for “assembly rules” (Keddy, 1992; Wilson, 1994; Wilson and Whittaker, 1995) suggests that deterministic factors could strongly affect species composition. When links are not found, historical factors, sampling error, unmeasured variables (McCune and Allen, 1985) or mutual exclusion (Frelich *et al.*, 1998) are invoked. Stochastic factors can produce multiple successional paths (Eggler, 1941), lack of convergence (Rydin and Borgegård, 1988; del Moral and Wood, 1993a; del Moral, 1998), low within-community similarity (Fridriksson and Magnusson, 1992; del Moral and Wood, 1993b), novel communities (Tagawa, 1992) or poor correlations between seed banks and standing vegetation (Lavorel and Lebreton, 1992; Tu *et al.*, 1998). Stochastic processes may be a major determinant of mature vegetation (Collins and Glenn, 1991) and should be considered when analyzing mature vegetation or planning restoration efforts (Lockwood, 1997).

Mount St. Helens, Washington (new elevation 2550 m a.s.l.), experienced a devastating lateral eruption on 18 May 1980 (Foxworthy and Hill, 1982). This eruption formed deep pumice deposits on the north slope that entrained large amounts of ice. A result was the creation of many small depressions (potholes) when the ice melted. These potholes have suffered little erosion and are characterized by fine decomposing pumice. Nearby, a smooth barren pumice plain was formed. Wind has removed fine-textured material, leaving the

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FIG. 1.—Typical pothole dominated by *Epilobium angustifolium*, with small numbers of *Anaphalis margaritacea*, *Carex mertensii* and other species

surface dominated by coarse pumice, with finer material below the surface. The substrates of these habitats are composed of pumice of equal age and similar fertility.

Summer precipitation is low and variable (del Moral and Bliss, 1993). The soil remains immature and low in organic matter and nutrients (del Moral, 1993; del Moral *et al.*, 1995; Tsuyuzaki and Titus, 1996; Tsuyuzaki *et al.*, 1997). Microtopography is crucial to seedling establishment on barren pumice (Tsuyuzaki *et al.*, 1997; Titus and del Moral, 1998). The potholes form a special habitat that has permitted more rapid species accumulation. Their flat bottoms are protected from wind and accumulate snow. Thus, they are less xeric than nearby barrens. Seeds reaching a pothole and seeds produced within a pothole rarely emerge. Seeds blow readily for tens of meters across the adjacent barrens, though they may be trapped in rills or beneath small rocks. Physiography suggests that individual pothole populations are initiated from stochastic long-distance dispersal, rarely from adjacent potholes. This report compares the vegetation in potholes with vegetation found on the adjoining barrens.

METHODS

Location.—Several hundred potholes occupy a small area centered at Lat. 46°13'51"N, Long. 122°9'10"W, between 1250 and 1305 m a.s.l. The surroundings are a barren pumice plain, dissected by gullies. A smooth area of pumice at Lat. 46°14'9"N, Long. 122°9'25"W, and between 1230 and 1240 m a.s.l., was selected for comparison. The centers of these two sample areas are about 380 m apart.

Potholes.—I sampled 111 potholes for cover and environmental factors in 1993. These potholes were undisturbed, had complete rims and were neither drained nor fed by drainages (see Fig. 1). Pothole area was determined by measuring eight radii located every 45°, and summing the areas of the triangles so formed. The potholes averaged 30 m² (range 10 m² to 150 m²). Pothole depth was measured as the vertical distance from a line joining opposite rims and the center. Typical potholes were 20 cm deep.

Each pothole was located to the nearest meter. Soil was collected adjacent to mature plants. Four soil samples were obtained between 2 and 6 cm below the surface in mid-July and mid-August. Soil moisture was determined gravimetrically from each sample. The par-



FIG. 2.—Aspect of pumice grid. Note sparse vegetation and nearly homogeneous surface

ticle size distribution was determined by sieving a 100 g subset of each July sample through 2 mm, 1 mm and 0.5 mm screens, forming four fractions. Soil pH was determined from a 1:1 soil paste of a 50 g subset of these samples. Soil organic matter was determined from a 20 g subset of these samples by loss on ignition at 400 C after 24 h.

