Vegetation Patterns 25 Years after the Eruption

In September 2004, Mount St. Helens commenced a renewed phase of dome-building activity that has continued with intermittent, small eruptions. Thus far, steam and ash have been released in several events, and a second dome is forming between the existing dome and the new glacier in the crater. Should a significant eruption occur, we are in an excellent position to estimate its impact on vegetation because we established a large number of plots in July and August 2004.

This in-depth survey of vegetation on the north side of the crater (Pumice Plains) was planned to gauge the development of the vegetation on stable pumice and pyroclastic sites as well as sites prone to repeated flooding compared to vegetation described in 1992 (del Moral, et al. 1995). We sampled 271 plots on the Pumice Plains that contained some vegetation and that represented the variety of primary sites available. We excluded wetlands (studied intensively in previous years) and relict sites (sampled in 2002 and 2003). Below is a slightly shortened draft of the manuscript describing this work. Citations are included, but the reference list is not included.

VEGETATION PATTERNS 25 YEARS AFTER THE ERUPTION OF MOUNT ST. HELENS, WASHINGTON

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ABSTRACT: We conducted a vegetation survey of newly formed sites on Mount St. Helens in 2004 and compared it to a 1992 survey. We asked whether vegetative heterogeneity had become reduced and sought evidence from floristic classifications, links between species and environment, and changes in community structure. From species composition in 271 250-m^2 plots we determined diversity and dominance. Six loosely defined community types (CTs) were recognized. Their habitats, based on geographic and surface features, differed primarily in their location, but also by surface characteristics. The CTs were separated by detrended correspondence analysis (DCA), and DCA axes were related to location, elevation, exposure and surface variables. Canonical correspondence analysis confirmed similar weak, but significant correlations. Comparisons to the 1992 survey (in four habitats) demonstrated a large increase in plant cover that accelerated only since 2001. Pioneer species such as *Anaphalis* and *Chamerion* declined while mosses increased significantly. Rank order correlations of each habitat were significant, but low. Vegetation structure developed from differential accumulations of species set against a large cover increase. In lupine colonies, dominance was reduced and diversity increased due to the increased abundance of many formerly uncommon species. In habitats found on pumice, pyroclastics and drainages, dominance increased, while diversity changed little. This pattern suggested an incipient development of competitive hierarchies and differential response to herbivory. Weak correlations between vegetation and the environment suggested that establishment initiated by stochastic processes had not been erased by deterministic factors. A vegetation mosaic weakly tied to environmental factors may produce different succession trajectories and produce alternative stable communities in similar habitats.

INTRODUCTION

The ways plant communities assemble during primary succession are rarely studied on a landscape basis. At best, permanent plots that cover only small areas are monitored (Roozen and Westhoff, 1985; Olff and Bakker, 1991; del Moral, 2000; del Moral and Jones, 2002), often for only a few years. The alternative employs chronosequences, in which differences in space are assumed to reflect temporal differences (Kitayama and Mueller-Dombois, 1995). Such chronosequences can be misinterpreted (De Kovel et al., 2000; Martínez et al., 2001; Sýkora, Van den Bogert, and Berendse, 2004), but good chronosequence studies were conducted on lavas in Hawaii (Clarkson, 1998) and Sicily (Poli Marchese and Grillo, 2000), where sites of different age are similarly situated and in close proximity.

Mount St. Helens erupted in 1980 to form an extensive barren plain on its north face. Ecologists continue to study this area intensively, and results have led to modifications our understanding of successional mechanisms (Walker and del Moral, 2003; Dale et al., 2005). Dispersal and establishment are spatially constrained (Fuller and del Moral, 2003; del Moral and Ellis, 2004). The relationship between vegetation and environment in wetlands (Titus et al., 1999) and other habitats was weak, but strengthened over time (del Moral, 1998, 1999a, b). Herbivory affects the growth and spread of key species and alters the rate and direction of vegetation development (Bishop et al., 2005).

Here, we compare vegetation on the north slope of Mount St. Helens in 2004 with that that was initially described in 1992 (del Moral, Titus, and Cook, 1995). Though the 2004 samples were obtained from the same general area, they were not the same sites as in our earlier study, which included vegetation on pumice, pyroclastic sites and drainages. Vegetation was sparse, and floristically heterogeneous. It was immature and stochastic factors appeared to dominate establishment patterns (del Moral and Jones, 2002).

The present landscape-scale study bridges intensive studies (e.g. Bishop and Schemske, 1998; Fagan, Bishop and Schade, 2004) with remote sensing studies (Lawrence, 2005). While the latter can demonstrate vegetation development, floristic community structure cannot be discerned. We address three questions: 1. Have community types (CTs) developed on these substrates? For CTs to be valid, vegetation must be homogeneous, dominated by a few species, and be related to either habitats or to some environmental factors. 2. Are there environmental patterns that are closely tied to species patterns? Linkages between environmental factors suggest the development of deterministic patterns, a step in the formation of communities. However, if species patterns are linked to spatial factors, or are weakly associated to any factor, then we conclude that dispersal and stochastic factors continue to play a major role in determining the vegetation. 3. Has vegetation structure developed in 12 years since the earlier survey? At that time, vegetation was sparse. Since then, surfaces have stabilized, fertility has increased and vegetation cover has developed substantially. If this development includes changes in dominance hierarchies, then we conclude that biological factors have been initiated that could eventually lead to vegetation that is more consistently tied to environmental factors.

METHODS

Study sites—The surfaces of the study area originated on May 18, 1980 following a series of cataclysmic events that included the largest landslide in recorded history (60 km^2), a directed blast (570 km^2) that deposited pumice over the blasted terrain, and a series of pyroclastic flows (15 km^2). At least five subsequent pyroclastic events in 1980 seared the Pumice Plain to form deposits at least 40 m thick. Spirit Lake was relocated to the northeast and its level rose by 60 m (all descriptions from Swanson and Major, 2005). The resultant landscape was devoid, not only of vegetation, but also of organic matter except in a few "refugia," northeast of the crater.

