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Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption

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Abstract

Recovery of herbaceous vegetation on Mount St. Helens was studied annually after the massive lateral eruption of May 18, 1980. Measures such as species richness, cover, and diversity were combined with detrended correspondence analysis to describe vegetation recovery rates under different combinations of initial impact intensity and degree of isolation from recolonization sources. A major key to recovery is whether any plants survived the devastation. Survival of even a few individuals markedly accelerated recovery. Where no plants survived, the degree of isolation becomes paramount. New, barren substrates, a few meters from undisturbed sites, have begun to develop some vegetation, while more isolated sites have scarcely any subalpine plants present. On any site, plant-mediated processes that improve conditions for growth and the invasion of other species predominate in the early stages, but as vegetation develops, biotic inhibition and establishment of seedlings from adults already in the habitat gain importance. The rate at which this conversion occurs is a function of the size and intensity of the initial impact.

Abbreviations: DCA, Detrended correspondence analysis

Nomenclature is that of Hitchcock & Cronquist (1973), The Flora of the Pacific Northwest. University of Washington Press, Seattle.

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Introduction

The eruptions of Mount St. Helens in Washington State commenced on May 18, 1980, and included a catastrophic lateral blast, a massive debris avalanche, pyroclastic flows, lahars, and tephra fallout (Rosenfeld 1980). These events created varied conditions to which the vegetation has responded. Succession is the population- and community response to perturbation, including invasion and extinction of populations and changes in their relative abundances. We studied these responses in treeless habitats that differed in size and severity of volcanic impacts and, therefore, in their biological legacy (Franklin *et al.* 1985) and rate of reinvasion (del Moral 1983b; del Moral & Wood 1986). The biological legacy results from survival of intact adults, buried vegetative organs, propagules, or merely organic matter.

This paper emphasizes species recovery above treeline, which is nevertheless at montane elevations due to the recency and frequency of prior eruptions. The major questions explored include: How does disturbance intensity affect recovery rate? What role do survivors play in determining this rate? What are the roles in facilitation and inhibition (sensu Connell & Slatyer 1977)? Do species richness and vegetation cover recover at the same rate?

We propose that disturbance intensity determines the relative importance of seed dispersal and that disturbance size determines whether the succession will be uniform or will proceed as a series of waves expanding from point introductions. This study explores recovery patterns as documented in permanent plots examined annually since 1980.

Natural history

Pre-existing conditions

Mount St. Helens is located in southwestern Washington State at 46°12′N, 122°11′W (Fig. 1). Formerly at an elevation of 2950 m, the top of the cone is now at 2550 m.

No quantitative descriptions of subalpine vegetation on Mount St. Helens prior to 1980 exist. Above the ragged timberline on the north side of the mountain, composed primarily of stunted *Pinus contorta* and *Abies lasiocarpa*, relatively sparse, xeric meadows prevailed (Kruckeberg 1987). The pumice supported sparse vegetation dominated by *Eriogonum pyrolifolium, Juncus parryi*, and *Spraguea umbellata.* Common species in more favorable sites *Agrostis diegoensis, Lupinus lepidus, Achillea millefolium, Luetkea pectinata, Festuca idahoensis, Antennaria rosea, Penstemon cardwellii, Arctostaphylos nevadensis,* and *Castilleja miniata.*

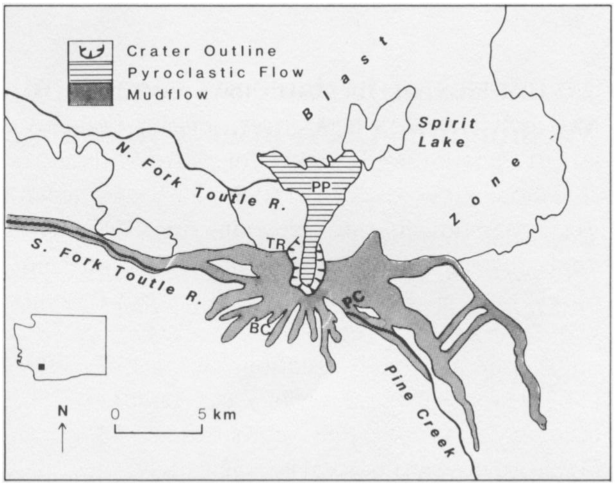

Fig. 1. Location of permanent plots near Mount St. Helens, southwestern Washington State. PP = Pumice Plains (pyroclastic zone); WR = Wishbone Ridge (blast zone); TR = Toutle Ridge (blast zone); BC = Butte Camp (mudflows and tephra deposits); and PC = Pine Creek (scours).

The flora of Mount St. Helens is depauperate compared to neighboring volcanoes. Kruckeberg (1987) noted 70 species were expected but not found in non-forested habitats, including several species of *Erigeron, Pedicularis, Potentilla, Eriogonum, Saxifraga,* and *Anemone.* Del Moral (unpubl.) estimated the vascular plant flora of Mount St. Helens above 1250 m to be about 95 vascular plants prior to 1980. The subalpine floras of nearby volcanoes are much greater. That of Mount Hood is 185 (Burnett 1986), that of Mount Adams is 198 (Riley 1986), and that of Mount Rainier is 261 (Dunwiddie 1983). Over 20 species may have become extirpated on this volcano as a result of the 1980 eruptions.

This limited flora probably resulted from the combination of small suitable area, absence of moist habitats, unstable soils, a limited alpine zone, frequent and recent eruptions (Crandell *et al.* 1975), and isolation from recolonization sources. Edaphic conditions for establishment are hostile, being deficient in nutrients and organic matter (del Moral & Clampitt 1985), thus making reestablishment of invading species difficult.

Climate

Pfitsch & Bliss (unpubl.) have shown productivity on Mount St. Helens to be positively correlated with total precipitation and weakly correlated with solar radiation. Reynolds & Bliss (1986) have maintained weather stations in three locations since 1981. Reynolds (pers. comm.) showed that his stations on Mount St. Helens are correlated with nearby stations with long-term records, providing a long-term record that permits the fluctuations during 1981–1986 to be viewed in perspective. July and August precipitation from 1981 to 1986 shows extreme variation (Table 1). Rain was normal in 1982, nearly twice normal in 1983. Extreme drought prevailed in 1984 while the 1985 growing season was dry. 1986 was moist through July 13, then dry for the rest of the summer. Mean July temperatures have differed by over 10 °C among years. These differing combinations led to favorable growing conditions in 1980–82, fair conditions in 1983, unfavorable conditions in 1986, and extremely poor conditions in 1984 and 1985.

Methods

Study area

The sample plots represent a gradient of eruption impacts in habitats that were at or above the suppressed timberline prior to 1980 (see Fig. 1). They were sampled using transects of permanent plots as described below.

Table 1. Summer precipitation (mm) for Upper Butte Camp (1500 m), Pine Creek (1450 m) and Spirit Lake (1150 m), July and August (Data summarized from Reynolds & Bliss, 1986).