I sampled 20 potholes to determine if internal soil patterns might explain species composition. The potholes were selected at random, but a selected pothole was replaced by a new selection if its size was not between 20 and 50 m² or if it would be the fourth selected pothole in a spatial sequence of ten potholes. Three soil samples were taken along a single radius at three locations from the center of the flat area, the edge of the flat area (*i.e.*, the “toe”, where the slope begins) and midway up the slope. The direction of each radius was south-southwest, towards the cone. Soils were examined as described above.

Absolute cover of each species was measured to the nearest 100 cm² as follows: a ¼ m² quadrat frame was divided into twenty-five 100 cm² squares. The number of squares occupied by each patch of each species was determined directly for the whole pothole, yielding an accurate cover estimate. I converted absolute cover to percent cover using the area of that pothole. (Vascular plant nomenclature follows Hitchcock and Cronquist, 1973; moss nomenclature follows Vitt *et al.*, 1988.) These potholes are “pseudoreplicates” (Hurlbert, 1984) because stochastic and position effects are large compared to deterministic effects (*see* Hefner *et al.*, 1996).

Barrens.—On the barrens, minor topographic heterogeneity created by water erosion and scattered rocks mitigated the inhospitable surface. There is no reason to believe that the seed rain differs from that of the potholes. A permanently marked grid (Fig. 2) was established in 1989 and continues to be sampled annually. The data reported here were collected in 1996. The grid had 10 rows and 10 columns of contiguous 10 by 10 m plots. The sample method sacrifices precise cover estimates for extensive coverage. These estimates have been shown to be consistent between years and provide reliable estimates of between plot similarity.

On this grid, I estimated quadrat cover as follows: 1 = one to five plants; 2 = six to 20 plants; 3 = over 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; and 7 = >4% to 8% cover (del Moral, 1998). Values were back-transformed to estimate total cover and to calculate between-plot similarity. Scores of

1 were converted to 0.06, 0.09, 0.12 or 0.15%, depending on the growth-form; scores of 2 were likewise converted to 0.08, 0.12, 0.16 or 0.20%. Scores of 3 were converted 0.25%, while higher scores were converted to the midpoint of their range.

Quantitative analysis—I characterized samples using richness and diversity. Richness is the number of species per sample. The information theory statistic (H') using percent cover estimated diversity:

$$H' = -\sum_{i=1}^S p_i \log_2 p_i \quad (1)$$

where s is the number of species and p_i is the proportion of the i^{th} species in a sample.

I used Canonical Correspondence Analysis (CCA; ter Braak, 1986), a direct gradient analysis method, to relate environmental variables to species patterns (Palmer, 1993). Oksanen and Minchin (1997) found that CCA was sensitive to input order due to lax convergence criteria. The corrected algorithm for CCA was used (McCune and Mefford, 1997). CCA performs a least-squares linear regression of environmental variables on site scores determined by correspondence analysis (*see* Gauch, 1982). New scores are predicted from the regression equation. I used eigenvalues, percentage of variance explained in the species data, Pearson correlation between species and environmental axes, regression coefficients of each environmental factor to two axes and intraset correlations of variables to each axis to evaluate the results. Monte Carlo simulations were used to determine if the observed correlations differed significantly from random.

Faith *et al.* (1987) showed that percentage similarity, long used in ordination studies (*e.g.*, Bray and Curtis, 1957), is a robust measure of ecological distance. PS was calculated by:

$$PS_{ij} = 200 \sum_{k=1}^S \min(X_{ik}, X_{jk}) / \sum_{k=1}^S (X_{ik} + X_{jk}) \quad (2)$$

where i and j are two samples, there are k species, X is the cover score and \min is the lower of the two values (Kovach, 1993).

Percent similarities among the 100 barren plots were calculated from back-transformed cover data. To make a fair comparison to these similarities, the cover of pothole species were similarly converted. For example, any small species with a cover 0.06% or less was given a score of 0.06%. Higher cover were converted to mid-points of the cover class in which they fell.

Classification.—The hierarchical structure of the two samples was compared using Ward's agglomerative method with nearest neighbor sorting and Euclidean distance. This metric is robust against many faults of hierarchical classification methods (Kent and Coker, 1992).

