Growth of Native Plant Species on Recent Volcanic Substrates from Mount St. Helens

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ABSTRACT: Subalpine vegetation on Mount St. Helens is recovering from the volcanic eruptions of May 1980. The recovery rate depends on the nature and intensity of destruction suffered by the vegetation at a particular site. New volcanic substrates were collected annually from 1980 through 1983 and bioassays were used to analyze their ability to support plant growth. The importance of soil structure and fertility was also investigated. Lack of soil nutrients appears to be a major factor limiting recovery. Soil weathering, the influx of airborne nutrients and the burrowing of small mammals enhance fertility. Some species now grow as well on these substrates as they do on an infertile loam. Despite the ability of some species to grow on these substrates, many areas of the mountain were devoid of vegetation as of October 1984. Immigration, a function of isolation, rather than soil development, may be the key to revegetation of totally devastated habitats.

INTRODUCTION

The subalpine vegetation on the slopes of Mount St. Helens suffered impacts ranging from deposits of a few centimeters of tephra to complete vaporization as a result of a series of eruptions that began on 18 May 1980. The early phases of recovery of subalpine vegetation on this volcano have been reported (del Moral, 1981, 1983). Other workers have documented plant recovery in other habitats surrounding the volcano (Antos and Zobel, 1983; Halpern and Harmon, 1983; Means *et al.*, 1982; Zobel and Antos, 1983). However, where landslides, pyroclastic flows or cold mudflows created surfaces devoid of residual living plants, recovery has been extremely slow and, in many places, there has been no primary succession to October 1984.

This report explores the ability of materials deposited by volcanic action to support the growth of native plant species. Do plants found on an active volcano vary in their abilities to reinvade barren surfaces low in nutrients (F. C. Ugolini, pers. comm.) and carbon (E. H. Franz, pers. comm.)? Since their deposition in 1980, has the ability of these substrates to support plant growth improved? Is it the lack of nutrients or adverse physical effects that suppress growth in these species? Is the observed paucity of recolonization (del Moral, 1983; J. F. Franklin, pers. comm.) a result of isolation from potential colonists?

Volcanic materials studied here differ in how they formed, their mode of deposition and their appearance. Pyroclastic materials were produced at high temperatures within the volcano and deposited in pulses over material laid down by a massive avalanche. Erosion removed most of the fine powder that comprised the bulk of the 1980 sample so that subsequent collections were coarse, gravelly materials of uncertain origin. However, none of this material was on the surface prior to the eruption and it is likely that all samples were thermally altered during the 1980 eruptions.

The Pine Creek mudflow deposited a veneer of fine-grained cold silt up to 12 cm thick on ridges above Pine Creek. By 1982, most of this material had eroded and no samples were collected thereafter.

The mudflows at Butte Camp produced deposits up to several meters thick that, despite considerable erosion, are now stable. Due to their proximity to vegetation that escaped major impacts, colonization has proceeded relatively quickly.

Much of the subalpine area on the S and W flanks received a blanket of coarse airborne material (= tephra) 6-8 cm thick during the eruption of 25 May 1980. This material has undergone little weathering since its deposition. Carbon content, however, has increased from none to ca. 0.2 mg-g^{-1} (F. C. Ugolini, pers. comm.) due to the activity of surviving plants that have grown through the tephra. In many places, the tephra was deposited over a mudflow produced by a mid-17th-century eruption (Crandell and Mullineaux, 1978). This more weathered material is brought to the surface by burrowing mammals, notably pocket gophers (*Thomomys bottae*), which are common and visibly active in this area (McMahon, 1984). Nutrients are being imported by rain and snow, which contain minerals and significant concentrations of nitrate (F. C. Ugolini, pers. comm.), and in insects and pollen blown onto our study sites from lower elevations (J. E. Edwards, pers. comm.). On the pyroclastic materials and mudflows, nutrient influx is the major cause of improved growing conditions.