	1981	1982	1983	1984	1985	1986
July						
Butte Camp	41	86	276	0	26	93
Pine Creek	23	–	–	0	26	86
Spirit Lake	–	–	–	0	25	54
August						
Butte Camp	27	180	64	3	68	7
Pine Creek	22	–	–	3	67	6
Spirit Lake	–	–	–	9	33	8

Blast zone ridges

Wishbone Ridge, comprised of old pyroclastic deposits separated by two lobes of the now defunct Wishbone Glacier, lies northwest of the Pumice Plains. The lateral blast destroyed the vegetation of this ridge. Transect 'Blast W' extends from 1 150 to 1 325 m and consists of 10 plots recorded since 1984. In only six have plants been recorded since the eruption. Remains of scattered *Pinus contorta* destroyed by the eruption are scattered along the lower portion of transect.

Toutle Ridge separates the Toutle Glacier from the Wishbone Glacier. The edge of the lateral blast seared this site killing all trees, but effects were less intense than on Wishbone Ridge. Some individuals of herbaceous and low woody plants survived due to protection by snow and subsequent regeneration from their below-ground perennating organs. Transect 'Blast T' has 9 plots recorded since 1981 arrayed along the ridge from 1 290 to 1 430 m.

Pine Creek

Pine Creek Ridge separates Pine Creek from the upper Muddy River. The rapidly melting Shoestring Glacier caused a large mass of mud to overtop the creek banks and scour the ridge. A silt deposit remained in its wake, tapering from a depth of over 30 cm at high elevations to less than 5 cm at the lowest site. Scoured habitats contrasted sharply with those on deep deposits formed on the Muddy River flood plain (Halpern & Harmon 1983). Scour plots, established in 1980, were clustered into three groups: 'Scour A', 3 scarcely impacted plots at the forest edge at 1 300 m; 'Scour B', 4 plots that were scoured and covered by a deposit of 10 to 15 cm of silt at 1 380 m; and 'Scour C', 5 plots that received intense scouring and deposits up to 30 cm at 1 525 m.

Butte Camp

Butte Camp is on the southwest side of the cone. Impacts were of two types: lahars and air-fall tephra. Lahars at Butte Camp were relatively small and often stopped on gentle slopes. The largest lahar flowed down the Kalama River, leaving a thick deposit in its wake. Others filled small canyons and abutted old ridges or were deposited on older lahars. A coarse air-fall tephra was deposited over the entire landscape on May 25, 1980. Tephra buried vegetation on depths ranging from 8 to 15 cm.

Plots on tephra were established in 1980, except as noted. They are grouped as follows: 'Tephra A', 3 plots from lower Butte Camp at 1 350 m; 'Tephra B', 4 plots from upper Butte Camp at 1 525 m; 'Tephra C', 4 upper Butte Camp plots (1 550 m); and 'Tephra D', established in 1981, 3 upper Butte Camp plots on the edge of a lahar from 1 580 to 1 680 m.

Lahar plots were grouped as follows: 'Lahar A', 3 plots established in 1980 on the edge of a small lahar at 1 500 m near sites that were merely tephra-impacted; 'Lahar B', 3 plots established in 1981 on a ridge at the edge of a large lahar at 1 650 m; and 'Lahar C', 7 plots established in 1982 on a large lahar at 1 400 m.

Permanent plots established on the upper Pumice Plains in 1983 were destroyed by mudflows. No plots have been reestablished here since there are virtually no established plants. Near Spirit Lake seedlings are establishing at lower elevations (Wood 1987; Wood & del Moral, 1988).

Field methods

Circular 250 m^2 permanent plots were established in open locations surrounding the volcano. Within habitats, plots were spaced along transects at 100 m intervals. Vegetation cover was monitored annually in six 20 by 50 cm subplots along each of four marked radii, yielding 24 subplots per plot. Observation errors were minimized since one observer determined all cover values. A species present in the plot, but not in any subplot, was given a cover value of 0.1%. All data were collected in late August of each year.

Analytical methods

Detrended correspondence analysis

Permanent plot data permit exploration of vegetation changes with sampling error reduced to between-year errors in observations of cover and placement of quadrats. Most studies of succession using permanent plots have reported the results by showing single species compositional change over time (e.g., Hogeweg *et al.* 1985). This approach is useful for long records or when a single succession is being studied. Van der Maarel (1969, 1980) and Austin (1977) appear to have pioneered the use ordination methods to study permanent plots, thus integrating floristic change over time. When multiple successions are compared, quantitative assessment is required. DCA (Hill & Gauch 1980) is a robust ordination method that provides useful analyses since plot shifts through time reflect floristic change in directly comparable units (floristic half – changes).

Permanent plots located in the same habitat and having experienced the same impacts were pooled to form composite plots. This gave a more clear trend assessment than did analyses of individual plots. Both absolute and relative cover of composite plots were analyzed, but since results are similar, only analyses of absolute cover, reflecting both cover increases and changes in composition, are presented.

Absolute cover data from 1986 samples were analyzed by DCA. Species with clear preferences for extreme habitat conditions in this environment were used to interpret the significance of composite plot shifts through time. These conditions were noted directly in the field and include exposure, slope, substrate depth and recent impacts. The indicators were used to interpret the full data.

DCA stand positions were plotted in two dimensions to show general changes. The Euclidean distances between successive years were calculated through the first four dimension of DCA space. These annual changes were plotted to facilitate between site comparisons. Together, these approaches demonstrate the magnitude of change vectors.

Synthetic measures

The mean number of species per plot within a transect is the mean plot richness while the total number of species in a transect is transect richness.

Percent cover was calculated from the 24 0.1 m^2 subplots per plot. Percent cover of a composite plot is the mean of all subplots in the composite, or (24 times *N*), where *N* is the number of permanent plots in the composite.

Diversity was calculated from percent cover of the subplots using the information theory statistic (H'). The goal was to assess recovery on a microscale. Changes were assessed by annual pairwise comparisons of subplots.

Results and discussion

General conditions

Survivors and isolation are extremely important determinants of recovery. Even after seven growing seasons, large expanses of the pyroclastic zone lacked plants, and few plants occurred on Wishbone Ridge. Recovery was more rapid where plants survived or where seed sources for colonists were nearby. For example, cover declined from Lahar A to C (Table 2), reflecting the shift from a small lahar near propagule sources to a large one far from potential colonists. A more dramatic example is the comparison of cover at Pine Creek, which declines from Scour A to C (Ta-

Table 2. Percent cover for common species in lahar plots at Butte Camp in the first year of observation, 1984 and 1986. t = <0.1%.

