Initial Recovery of Subalpine Vegetation on Mount St. Helens, Washington

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ABSTRACT: A network of permanent plots has been established on the subalpine slopes of Mount St. Helens. Plants in sites receiving only tephra or thin mud deposits survived the 18 May 1980 eruption and re-established themselves by late summer. Richness and cover on these substrates increased dramatically by 1981. Sites receiving thick cold mudflows have little vegetation after two growing seasons, and the few scattered individuals encountered are residual survivors, not seedlings. Subalpine sites destroyed by the directed blast, debris flow or pyroclastic flows had no surviving vascular plants and have yet to be recolonized. Such sites will require import of organic debris, nitrification and seed invasion for recovery to commence. Community analysis shows that subalpine herb composition is changing on all sites and that the magnitude of change, except on totally devastated sites, is proportional to the magnitude of the initial impact. Based on two seasons of observations, future changes in species number and cover are projected.

INTRODUCTION

Mount St. Helens resumed volcanic activity, highlighted by its lateral eruption, on 18 May 1980. Triggered by a massive landslide (Rosenfeld, 1980), the subsequent eruptions produced a complex disturbance pattern on subalpine habitats. Other studies of the consequences of these eruptions for plant life have been published (Cook *et al.*, 1981; Mack, 1981), but these concentrated on vegetation away from the cone. Here I report the initial response of subalpine vegetation to major eruption events and describe changes through September 1981.

Tree line on Mount St. Helens is ca. 800 m lower than that of nearby Mt. Adams (Lawrence, 1954); therefore, subalpine herbaceous vegetation occurs as low as 1275 m in the areas studied. Though the subalpine flora was well known before the eruption (St. John, 1976; A. R. Kruckeberg, pers. comm.), plant community structure and distribution were not. It is therefore difficult to assess the degree to which subalpine vegetation has recovered.

Volcanic damage is categorized as follows: (1) A huge area on the N face was devastated by a massive landslide, a debris flow and pyroclastic flows (Rosenfeld, 1980). This volcanic effluvium contained no residual vascular plant life. The E flank received hot aerial blasts, incandescent pumice flows and mudflows that also destroyed all plant life. (2) Rapid deglaciation scoured upper glacier valleys on the NW, S and SE slopes and deposited varied thicknesses of fine mud at lower elevations (del Moral, 1981). Survivorship varied depending on the degree of scouring and the depth of mud deposits. (3) Ridges within the blast zone, near the crater but above mudflows, were exposed to searing, gale-force winds. Some dormant individuals survived, but most plants were destroyed. (4) Tephra and mud were often deposited on snow. Dormant herbaceous plants on the SE to western slopes were often protected from tephra and mud deposits, though these deposits inhibited the emergence of many plants. (5) Sites on the northwestern edge of the blast zone were protected by snow and sufficiently close to the cone to receive limited tephra deposits. Here, by September 1980, herbaceous vegetation appeared normal.

During the winter, 1980-1981, water eroded massive quantities of material from the cone (F. J. Swanson, pers. comm.). Erosion altered conditions in many places and arrested reinvasion of devastated areas. This report summarizes observations made of subalpine vegetation during 1980 and 1981.

METHODS

I established 42 permanently marked 250 m² circular plots in 1980. In 1981, 37 were resampled and 20 new ones were established. Four radii were marked in each plot and sampled using six 20 by 50 cm quadrats at 1-m intervals. This report summarizes data from the plots (Fig. 1). Data obtained both years: Butte Camp (Bc)—horizontal transects at 1350 m (BcA, n = 7), 1550 m (BcB, n = 12) and 1620 m (BcC, n = 5) and Pine Creek (Pc)—horizontal transects at 1280 m (PcE, n = 4), 1370 m (PcA, n = 4) and 1530 m (PcB, n = 5). Data obtained only in 1980: South Fork Toutle Ridge at 1500 m (SFT, n = 4) and the Plains of Abraham at 1375 m (n = 1). Data obtained in 1981: a vertical transect ranging between 1275 m and 1430 m on a ridge above the Talus Glacier (Er, n = 10) and a vertical transect ranging from 1620-1700 m above Butte Camp (BcD, n = 5). Nomenclature is that of Hitchcock and Cronquist (1973).