METHODS

Soils were collected each summer between 1980 and 1983. Logistical problems made it impractical to obtain samples from precisely the same location each year. For our present purposes, pyroclastic materials result from direct volcanic events and are deposited at high temperature; tephra is any airborne deposit; mud is any water-borne deposit; and silt is any well-sorted deposit of particles ranging in size from sand to clay. The substrates we collected and their general locations are: (1) Pyroclastic materials (1980, 1981, 1982) and debris avalanche residue (1983), collected in the blast zone on the NE flank of the crater (the "north face") between 1000 and 1200 m; (2) Pine Creek silt, collected at 1300 m on an exposed SE-trending ridge above Pine Creek (this deposit was eroded away by 1983); (3) Butte camp mud, collected on the W flank of the volcano between 1300 and 1550 m from a series of cold mudflows several meters thick deposited in creek beds; (4) Butte Camp tephra, coarse airborne deposits collected from between 1350 and 1450 m, and (5) Gopher mound soil, collected immediately adjacent to tephra collections at Butte Camp.

In August and September of each year, available seeds were collected for use in bioassays. The species are representative of those common at Butte Camp and Pine Creek. However, species with fleshy fruits (*e.g., Fragaria virginiana*), minute seeds (*e.g., Juncus* spp.) and woody habits (*e.g., Phlox diffusa*) were not collected. The availability of seeds of these species varied from year to year due to poor growing seasons in 1982 and 1983 and to logistical difficulties.

The standard bioassay was as follows: Seeds of each species were germinated in petri plates or flats containing vermiculite. Several species required stratification for 6-12 weeks before they would germinate. For each species, four 250 cc styrofoam cups with drainage holes were filled with each substrate to be tested. Six small seedlings were planted in each cup. Plants were kept well-watered for 30 days under a 16-hr photoperiod with temperatures at 20 C when lit and at 10 C when dark in a model 3 EGC growth chamber with a light intensity of 1350 uE m^{-2} sec^{-1}PAR. Most of the 1983 trials were run in this way, but some were run under 16-hr photoperiods in the greenhouse. Plants were then harvested, washed, dried and weighed.

Control soils were either unaltered subalpine loam from Deer Park (DPL) in the Olympic Mountains (1800 m) or loam from the University of Washington greenhouse (UWL).

The relative importance of soil type, nutrients and soil structure for plant growth was compared in a factorial experiment. In this experiment four soils, collected in 1981, were used: (DPL; pyroclastic surface; Pine Creek silt and tephra). Each soil was used (a) as collected; (b) with 1 g kg^{-1} of 18% N, 24% P, and 6% K slow-release fertilizer; (c) with 25% perlite (by volume) added, and (d) with both nutrients and perlite added. Four species were used: *Achillea millefolium, Agrostis diegoensis, Lupinus latifolius* and *Sitanion jubatum*. The nutrient level was previously determined to be optimum for the grasses used. Perlite was added to improve soil aeration and reduce compaction. Soils were bioassayed as described above.

The degree to which gophers improve surface soil conditions was explored in two experiments. The first used soil cores collected in 1982 from gopher mound material, a new mudflow and tephra through which vegetation rooted in the original surface had penetrated. Control cores were made using DPL. These cores were 7 cm in diam and 5 cm deep. They were placed in flats containing UWL under artificial illumination at 20 C, planted with *Achillea millefolium* and *Agrostis diegoensis* and kept well-irrigated for 30 days. Plants were then harvested, washed, dried and weighed. The second experiment used tephra and gopher mound material collected in bulk in adjacent areas. These were bioassayed under the standard conditions.

Statistical tests used SPSS (Nie *et al.,* 1979) or Minitab (Ryan *et al.,* 1981). Treatments were compared to their controls with t-tests in the standard bioassays. The relative growth of all species on a given substrate was compared by the Honestly Significant Difference (HSD, $\alpha = .05$) test. The rank orders of species on the various substrates were compared using Spearman's nonparametric test. The factorial experiment was analyzed using a 3-factor nested ANOVA.