Species	Lahar A			Lahar B			Lahar C		
	1980	1984	1986	1981	1984	1986	1982	1984	1986
Achillea millefolium	0.1	t	t	t	t	t	t	t	t
Agrostis diegoensis	0.1	0.1	0.1	0.8	0.4	0.6	t	t	0.1
Aster ledophyllus	0.1	0.1	0.1	0.1	0.1	0.1	t	t	0.1
Carex mertensiana	–	0.1	0.9				–	t	t
Eriogonum pyrolifolium	–	0.1	0.1	–	0.2	0.3	–	t	0.1
Fragaria virginiana				t	t	t			
Juncus parryi	–	t	0.1	t	0.1	0.1			
Lomatium martindalei				t	t	–	–	t	–
Luetkea pectinata	t	0.1	0.1				–	t	t
Lupinus lepidus	t	0.1	0.1	t	t	0.1	0.1	0.1	0.1
Penstemon cardwellii	t	0.1	0.1	0.5	0.4	0.9	–	–	0.1
Polygonum newberryi	0.1	1.7	1.6	0.4	0.5	1.0	t	0.2	0.3
Total cover	0.1	3.3	3.6	1.6	2.0	3.1	0.2	0.7	1.4

Table 3. Percent cover for common species in scoured plots at Pine Creek in 1980, 1984 and 1986. t = <0.1%.

Species	Scour A			Scour B			Scour C		
	1980	1984	1986	1980	1984	1986	1980	1984	1986
Achillea millefolium	0.5	4.9	5.5	t	0.1	0.1			
Agrostis diegoensis	0.3	1.6	5.7	0.7	5.2	8.9	t	0.8	1.9
Aster ledophyllus	0.4	1.6	1.8	0.2	1.2	1.4	t	t	t
Carex rossii	–	0.2	0.5	–	0.3	0.3	–	t	t
Carex spectabilis	6.8	24.4	25.0						
Eriogonum pyrolifolium				0.2	0.7	0.6	<0.1	0.9	0.7
Juncus parryi	–	t	t	t	0.1	0.1	–	t	t
Lomatium martindalei	0.2	3.2	0.5	–	t	t			
Luetkea pectinata	0.1	10.4	14.5	t	6.9	8.0	<0.1	1.8	1.7
Lupinus latifolius	10.6	33.4	21.7	0.1	2.9	2.7			
Lupinus lepidus				t	0.8	1.4	<0.1	0.3	0.5
Polygonum newberryi	0.3	0.8	1.0	0.4	2.2	1.1			
Total cover	19.7	84.9	80.4	1.3	21.4	25.3	0.2	5.6	7.1

Table 4. Percent cover for common species in the composite plot on Toutle Ridge, 1981, 1984, 1985. t = <0.1%.

Species	Year		
	1981	1984	1986
Achillea millefolium	0.3	1.5	1.1
Agrostis diegoensis	0.3	0.6	0.6
Carex phaeocephala	t	0.1	0.3
Eriogonum pyrolifolium	t	0.2	0.3
Fragaria virginiana	0.1	0.3	0.3
Lomatium martindalei	0.9	2.1	1.1
Lupinus lepidus	0.5	0.8	4.2
Penstemon cardwellii	t	t	0.4
Polygonum newberryi	0.1	0.7	0.2
Sitanion hystrix	t	0.1	0.1
Spraguea umbellata	–	0.2	0.4
Total	3.1	6.7	9.4

ble 3). In Scour A, most individuals survived and changes primarily reflect competitive reassortments. Scour C, in contrast, remains relatively barren and supports fewer than half the species that probably occurred prior to the eruption.

Plots on Toutle Ridge have developed little plant cover (Table 4), suggesting that even expansion from local survivors into a devastated landscape will be slow. Annual compositional changes have been large, but there have been few invasions by new species and only minor cover increases.

Tephra zone vegetation was neither greatly impacted nor isolated. This vegetation had recovered by 1982 and subsequent changes reflect varied summer rainfall regimes and competitive rearrangements (Table 5).

Detrended correspondence analysis

Species indicators

Analysis of the first axis by species indicators suggests that it is a moisture gradient, trending from species common at the former forest edge (*Xerophyllum tenax*), in late snow melt areas (*Luetkea pectinata*), or stable, protected sites (*Carex spectabilis, Lupinus latifolius*, and *Phyllodoce empetriformis*) to more exposed and xeric (*Anaphalis margaritacea, Phlox diffusa, Lomatium martindalei, Lupinus lepidus, Spraguea umbellata*, and *Juniperus communis*) or unstable sites (*Saxifraga*

Table 5. Percent cover for common species in composite Tephra plots: A, B, and C, for 1980, 1983 and 1986; D, for 1981 and 1986. t = <0.1%.

Species	Tephra A			Tephra B			Tephra C			Tephra D	
	1980	1983	1986	1980	1983	1986	1980	1983	1986	1981	1986
Agrostis diegoensis	4.6	27.3	28.1	3.9	10.1	8.6	2.4	7.7	3.4	0.3	1.1
Aster ledophyllus	0.7	0.6	0.4	1.3	1.2	1.7	0.2	0.4	0.8	0.3	0.6
Carex rossii	0.4	0.4	0.2	t	1.4	1.5	0.9	0.9	1.4	t	0.2
Danthonia intermedia				0.3	0.2	0.8	0.4	1.1	1.3		
Eriogonum pyrolifolium	3.0	4.1	1.3	1.1	1.2	1.0	1.6	2.6	2.0	0.1	0.3
Juncus parryi	0.2	0.2	0.1	1.3	1.3	1.4	0.9	1.5	1.1		
Lomatium martindalei	1.4	3.2	0.3	0.5	0.3	0.1	0.2	0.8	0.1	0.9	1.1
Lupinus lepidus	5.9	3.4	1.3	4.1	3.1	2.3	5.5	3.1	2.3	0.5	4.0
Phlox diffusa		t	0.3	1.5	3.9	4.6	1.5	4.4	2.8	t	t
Phyllodoce empetriformis				0.4	1.4	2.4	0.3	0.2	1.4		
Polygonum newberryi	0.4	1.0	0.3	2.5	3.5	4.6	t	1.1	1.0	0.1	0.1
Sitanion jubatum	0.3	0.6	0.5	0.1	0.1	0.2	0.4	1.0	0.4	t	0.1
Spraguea umbellatum	0.3	0.6	0.2		t	t	t	0.2	t		0.4
Stipa occidentalis	0.7	0.6	0.5		0.1	0.2	0.2	0.5	0.4		0.1
Total cover	21.3	43.0	34.3	19.8	36.2	39.2	17.8	29.7	24.3	20.9	18.0

tolmiei). The second axis may reflect trends from more to less stable sites.

Lahars

The lahars show large shifts in DCA space over time, but cover remains scant (Fig. 2). Lahar A changes primarily in the second axis, reflecting the development of *Polygonum* and *Carex mertensiana*, two large, long-lived species. Lahar B fluctuates annually and *Polygonum* and *Penstemon* gradually increase. Lahar C, where there were no survivors, shows increasing *Lupinus lepidus, Juncus, Agrostis*, and *Polygonum.*

Fig. 3 summarizes how composite lahar plots through a four-dimensional DCA space. The greatest changes in Euclidean distances occur between the first two years. These changes may reflect the development of a more permanent flora against the background of fluctuating summer moisture conditions. Lahars B and C plots changed similarly since most species retain equal, minimal values. There has been little recruitment of new species after three years and further increases in richness will be slow. Means for annual change are relatively high (Table 6). Note that the net shift from first to last year is very high for Lahars C and A.