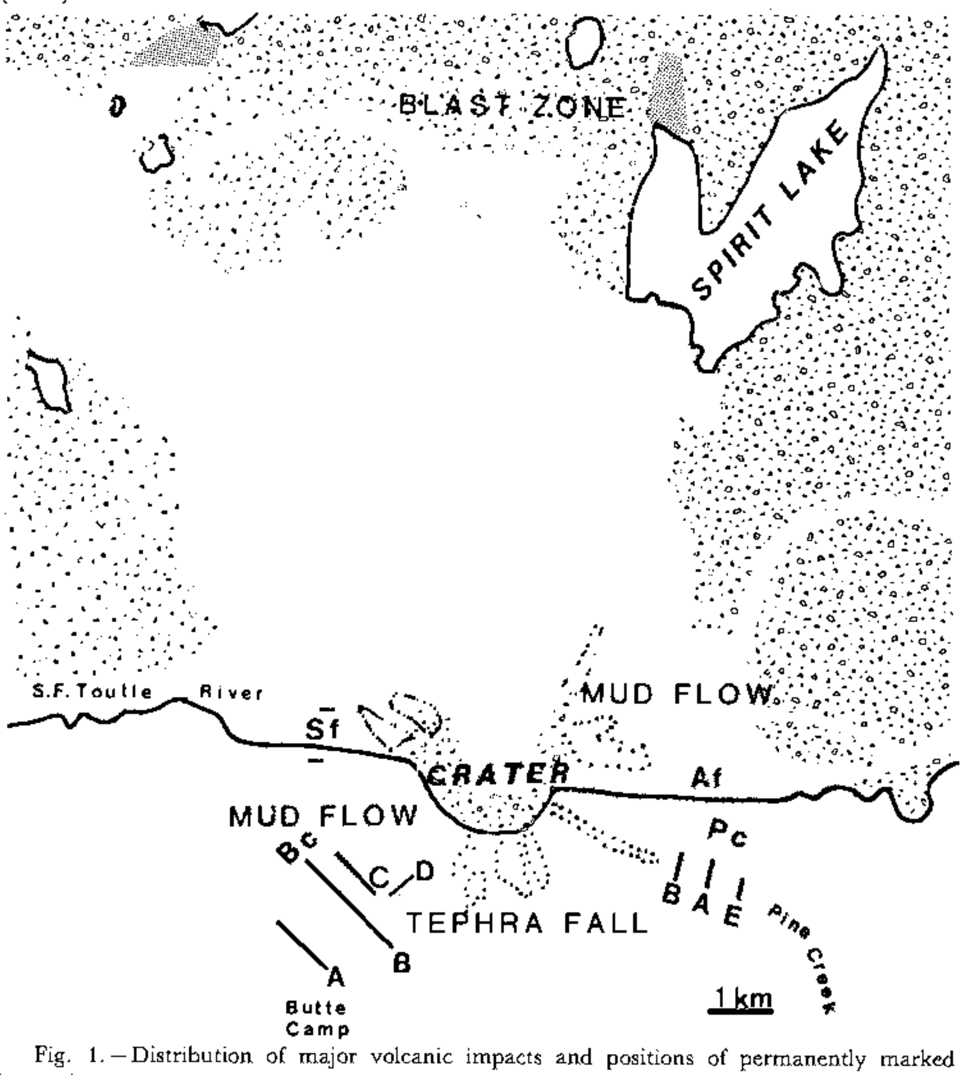

Fig. 1.—Distribution of major volcanic impacts and positions of permanently marked transects

Stand structure was estimated in three ways. The number of species (richness) was determined for each plot. Percent cover was determined for each species from the 24 quadrats and averaged to obtain an estimate of total plot cover. Where cover was very low, total plot cover was also estimated directly. From these data, an estimate of diversity was calculated using the Shannon-Weiner Index (H′).