We sampled 271 plots on the north slope of Mount St. Helens that extended over 25 km^2 in order to sample the range of existing variation on new substrates outside wetlands. Plots were centered at UTM 56-3800 E, 512-1500 N on stable substrates (Fig. 1). Elevations ranged from 1056 to 1387 m. Early descriptions of this area are in Wood and del Moral (1988).

Three surface types were sampled. Pyroclastic ejecta were deposited north of the crater. Most of the fine material has been eroded, leaving mixtures of harder rock and pumice. Pumice, deposited during the initial blast was concentrated to the east and south of the study area. Melting snow created drainage channels characterized by larger rocks and unstable surfaces.

Sampling—A plot was established in a homogeneous location with some vegetation at least 100 m from another plot. Approximate locations were determined *a priori* such that from 200 to 300 plots would be distributed within the target area. Plot locations were determined by GPS to within 5 m. "Easting," the longitude, increased west to east. "Northing," the latitude, increased south to north. Those sites within 50 m of Spirit Lake, lacking vegetation, or recently disturbed by elk or by erosion were excluded. Vegetation was sampled by estimating cover in 12 1-m^2 quadrats per plot. Quadrats were arrayed on four 9-m radii, starting at 2, 4 and 6 m. Additional species within the plot were noted and assigned a score of 0.01%. Plots were 250 m^2 in size.

Geographic and geomorphic features of each plot were determined. Plot location relative to refugia and to wetlands were recorded (1 = within 20 m; 2 = 20 to 50 m; 3 = > 50 m). Previous studies demonstrated that biologically rich sites have little impact beyond 20 m (Fuller and del Moral, 2003; del Moral and Eckert, 2005). Aspect was determined by compass and confirmed with a digital topographic map. Directions were converted to a scale to reflect increasing solar insolation (1 = 45° to 330°; 2 = 45° to 80° and 280° to 330°; 3 = 80° to 115° and 245° to 280°; 4 = 115° to 135°and 210° to 245°; 5 = 135° to 210°). Slope was determined by inclinometer and converted to a 5-part scale (1 = 0 to 5°; to 5 = over 21° in 5° increments). Exposure, determined from position on slope, protection from prevailing westerly winds, and local topography, was determined as follows: 1 = ravines or bottom of slope; 2 = shielded from wind or north-facing; 3 = gentle slopes open to some wind; 4 = exposed to prevailing winds; 5 = ridges). The elevation was determined by plotting GPS coordinates on the USGS digital topographic map. The habitat type (pumice or pyroclastic area) was determined from the impact map (Swanson and Major, 2005). Rills and drainage courses were recorded separately. Habitat, rills and drainage were binary functions. The surface texture was estimated by determining percentage (nearest 5%)for rocks (> 2 cm), gravel (0.5 to 2.0 cm), sand (< 0.5 cm) and fines (very smooth when rubbed between fingers). The total cover of pumice was estimated visually. Species nomenclature is that found in the Integrated Taxonomic Information System (ITIS; http://www.itis.usda.gov).

Data summary—The number of species (richness, S), their percent cover and three measures of vegetation structure were calculated for each plot. We used the Shannon Index ($H' = -\Sigma p_i \ln p_i$), which combines richness and the relative abundances of each species. The complement of Simpson's dominance index [$D = (1 - \Sigma p_i^2)$] and evenness [$E = H' / \ln(\text{richness})$] both vary from 0 to 1. E is insensitive to richness, while D is insensitive to small sample size and to rare species. Each measure depends on p_i, the proportion of the cover represented by species i (McCune and Mefford, 1999).

Floristic analyses—For descriptive purposes, plots were clustered into groups with similar species composition using flexible sorting (ß = -0.25) with Euclidean distance. Multi-response permutation procedures (MRPP; McCune and Grace, 2002) were applied to assess the validity of the classification. Percent similarity among the groups was determined by Euclidean distance.

Nonmetric multidimensional scaling (NMS) was used to determine the number of effective dimensions in the floristic data, but its result was no better than detrended correspondence analysis (DCA; McCune and Grace, 2002). Because DCA provides scaling in floristic units, we used this method. All ordinations were conducted using PC-ORD (McCune and Mefford, 1999).

Statistical analyses—One-way analysis of variance (ANOVA) followed by the conservative Bonferroni test of differences among the means were used to assess structural parameters among floristic groups and habitat groups. In a few cases, ANOVA indicated small significant differences, but the conservative multiple means test did not separate groups.

RESULTS

Clusters**—**Cluster analysis produced six community types (CT) that were significantly different from each other as determined by MRPP. The chance-corrected within-group agreement, **A**, was 0.255 (P >>0.0001), overall indicating distinctive groups (t = -59.9). Pair wise comparisons were all significant. The internal Euclidian distances varied from 14.3 (CT-C) to 38.6 (CT-A). There were 14 dominant species (cover > 1%) and nine additional species that demonstrated significant differences between the community types (Table 1). *Agrostis scabra* was the only common species that did not differ significantly among CTs. Mean DCA-1 scores were used to order the clusters and species were listed by their DCA-1 sequence.

The distribution of the CTs indicates moderate correlation to geographic position, though anomalies occur (Fig. 1). While most CT-A plots were at higher elevations in the southeast portion of the study area, two occurred to the northwest. The low ridge in this area also included plots from three other types. CT-D was scattered throughout the study area, but was most common on pumice to the east. The pyroclastic area contained samples of CTs C, E and F.

The habitat variables of the CTs were compared by ANOVA for descriptive purposes. The CTs did not differ with respect to aspect, exposure, distance-to-wetlands, presence of rills or presence of sandy surfaces. Rather, CTs were arrayed with respect to habitat features that were spatially based (Table 2). We ranked each variable from 1 to 6 and recorded the rank of each CT to facilitate comparisons.