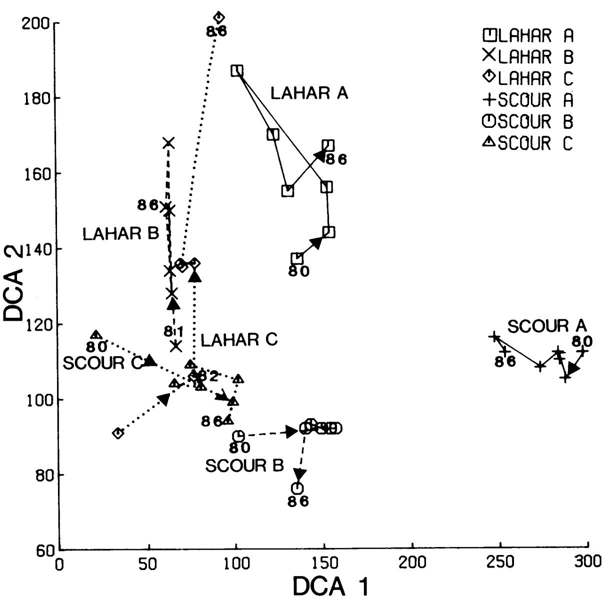

Fig. 2. Detrended correspondence analysis of composite lahar and scour plots determined from absolute cover percentage. Arrows show direction of annual change; numbers refer to first and last year of record.

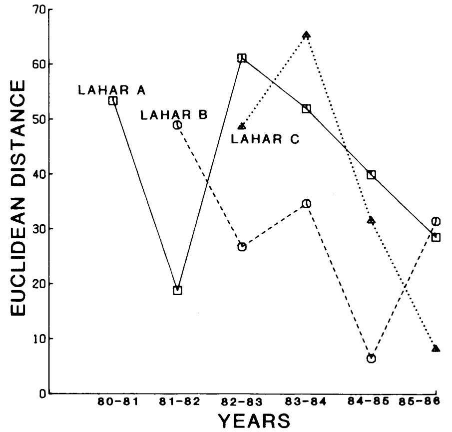

Fig. 3. Annual changes (Euclidean distance between successive positions of a sample) of composite lahar samples in four dimensions of detrended correspondence analysis determined using absolute cover.

Scour

Scoured plots recovered primarily as a result of the redevelopment of adults (Fig. 2). Scouring had relatively little impact on Scour A. Where changes may reflect increased post-eruption insolation (due to the destruction of scattered *Abies lasiocarpa*). *Lomatium* and *Aster* are increasing more than *Lupinus*

Table 6. Mean Composite Euclidean distance changes through four dimensions of DCA, in four habitat types. Mean Score is the average annual shift in the position of a composite plot. Net Score is its total shift from the first sample year to the last.

Habitat	Mean score		Net score	
	Distance	Rank	Distance	Rank
Lahar A	42.3	2	84.6	5
Lahar B	29.7	6	49.9	10
Lahar C	38.5	3	114.6	1
Scour A	14.3	11	57.1	9
Scour B	25.3	8	85.4	4
Scour C	34.8	4	93.1	2
Blast	58.8	1	68.6	7
Tephra A	23.0	10	92.9	3
Tephra B	24.7	9	66.8	8
Tephra C	26.4	7	79.6	6
Tephra D	31.9	5	27.7	11

latifolius and *Carex spectabilis. Polygonum* and *Luetkea* also are increasing in importance. In contrast, species of Scour B reflect a more mesic habitat as cover develops. Scour C shifted towards mesic species composition between 1980 and 1981, then changed little, reflecting only cover increases.

Fig. 4 summarizes scoured plot shifts through the four-dimensional DCA space. Uncharacteristically large changes in Scour A during 1985 and 1986 result from the large cover decline in *L. latifolius* caused by the 1985 drought. Scour C changed dramatically in the first comparison. Mean movement and net movement of Scour plots increases from A to C as a function of initial intensity (Table 6).

Blast

The DCA of Blast T vegetation shows large fluctuations (Fig. 5), with little trend. Species responses may reflect desiccation due to greater openness and soil loss. Euclidean distance changes (Fig. 6) are greater than those of lahars suggesting that species composition on this ridge is unstable. The mean increment of change approaches that of the net (Table 6).

Tephra

In contrast to other sites, trends on tephra are primarily a function of shifting dominance, not recovery. Tephra sites either show species compositional changes that suggests more mesic conditions or no trend (Fig. 5). They appear to be increasingly stable over time. During the drought years, these trends were arrested. Euclidean distances (Fig. 6) indicate that tephra plots changed little annually relative to other sites, but that changes have accumulated in Tephra A, B, and C. These changes reflect the increasing dominance of *Agrostis diegoensis* (Table 5). Annual increments in tephra plots are low, but net movements are relatively large.

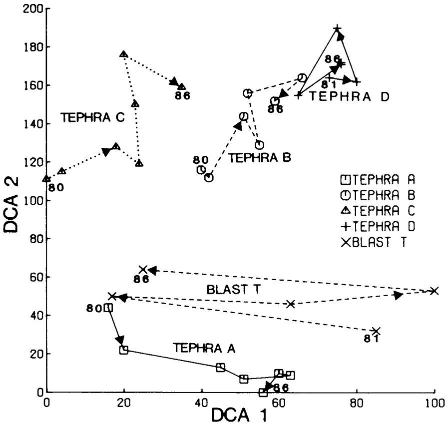

Fig. 5. Detrended correspondence analysis of composite blast T and tephra plots determined from absolute cover percentage. Arrows show direction of annual change; numbers refer to first and last year of record.

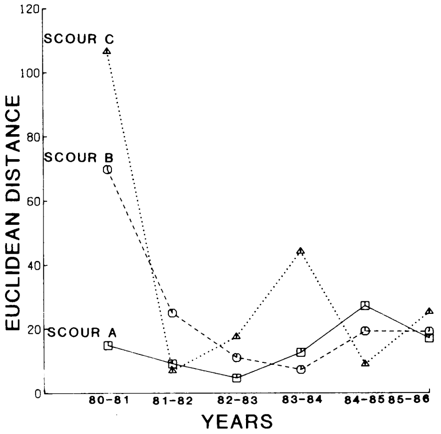

Fig. 4. Annual changes (Euclidean distance between successive positions of a sample) of composite scour samples in four dimensions of detrended correspondence analysis using absolute cover.