Data analyses were aided by detrended correspondence analysis (DCA; Hill and Gauch, 1980), an ordination method that minimizes quadratic distortions inherent in other methods and that scales the axes in constant units related to floristic changes along the ordination. To improve interpretability of these data, characterized by large differences in absolute cover, data were transformed logarithmically and rare species down-weighted. The contribution of those species found in fewer than 20% of the samples was reduced by an amount dependent on their frequency (Hill, 1979).

RESULTS

Species responses. — Figure 1 locates principal geographic features, major volcanic impacts and permanent plots. Tephra was deposited throughout the area during several eruptions, primarily in May and June 1980. Blast effects, the debris flow and mudflows destroyed existing vegetation.

Plots were grouped into five categories based on similarity of volcanic effects received (Table 1). Except for "thick mud," each group is comprised of plots from a compact area, *e.g.*, Butte Camp and Pine Creek. The thick mud group includes plots from transects A and B at Pine Creek and appropriate ones from transects B and C at Butte Camp. Plots sampled in both years were tested for cover increases by a 1-tailed paired t-test (Steel and Torrie, 1960) in two ways. Plot means were compared and significant differences ($P < .05$), marked by an "a," noted. Individual quadrats were also compared. Species showing significant differences by this more detailed analysis are marked with a "b."

South Fork Toutle Ridge plots are just S of the direct blast-effect boundary. Trees near these plots were killed, but the herb layer was dormant and protected by snow. These sites were sufficiently close to the crater to receive only light tephra deposits. Logistical problems precluded resampling these plots in 1981. This group of plots had high cover and richness and was the least disturbed of my sample.

Of four plots established at lower Pine Creek (PcE), only three could be relocated. A thin veneer of mud debris was deposited here as a result of the rapid melting of the Shoestring Glacier. By spring 1981 most mud was gone and cover increased substantially.

Plots that received only tephra deposits were sampled in the Butte Camp area. Though ca. 6-8 cm of coarse material fell on or after 18 May 1980, many species emerged that summer. This vegetation is rooted on a mudflow estimated to be ca. 500 years old (F. C. Ugolini, pers. comm.). Tephra was partially eroded from steeper sites and all samples showed dramatic cover increases. Every species except *Fragaria* increased in cover in each 0.1 m^2 quadrat it occupied. In eight cases, based on mean cover values, these increases were statistically significant. Secondary deposits of tephra, washed down from steeper slopes, markedly inhibited vegetation in 1981. Where deposits exceeded 20 cm in depth, no vegetation emerged. *Polygonum newberryi* and *Aster ledophyllus* were best able to penetrate such deposits.

Thick mud deposits above Butte Camp and along Pine Creek scoured the substrate and then covered it with varied mud deposits. There were few plants on these sites in 1980. Though cover remained low in 1981, substantial recovery has occurred. *Luetkea pectinata*, which failed to emerge in many places in 1980, and *Agrostis diegoensis* were significantly more abundant in 1981.

In 1981, a transect was established on an exposed ridge (Er) just N of the South Fork, Toutle River (Fig. 1), within the blast zone. Close aerial reconnaissance in 1980 revealed no vegetation on this ridge. It received an intense heat blast followed by tephra deposits, but otherwise escaped direct effects of the calamitous May 18 eruption. Cover on this transect is scant and since much of the original soil appears to have been blasted, nitrogen, phosphorus, cation exchange capacity and several cations may be limited.

Except where residual vegetation produced substantial cover, seedlings were rarely encountered. Plants that were observed had survived the eruption and re-established from underground vegetative parts. In some cases, notably *Juncus parryi* and *Luetkea pectinata,* survivors had remained dormant and buried by snow or mud from late 1979 to spring of 1981. Burial caused high mortality in these and other species. Trenches dug in 1980 suggested that graminoids had suffered disproportionately when buried by tephra. At Pine Creek, erosion revealed many clones of *Agrostis, Carex spectabilis* and *Juncus* killed by burial. Substrates from which all vegetation was removed, either by mudflows or pyroclastic flows, have yet to be recolonized. Low soil nitrogen in these materials implies that nitrogen-fixing lupines will be the most successful early colonists.