CT-A occurred primarily in the southeast, at higher elevations on steeper pumice slopes (Fig. 1). Most of these plots were near relict sites and had stable surfaces, evidenced by limited rocks and gravel and few rills. Surface soil texture was sandy. CT-A was characterized by *Lupinus latifolius*, *Penstemon cardwellii* and *Saxifraga ferruginea*, while mosses (*Grimmia* and *Racomitrium canescens*) were scattered among the larger plants. *Agrostis pallens* and *Hypochaeris radicata* were common, as were species that were common in nearby refugia, e.g. *Castilleja miniata* and *Alnus viridus*.

The mean position of CT-B plots was at higher elevations on slopes of moderate slope, with substantial gravel. Most sites were on pumice and some were near relicts. Only *L. lepidus* occurred consistently, with mosses, grasses and *Penstemon* common.

CT-C was significantly farther west than CT-A and was the most northern type, found at the lowest elevations, far from relicts, primarily on pyroclastic substrates. Rills, rocks and gravel were uncommon. *Lupinus lepidus* reached its greatest abundance, and mosses were common.

CT-D was well scattered throughout the study area and had intermediate environmental characteristics. Rills were common. The vegetation had substantial *Lupinus* and high cover by *Polytrichum*, *Racomitrium* and *Hypochaeris*, with some *Salix*.

CT-E was concentrated on pyroclastic surfaces to the west of the study area and lower elevations, but on steeper slopes. Surfaces were coarse textured and rills common. Racomitrium and Lupinus were the leading dominants.

CT-F occurred to the west and as a result, pyroclastic surfaces were common. Surfaces were coarse, with high values for rocks, gravel and rills. *Racomitrium* dominated this CT, with *Lupinus* common. CT-E and CT-F were similar floristically and environmentally.

The CTs differed in total and mean richness, percent cover, diversity, evenness and dominance (Table 3). CT-A had the highest total richness, while other CTs had similar total richness. Mean richness was highest in CT-A and least in CT-B and CT-F.

Total cover was highest where mosses were dominant and *Lupinus* common (CT-E), and lowest in CT-C where mosses were less common and *L. lepidus* uncommon. Diversity (H') was least in CT-F, where *Racomitrium* reached its highest levels. Diversity was higher in CT-E, where several other species were common. Diversity in CT-D was similar to CT-E, resulting from reductions in cover in mosses and *Lupinus*. Diversity was highest in the remaining CTs. CT-B had the lowest plant cover, and many species were relatively abundant. In CT-A, dominance by *Lupinus latifolius* was compensated for by high species richness and several common species. CT-C, only slightly less diverse, had only one abundant species, but several relatively common ones. Variation within each CT was large, so that values overlapped greatly and structural patterns were individualistic, not truly representative of a community.

TABLE 1. Cover of common species in six community types (CTs). P is from ANOVA of cover; group sample size is in parentheses; superscripts unite members of homogeneous groups (Bonferroni comparisons, $P < 0.05$). These species exceeded 1% in at least one CT or they had significant differences; tr = trace occurrence. Species with significant ANOVA, but no superscripts lack differences by the Bonferroni test. CTs and species are each in order of DCA-1 scores.

		Community Type (CT)					
Species	**P <**	**A (16)**	**B (21)**	**C (20)**	**D (83)**	**E (69)**	**F (62)**
Lupinus latifolius	0.000	23.0^{a}	1.13^{b}	0^{b}	0.24^{b}	0.04^{b}	0.38^{b}
Luzula parviflora	0.000	0.48^{a}	tr^{b}	0^{b}	0.04^{b}	0.20^{b}	0.02^{b}
Saxifraga ferruginea	0.000	1.25^{a}	0.07^{b}	0^{b}	0.15^{b}	0.02^{b}	0.02^{b}
Carex paysonis	0.000	0.29^{a}	tr^{b}	tr^{b}	0.04^{b}	tr^{b}	tr^{b}
Carex microptera	0.000	0.51^{a}	0.05^{b}	tr^{b}	0.04^{b}	0.01^{b}	tr^{b}
Penstemon cardwellii	0.000	6.37^{a}	0.65^{b}	0.06^{b}	0.82^{b}	0.54^{b}	0.40^{b}
Alnus viridus	0.000	1.74^{a}	0.07^{b}	0.07^{b}	0.35^{b}	0.07^{b}	tr^{b}
Chamerion angustifolium	0.001	0.35^{a}	0.04^{b}	0.07^{b}	0.08^{b}	0.07^{b}	0.06^{b}
Phacelia hastata	0.02	0.17	0.16	0	0.05	0.20	0.02
Penstemon sericea	0.04	0.28	0.32	0.10	0.03	0.34	0.03
Agrostis pallens	0.003	2.58^{a}	1.94^{a}	0.78^{b}	1.39^{a}	0.20^{b}	0.08^{b}
Grimmia sp.	0.01	2.48^{a}	0.11^{b}	1.71^{b}	0.30^{b}	0.51^{b}	0.15^{b}
Achillea millefolium	0.05	0.80^{a}	0.52^{ab}	0.47^{ab}	0.20^{b}	0.10^{bc}	0.08^{c}
Carex mertensii	0.01	0.87^{a}	0.23^{ab}	0.29^{ab}	0.35^{ab}	0.22^{b}	0.19^{b}
Castilleja miniata	0.009	1.93^{a}	0.16^{b}	2.10^{b}	1.30^{ab}	0.65^{b}	0.20^{b}
Anaphalis margaritacea	0.000	0.96^{a}	0.29^{b}	0.19^{c}	0.79^{a}	0.25^{c}	0.28^{bc}
Epilobium paniculatum	0.02	0.05^{b}	0.02^{b}	0.06^{b}	2.52^{a}	0.06^{b}	0.02^{b}
Salix commutata	0.000	0.34^{b}	0.42^{b}	1.26^{b}	4.97^{a}	0.96^{b}	0.62^{b}
Hypochaeris radicata	0.000	1.57^{b}	0.67^{b}	1.00^{b}	5.53^{a}	2.03^{ab}	1.27^{b}
Polytrichum juniperinum	0.000	0.75^{c}	0.73^{c}	3.63^{b}	11.6^{a}	2.16^{bc}	0.82^{c}
Elymus elymoides	0.04	0.0^{b}	0.19^{ab}	0.04^{b}	0.28^{a}	0.05^{b}	0.03^{b}
Agrostis scabra	ns	0.19	1.53	0.87	0.90	0.63	0.73
Hieracium albiflorum	0.02	0.37	0.34	0.48	0.84	0.70	0.45
Lupinus lepidus	0.000	0.66^{c}	8.87^{b}	28.1^{a}	9.24^{b}	26.7^{a}	11.3^{ab}
Cistanthe umbellata	0.02	0.04^{b}	0.41^{a}	0.31^{a}	0.03^{b}	0.36^{a}	0.36^{a}
Racomitrium canescens	0.000	2.45^{c}	1.41^{c}	4.10^{c}	7.85^{c}	32.2^{b}	46.7^{a}