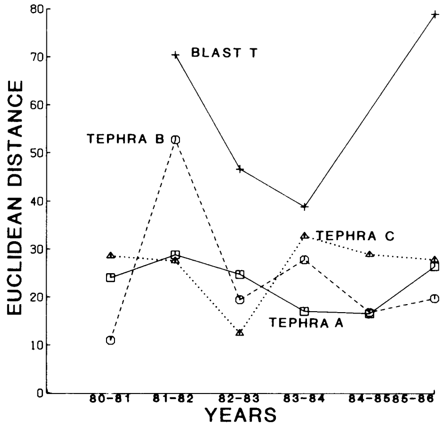

Fig. 6. Annual changes (four dimensional Euclidean distance between successive sample positions) of composite blast T and composite tephra samples in detrended correspondence analysis space using absolute cover.

Relative composition

Scours

Species composition may change significantly where recovery has been great. Fig. 7a–c show the relative cover ([absolute species cover/total plot cover]*100%) for selected species in the three scoured sites. At Scour A, there has been a gradual increase in three aggressive rhizomatous species, *Luetkea, Agrostis*, and *Achillea. Carex spectabilis* has remained essentially constant, except in 1985, where its increase reflects the large decline of *Lupinus latifolius* due to early-season drought in that year. In 1986 *Lupinus* recovered. *Luetkea*, a low-growing strongly rhizomatous species, has continued to increase annually.

There are several significant patterns at Scour B. Erosion uncovered *Luetkea*, and it has increased steadily. *Agrostis*, a significant survivor, declined proportionally as other species recovered. However, it suffered less than other species through the drought and is reasserting dominance at the expense of *Aster* and *Polygonum. Aster* has been subject to several types of severe seed predation (Wood & Andersen manuscr.) and has not established many new individuals. Absolute cover of *Polygonum* has remained constant since 1980, with little seedling establishment.

The survival of *Luetkea* at Scour C permitted it to dominate through 1983, but as conditions became more favorable, *Agrostis* began to assert dominance. *Eriogonum* has gradually declined while *L. lepidus* and *Juncus* have stabilized at moderate levels.

Blasted ridge

Changes have been erratic at Toutle Ridge (Fig. 8). *Achillea* thrived during drought years, but declined in 1986. *Lupinus lepidus* increased dramatically in 1982 then declined in 1984. It has since recovered due to a new wave of seedlings. *Lomatium* and *Lupinus*, both short-lived perenials, both responded after disturbance. Their patterns mirror each another.

Tephra

On dry tephra-impacted slopes, rhizomatous, drought-tolerant species gained dominance during the drought years. Short-lived species suffered major seedling establishment failures in 1984 and 1985

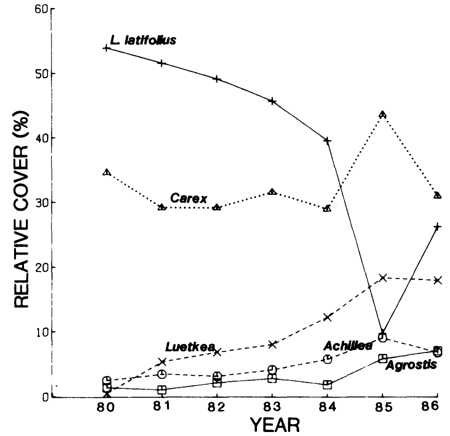

Fig. 7A. Relative cover of *Achillea millefolium, Agrostis diegoensis, Carex spectabilis, Lupinus latifolius*, and *Luetkea pectinata*: Scour A.

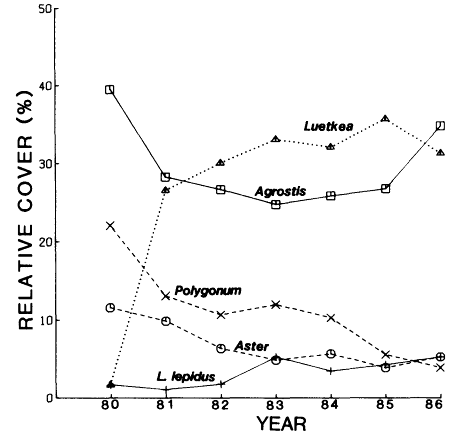

Fig. 7B. Relative cover of *Agrostis diegoensis, Aster ledophyllus, Luetkea pectinata, Lupinus lepidus*, and *Polygonum newberryi*: Scour B.

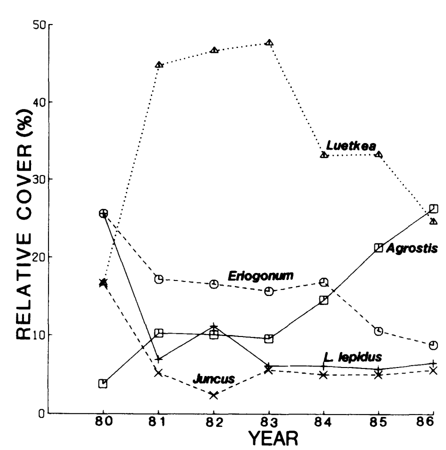

Fig. 7C. Relative cover of *Agrostis diegoensis, Eriogonum pyrolifolium, Luetkea pectinata, Lupinus lepidus*, and *Juncus parryi*: Scour C.

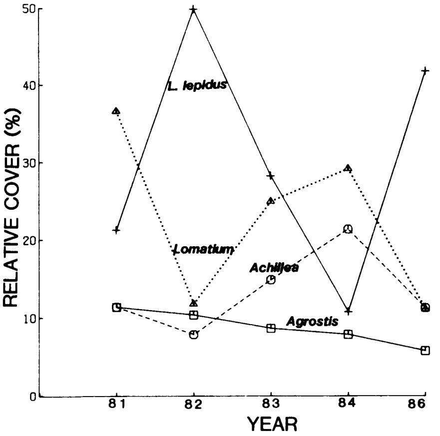

Fig. 8. Relative cover of *Achillea millefolium, Agrostis diegoensis, Lomatium martindalei,* and *Lupinus lepidus*: Blast T.

(Fig. 9a–c). *Lupinus* has declined steadily, whether or not *Agrostis* has increased. This decline relates to its life history characteristics (*Lupinus* normally dies in 3–4 years) and possibly to a nutrient pulse in 1981, generated by the decomposition of plants killed by tephra burial. Seedling establishment in 1982–85 was limited by drought, competition from established plants (del Moral & Wood 1986), and by reproductive failure due to extensive seed predation. In the driest of these plots, Tephra A, *Agrostis* steadily developed dominance. In Tephra B, *Polygonum* has become dominant, while other species have remained relatively stable. In Tephra C, *Agrostis* increased during the dry years, but a collection of other species have subsequently increased.

Richness and cover

Table 7 summarizes species richness and cover data for all composite plots.