Model.—A simulation model, SIMCOM, was created in Visual Basic Professional® 4.0 to estimate community structure that would occur in the absence of deterministic mechanisms such as environmental gradients or competition. The model calculated richness, cover and frequency from a random draw of species found in the data. The species composition of each plot was entered into an Excel® file. The simulation randomly selects a cover value for each species in turn. If the value was positive, plot richness and species cover and frequency were incremented. If negative, no changes occur and the next species was checked. The probability of a species being selected for each plot is its frequency in the entered data. Therefore, plot cover and richness were not constrained by real data. Simulations consisted of 100 runs of 100 samples. The mean richness, cover, frequency and ranks for each run were written to an Excel file. Cover in 100 plots of the first 20 simulations was written to a separate file for use in calculating percent similarity. Simulated plots were

TABLE 1.—Frequency and cover of common species found in potholes and on the grid. Species are in order of descending frequency (rounded to whole percent) in potholes, including only species with at least 10% frequency in either set of data. Dominance is by percent cover

Species	Potholes				Grid	
	Frequency (%)	First dominant	Second dominant	Cover (%)	Frequency (%)	Cover (%)
<i>Anaphalis margaritacea</i>	98	82	12	1.05	99	0.28
<i>Epilobium angustifolium</i>	97	2	27	0.23	99	0.11
<i>Carex mertensii</i>	96	12	33	0.40	91	0.14
<i>Hypochaeris radicata</i>	87	1	6	0.17	90	0.07
<i>Hieracium albiflorum</i>	68	0	5	0.07	88	0.06
<i>Penstemon cardwellii</i>	65	5	13	0.12	97	0.24
<i>Agrostis diegoensis</i>	59	3	9	0.11	93	0.11
<i>Juncus parryi</i>	39	0	4	0.04	36	0.03
<i>Carex limnophila</i>	36	1	3	0.06	40	0.04
<i>Saxifraga ferruginea</i>	36	3	7	0.09	50	0.06
<i>Polytrichum piliferum</i>	35	0	0	0.03	2	<0.01
<i>Agrostis scabra</i>	23	0	0	0.04	74	0.08
<i>Spraguea umbellata</i>	23	0	1	0.02	7	<0.01
<i>Luetkea pectinata</i>	19	0	1	0.01	28	0.03
<i>Lupinus lepidus</i>	14	0	6	0.02	83	0.08
<i>Poa incurva</i>	13	0	0	0.01	7	0.01
<i>Epilobium alpinum</i>	12	0	0	0.01	28	0.02
<i>Salix</i> sp.	11	0	0	0.03	46	0.08
<i>Orthotrichum</i> sp.	10	0	0	0.01	23	0.01
<i>Luzula parviflora</i>	5	0	0	<0.01	16	0.02
<i>Carex paysonis</i>	3	0	0	<0.01	10	0.01

compared to the observed plots with non-parametric Spearman's rank order correlations and t-tests of cover of species in the two sets of plots. Total richness and cover were compared directly.

Statistics.—I used StatMost for Windows® (DataMost, 1994) for the ANOVA described below and Statistix (Analytical Software, 1994) for simple data description.

RESULTS

Vegetation structure.—Richness per pothole varied from 3 to 17 species (mean = 8.8 ± 2.5) and was correlated ($P < 0.0001$; $r = 0.52$) to pothole size. There were 39 species in potholes, but 18 occurred fewer than four times (Table 1). These species included annuals, spreading or compact perennial forbs, perennial graminoids and shrubs. Pothole cover varied from 0.005% to over 10% (mean = $2.58 \pm 1.75\%$). Mean H' of potholes was 2.17 ± 0.45 (0.61 to 2.88). Thirteen species were first or second most abundant species in at least one pothole (Table 1).

On the barrens, species that had the highest or second highest cover in a quadrat occurred in more quadrats, but had lower cover than dominants of the potholes (Table 1). The ten most common species were more narrowly distributed in the potholes than on the grid. In potholes, they had a mean frequency of 68.1%, whereas the ten leading species on the grid had a mean frequency of 81.4%. Richness was 12.22 ± 2.91 species per 100 m², significantly higher than the potholes ($t = 9.07$, $P < 0.0001$). However, since the mean area of potholes is 28.9 m², this comparison must be viewed cautiously. The regression predicts

TABLE 2.—Soil characteristics of twenty potholes, stratified by location. Means \pm standard deviation of the parameter. Repeated measures AOV was used to determined if there were any significant differences. For parameters with significant differences, paired t-tests were used to assess which means differed