Samples of each soil were sent to the Analytical Testing Laboratory, Idaho State University, for analysis of *p*H, nitrate, potassium and phosphorus. Nomenclature follows Hitchcock and Cronquist (1973).

RESULTS

There is a high degree of variation in the substrates under study, but the nutrient values are all very low (Table 1). Statistical comparisons were not made because it was not clear that such differences would be biologically meaningful.

On the N face of Mount St. Helens, erosion of the pyroclastic materials resulted in substantially different substrates each year. In 1980, the surface was pumice in a fine powder deposited by a pyroclastic flow. By 1981 meltwater had eroded the pyroclastic surface and in 1982, the surface had been eroded primarily by wind, rather than water. By 1983, all surfaces had been eroded and the material collected probably had been deposited by the debris avalanche.

Pyroclastic materials, though variable, appear to have been more fertile than the other materials of recent origin. Potassium appears to become depleted in each material, possibly as a result of leaching or, in some substrates, incorporation into plants. Material derived from an old mudflow under the new tephra and deposited on the surface by gophers has comparatively high nitrogen levels.

The nutrient data suggest that no species should grow well and that pyroclastic materials should support the best relative growth if nutrients are the limiting factor.

In 1980, no species grew well in pyroclastic materials, while there was an array of growth patterns in other substrates (Table 2). That nitrogen-fixing lupines grew well on other substrates while most other species did not suggests that nitrogen is a limiting factor. Grasses and *Achillea millefolium* did especially poorly. These data imply that although growth would have been retarded, some species could have colonized mudflows and tephra. However, the physical structure of the pyroclastic material would preclude the establishment of immigrating seeds.

On each of the substrates collected in 1981, only a few forbs did poorly (Table 3). Grasses, except for *Danthonia,* fared poorly on all substrates, while several forbs did well on pyroclastic material. In 1982 the ability of the substrates to support plant growth continued to improve, and the yield of some species increased markedly (Table 4). *Agrostis diegoensis,* a dominant subalpine grass, continued to do poorly, suggesting that it is quite sensitive to infertility. Improvement continued in 1983 (Table 5), by which time the yield of most species was not significantly less than that of controls, especially on pyroclastic materials. Grasses tended to do less well than forbs.

Analysis of variance of the data from the factorial experiment (Table 6) indicates that nutrient addition and soil type each have major effects, but that structural modifications do little to improve growth. For *Achillea,* the soil and nutrient effects were significant, but soil structure had no effect on yield. Structure affected *Agrostis* when it was grown on mud with added nutrients, but on other substrates only nutrients had an effect. The nutrient effects for *Lupinus* were small, probably because this species can fix nitrogen. For *Sitanion,* there were moderate soil and nutrient effects.

In the absence of compaction and with adequate water, nutrients (primarily nitrogen) were the major determinants of plant growth on a given substrate. On each substrate, *Achillea,* an aggressive species, was the most responsive to nutrients, while *Lupinus latifolius,* a nitrogen-fixing species, was the least responsive (Table 6). In no case did soil structure alone enhance growth and only in the case of *Agrostis* on Pine Creek silt does the interaction of nutrient and perlite yield greater growth.

Gophers and other burrowing rodents are thought to increase surface fertility by processing and returning weathered material to the new surface (Andersen and Mac-

TABLE 1.—Soil characteristics for bioassay materials. Values are means of two determinations each, except n = 3 for loams. Values for nutrients are μg per gram. PC = Pine Creek, BC- = Butte Camp, and UWL = loam from the University of Washington greenhouse