Lahars

The flora on lahars at Butte Camp is similar to that of scours at Pine Creek and to adjacent tephra-impacted plots. Individual plants occasionally survived on Lahar A, where there has been a gradual increase in richness. No annual increment is statistically significant, but the overall trend (Kruskal-Wallis test) is strongly so. Lahars should come to resemble vegetation on Tephra C, which surround

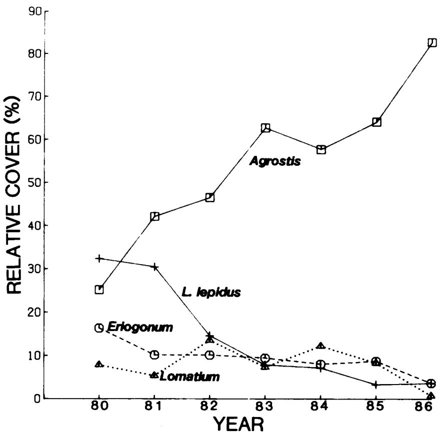

Fig. 9A. Relative cover of *Agrostis diegoensis, Eriogonum pyrolifolium, Lomatium martindalei,* and *Lupinus lepidus*: Tephra A.

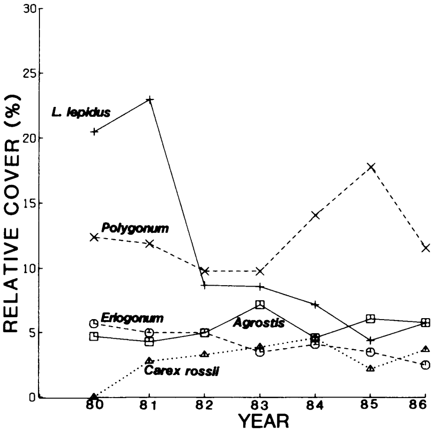

Fig. 9B. Relative cover of *Agrostis diegoensis, Eriogonum pyrolifolium, Carex rossii, Lupinus lepidus,* and *Polygonum newberryi*: Tephra B.

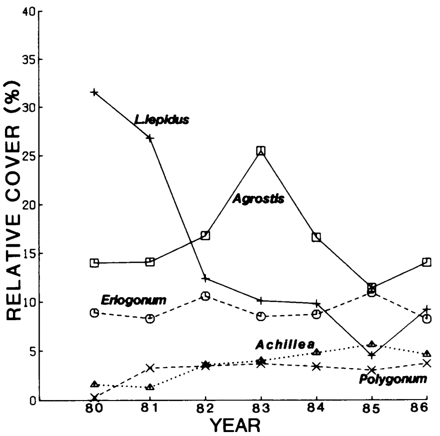

Fig. 9C. Relative cover of *Achillea millefolium, Agrostis diegoensis, Eriogonum pyrolifolium, Lupinus lepidus,* and *Polygonum newberryi*: Tephra C.

Table 7. Species richness (mean number of species per 250 m^2 plot) and mean percent cover per plot in composite samples from lahars, scoured ridge, blasted ridges and tephra-impacted sites over 7 years. (n.s. is given when plots were not sampled.)

Habitat	Measure	Year						
		1980	1981	1982	1983	1984	1985	1986
Lahar A	richness	4.3	8.3	8.3	10.0	10.0	10.3	12.0
	cover	0.1	1.3	1.7	2.4	3.3	3.5	3.6
Lahar B	richness	n.s.	6.0	8.3	8.3	9.7	9.0	9.3
	cover	n.s.	1.6	2.1	2.8	2.0	2.7	3.1
Lahar C	richness	n.s.	n.s.	2.6	3.1	4.7*	8.0**	11.3**
	cover	n.s.	n.s.	0.2	0.3	0.7	1.1	1.4
Scour A	richness	10.0	14.3*	15.3	18.0*	16.7	16.3	16.7
	cover	19.7	60.7**	76.3*	86.6*	84.9	71.0*	80.4
Scour B	richness	5.0	9.3*	13.0**	14.0	13.8	13.8	13.8
	cover	1.3	7.6*	13.9*	19.3*	21.4	22.7	25.3
Scour C	richness	2.0	5.4	7.2*	8.2	7.8	7.8	8.0
	cover	0.1	0.6	3.3*	4.1	5.6	5.6	7.1
Blast-Wishbone	richness	n.s.	n.s.	n.s.	n.s.	0.8	1.1	1.3
	cover	n.s.	n.s.	n.s.	n.s.	<0.1	0.1	0.4
Blast-Toutle	richness	n.s.	7.6	11.0	12.0	11.8	n.s.	11.8
	cover	n.s.	3.1	7.0	5.5	6.7	n.s.	9.4
Tephra A	richness	11.3	15.7*	15.7	17.3	17.0	17.7	16.7
	cover	21.3	54.4**	41.8*	43.0	22.2*	22.7	34.3*
Tephra B	richness	11.3	18.5*	20.5	18.5	20.5	18.3	18.3
	cover	19.8	38.4*	38.0	36.2	34.2	32.0	39.2
Tephra C	richness	15.3	19.8*	20.8	18.8	19.0	18.8	19.8
	cover	17.8	31.5**	30.3	29.7	23.2	20.9	24.3
Tephra D	richness	n.s.	15.3	15.3	14.7	15.7	14.3	14.7
	cover	n.s.	20.9	22.4	26.1	16.9*	15.4	18.0

* = significantly different from previous season, determined by paired *t*-test, $P<0.05$; ** = $P<0.01$.

them. Richness should increase by from 5 to 8 species per plot. In 1986, the first two DCA coordinates of Tephra C were 38 and 161, those of Lahar A were 152 and 162. Cover of Lahars A and B has increased gradually from the expansion of residual species, though a few species have invaded Lahar B. Richness here is lower than in adjacent plots and the colonization rate is low. Lahar C smothered existing vegetation and all recorded plants began from seeds. Richness has increased significantly. A comparison between cover of Lahar C and Scour B and C suggests that lahars are difficult habitats for seedling establishment and that turnover rates are great.

Scours

Scoured plots recovered rapidly (Table 7). Compared to the surrounding desolate landscapes, vegetation at Scour A was lush in 1980. Richness recovered fully by 1983. Cover tripled by 1981 and peaked in 1983. The reduced value in 1985 was due to the large drought-induced decline of *Lupinus latifolius.*

Small rill erosion channels dissected the silty veneer at Scour B. Most survivors occurred in the rills. Erosion removed the veneer by 1981, exposing surviving species and leading to significant richness increases which were augmented to a limited degree by seeds invading from surrounding areas. Species richness stabilized by 1983. Despite drought, Scour B gradually increased cover. From plants largely confined to rills, the community has come to resemble that of Tephra C.

Mortality at Scour C was high and it is likely that several species were extirpated. There is no reason to believe that these sites should have fewer species than

Scour B, but richness is less than 70% of Scour B plots. The absence of species such as *Lomatium* and *Agoseris aurantica* and low cover values for *Trisetum* and *Lupinus latifolius* may result from the intensity of the initial impact. Cover in Scour C was virtually nil in 1980, but since then cover has increased slowly due mainly to expansion of strongly vegetative species.

Blast zone

The Wishbone Ridge sites had only 3 species in 1984, when first sampled: *Lupinus lepidus, Anaphalis margaritacea*, and *Pseudotsuga menziesii*. A *Carex* seedling was added in 1985; in 1986, two *Epilobium* species were added to the list. Cover is not yet measurable.