FIG. 1. SPATIAL DISTRIBUTION OF SAMPLES DISTINGUISHED BY COMMUNITY TYPES. EASTING IS THE LONGITUDE, FROM WEST TO EAST; NORTHING IS THE LATITUDE FROM SOUTH TO NORTH. LEGEND LISTS DOMINANT SPECIES FROM EACH OF THE SIX COMMUNITY TYPES.

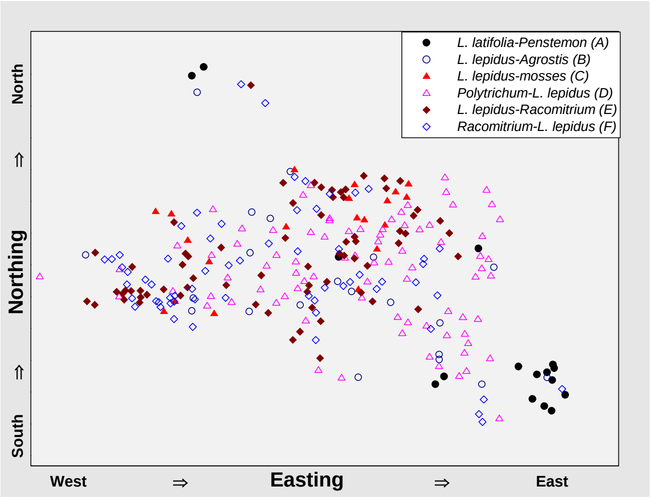


Table 2. Environmental parameters that differed among the CTs. Values were ranked from 1 to 6 as indicated. Habitat ratio is from all plots on pumice sites to all plots on pyroclastic sites. P is the ANOVA for the comparison; superscripts indicate membership in homogenous groups. Lack of a subscript indicates no differences by the Bonferroni test. Sample size is in parentheses.

			Community Types (CT)					
Parameter	**Type**	**P <**	**A (16**	**B (21**	**C (20**	**D (83**	**E (69**	**F (62**
Easting	East→West	0.000	1^{a}	3^{bc}	4^{bc}	2^{b}	5^{c}	6^{c}
Northing	South→North	0.000	1^{a}	2^{ab}	6^{c}	3^{bc}	4^{bc}	5^{bc}
Elevation	High→Low	0.000	1^{a}	2^{b}	6^{d}	3^{bc}	5^{bc}	4^{cd}
Slope	Shallow→Steep	0.02	1	4	6	2	3	5
Relict proximity	Near→Distant	0.002	1^{a}	2^{ab}	6^{b}	3^{b}	4^{b}	5^{b}
Gravel	Low→High	0.001	1^{a}	6^{b}	2^{ab}	4^{b}	3^{b}	5^{ab}
Rock	Low→High	0.01	1^{a}	3^{ab}	2^{ab}	4^{ab}	5^{b}	6^{b}
Rills	Rare→Common	0.007	2^{ab}	4^{ab}	1^{a}	6^{b}	3^{ab}	5^{ab}
Habitat ratio	Pumice→Pyroclastic	0.000	1^{a}	2^{a}	6^{b}	3^{a}	5^{b}	4^{b}

Table 3. Structural features of community types. Statistics as in Table 1.

		Community Types (CT)					
Structural measure	**P <**	**A (16)**	**B (21)**	**C (20)**	**D (83)**	**E (69)**	**F (62)**
Total Richness (S)	---	64	44	55	55	55	60
Species Richness	0.002	19.7^{a}	15.0^{b}	16.9^{ab}	16.0^{b}	16.5^{ab}	15.0^{b}
Percent Cover	0.000	54.7^{abc}	21.9^{c}	53.1^{abc}	47.7^{bc}	70.2^{a}	65.3^{bc}
Diversity (H')	0.000	1.69^{a}	1.79^{a}	1.61^{ab}	1.35^{b}	1.34^{b}	1.02^{c}
Evenness (E)	0.000	0.576^{ab}	0.671^{a}	0.581^{ab}	0.492^{bc}	0.482^{c}	0.379^{d}
Dominance (D)	0.000	0.684^{ab}	0.751^{a}	0.705^{ab}	0.573^{c}	0.638^{b}	0.468^{d}

Patterns in Evenness and Dominance differed in their details, but follow those of diversity. Both peak in CT-B, the least dense CT. They reach their minimum value in CT-F, where *Racomitrium* and *L. lepidus* dominate. Intermediate values occur in CT-D and CT-E. CT-D has moderate cover and a variety of common species (e.g. *Penstemon, Hypochaeris,* and *Salix*) that reduce the dominance of *Racomitrium* and *Lupinus*. The high cover of CT-E would suggest strong dominance, but moderate environmental conditions support several common species in most plots.