Year	Substrate	*p*H	P	K	NO_3
1980	Pyroclastic	6.43	2.5	87	0.35
	Mud-PC and BC	—	—	—	—
	Tephra	6.15	1.4	80	0.15
1981	Pyroclastic	5.10	2.9	53	0.30
	Mud-PC	4.66	3.2	50	0.38
	Mud-BC	4.75	1.5	40	0.08
	Tephra	5.47	1.5	49	0.08
	Gopher mound	5.29	1.3	20	4.72
1982	Pyroclastic	5.94	0.9	47	0.76
	Mud-PC	4.52	2.1	23	0.03
	Mud-BC	4.33	3.1	24	0.05
	Tephra	5.20	1.9	40	0.12
	Gopher mound	5.58	1.7	47	5.85
1983	Pyroclastic	4.30	4.7	18	0.29
	Mud-BC	4.76	2.0	43	0.22
	Tephra	5.10	2.2	25	0.17
	UWL	5.73	121.0	1350	326.
	Deer Park loam	5.59	3.2	84	6.50

TABLE 2.—Growth response, expressed as percent of growth in greenhouse loam (UWL) control, and rank of native species growing in four substrates collected on Mount St. Helens, summer 1980. All comparisons are by t-test. All values are significantly different from UWL control. *a* = different from pyroclastic material; *b* = different from PC mud; *c* = different from BC mud; and *d* = different from tephra, all at $P < .05$

Species	Substrates							
	Pyroclastics		PC Mud		BC Mud		Tephra	
	% Cont.	R	% Cont.	R	% Cont.	R	% Cont.	R
Achillea millefolium	2.2	5	0.0	10	1.0	10	1.1	10
Agrostis diegoensis	1.4	6	2.9	8	2.6	9	2.9	9
Aster ledophyllus	10.6^{bc}	1	22.9^{a}	5	22.9^{a}	7	14.9	7
Carex spectabilis	5.8^{bcd}	2	29.6^{ad}	3	30.3^{ad}	6	43.3^{abc}	4
Eriogonum pyrolifolium	4.2^{bcd}	3	31.0^{a}	2	35.0^{a}	4	35.0^{a}	6
Luetkea pectinata	0.0^{bcd}	9	17.6^{acd}	6	48.0^{ab}	1	48.0^{ab}	3
Lupinus latifolius	0.0^{bcd}	9	17.3^{acd}	7	36.8^{ab}	2	79.1^{abc}	1
L. lepidus	2.4^{bcd}	4	27.6^{ad}	4	35.1^{ad}	3	62.8^{abc}	2
Poa incurva	1.1	7	1.6	9	3.0	8	3.8	8
Spraguea umbellata	0.0^{bcd}	9	36.9^{a}	1	32.6^{a}	5	41.3^{a}	5

TABLE 3.—Growth response, expressed as percent of growth in greenhouse loam (UWL) control, and rank (R) of native species growing in four substrates collected on Mount St. Helens, summer 1981. All comparisons are by t-test. All values are significantly different from UWL control. *a* = different from pyroclastic material; *b* = different from PC mud; *c* = different from BC mud; and *d* = different from tephra, all at $P<.05$

Species	Substrates							
	Pyroclastics		PC Mud		BC Mud		Tephra	
	% Cont.	R	% Cont.	R	% Cont.	R	% Cont.	R
Achillea millefolium	20.9^{bc}	7	5.9^{a}	16	8.3^{a}	15	14.3	13
Agrostis diegoensis	1.2	18	2.7	19	2.3	19	8.2	17
Antennaria microphylla	10.8	10	9.1	14	10.8	14	12.4	14
Arnica latifolia	0.0	20	5.4	17	0.0	20	9.2^{ac}	16
Aster ledophyllus	9.9^{bcd}	11	21.4^{ad}	9	24.9^{ad}	10	15.6^{abc}	11
Carex pachystachea	8.7^{bcd}	12	40.7^{ad}	3	32.7^{ad}	6	17.2^{abc}	10
C. spectabilis	5.2^{bcd}	16	29.5^{ad}	6	30.1^{ad}	7	41.9^{abc}	6
Danthonia intermedia	56.6^{bc}	1	28.6^{a}	7	26.2^{a}	9	—	—
Eriogonum pyrolifolium	17.2^{bcd}	8	60.0^{ad}	1	61.1^{ad}	1	45.8^{abc}	4
Hieracium gracile	4.0	17	2.4	20	3.8	17	3.2	19
Lomatium martindalei	30.1^{cd}	4	26.5	8	22.3^{a}	11	22.8^{a}	8
Luetkea pectinata	0.0^{bcd}	19	18.7^{ad}	10	45.8^{ab}	2	50.5^{ab}	3
Lupinus latifolius	6.1^{cd}	14	16.1^{cd}	11	34.1^{abd}	5	61.9^{abc}	1
L. lepidus	40.9	3	41.9	2	40.5	3	44.0	5
Penstemon cardwellii	25.0^{bcd}	5	9.5	13	6.1^{ad}	16	11.5^{ac}	15
Poa incurva	23.0^{b}	6	9.6^{d}	12	13.3	12	20.2^{b}	9
Polygonum newberryi	44.8^{bcd}	2	30.8^{ad}	5	34.9^{a}	4	37.2^{ab}	7
Sitanion jubatum	5.4^{cd}	15	6.4^{a}	15	11.4^{ab}	13	15.3^{ab}	12
Spraguea umbellatum	6.6^{bcd}	13	33.4^{a}	4	29.1^{a}	8	50.7^{a}	2
Trisetum spicatum	11.3^{bcd}	9	3.5^{a}	18	3.1^{a}	18	4.2^{a}	18