At Toutle Ridge species richness quickly increased to about 12 species per plot and has remained steady. Due to isolation, the paucity of vegetation at higher elevation, its environmental harshness, and the inability of lowland species to establish, further increases are likely to be small. The ridge lacks at least six species compared to tephra plots. Cover in 1981 was relatively high and measurable cover must have existed in 1980. Cover was lower during the drought years, but increased during 1986. Cover should continue to increase. The ridge is environmentally similar to Pine Creek, where cover now averages about 25%.

Tephra

Species richness stabilized within three years, probably at their pre-eruption levels. Subsequent changes merely reflect variation in summer rainfall. Cover recovered quickly and peaked in 1981, a favorable growing season. In addition, the mortality and decay of many plants, followed by their mineralization, may have released nutrients into a nutrient-limited system. After 1982, the combined effects of mortality among short-lived species, limited recruitment due to extreme droughts, and competition from *Agrostis* led to reduced community cover.

Paired cover changes

Changes in individual species cover were monitored in all plots (Table 8) to explore species dynamics.

Table 8. Number of species changing their cover between years. Significance determined by paired *t*-tests ($P<0.05$) of individual species cover in 24 0.1 m^2 subplots per plot.

Habitat	Species number	Change	Years					
			80 – 81	81 – 82	82 – 83	83 – 84	84 – 85	85 – 86
Scour A	9	increase	6	5	3	2	4	1
		decrease	1	1	2	1	2	2
Scour B	8	increase	5	3	3	2	3	2
		decrease	0	0	0	0	0	0
Scour C	7	increase	2	3	2	2	0	1
		decrease	0	0	0	0	1	0
Blast	9	increase	n.s.	5	1	2	n.s.	5*
		decrease	n.s.	0	1	1	n.s.	2
Tephra A	12	increase	8	4	1	0	1	1
		decrease	0	3	5	5	1	4
Tephra B	13	increase	10	3	1	1	1	5
		decrease	0	2	3	2	6	0
Tephra C	14	increase	8	4	4	0	0	5
		decrease	0	3	2	5	4	2
Tephra D	8	increase	n.s.	1	1	0	0	0
		decrease	n.s.	2	0	1	1	0

* based on 1984 – 1986 comparison.

Scour

Species increased and decreased each year on Scour A, but increasers initially outweighed decreasers, then an equilibrium with climatic fluctuation was reached. Xerophytic species are now increasing at the expense of mesophytic species. Scour B and C show gradual increases for *Eriogonum, Agrostis, Juncus, Carex rossii*, and *Luetkea*. These sites are not in equilibrium with climatic factors.

Blast

Initially many species increased dramatically on Toutle Ridge. After several years of minor change, species such as *Agrostis, Eriogonum, L. lepidus*, and *Spraguea* commenced increasing.

Tephra

Many species showed significant increases in the first comparison on tephra, followed by a steep decline triggered by the drought of 1984–85. In 1986, Tephra A, where *Agrostis* is most strongly developed, had 5 species decline, while Tephra B and C, where dominance is less strong, each had 5 species increase.

Species diversity

Diversity (H') is a composite measure of species richness and relative abundance. Diversity of subplots was calculated (Table 9) for transects with significant cover. In this way, diversity changes on the scale of 0.1 m^2 could be determined.

Scour

In Scour A, diversity increased significantly in each plot (Table 9). Increases were concentrated between the first two years. Diversity in Scour B is much lower due to low frequency; increases here are due primarily to the increased number of plots with two or more species.

Blast

Only plots 5 and 6 are sufficiently dense to warrant diversity calculations (Table 9). Both show significant increases. The jump in 1986 suggests that recovery will accelerate in 1987.

Tephra

Subplot diversity was initially low, then pulsed in

Table 9. Mean diversity comparisons in paired sub-plots of composite samples. Symbols *between* mean H′ scores indicate level of significance: * = $P<0.05$; + = $P<0.01$; # = $P<0.001$. Overall significances are given for Kruskal-Wallis (KW).

Site	Overall	1980	1981	1982	1983	1984	1985	1986
Scour A1	$P<0.001$	0.28^{+}	0.63^{+}	0.78	0.78	0.79	0.73*	0.82
Scour A2	$P<0.001$	0.16^{+}	0.49	0.59	0.56	0.63	0.59	0.61
Scour A3	$P<0.005$	0.39	0.49	0.61	0.60	0.68	0.71	0.74
Scour B1	$P<0.03$	0.05	0.11	0.13	0.19	0.23	0.32	0.22
Scour B2	$P<0.001$	0.02	0.06	0.04	0.25	0.27	0.32	0.31
Scour B3	$P<0.001$	0.11	0.14	0.28	0.36	0.40	0.34	0.43
Scour B4	$P<0.001$	0.00	0.03	0.05	0.18	0.19	0.29	0.32
Blast 5a	$P<0.03$	n.s.	0.00	0.12	0.04	0.03	n.s.	0.16
Blast 6	$P<0.001$	n.s.	0.00	0.16	0.03	0.04	n.s.	0.27
Tephra A1	$P<0.001$	0.83*	1.06	1.14^{+}	0.82	0.76	0.72	0.42
Tephra A3	$P<0.001$	0.82	0.86	0.93*	0.75	0.65*	0.50^{+}	0.27
Tephra A4	$P<0.001$	0.84	0.91^{+}	1.17*	1.02^{+}	0.71	0.75^{+}	0.45
Tephra B1		1.06	1.06	1.02	1.13	1.12	0.93	0.87
Tephra B2		0.83	0.86	0.84	0.80	0.74	0.73	0.71
Tephra B3		0.40	0.42	0.51	0.49	0.51	0.38	0.44
Tephra B4		0.68	0.77	0.72	0.67	0.74*	0.54	0.68
Tephra C1	$P<0.009$	0.75	0.78*	0.99	0.99	0.92^{+}	0.67	0.66
Tephra C2		0.60	0.72	0.81	0.76	0.71*	0.61	0.67
Tephra C3		0.21	0.28	0.40	0.35	0.29	0.31	0.32
Tephra C4	$P<0.001$	0.78*	1.01^{+}	1.23	1.15	1.06	0.91	0.82

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[a] Other Blast Plots showed increased diversity, but no significant trends.

1981 and 1982 as cover and local richness increased (Table 9). The 1984-85 drought reduced H' greatly. In Tephra A this trend continues with the dominance of *Agrostis*. Tephra B showed no significant overall trend, though H' in the midyears was higher than in the last two.

Conclusions

Subalpine herbaceous vegetation on Mount St. Helens appears to be recovering through two principal phenomena: expansion of plants surviving the eruption and dispersal. As was found in other studies of volcano succession (Riviere 1984), dispersal barriers are great. Impact scale determines the degree of isolation and dictates immigration rates. The presence of a few survivors can strongly influence recovery (cf. Griggs 1933). Therefore, initial impact intensity is important, but a wide range of less-than-catastrophic impacts may produce similar responses. As has occurred on other volcanoes, these impacts have locally lowered treeline (Lawrence 1938; Ohsawa 1984) and reduced richness (Kruckeberg 1987).