Plot distribution**—**The plots were assigned to one of four habitat categories: pumice, pyroclastic, drainages and dense *Lupinus* (greater than 50% cover) for comparison to the 1992 data (see below). The χ^2 test of the six CT by four habitat types demonstrated a significant relationship ($\chi^2 = 59.9$; $P < 0.0001$). CTs were all distributed in two or more habitats. CT-A and CT-B were confined to pumice and a few drainages. CT-C was primarily on pyroclastic and drainage sites, with a few plots on pumice. CT-D, the largest cluster occurred on all sites, approximately as would be expected. CT-E and CT-F occurred widely on pumice and pyroclastic sites, but had few drainage or lupine occurrences. *Lupinus* colonies were largely assigned to CT-D, with a few in CT-E and CT-F.

Indirect ordination—The DCA position of each plot, identified by CT, demonstrated considerable floristic variation within these communities (Fig. 2). Variation was concentrated on DCA-1, whose eigenvalue was 0.448, compared to eigenvalues of 0.182 on DCA-2 and 0.130 on DCA-3. DCA-1 spanned 3.53 half-changes (HC), A DCA-2 spanned 2.55 HC and DCA-3 spanned 3.06 HC. DCA scores for each CT were compared by ANOVA (Table 4).

Table 4. DCA scores for community types. Statistics based on DCA scores as Table 1. S.D. = standard deviation. (See Fig. 2.)

		Community Type					
Axis, S.D.	P <	A (16)	B (21)	C (20)	D (83)	E (69)	F (62)
DCA-1	0.0000	254.2^{a}	138.4^{b}	134.6^{bc}	117.4^{c}	65.5^{d}	36.1^{e}
S.D.	---	47.9	20.0	34.4	21.9	22.8	32.7
DCA-2	0.0000	150.8^{ab}	154.4^{ab}	134.6^{bc}	163.0^{a}	137.8^{bc}	119.5^{c}
S.D.	---	72.1	26.6	93.1	24.8	15.5	13.2

CT-E and CT-F are relatively tight-knit, while the others distributed along both axes. The six CTs were well distributed on DCA-1, with only CT-C overlapping CT-B and CT-D. On DCA-2, CT-C was distinguished from CT-D, but not CT-B, to which it is closely related.

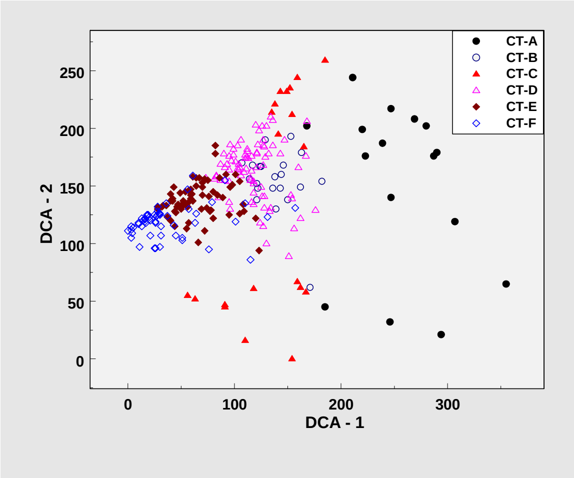


Fig. 2. Position of plots determined by DCA. Plots symbolized by community type (see Fig. 1).

Stepwise regression of environmental variables vs. DCA-1 indicated strong correlations with Easting (+; $P < 0.000$), Elevation (+; $P < 0.000$), Exposure (-; $P < 0.02$), Rocks (-; $P < 0.03$), Gravel (-; 0.04) and fines (+; 0.05). The analysis of DCA-2 indicated weak correlations with Elevation (+; 0.006), Pumice (+; 0.01) and Distance to Wetland (-; 0.05).

Many common species were correlated with the first or second axes. Species abundant in CT-A were positively correlated to DCA-1 (e.g. *Lupinus latifolius*, *Penstemon cardwellii*, *Saxifraga ferruginea*, and *Castilleja miniata*.) *Racomitrium* was strongly negatively correlated and *L. lepidus* weakly so. Many species were negatively correlated to DCA-2. These included the early pioneer species *Hypochaeris*, *Hieracium albiflorum*, and *Chamerion*, as well as *Achillea*. Both common mosses were strongly negatively distributed. *Carex paysonis* and *Penstemon* were positively correlated.

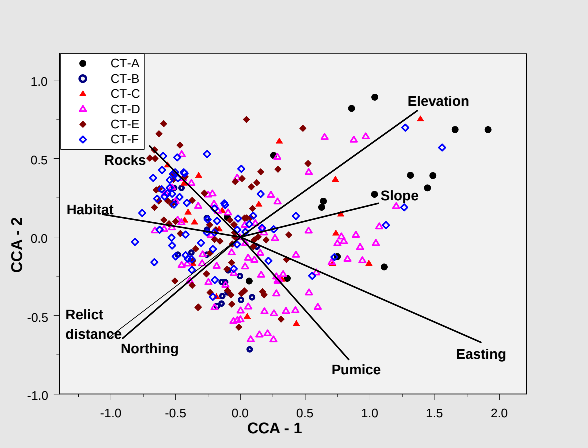
Direct ordination—Canonical correspondence analysis was applied to determine the degree to which these environmental factors could predict species patterns. The 271 plots were analyzed using 41 species that occurred in at least 3% of the plots ($n > 8$ plots). Because variables Rocks, Gravel, Sand and Fines totaled to 100%, we excluded Sand a priori to reduce autocorrelations that render the analysis problematic.