Parameter	Center	Toe	Slope
Soil moisture (%)	13.6 \pm 4.5	13.1 \pm 3.3	15.2 \pm 3.8
Soil pH	4.8 ^c \pm 0.05	4.8 ^c \pm 0.05	5.2 ^{ab} \pm 0.10
Organic matter (%)	0.8 \pm 1.03	0.9 \pm 1.44	0.5 \pm 0.06
Gravel (%)	4.9 ^{bc} \pm 5.4	10.4 ^{ac} \pm 10.2	18.8 ^{ab} \pm 8.0
Sand (%)	5.4 ^{bc} \pm 8.2	8.2 ^{ac} \pm 5.2	13.7 ^{ab} \pm 3.1
Silt (%)	51.5 ^{bc} \pm 16.9	42.9 ^a \pm 11.6	41.8 ^a \pm 13.3
Clay (%)	37.5 ^c \pm 19.9	38.9 ^c \pm 20.7	25.4 ^{ab} \pm 10.3

a = different from center; b = different from toe; c = different from slope, $P < 0.05$

12 species for a pothole of 100 m², though most large potholes have fewer species. Percent cover ($1.42 \pm 0.57\%$) was lower than that of the potholes ($t = 7.80$, D.F. = 99, $P < 0.0001$). Mean H' was 2.29 ± 0.24 , similar to that of the potholes. Spearman's rank correlation between the species abundance in the two samples was 0.77 ($P < 0.0001$).

Internal pattern.—Pothole vegetation showed distinct patterns. Plants usually were concentrated near edges and on the lower slopes. Pothole centers were sparsely vegetated. Soil moisture, texture, pH and organic matter of 20 potholes in the center, at the edge and on the slope were compared (Table 2). Repeated measures AOV revealed no significant differences in soil moisture or organic matter. Pairwise comparisons of the remaining factors revealed some significant differences. Slopes were less acid than either edge or center. Centers were dominated by silt and clay fractions. The slopes had more gravel and sand and less clay than the centers. The edges were intermediate in sand and gravel and had more clay than the slopes.

Classification structure.—Numerical classification of pothole vegetation demonstrated high heterogeneity despite their close proximity. Pothole percent similarity among the 111 samples was $46.0 \pm 16.1\%$. Table 3 summarizes species composition of nine groups formed by fusion below $SS = 1$. Ten potholes were either unfused or merely paired at this similarity level and are not shown. Group A was characterized by *Penstemon* and *Epilobium*, with low cover and sparse *Anaphalis*. The remaining groups were dominated by *Anaphalis* with other species. *Epilobium* was characteristic of all groups except G and H and was often common. *Carex mertensii* was abundant in, groups C, D, E, F and G. Group C, though dominated by other species, was uniquely characterized by *Saxifraga*. Of the remaining species, only the wind-dispersed *Hypochaeris* and *Hieracium* were characteristic of any group.

If these groups were correlated with environmental factors, there would be evidence for deterministic vegetation control. Tukey's HSD test was applied to each variable after one-way AOV, but no mean was significantly different from any other ($P < 0.05$; Table 4).

No spatial pattern of groups emerged (Table 5). Members of most groups lacked spatial cohesion. Moisture varied little among groups, though Group B was drier in August and Group F slightly drier in July than other groups. Group C was lowest in clay and soil pH and highest in silt among the groups. Only Group C displayed weak correspondence between environment and species composition. Most potholes in this group were adjacent to each other.

The barrens quadrats occupied 1 ha and had a mean PS of $63.0 \pm 11.5\%$, larger than that of the potholes ($P < 0.0001$). The classification indicated little heterogeneity (Table

TABLE 3.—Composition (percent cover) of leading species in potholes, determined from agglomerative classification. Groups were divided at SS = 1.0. (Species listed in order of overall frequency; those in bold occur in all plots of a group)