Subalpine herbs on Mount St. Helens are adapted to more xeric conditions than on surrounding volcanoes and the resulting communities are depauperate in species despite having a wider-than-normal elevational range. However, each community has an analog on other volcanoes and we cannot demonstrate unique communities comparable to those found on Krakatau (cf. Tagawa *et al.* 1985). Isolation appears insufficient for this to occur. Successional rates vary due to isolation effects even when the substrates are similar (Tagawa 1965). Thus far, there is little evidence that 'succession recapitulates phylogeny' on Mount St. Helens. Whereas Griggs (1933) believed algae and mosses were required to begin succession, our results support Tagawa (1964) who found vascular plants to be pioneers. It may be that aeolian fallout adds sufficient organic matter and nutrients to lahars and pumice to permit some vascular plant species to invade directly without cryptogamic influence (Edwards *et al.* 1986).

Table 10 summarizes conditions of each habitat described in terms impact intensity determined from geological descriptions and conditions in 1980 and the degree of isolation determined from direct observations. There is no vegetation in higher elevation pyroclastic zone sites, so here only immigration can produce recovery. Nutrient additions and microsite amelioration should dominate this extremely harsh habitat for many years. Climatic variation also plays a large role in reestablishment since the series of dry summers has thus far prevented establishment of many species.

Wishbone Ridge is several kilometers distant from sources of potential colonists. The lateral blast killed all individuals of most species. Richness is low and

Table 10. Comparison of recovery in each subalpine habitat on Mount St. Helens. Codes: VH = very high; H = high; M = moderate; L = low; VL = very low. Richness (% Max) is current number of species in 1986 as a percentage of the projected equilibrium richness; Cover (% Max) is the 1986 cover as a percentage of the projected equilibrium cover; Immigration is the importance of dispersal to recovery. F81 is putative importance of facilitation in 1981; F90 is expected importance of facilitation in 1990.

Impact	Isolation	Example	Richness (% max)	Cover (% max)	Immigration	F81	F90	Chance
VH	H	Pumice	<1	⩽0.1	VH	VH	VH	VH
H	H	Wishbone	<10	<0.1	VH	VH	H	H
H	M	Lahar C	<60	<3	VH	VH	H	H
H	L	Lahar A, B	60	10	H	M	M-L	H
M	M	Scour C	60	<25	M	H	M	M
M	M	Toutle	70	25	M	H	M	M
M	L	Scour B	75	<75	L	M	L	M
L	L	Scour A	>90	100	L	L	VL	L
VL	L	Tephra	>90	100	VL	L	VL	VL

cover scant. Immigration remains very important and facilitation dominates biotic interactions. Species have appeared and disappeared in the four years of observation.

Lahar C, a new habitat, is near sources of immigrants. It has moderate richness and species continue to accumulate slowly (cf. Eggler 1963; Rejmánek *et al.* 1982), but cover is very low. Plant mediated colonization should become less important as cover increases and vigorous vegetative species become dominant. The other lahars abut adjacent recovered vegetation and a few individuals may have survived. Nevertheless, only half the expected species have become established and cover remains very low.

Scour C is isolated by deep canyons but it is only ca. 700 m above Scour B. It received a moderate impact. A few species survived in our samples and others survived nearby on the ridge. Immigration will be required to produce a complete complement of species and facilitation will be required to modify invasion conditions. Chance survival and the location of rills has played an important role in recovery.

The lateral blast on Toutle Ridge was attenuated and permitted some species survival. The ridge is somewhat isolated, but downwind of potential sources. Cover remains low, a testament to soil lost during the blast. Inhibition is already operative and will accelerate in the next several years. Now that an initial phase of richness increase has occurred, further increases may be quite slow due to limited dispersal (Peterkin & Game 1984).

Scour B was impacted moderately, but as it is close to sources of colonists, richness and cover already approach equilibrium values. Because there were so many survivors, immigration has played a minor role in recovery. Facilitation has been moderately important and there is evidence for increasing inhibition (del Moral & Wood 1986).

Scour A was lightly impacted – most species survived. Therefore, immigration has always been a minor factor and cover is completely recovered. Inhibition will continue to be a major factor in structuring this community.

Tephra plots suffered minor impacts and are recovered. Immigration has only been locally important and there is much evidence for inhibition.

Evidence for the assessments of Table 10 is found in the structural measures. Analysis of species cover changes implied facilitation in Blast T while cover changes in Scour B, Scour A and Tephra sites implied inhibition.

Relative abundance changes are consistent with an inhibition mechanism in Scour A and B as longer lived, aggressive species such as *Luetkea* expand. There is evidence for facilitation on tephra in 1981, when *Lupinus lepidus* dominated, followed by strong inhibition by *Agrostis* in Tephra A and *Polygonum* in Tephra B.

Further evidence comes from experiments conducted since 1981. Seed availability is the major constraint for establishment of tolerant species under harsh conditions (del Moral & Wood 1986). Where dense cover exists, its removal becomes the dominant factor, promoting seedling establishment. Seedling densities across tephra-lahar boundaries decline rapidly, approaching zero within a few meters for all species (Wood & del Moral 1987).

Once established, a plant improves the establishment probability of other seedlings, provided that its density is not too great (Wood 1987). This 'nurse plant' effect, in which the microsite is ameliorated and wind-blown seeds are trapped, is well known. Wood & del Moral (1987) found that most seedlings on lahars occurred with a moderate concentration of adults. Plots with very low cover are harsh environments precluding seedling establishment, while those with higher cover create adverse competitive conditions.

The recovery process on Mount St. Helens results from a tapestry of events woven over a patchy environment. The biological legacy, a signal from predisturbance vegetation to the post-disturbance community, varies from strong to weak or non-existent. In habitats where the legacy was weak, recovery has been slow because rescue by surrounding populations is limited by poor dispersal of those species tolerant of harsh conditions.

As disturbance intensity increases, the ecosystem increasingly loses nutrients, soil, biomass, and species, resulting in a system that requires plant-mediated improvements (facilitation) for recovery. Distance (or scale of impact) decreases the importance of biotic inhibition by limiting the rate of reinvasion and initial richness. Implicit in this model is the view that competitive inhibition is limited under conditions of low productivity (Grime 1977; del Moral 1983a).

Future vegetation development on extensive lahars and pyroclastic surfaces should be slow, characterized by increasing cover and gradual accumulation of species. High elevation lahars have begun their recovery, with many species per 100 m^2 (del Moral unpubl.), while high elevation pyroclastic areas have scarcely begun. We may see the development of structurally normal meadows on lahars at lower elevation within decades, but it may require well over a century for the same development to occur above 1400 m in the pyroclastic zone.

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