Total variance, the inertia, was 3.127, of which 7.4%, 3.5% and 1.9% were associated with the first 3 axes, respectively. Pearson Correlations between species and environment were low, 0.662, 0.561 and 0.458, respectively. These low correlations indicate that factors operating at a smaller scale than those measured were important. They also suggest that stochastic factors continue to be important. However, both the eigenvalues and the correlations were significantly greater than what was obtained by the Monte Carlo simulation of 100 trials on each axis. No simulation produced a higher eigenvalue or correlation for the first three axes. Given the low degree of explanation, only Axis 1 and Axis 2 will be explored.

Of the 15 variables used, eight were included in the multiple regression. We interpret these results with caution, treating them as hypotheses, not explanations. Variables with the greatest explanatory power and the position of each plot (which is determined as a linear combination of its environmental variables) demonstrate general patterns (Fig. 3). Plots were coded as in other figures. Vectors indicate the relative strength of the variables along two axes (but we multiplied the vector length by five for clarity).

Clearly, position effects were the strongest (Table 5). Easting was the strongest contributor to CCA-1 and significant on CCA-2. Elevation, which was strongly correlated ($r = -0.83$) to northing, was the second strongest factor on CCA-1 and the strongest factor on CCA-2. It was inversely related to habitat because pumice sites typically were at elevations higher than to pyroclastic sites. Similarly, slope increased with elevation, and inversely with northing, so it is not surprising that this factor was significant. Distance from relicts was also significant on CCA-1. The degree of pumice-covered surface was the only significant factor on CCA-1 that was not spatially related. On CCA-2, slope, pumice and easting were the leading variables. The fraction of the surface covered by rocks was the only significant surface feature. The presence of rills or a drainage area had little effect on species composition at the scale of this study. Neither did the vegetation vary greatly with respect to aspect, exposure or distance to wetlands.

FIG. 3. CCA RESULTS. PLOTS SYMBOLIZED BY COMMUNITY TYPE. VECTORS ARE MULTIPLIED BY 5 FOR BETTER RESOLUTION. "HABITAT" IS EITHER PUMICE OR PYROCLASTIC SITES. "PUMICE" IS THE PERCENTAGE OF PUMICE ON THE SURFACE.



The six CTs were only weakly correlated to the canonical axes (Fig. 3). Since less that 13% of the vegetation variation is explained, this is not surprising. The major canonical correlates were spatial, even though the CTs are also broadly distributed in space (Fig. 1).

TABLE 5. CANONICAL CORRELATIONS FOR VARIABLES INCORPORATED IN THE MULTIPLE REGRESSION (BOLD) OR WHICH DIFFERED BETWEEN THE COMMUNITY TYPES.

Parameter	**CCA-1**	**CCA-2**
Easting	**0.807**	**-0.407**
Northing	**-0.379**	**-0.392**
Elevation	**0.567**	**0.490**
Slope	**0.442**	**0.130**
Relict proximity	**-0.421**	**-0.338**
Pumice	**0.348**	**-0.475**
Gravel	-0.041	-0.025
Rocks	**-0.299**	**0.352**
Rills	-0.079	-0.100
Habitat type	**-0.443**	**0.089**

Comparison to 1992—Sampling in 1992 differed in several respects from the 2004 study. In 1992, plots were 100 m^2, but it was possible to measure the cover of all species with cover < 5%. In the few cases where cover exceeded 5%, visual estimates were used. Plots were dispersed over a similar range of sites, but included refugia, which are not considered here. GPS technology was not available, so plot positions were not determined accurately. Plots were divided into three habitat types and lupine patches, as in the present study. Sampling appeared to adequately cover the range of variation (del Moral, Titus, and Cook, 1995).

Total richness increased from 79 in 1992 to 105 species in 2004 (Table 6). There were 61 species in 1992 and 74 species in 2004 that occurred more than once. Richness within *Lupinus* colonies declined slightly, and the numbers on pumice were comparable. Pyroclastic and drainage areas, habitats in which cover has developed substantially, also produced a substantial increase in species richness.

The mean number of species per plot in the four habitats did not differ significantly in 1992. By 2004, there were small differences among habitats, and all had increased species richness significantly (Table 6). In 1992, *Lupinus* colonies had substantial cover, over ten times most other plots. By 2004, they were even denser, largely due to the development of moss layers. Percent cover in each type had increased markedly. In particular, drainages appear to have stabilized, with erosion being increasing confined to stream courses. This has allowed vegetation to develop on formerly unstable surfaces.

Hierarchical structure was estimated by evenness and dominance, both bounded by 0 (only 1 species) and 1.0 (all species equally abundant). Each demonstrated strong dominance by *Lupinus lepidus* in lupine colonies (naturally), and higher equitability in the other habitats. By 2004, *Lupinus* colonies had become more diverse and lupines less dominant. In contrast, dominance hierarchies had developed on the other sites reducing equitability. Dominant species varied, but included mosses, *Agrostis*, and *Penstemon* in various locations. Equitability in 2004 retained significant differences among the sites (Table 6). In 2004, evenness and dominance were both significantly higher in lupines and significantly lower in the other sites compared to 1992. Diversity (H') mirrored the equitability trends. However, increased richness was countered by increased dominance so that in 2004 pumice and drainages were not significantly different from 1992. Lupine colonies were more diverse, and drainages less diverse.

Table 6. Structure comparisons between 1992 and 2004. Superscripts within a column of a group indicate membership in homogeneous groups (Bonferroni comparisons, $P < 0.05$). Contrasts between sample years were made with simple t-test with P provided in last column. Richness in habitat types reported for all species (those with two or more occurrences are in parentheses).