Species	Vegetation group (membership size)								
	A (10)	B (23)	C (7)	D (9)	E (8)	F (11)	G (8)	H (14)	I (11)
<i>Anaphalis margaritacea</i>	0.26	0.73	1.24	2.45	1.36	1.29	0.63	1.41	0.72
<i>Epilobium angustifolium</i>	0.15	0.13	0.30	0.12	0.30	0.50	0.41	0.09	0.48
<i>Carex mertensii</i>	0.18	0.18	1.21	0.21	0.82	0.23	0.80	0.16	0.15
<i>Hypochaeris radicata</i>	0.07	0.12	0.09	0.17	0.07	0.09	0.05	0.11	0.07
<i>Hieracium albiflorum</i>	0.03	0.06	0.07	0.06	0.07	0.14	0.06	0.10	0.06
<i>Penstemon cardwellii</i>	0.15	0.12	0.02	0.10	0.13	0.11	0.10	0.07	0.01
<i>Agrostis diegoensis</i>	0.07	0.05	0.04	0.12	0.10	0.07	0.15	0.10	0.02
<i>Juncus parryi</i>	0.04	0.06	0.01	0.11	0.03	0.03	0.04	0.02	0.02
<i>Carex limnophila</i>	0.03	0.03	0.06	0.01	0.08	0.08	0.05	0.03	0.02
<i>Saxifraga ferruginea</i>	0.10	0.02	0.58	0.13	0.05	0.02	0.03	0.05	0.01
<i>Polytrichum piliferum</i>	0.01	0.01	0.06	0.01	0.04	0	0.04	0.04	0.04
<i>Agrostis scabra</i>	0.08	0.01	0	0.08	0.11	0.03	0.04	0.03	0
<i>Spraguea umbellata</i>	0.01	0.01	0.02	0.07	0.01	0.02	0.10	0.01	0.01
<i>Luetkea pectinata</i>	0.01	0.01	0.02	0	0.01	0.01	0.01	0.02	0.01

5). The last two groups of the grid had SS of 0.99 and 1.44. Total SS was 2.78, <20% of that of the potholes. There remained only one single plot at SS = 0.5.

Canonical correlation analysis.—Though pothole vegetation was variable, it might be correlated with environmental factors (*cf.*, Tsuyuzaki and del Moral, 1994). CCA, with the variables shown in Table 6, was used to assess this possibility. Clay was deleted because of colinearity with other texture values. The highest correlations were achieved with no down-weighting of rare species, no species transformations and deletion of species with three or fewer occurrences (Table 6).

The Monte Carlo simulation (1000 trials) of the first three axes indicated that the envi-

TABLE 4.—Mean values of environmental factors in each vegetation group in the pothole sample. Variables include any in which the 95% confidence interval does not include the grand mean. Values differing by at least 1 SD from overall mean are in bold. X, Y and gravel are shown for reference. No mean within a column is significantly different, based on AOV followed by Tukey's H.S.D. test ($P < 0.05$), from any other

Factor	Vegetation group									Mean
	A	B	C	D	E	F	G	H	I	
X (meters)	196	156	204	80	158	158	171	141	124	152
Y (meters)	56	61	54	43	62	54	49	44	45	53
H ₂ O–July (%)	30.3	30.3	29.3	29.3	30.1	28.5	34.6	29.8	28.7	30.1
H ₂ O–Aug (%)	14.4	12.3	12.3	13.0	14.4	16.4	16.3	12.8	13.6	14.3
Gravel (%)	10.6	8.5	11.7	8.3	8.4	8.1	8.1	9.4	6.9	8.8
Silt (%)	12.3	7.6	18.1	10.5	14.9	13.0	11.5	9.8	9.5	10.9
Clay (%)	68.8	77.0	59.0	74.1	69.3	69.8	72.6	72.1	71.3	74.8
pH	4.24	4.23	3.96	4.17	4.21	4.15	4.09	4.27	4.31	4.20

TABLE 5.—Classification structure in potholes and barren plots. Samples were clustered using Ward's method and Euclidean distance

Parameter	Potholes	Grid
Number of plots	111	100
Total sums of squares (SS)	15.38	2.78
SS at 10 nodes	0.13	0.063
SS at 50 nodes	0.26	0.11
SS at 80 nodes	0.58	0.25
Number of single plots SS = 0.5	21	1

ronmental data predicted species-environmental correlations no better than sets of scores randomly assigned to samples. The probabilities of achieving the relationships by chance were $P = 0.242$, $P = 0.445$ and $P = 0.715$, respectively. Preliminary analyses with CANOCO provided low t-values for individual environmental factors. To the extent that variation was associated with any factors, July moisture and X position were associated with the first axis and X position and Y position associated with Axis 2.

Model.—The pothole simulation produced samples with species richness between 4 and 15 species (mean = 8.79 species per pothole). Spearman's rank order of frequencies correlation between pothole vegetation and twenty selected simulations were highly significant and varied from $r = 0.920$ to $r = 0.981$. Predicted mean cover percentage was $2.65\% \pm 0.24$ (ranging from 2.43 to 2.93%) compared to the observed 2.58%.