TABLE 4.—Growth response, expressed as percent of growth in greenhouse loam (UWL) control, and rank of native species growing in four substrates collected on Mount St. Helens, summer 1982. All comparisons are by t-test. Except where indicated by *N*, all values are significantly different from UWL control. *a* = different from pyroclastic; *b* = different from PC mud; *c* = different from BC mud; and *d* = different from tephra, all at $P<.05$

Species	Substrates							
	Pyroclastics		PC Mud		BC Mud		Tephra	
	% Cont.	R	% Cont.	R	% Cont.	R	% Cont.	R
Achillea millefolium	20.7^{cd}	13	14.7	10	10.1^{a}	11	11.8^{a}	11
Agrostis diegoensis	52.3^{bcd}	5	5.5^{a}	15	5.2^{a}	13	5.8^{a}	15
Antennaria microphylla	14.0	14	10.2	12	6.5	12	9.4	12
Arnica latifolia	43.2	8	49.2^{cd}	4	34.5^{b}	4	33.8^{b}	6
Carex pachystachea	12.2	15	9.8	13	3.5	15	8.5	13
C. spectabilis	45.0^{bc}	7	27.9^{acd}	9	11.7^{abd}	9	44.1^{bc}	5
Danthonia intermedia	43.0^{cd}	9	31.0^{d}	6	21.2^{a}	6	15.3^{ab}	7
Hieracium gracile	30.9^{bd}	10	48.6^{acd}	5	20.6^{b}	7	14.2^{ab}	8
Lomatium martindalei	28.1^{d}	12	28.3^{d}	7	26.6^{d}	5	74.0^{abcN}	3
Luetkea pectinata	57.7^{bc}	4	82.0^{adN}	2	84.5^{abN}	2	56.7^{bc}	4
Lupinus latifolius	109.4^{bcN}	1	79.8^{aN}	3	79.4^{aN}	3	86.4^{N}	1
L. lepidus	108.0^{dN}	2	96.6^{dN}	1	102.5^{dN}	1	77.6^{abcN}	2
Poa incurva	95.0^{bcdN}	3	11.2^{a}	11	11.3^{a}	10	12.6^{a}	10
Sitanion jubatum	30.2^{cd}	11	28.2^{cd}	8	13.5^{ab}	8	13.1^{ab}	9
Trisetum spicatum	48.0^{bcd}	6	6.0^{a}	14	4.0^{a}	14	6.3^{a}	14

Mahon, 1985). Two bioassays explored the question of whether such material was a better growth medium than the tephra deposited over it. Experiment 1 used cores obtained in the field and tested with minimum disturbance. The cores were small, the material sampled lacked cohesiveness and the edge effect was large. These factors combined to produce a large standard error. Despite these circumstances, gopher mound substrate permitted both bioassay species to grow nearly twice as large as they did in tephra (Ta-