TABLE 1. — Mean cover of common species in paired plots, 1980 and 1981. Habitats were grouped according to the major form of impact received and are listed in order of increasing damage

	Thin tephra (n = 4)	Thin mud (n = 3)		Tephra (n = 14)		Thick mud (n = 12)		Blast area (n = 9)
Species	1980	1980	1981	1980	1981	1980	1981	1981
Gentiana calycosa	0.2							
Penstemon confertus	3.2							p
Phyllodoce empetriformis	0.9	p	p	0.1	0.1		p	
Fragaria virginiana	3.0	0.1	0.2	0.5	0.6			0.1
Achillea millefolium	8.5	1.5	2.2	0.3	2.2[ab]	0.1	0.1	0.2
Agoseris aurantiaca	0.4	0.1	0.2	p	0.2[b]	p	p	
Lupinus latifolius	12.0	10.6	31.2[ab]	p	p			p
Carex spectabilis	1.6	6.7	17.8[ab]			p	0.1	
Spraguea umbellata	0.1			p	0.1			
Antennaria microphylla		p	0.1		p			
Xerophyllum tenax		0.1	0.4					
Castilleja miniata	0.1		p	0.1	0.2			
Hieracium gracile	p		0.1		0.1		p	
Carex rossii			0.3	0.5	1.2[ab]			p
Luetkea pectinata		0.1	3.3[b]	0.1	0.3[b]	0.1	0.7	
Agrostis diegoensis	4.2	0.3	0.6[b]	3.9	10.1[ab]	0.2	0.8[ab]	0.3
Danthonia intermedia		0.1	0.1	0.2	0.5			
Lomatium martindalei	0.3	0.2	2.5[ab]	1.2	2.1[ab]			0.9
Polygonum newberryi	0.2	0.3	1.2	0.9	1.8[ab]	0.1	0.4[b]	0.1
Aster ledophyllus	p	0.3	0.3	0.7	1.9[ab]	0.1	0.3[b]	p
Hieracium albiflorum				p	p		p	0.1
Sitanion jubatum	0.5			0.3	1.2[b]		0.1	0.1
Phlox diffusa				0.9	1.8			
Carex pachystachya				p	p			0.1
Eriogonum pyrolifolium	0.2			1.6	3.1[ab]	0.1	0.1	0.1
Juncus parryi				0.8	1.4[b]	p	0.1	
Juniperus communis				p	p			
Penstemon cardwellii				0.2	0.5		p	
Stipa occidentalis				0.2	0.4[b]		0.1	
Poa incurva				0.1	0.6[b]	p	p	p
Lupinus lepidus	0.2			3.2	9.8[ab]	0.1	0.1	4.5
Trisetum spicatum			p	p	0.2		0.1	p

[a]p < 0.05, determined by one-tailed paired t-test of plot means
[b]P < 0.05, determined by one-tailed paired t-tests of individual 0.1 m^2 quadrat values
p = present less than 0.05% cover

Since these lupines have poor long-distance dispersal mechanisms, reinvasion may proceed quite slowly.

In most plots, density has yet to reach values where competition may be expected to affect community structure. Tephra-impacted plots are closest to this stage. Here opportunities for invasion by new species and genets appear limited. On mudflows and other low density plots, invasion opportunities are greater and strong competitive interactions are unlikely for several years.

Overall recovery patterns can be characterized by species richness, cover and H'. Plots are grouped geographically in Table 2, where these structural features are compared by a 1-tailed paired t-test. (1980 values for South Fork Toutle plots and 1981 values for the Exposed Ridge transect are also shown for comparison.) Richness and cover increased significantly ($P < .05$) from 1980 to 1981 in every comparison except the small BcC sample. A pattern of further recovery by residual species and the emergence of completely buried species are implied.