The observed cover values of individual species were compared to their simulated values in a randomly selected simulation (Table 7). Differences among the species were small. None of the species had significant cover differences. Frequency is the percentage of times a species occurred, either in the simulations or in the actual data. SIMCOM accurately

TABLE 6.—Eigenstructure and canonical coefficients for environmental factors best predicting sample distributions

General structure	Axis 1	Axis 2
Eigenvalues	0.115	0.061
Pearson species-environment correlation	0.562	0.610
Monte Carlo Test result	$P = 0.242$	$P = 0.445$
% Variance—Species data	4.7	2.5
Predictor variables	Axis 1 coefficient	Axis 2 coefficient
X-distance (m)	0.498	−0.585
Y-distance (m)	−0.218	−0.720
Area of pothole (m ²)	−0.048	0.314
July moisture (%)	0.510	−0.373
August moisture (%)	0.010	0.309
Gravel (%)	−0.237	−0.045
Sand (%)	0.009	−0.324
Silt (%)	0.006	−0.138
Organic fraction (%)	−0.055	0.208
pH	−0.310	−0.142

TABLE 7.—Mean cover percentage and mean frequency of pothole species in the simulation compared to the observed means in 111 potholes. None of the cover values differed significantly ($P < 0.05$ by t -test)

Species	Simulation mean cover	Observed mean cover	Simulation mean % frequency	Observed % frequency
<i>Anaphalis margaritacea</i>	1.107	1.050	98.6	98.2
<i>Epilobium angustifolium</i>	0.212	0.232	96.9	97.3
<i>Carex mertensii</i>	0.405	0.402	92.2	92.8
<i>Hypochaeris radicata</i>	0.131	0.165	85.5	87.3
<i>Hieracium albiflorum</i>	0.602	0.072	66.8	67.6
<i>Penstemon cardwellii</i>	0.161	0.128	65.4	64.9
<i>Agrostis diegoensis</i>	0.112	0.105	57.8	58.6
<i>Juncus parryi</i>	0.057	0.043	37.9	38.7
<i>Carex limnophila</i>	0.064	0.060	34.0	36.0
<i>Saxifraga ferruginea</i>	0.150	0.088	35.6	36.0
<i>Polytrichum piliferum</i>	0.031	0.032	33.1	35.1
<i>Agrostis scabra</i>	0.048	0.037	24.0	22.5
<i>Spraguea umbellata</i>	0.021	0.023	23.3	22.5
<i>Luetkea pectinata</i>	0.009	0.013	19.2	18.9
<i>Lupinus lepidus</i>	0.026	0.017	15.0	15.3
<i>Poa incurva</i>	0.010	0.009	13.2	13.5

recaptured the observed frequencies (Table 7). The percentage similarities between the potholes (absolute cover) and the plots in five randomly selected simulations were compared. The pothole similarity ranged from 1.66 to 90.35%, with a mean of $46.0 \pm 16.1\%$. The simulation PS ranged from 1.84 to 93.04% in the five runs. The distribution of similarities between potholes and the simulations was similar. In each case, the mean PS exceeded the observed mean value or was not significantly different.

SIMCOM was applied to the barrens with similar results. Correlations of frequency ranks between barrens plots and the simulations ranged from 0.969 to 0.993. Between-simulation rank correlations were similar (0.946 to 0.985). Species richness was predicted closely (12.23 species per sample) and cover was accurately predicted to be 1.40% (vs. 1.42%). The frequencies of all species were accurately predicted.

The barrens were also simulated using pothole frequencies to determine selection probabilities. If pothole data sample a community more representative of the original seed input, and the barren site is more developed, then this simulation should differ significantly from the actual data. Frequencies of species absent from the potholes were left unchanged.