TABLE 5.—Growth response, expressed as percent of growth in greenhouse loam (UWL) control, and rank of native species growing in three substrates collected on Mount St. Helens, summer 1983. All comparisons are by t-test. Except where indicated by *N*, all values are significantly different from UWL control. *a* = different from pyroclastic; *c* = different from BC mud; and *d* = different from tephra, all at P<.05

Species	Substrates					
	Pyroclastics		BC Mud		Tephra	
	% Cont.	R	% Cont.	R	% Cont.	R
Achillea millefolium	4.3^{cd}	14	14.7^{ad}	13	6.6^{ac}	13
Agrostis diegoensis	50.7^{d}	9	41.8^{d}	8	8.6^{ac}	12
Arnica latifolia	59.7	6	46.6	7	44.2	5
Carex pachystachea	54.2^{cd}	8	70.2^{adN}	4	11.8^{ac}	11
C. spectabilis	55.2	7	35.4^{d}	10	65.5^{c}	4
Danthonia intermedia	81.7^{dN}	3	51.4^{d}	6	36.9^{ac}	6
Hieracium gracile	9.1^{cd}	12	7.0^{ad}	14	5.1^{ac}	14
Lomatium martindalei	70.0^{N}	4	86.1^{N}	3	78.7^{N}	3
Luetkea pectinata	64.5^{cdN}	5	24.2^{a}	11	32.6^{a}	8
Lupinus latifolius	112.9^{N}	2	112.4^{N}	2	105.7^{N}	2
L. lepidus	136.6^{N}	1	130.5^{N}	1	116.6^{N}	1
Poa incurva	21.0	12	15.1	12	18.2	9
Sitanion jubatum	40.0	10	56.1^{d}	5	35.1^{c}	7
Trisetum spicatum	25.2^{cd}	11	35.5^{ad}	9	14.3^{ac}	10

TABLE 6.—Effects of 1981 soil, nutrient addition and structural modification on the growth of four representative species. Values are expressed as percent of the unmanipulated control soil. Significance of the differences from control are indicated by *a* = P<0.05; *b* = P<0.01; and *c* = P<0.001

Treatment	Species							
	Achillea		*Agrostis*		*Lupinus*		*Sitanion*	
	Wgt.	%	Wgt.	%	Wgt.	%	Wgt.	%
DPL-control	517	100	893	100	2015	100	141	100
+ perlite		101		68^{a}		84		83
+ nutrient		527^{c}		141^{b}		101		126^{b}
+ both		469^{c}		137^{b}		112		126^{b}
Pyroclastic-control	260	100	106	100	1412	100	92	100
+ perlite		119		136		100		92
+ nutrient		874^{c}		538^{b}		156^{a}		165^{a}
+ both		984^{c}		469^{b}		152^{a}		150^{a}
PC Silt-control	129	100	28	100	1510	100	57	100
+ perlite		166		104		90		123
+ nutrient		1082^{c}		318^{b}		153^{b}		160^{b}
+ both		1363^{c}		1432^{c}		132^{a}		246^{c}
Tephra-control	230	100	104	100	1492	100	59	100
+ perlite		155		99		108		122
+ nutrient		1011^{c}		712^{c}		143^{b}		226^{b}
+ both		635^{b}		416^{b}		159^{b}		230^{b}

ble 7). Growth of *Achillea* was significantly lower in gopher soil than in the control while the growth of *Agrostis* was not significantly different from the control. The mud supported growth intermediate between tephra and gopher soil.

Experiment 2 (Table 8) compared four species under standard bioassay conditions, growing on DPL, gopher soil and tephra. In each case, growth was greater on the gopher soil than on tephra, though for *Danthonia* the difference was not statistically significant.

These experiments suggest that older, more weathered substrates are better growing media than recent, volcanically altered materials. It is therefore likely that small mammals play an important role by returning such material to the surface, thus enhancing the nutrient status of the tephra.