Species richness increased in every plot, but was not due to seedling establishment because species not recorded in 1980 were nearly always mature and in flower when sampled. In 1981, mean cover of species absent in 1980 was low, suggesting that these plants suffered high mortality due to burial. Survival often appeared to be serendipitous, resulting from protection by overhanging rocks or release by rill erosion on mudflows. Burial by tephra produces a loosely consolidated and porous surface, while the fine texture of most mudflows in this area produce cement-like surfaces that inhibit gas exchange and water penetration.

Increased cover on tephra resulted primarily from vegetation expansion and secondarily from tephra removal. In contrast, on mudflows, rill erosion permitted limited recovery in 1980; sheet erosion during winter of 1980-1981 cleared the surface of ridges along Pine Creek and led to enhanced recovery. However, vegetation often remained confined to strips corresponding to the rills formed in summer 1980. One season of burial appears to produce high mortality.

Diversity did not change significantly, despite an *a priori* expectation that it would. Where cover was initially quite low, relative cover could not be assessed accurately and H' was overestimated in 1980 because most species were assigned the same minimum

TABLE 2.—Structural features of permanent plots in 1980 and 1981. Significance levels determined by one-tailed t-tests, with standard errors reported in parentheses. Plots are grouped by region. South Fork Toutle and Exposed Ridge plots are shown for comparison

Group[1]	Year	Richness (n)	Cover (%)	H'
BC-A; 1 to 6	1980	10.8 (0.94)	14.4 (3.90)	1.56 (0.18)
	1981	15.3 (0.82)[b]	37.7 (10.9)[a]	1.55 (0.08)
BC-B; 1 to 6	1980	13.5 (1.42)	20.5 (3.14)	2.01 (0.13)
	1981	16.6 (2.12)[a]	37.3 (6.18)[a]	2.12 (0.13)
BC-B; 7 to 12	1980	10.8 (1.60)	5.6 (1.20)	1.78 (0.11)
	1981	14.0 (2.31)[a]	15.4 (3.73)[a]	1.58 (0.19)
BC-C; 1 to 4	1980	6.5 (2.32)	4.9 (4.80)	1.46 (0.29)
	1981	10.2 (2.82)	10.0 (8.48)	1.74 (0.28)
PC-A; 1 to 4	1980	3.7 (0.92)	0.7 (0.28)	0.92 (0.21)
and PC-B; 1 to 5	1981	7.2 (1.10)[b]	4.0 (1.49)[a]	1.35 (0.16)
PC-E; 2 to 4	1980	10.0 (1.53)	19.8 (0.70)	1.11 (0.09)
	1981	15.0 (1.01)[a]	60.7 (3.10)[b]	1.27 (0.04)
SFT; 1 to 4	1980	14.8 (2.70)	37.1 (14.0)	1.71 (0.25)
ER; 2 to 10	1981	7.5 (0.57)	3.3 (0.32)	1.52 (0.07)

[1]BC = Butte Camp; PC = Pine Creek; SFT = South Fork, Toutle Ridge; ER = Exposed Ridge; letters and numbers refer to transect and plot numbers, respectively

[a]$P < 0.05$

[b]$P < 0.01$

values. In 1981, descriptions of these plots were more precise due to higher cover, and H′ estimates better reflected the true dominance hierarchy. In other cases, H′ declined because the dominant species present in 1980 increased proportionately more than newly emerged species. As conditions stabilize over the next several years, H′ should reveal distinct patterns.

Plant community analysis.—Plots sampled in both years were compared using DCA (Hill, 1979) as described above. Absolute cover varies from trace amounts to 80% and, though beta diversity (ca. three half-changes) is moderate, geographic effects accentuate its impact. Unfavorable conditions are thus created for detailed interpretation. Site Er-1 was eliminated because it consisted of a single *Lupinus latifolius* plant and its presence distorted the total configuration. Alternative analytical methods did not improve interpretations.

Plots sampled in both years are connected by solid lines at Butte Camp and by dashed lines at Pine Creek. Figure 2 is labeled to combine preexisting habitat conditions with the dominant impact received.