This simulation yielded a mean richness of 8.75, significantly lower than the observed data (12.22 species per plot; $P < 0.001$, t -test). This result is expected since the simulation is driven by pothole richness. Total percent cover was 1.39%, similar to the observed value (1.42%) because the pumice cover values were used. The rank order correlations of species frequencies in the simulations varied from 0.885 to 0.959, indicating a robust simulation. These ranks, when compared to the actual species frequency rank, yielded correlations ranging between 0.781 and 0.857. These lower, nonoverlapping correlations demonstrate that the simulation based on pothole vegetation structure is distinct from the barrens vegetation structure. Cover values of the pothole-driven simulation of barrens vegetation differs little from the actual cover values. However, the simulation overestimated these common species by at least three steps: *Agrostis diegoensis*, *Carex limnophila*, *Hypochaeris radicata*,

Lupinus lepidus, *Racomitrium* sp. and *Spraguea umbellata*. The simulation underestimated the rank of *Agrostis scabra*, *Carex pachycephala*, *Luzula parviflora*, *Lupinus latifolius* and *Luzula parviflora*, *Luetkea pectinata* and *Salix* sp.

DISCUSSION

Comparison between sites.—Pothole vegetation was concentrated on flats near the slope and on the lower slope of most potholes. This pattern may be related to the observed coarse texture of these habitats. Tsuyuzaki and Titus (1996) showed that seed germination was poor in silt and clay, and was best in sand. Seeds also may be more likely to be trapped near the toe of the slope. Barren vegetation lacked significant spatial heterogeneity at this scale.

The two samples were drawn from the same actual species pool (*cf.*, Pärtel *et al.*, 1996) since their Spearman's rank order correlation was significant, with 29 species in common. Of the top 20 pothole species, 17 were also in the top 20 of the grid. However, the barren quadrats have higher mean richness, higher frequencies and lower cover than do the potholes. This implies that secondary dispersal is more common on the grid. Individual potholes have higher cover and lower between pothole similarity than do barrens samples.

Many of these species have good wind dispersal mechanisms, but *Penstemon*, *Saxifraga*, *Carex mertensii* and *C. limnophila* have modest to poor dispersal abilities (del Moral, 1998). The large between-pothole variation of these species is consistent with strong founder effects and limited secondary dispersal. Subsequent expansion within potholes appears to favor species that produce many poorly dispersed seeds (*e.g.*, *Carex* spp., *Saxifraga* and *Spraguea*), those with strong rhizomatous growth (*e.g.*, *Anaphalis* and *Agrostis*) and woody species (*e.g.*, *Penstemon* and *Luetkea*). Species with limited seed dispersal abilities, such as *Lupinus lepidus*, both *Agrostis* species, *Penstemon* and *Carex paysonis*, were more frequent on the grid. Species such as *Spraguea umbellata* and *Polytrichum* sp. were more common in potholes, where conditions were more moist than on the grid. Grid cover was substantially lower than the potholes, suggesting that the grid is more stressful than the potholes. However, limited species interactions and the presence of numerous safe-sites (*see* del Moral and Bliss, 1993) permit frequent establishment of individuals derived from earlier colonists.

Dispersal barriers.—Ash *et al.* (1994) noted that composition in early succession is affected strongly by dispersal barriers and Blundon *et al.* (1993) described how first colonists influenced subsequent successional patterns. Stöcklin and Bäumlér (1996) noted that species with good wind dispersal and strong clonal growth should dominate early primary succession and influence the subsequent course of development. Lockwood (1997) noted that arrival order can alter composition, richness and succession. The potholes are so isolated that few seeds arrive and their order is highly variable. Fewer still establish, so founder effects can be pronounced. Each pothole was self-contained and individuals within a pothole appeared to be derived from few long-distance dispersal events. Most species within a pothole usually occurred in only one place. The annual probability of a seed of a less common species reaching a pothole is much less than 1.0 (D. M. Wood, pers. comm.). As the few progeny of founders are rarely dispersed beyond the pothole, within-pothole dispersal has accentuated these stochastic effects.

Heterogeneity.—Secondary dispersal between potholes is restricted, so that the initial floristic composition persists and heterogeneity among the potholes remains large. Classification substantiated that internal variation among potholes was much greater than among grid samples. Ground dispersing species (*e.g.*, *Penstemon*, *Lupinus* and *Agrostis*) were more frequent on the grids than they were in potholes. The heterogeneity of vegetation on other grids on Mount St. Helens has declined since 1987 (del Moral and Wood, 1993a; del Moral,

1998). Barriers to secondary migration have delayed potential homogenization of the potholes.