DISCUSSION AND CONCLUSIONS

The species tested vary widely in their tolerance of particular substrates. Differences appear to be related to substrate chemical and physical features and perhaps to the growth-forms characteristic of the species. Since these were short-term experiments, using germinated seedlings, conducted over several years with several seed sources and substrates from various localities, detailed comparisons are inappropriate. However, we believe some general observations are appropriate.

Each year there was a wide range of responses on each substrate (Table 9). The average performance of all species taken together improves annually. Considering only the seven species common to all years, the drop on tephra in 1981 is primarily due to substantial declines in both lupines, for which we have no explanation.

In 1980 and 1981, response of species on pyroclastic materials was not correlated (Spearman's rank test) with that of species on the remaining substrates; the rank-order correlations among the other substrates were high. For example, in 1980 correlation between plant growth on silt and on mud was $r = 0.61$ ($P < 0.002$) and between plant growth on tephra and on mud it was $r = 0.93$ ($P < 0.001$). In 1981, correlations among yield on pyroclastic materials and on other substrates were no higher than $r = 0.42$ ($P < 0.03$), while correlations between the yield on silt and on mud was $r = 0.85$ ($P < 0.001$), that between yield on silt and on tephra was $r = 0.66$ ($P < 0.001$) and that between plants on mud and those on tephra was $r = 0.62$ ($P < 0.002$). Correlations of the yield of plants growing on pyroclastic substrate with those of plants on silt, on mud, and on tephra were $r = 0.50$ ($P < 0.026$), $r = 0.57$ ($P < 0.011$) and $r = 0.58$ ($P < 0.01$), while correlations among the latter substrates were $r = 0.92$ ($P < 0.001$) or more. These correlations imply that the native species tested initially responded differently to the thermally altered substrates than they did to the other surfaces. By 1983, material collected from the N side of the mountain was coarse and resembled mudflow material more than previous collections. Rank correlations among the substrates showed that the responses of all species were similar. The pyroclastic substrate more closely resembled the mud ($r = 0.89$, $P < 0.001$) and the tephra ($r = 0.77$, $P < 0.001$) than the Butte Camp materials resembled each other ($r = 0.75$, $P < 0.001$).

Derived from this is the prediction, to be tested, that early colonists will be comprised of a different subset of the available flora than those already colonizing the high-elevation mudflows. For example, in 1981 *Achillea, Danthonia, Penstemon, Poa* and *Trisetum* did remarkably better in pyroclastics than they did in other substrates; species such as *Aster ledophyllus, Carex spectabilis, Eriogonum pyrolifolium, Luetkea pectinata* and *Lupinus latifolius* did much worse. In 1982, improvements by species such as *Lupinus latifolius* and *Carex spectabilis* reduced these differences. The species that do well in the pyroclastics do not share any obvious characteristics though they tend to be more xerophytic. The bioassay results suggest that there is a spectrum of species now capable of invading the subalpine habitats created by the 1980 eruptions.

There is some evidence that some of these soils are changing in character. The weathering process is slow and the changes observed thus far have been caused by erosion. Leaching has lowered *p*H in tephra, but its ability to support plant growth has not changed since the first year, and vegetative cover on this substrate has stabilized since 1981. Fine material has been removed from the silt and the pyroclastic substrates. There has been a general improvement in porosity and aeration in these soils. Nutrient inputs from precipitation and insects are small, but may be significant. Where original surfaces were buried, burrowing rodents serve to bring nutrients to the surface.

Since nutrient changes appear to have been modest, the large increase in growth shown in pyroclastic materials probably results from improved structure. Further improvement may depend on weathering, nitrogen fixation and the continued influx of nutrients through fallout.

The results of the factorial experiment support the hypothesis that further improvements in growth potential must result from nutritional factors. Only nutrient addition led to major improvements. Because *Lupinus latifolius* had the least response, it is likely that nitrogen is a major limiting nutrient.