Plots covered only by a thin mud layer at Pine Creek retain relatively lush vegetation. These plots, with high DC-1 scores, occur on mesic sites. The dry end of this axis is characterized by plots on steep slopes that received tephra. Plots at the low extreme of DC-2 are from ridges above the South Fork, Toutle River (SFT) with lush vegetation. Those at the upper extreme are from xeric sites that received heavy mud deposits.

The greatest compositional changes occurred on mudflows. Percent distance between samples of each plot in successive years averaged .765 ± .223 on Butte Camp mudflows; .877 ± .095 on upper Pine Creek mudflows; and .665 ± .309 on thin Pine Creek mudflows. In contrast, tephra-impacted sites changed relatively little. For the BcA transect, distances averaged .398 ± .196; at BcB, plots 1 to 6, distances averaged .249 ± .049; while on BcB-7, 10, 12 and BcC-3 they averaged .339 ± .117. Distances

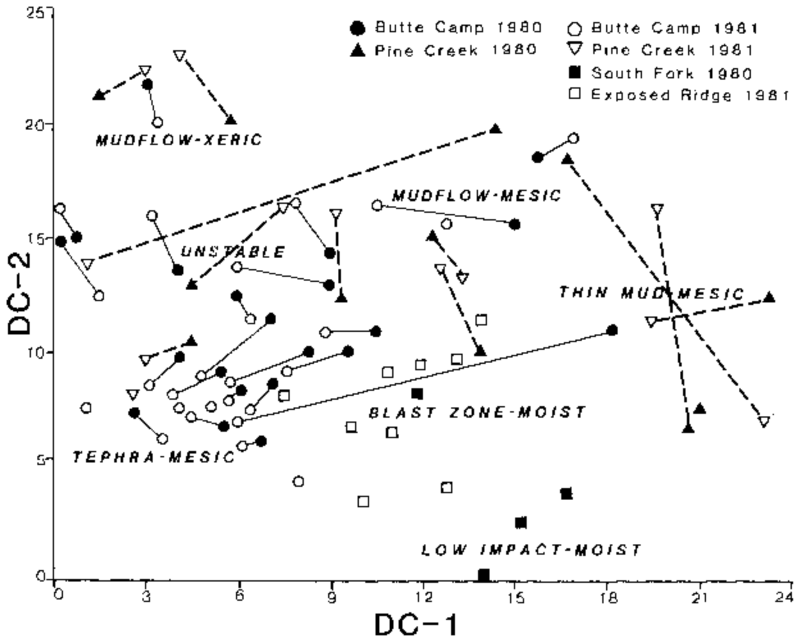

Fig. 2.—Detrended correspondence analysis of plant community data. Plots measured in 1980 and 1981 are connected by solid lines (Butte Camp) or dashed lines (Pine Creek). Regions on graph are designated by a combined volcanic impact and habitat characterization

on unstable plots receiving tephra averaged .253 ± .089.

The exposed ridge transect, though low in cover, is relatively diverse and rich in species. The transect is geographically close to lush, low impact sites and several sample plots fall near them in Figure 2. This implies that the ridge will eventually support lush meadows and that these plots should converge floristically towards those of the protected ridges to the S.

DISCUSSION

Recovery of subalpine vegetation will depend upon the impact history and its interaction with local conditions. Sites impacted primarily by coarse tephra have recovered quickly. Seedling recruitment is relatively unimportant. Though tephra appears to have little available nitrogen (Fruchter *et al.*, 1980), plants rooted in soil show no deficiency symptoms. Seedling establishment is limited to areas of thin tephra and where much of it has eroded. This habitat will equilibrate rapidly as biological and physical factors incorporate tephra into the existing profile and as organic matter is added to the surface.

Mudflows N of Butte Camp are extensive (Fig. 1), but relatively close to recovered vegetation. Erosion has cut deeply to the original surface in places where a few preexisting individuals survive. For example, erosion produced a gully that reached the original surface where *Aster ledophyllus, Agrostis diegoensis, Lupinus lepidus, Phlox diffusa* and other species were noted in 1981.