Though potholes are relatively moist and protected, establishment was spatially confined. The central part of most potholes is fine-textured, lacking seed-trapping features. Del Moral and Clampitt (1985) and Tsuyuzaki and Titus (1996) showed that many of the taxa common in potholes (e.g., *Anaphalis* and *Epilobium*) germinated poorly in fine-textured substrates. There was little evidence that species composition was linked to environmental factors, so structure should not be predictable. Deterministic factors such as competition have yet to start to structure pothole vegetation. Rather, community structure has resulted from an accumulation of rare events and each pothole is initially a nearly independent sample of a diffuse seed rain.

Environmental control.—Numerical classification of the potholes produced nine poorly defined groups with fuzzy boundaries. The mean values of environmental factors in these groups did not differ significantly. Only Group C, characterized by *Saxifraga*, was spatially coherent and it had coarser soil and lower pH than did the other groups. Factors with modest predictive value in CCA (X, Y and July moisture) did not vary significantly among vegetation groups.

Individual potholes, when assessed with CCA, demonstrated little linkage between environmental factors and species composition. Pothole location, as indicated by spatial coordinates, was weakly related to composition. This weakly suggests that founder effects in poorly dispersed species such as *Saxifraga ferruginea* may play a role in early succession.

The failure of CCA to reveal strong species to environment patterns has four possible causes (Kazmierczak *et al.*, 1995): species dominance overrides environmental factors, factor interactions, unmeasured variables and chance. Densities are low, so competition could not produce dominance hierarchies. It is unlikely that subtle nutrient interactions could control this vegetation since nutrient levels are low (del Moral and Bliss, 1993). There was no evidence for an underlying gradient since the first species axis accounted for only 4.7% of the variation. By exclusion, chance is the remaining explanation for the observed pattern.

Simulations.—Simulation of the community structure of both potholes and barrens was consistent with the hypothesis that these communities have assembled by stochastic factors and that deterministic factors are weak. SIMCOM accurately reproduced the vegetation structure of both. The simulations resulted in richness, cover, species ranks and distribution of percent similarity that were very similar to the observed patterns. These results were obtained even though plot richness and cover were not constrained. The simulation method can be used to generate null-model communities for comparison to observed vegetation.

Stochastic control.—Many factors affect succession (Walker and Chapin, 1987; Chapin *et al.*, 1994; Fastie, 1995), but chance effects have not been well documented. Stochastic effects have been proposed as major determinants of initial species composition (del Moral, 1972; Finegan, 1984; McCune and Allen, 1985; Chesson and Case, 1986; Primack and Miao, 1992; Davey and Rothery, 1993; Grishin *et al.*, 1996). Dispersal into isolated sites can produce highly variable vegetation in the early stages of succession. Secondary dispersal and biomass accumulation accelerate vegetation homogenization. In any system where either dispersal or development time is limited, vegetation should be heterogeneous. The potholes are isolated and physically stressful, suggesting that their heterogeneity should be expected.

This study demonstrated that this primary succession is initiated by stochastic factors. Sale (1977) formalized the role of chance as “the lottery model.” The colonizing species have broadly overlapping tolerances (del Moral and Wood, 1993a) and few seeds arrive. Since many different species could occupy a particular pothole, initial colonists in a pothole were a stochastic subset of the source pool. Hanski (1982) described the carousel model to

extend the lottery model through time (*see* Shmida and Ellner, 1984; Collins *et al.*, 1993; Kikvidze, 1993; van der Maarel and Sykes, 1993; Sykes *et al.*, 1994; van der Maarel *et al.*, 1995). Each individual replacement is stochastic, based on dispersal ability and proximity of seed sources. This creates, at best, a weak relationship between a species and its environment. An implication is that strong species-environment relationships cannot be expected early in primary succession. It appears that species have assembled in potholes by a lottery. However, their persistence makes it premature to seek direct evidence for a carousel in time. Secondary dispersal between potholes is restricted by topography, which limits the spread of rarer species. Even the largest potholes had fewer than half of all species, yet there was much empty surface. A mosaic of distinct species assemblages is being created that is isolated from factors that, under normal conditions, blur such mosaics. Low soil fertility limits biomass accumulation, slows the succession "clock" and retards the development of competitive dominance. Vegetative growth and poor dispersal may preclude deterministic species replacement patterns (*see* Tilman *et al.*, 1997). The result is a persistent, chaotic pattern interpretable as a carousel in space. Therefore, explainable variation in mature vegetation may be low because initial stochastic processes permit several equivalent species to establish and persist, generating different communities occupying similar environmental conditions.

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