Parameter	Habitat Type[a]	1992	2004	P <
Total Richness	**All sites**	**79**	**105**	**n.a.**
Richness	Lupine colonies	52 (38)	44 (31)	n.a.
	Pumice	66 (50)	69 (54)	n.a.
	Pyroclastic	36 (26)	63 (49)	n.a.
	Drainages	42 (35)	68 (43)	n.a.
Mean Richness	Lupine colonies	12.5	17.1^{a}	0.02
	Pumice	11.7	17.0^{a}	0.0000
	Pyroclastic	9.8	15.3^{b}	0.0000
	Drainages	11.2	15.2^{b}	0.0006
Percent Cover	Lupine colonies	68.6^{a}	107.3^{a}	0.0001
	Pumice	7.2^{b}	56.8^{b}	0.0000
	Pyroclastic	2.9^{b}	56.5^{b}	0.0000
	Drainages	2.6^{b}	38.3^{c}	0.0000
Evenness	Lupine colonies	0.254^{a}	0.384^{a}	0.03
	Pumice	0.610^{b}	0.515^{b}	0.0005
	Pyroclastic	0.644^{b}	0.455^{c}	0.0000
	Drainages	0.629^{b}	0.518^{b}	0.01
Dominance	Lupine colonies	0.301^{a}	0.512^{c}	0.005
	Pumice	0.646^{b}	0.627^{b}	n.s.
	Pyroclastic	0.654^{b}	0.563^{a}	0.03
	Drainages	0.637^{b}	0.600^{ab}	n.s.
Diversity	Lupine colonies	0.668^{a}	1.099^{b}	0.007
	Pumice	1.466^{b}	1.447^{a}	n.s.
	Pyroclastic	1.443^{b}	1.228^{b}	0.05
	Drainages	1.503^{b}	1.398^{ab}	n.s.

[a] Sample sizes: Lupine colonies 19 (1992) and 17 (2004) plots; pumice, 49 and 117 plots; pyroclastic 17 and 84 plots; drainages 21 and 53 plots.

The rank correlations of species in similar habitats were compared. Before the analysis, uncommon species (< 0.02% cover) were removed, leaving 50 species in the rank order analysis (1992 = 43 species; 2004 = 50 species). When ranks are compared, species that occur in only one of the two years are excluded. Spearman rank order correlations (S_r) showed substantial changes between years in each habitat type. S_r within types, between years, were low, but significant (Table 7). Pumice and pyroclastic habitats changed the most, while drainages were relatively similar between years. To provide perspective, we compared habitat types within years. In 1992, none of the comparisons were significant, and some of the rank correlations were negative. The highest correlation was 0.156 between pumice and lupine patches. In contrast, as vegetation developed, the vegetation between habitat types became more similar. The lowest S_r, that of pumice compared to pyroclastic, was not significant ($S_r = 0.190$). All other comparisons were significant: Pumice vs. Drainage ($S_r = 0.320$; $P < 0.035$) and vs. Lupine colonies ($S_r = 0.531$; $P < 0.0006$); Pyroclastic vs. Drainage ($S_r = 0.519$; $P < 0.0005$) and vs. Lupine colonies ($S_r = 0.545$; $P < 0.0006$); and Drainage vs. Lupine colonies ($S_r = 0.591$; $P < 0.0001$).

TABLE 7. CHANGES IN THE RELATIVE ABUNDANCE OF SPECIES INDICATED BY THEIR ABUNDANCE RANKS, STRATIFIED BY HABITAT IN 1992 AND 2004.

	Pumice		Pyroclastic		Drainage		Lupine Patch	
Species	**1992**	**2004**	**1992**	**2004**	**1992**	**2004**	**1992**	**2004**
Achillea millefolium	20	15	21	22	20	18	22	23
Agrostis pallens	6	7	5	16	13	8	9	5
Agrostis scabra	21	9	13	7	10	10	17	7
Alnus viridus	18	16	---	28	29	23	13	8
Anaphalis margaritacea	5	18	1	10	3	15	6	20
Carex mertensii	12	14	10	19	7	14	10	19
Castilleja miniata	26	8	---	6	---	9	20	9
Chamerion angustifolium	13	26	2	21	4	21	12	22
Cistanthe umbellata	15	19	19	9	14	17	21	24
Elymus elymoides	---	24	---	24	---	28	24	---
Epilobium anagallidifolium	24	21	15	20	25	24	---	15
Eriogonum pyrolifolium	11	31	16	29	19	31	26	---
Grimmia sp.	---	10	24	11	---	7	---	10
Hieracium albiflorum	17	12	8	8	11	11	14	11
Hypochaeris radicata	10	5	4	4	6	4	4	6
Juncus parviflora	16	17	14	15	8	13	19	13
Luetkea pectinata	17	29	18	27	18	27	15	16
Lupinus latifolius	9	4	---	14	5	12	2	---
Lupinus lepidus	1	1	3	2	2	2	1	1
Luzula parviflora	7	27	11	---	16	26	16	25
Penstemon cardwellii	2	6	6	13	12	6	5	12
Penstemon sericea	14	23	---	23	21	29	27	27
Phacelia hastata	23	28	22	28	22	20	25	26
Polygonum minimum	22	13	20	3	15	5	---	3
Polytrichum juniperinum	---	3	---	12	---	16	30	14
Populus balsamifera	---	22	---	17	---	19	31	21
Pseudotsuga menziesii	25	30	12	18	23	26	18	18
Racomitrium canescens	8	2	9	1	9	1	3	2
Salix commutata	3	11	7	5	1	3	7	4
Saxifraga ferruginea	4	20	17	26	17	22	23	17
Vaccinium membranaceum	27	25	---	---	27	30	11	28

The low correlations between years indicated that species abundances changed greatly. *Agrostis scabra*, *Castilleja*, *Elymus*, *Polygonum* and *Populus* all became more common. The mosses all became substantially more abundant, with *Racomitrium* assuming dominance in many places and *Polytrichum* becoming an important subordinate. *Lupinus latifolius* became more abundant on pumice and pyroclastic habitats, but declined in drainage sites. Many of the initial colonists became proportionally less abundant (e.g. *Anaphalis*, *Chamerion*, *Eriogonum*, and *Luzula*). Only *Hypochaeris* retained its share in most places and increased it on pumice, while *Saxifraga* declined on typical sites, but increased in lupine colonies.