Such remnants may accelerate reinvasion of mudflows, which are grossly deficient in nitrogen and phosphorus and which have a low cation exchange capacity (R.B. Walker, pers. comm.). These flows are too thick to permit any residual vegetation from emerging without substantial erosion. However, rootstocks of *Lupinus lepidus,* washed down with these flows, sometimes ended up near the surface. Because the flows were cold, such material survived and sprouted. Where mud deposits are stable, low densities of flowering individuals of *L. lepidus* and *Agrostis diegoensis* were observed in 1981. These plants will be important to further recolonization of mudflows. The thick subalpine mudflows formed primarily on gentle slopes. Soil erosion and, in more stable sites, soil development must occur before immigrants initiate significant establishment.

Mudflows near Pine Creek scoured vegetation less. Here, residual plants will develop to form vegetation like that previously existing on the site. Most mud, which was low in all nutrients (R. B. Walker, pers. comm.), has now been removed to reveal the original barren pumice surface. Seedling establishment will occur and accelerate recolonization, but only short distance dispersal is required.

Canyons below glaciers received scouring mudflows and have since eroded very quickly. Cold-adapted mesophytic subalpine species that colonize such places were destroyed. Though vegetation is plentiful on adjacent ridges, it remains to be seen which species can invade these canyons.

Regions that received direct aerial heat blasts but that escaped mud or pyroclastic flows suffered high mortality. The exposed ridge, seared by heat and smothered by tephra, showed no signs of life in 1980, yet, though mortality was high, a few survivors emerged in 1981. Recolonization will require some soil development, surface erosion of tephra, recovery of residual plants and seedling establishment. *Lupinus lepidus* is likely to remain the dominant species until soil nitrogen levels increase.

Permanent plots have yet to be established on portions of the cone that were massively perturbed by the debris flow, pyroclastic flows or steaming mudflows because here vascular plants have yet to be observed. R.B. Walker (pers. comm.) reports that pyroclastic materials are very low in nitrogen, phosphorus and major cations, but high in sulfur and sodium. Soil cooling, *in situ* nitrification, importation of nutrients by fallout of pollen, detritus, arthropods (J. S. Edwards, pers. comm.) and relatively long distance seed dispersal will be required as prelude to vascular plant succession.

CONCLUSIONS

Several schemes for recovery of cover and richness may be envisioned, depending upon the nature of the original impact. Biomass recovery should be inversely proportional to the severity of initial impacts.

Tephra-covered sites have recovered quickly and future vegetative changes will be moderate. Cover and biomass may continue to increase, but richness is probably already near equilibrium. It is unlikely that richness will temporarily exceed this value. The opportunity for invasion by species absent prior to the eruption is limited, and it is unlikely that tephra deposits totally extirpated any species from the cone.

Survivors on mudflows were few, but enduring plants should accelerate reclamation of such sites. Either further erosion to original surfaces or mudflow stabilization will permit survivors to act as foci for restoration by clonal expansion and seedling establishment. Soil development and nutrient inputs will be required for complete rehabilitation. Biomass will accumulate slowly. Because the habitat is quite open, opportunities exist for species not previously present to invade and it is possible that species richness might exceed pre-eruption values.

Regions on the edge of the blast zone are similar to mudflows, but substrates are more stable. Rehabilitation may follow a path similar to that of mudflows. Because surviving residual plants may quickly re-establish competitive dominance, richness equilibrium may be reached sooner than on mudflows at values comparable to those that occurred prior to the eruption.

Sites totally destroyed will develop slowly. The pioneer phase promises to be prolonged and will be materially inhibited by the lack of nutrients, poor soil texture and dispersal problems. To the extent that invaders may be unable to persist as succession proceeds, species composition may change more often than in other cases. It is likely that species richness will differ from that found on such sites prior to the eruption and that a new equilibrium will be established.

The subalpine vegetation of Mount St. Helens continues to change in response to volcanic and physical factors. As these processes continue, the biotic factors of dispersal, competition and grazing will become increasingly important. Comparisons between recovery from surviving residual plants and recovery totally dependent on seed invasion promise to produce interesting results.

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