Despite the fact that pyroclastic materials supported the best growth in 1982 and

TABLE 7.—Growth of two species in cores obtained from primary tephra (teph 1), secondary tephra (teph 2, redeposited) and gopher mounds compared to DPL controls. Values are mean weight (mg) per plant. Weights underlined are not significantly different from one another (multiple range test, $P < 0.05$)

Species	Control	Gopher	BC mud	Teph 1	Teph 2
Achillea millefolium	72	49	36	29	27
Agrostis diegoensis	30	28	23	17	16

TABLE 8.—Growth of four species in gopher mound soil and tephra compared to DPL control. Values are mean weight (mg) per plant. Differences were determined by t-test; *a* = different from control; *b* = different from gopher soil ($P < 0.05$ in each case)

Species	Control	Gopher mound	Tephra
Antennaria microphylla	33.3	22.5^{a}	16.4^{ab}
Danthonia intermedia	68.3	65.6	59.5
Lupinus lepidus	192.0	178.0	141.1^{ab}
Poa incurva	117.1	87.9^{a}	28.9^{ab}

TABLE 9.—Changes in plant responses to substrates collected from 1980 to 1983. Values are mean percent of control, with range shown for comparison

	Substrate			
Year, N of species	Pyroclastic	Silt	Mud	Tephra
1980 (n = 10) mean	2.7	18.7	24.7	33.2
range	(0-10.6)	(0-36.9)	(1.0-48.0)	(1.1-79.1)
1981 (n = 20) mean	16.4	20.1	23.7	26.4
range	(0-56.6)	(2.4-60.0)	(0-61.1)	(3.2-61.9)
1982 (n = 15) mean	49.2	35.3	29.0	31.3
range	(12.2-109.4)	(5.5-96.6)	(3.5-102.5)	(5.8-86.4)
1983 (n = 14) mean	56.2	—	51.9	41.4
range	(4.3-136.6)	—	(7.0-130.5)	(5.1-116.6)

1983, there is virtually no growth on pyroclastic surfaces in the field. Where a few colonists are found, they are healthy and expanding, but the upland landscape is generally barren. Over most of this large area (over 40 km^2), the surface has come to resemble a "desert pavement" (F. C. Ugolini, pers. comm.) that offers limited opportunities for successful seed germination. Distances to the nearest potential colonizing subalpine herbs are great. Field experiments have indicated that mudflows will support successful seedling growth if the seeds are sown, but that the most successful species are poor dispersers (D. M. Wood, pers. comm.). Combined with the results of experiments reported here, it appears that recolonization is limited first by isolation and second by a hostile surface. Seedlings of many species that can reach a site and chance into a favorable microsite may be retarded, but not excluded by limited nutrients. The species best able to reach this area are composites such as *Aster* and *Hieracium.* However, species best able to grow in the devastated subalpine zones include *Lupinus latifolius, L. lepidus, Luetkea pectinata* and some grasses. The lupines are currently the most successful colonists.

Natural revegetation of devastated surfaces surrounding Mount St. Helens requires several conditions. Mudflows that were surrounded by intact or recovered vegetation are being colonized. Though low in nutrients and with harsh surface properties that further reduce the density of safe-sites, dispersal distances are short and invasion has commenced. High-elevation sites in the massively devastated zone are up to several kilometers from potential colonists. Though surface characteristics and nutrient levels have become at least as favorable as cold mudflows, distance effects have greatly inhibited colonization. Recovery in such locations will be exceedingly slow in comparison to forests, clear-cuts, lake margins (Means *et al.,* 1982), and lower elevation mudflows (Halpern and Harmon, 1983).

The evidence presented here suggests that now that substrates have stabilized, the restoration of devastated subalpine meadows is constrained by the lack of suitable colonists. Reclamation in similar circumstances should therefore concentrate on supplying suitable species. A stable surface and adequate nutrients are important preconditions, but after 5 growing seasons, the devastated subalpine surfaces of Mount St. Helens are capable of supporting pioneering vascular plant species. They need only to be dispersed from surrounding areas.

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