DISCUSSION

The landscape created by the eruption of Mount St. Helens has developed rapidly since 1992. At that time, vegetation was sparse. Other than wetlands, only *Lupinus* colonies were densely populated by plants. Since then, the pace of recovery accelerated. *Lupinus* and mosses became broadly distributed, and many other species achieved broad distribution. Based on permanent plot data, much of the increase occurred since 2000, and has accelerated since 2002 (see http://protist.biology.washington. edu/delmoral/GridPumPlain2004.pdf and http://protist.biology.washington.edu/delmoral/GridPumPlain 2004.pdf). As sites developed, *Lupinus* has tended to promote other species through N-fixing, while other species have developed greater competitive abilities. The balance between facilitation and inhibition has therefore been altered, changing the rules for success (cf. Callaway and Walker, 1997).

Community types—While we describe six community types, each is highly variable and none has a close correlation to either habitats or to environmental variables. Each has a wide geographic distribution (Fig. 1). While they can be distinguished by indirect ordinations (DCA), plots demonstrate overlap and considerable variation (Fig. 2). Vegetation can only poorly be predicted by canonical correspondence analysis (Fig. 3), and none of the predictors is strong (Table 5). While the CTs do show a modest degree of pattern, there is much overlap among samples of different composition. The principal determinants were, as in 1992, related to spatial landscape factors, not to local conditions. Thus, geographic coordinates and elevation were the leading predictors. We conclude that stochastic factors related to dispersal and establishment continue to determine species composition, while in most places deterministic factors related to competition and local soil conditions have not resulted in significant species turnover.

***Species patterns*—**Species also lacked the strong ties to environmental factors that are typical of developed vegetation. A few species were concentrated in a single community type (e.g. *L. latifolius*, *Saxifraga ferruginea*, *Carex microptera, Epilobium paniculatum*), but even these occurred in several others. In contrast, many species were common in all community types. These included *Agrostis pallens*, *A. scabra*, *Carex mertensii*, *Anaphalis margaritacea*, *Lupinus lepidus* and several mosses.

These patterns imply that many species remain where they established when there were few competitors. They persist, and have expanded, even though they occupy sub-optimal habitats. As the vegetation develops, it is likely that competitive interactions will limit many species to environments to which they are better adapted. As that process unfolds, we expect that analyses such as the CCA reported here will yield higher correlations.

Dominance hierarchies—The six community types demonstrated strong differences in cover, diversity and equitability. Percent cover was highest where mosses and *L. lepidus* dominated (CT-E, CT-F) and least where *Agrostis* and *L. lepidus* were common. Diversity and equitability were, as would be expected, were lowest when percent cover was highest since only a few species produce the cover, leading to pronounced dominance.

Dominance hierarchies have developed since 1992, due to developing dominance of a few species (Table 7). In 1992, vegetation was dense only in *Lupinus* colonies. Here, strong dominance, with little moss cover, was reflected in very low equitability and diversity values. In *Lupinus* colonies, increased diversity led to reductions in measures of community structure. In the other habitat types, dominance either was reduced or it remained the same, even though the number of species increased. In pumice, pyroclastic, and drainage habitats, a few species became dominant. Often these dominants were mosses that were not pioneers, rather they were later colonists. Thus, we observe the initial stages of the development of typical dominance hierarchies. It is likely that until dramatic changes in physical vegetation structure occur (e.g. through the invasion of conifers), existing species will expand differentially and dominance values will continue to decline. Because the developing dominants will be those better adapted to a particular site, one result is that closer ties to the local environment should develop.

Implications—This study demonstrated that vegetation development has accelerated since 1992. Correlations between vegetation patterns and environmental and landscape factors remained weak suggesting that heterogeneous patterns of invasion and establishment have not yet been obliterated by deterministic factors such as competition or environmental gradients. In addition, species composition of community types was variable. Økland (1999) discussed the general observation that both indirect (e.g. DCA) and direct (e.g. CCA) methods retain large amounts of unexplained variation, even in mature vegetation. We expect that unexplained variation of vegetation patterns in this study area will decline with time, but that a large residual will remain. It is possible that low correlations in this study are related to floristic variations controlled at a scale smaller than our sample plots, but other factors are more likely. The floristic correlations to spatial factors imply that dispersal effects are strong. If a given species has a low probability of reaching identical sites, then links between distributions of species and their environment are weakened (c.f. Ozinga, et al. 2005).

Once established, many species can persist even when confronted by superior competitors (Tagawa, 1992; Eriksson and Eriksson 1998). Continued occupancy of a site also alters soil conditions. As a result, pioneers can dictate conditions for future colonization (Magnússon, Magnússon, and Sigurđsson, 2001). Stochastic events that permit the development of a heterogeneous mosaic of species may promote the eventual development of a mosaic representing alternative stable states (Belyea and Lancaster, 1999; Petraitis and Latham, 1999; Savage, Sawhill, and Askenazi, 2000). *Lupinus* colonies, in particular, create conditions where a few species thrive (*Agrostis scabra, Hypochaeris,* and *Polytrichum*) and vegetation development is hastened. Less dense vegetation with little moss may be better suited to invasion by conifers.

The barren landscape on the north slope of Mount St. Helens continues to develop, but the process remains incomplete. Existing vegetation continues to expand, a few new species invade, competitive hierarchies are becoming established and herbivores everywhere alter the patterns (Bishop, 2002; Bishop et al., 2005). The maturation of this vegetation should continue to manifest a mosaic of persistent communities at least until conifers (or in a few sites, *Alnus viridus*) establish. Landscape level studies such as this one complement experimental and monitoring studies and remote sensing approaches. Future studies of the effects of dominant species (e.g. *Lupinus, Racomitrium, Alnus*) on the invasion of species characteristic of more developed vegetation will provide insight into how late stages of primary succession function. This knowledge will improve the efficiency of vegetation rehabilitation projects.

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