

Early primary succession on the volcano Mount St. Helens

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Abstract. Primary succession on Mount St. Helens, Washington State, USA, was studied using long-term observational and experimental methods. Distance from potential colonists is a major factor that impedes early primary succession. Sites near undisturbed vegetation remain low in plant cover, but species richness is comparable to intact vegetation. Sites over 500 m from sources of potential colonists have as many species, but mean species richness is much lower than in undisturbed plots. Cover is barely measurable after 11 growing seasons. Highly vagrant species of *Asteraceae* and *Epilobium* dominate isolated sites. Sites contiguous to undisturbed communities are dominated by large-seeded species.

For a new surface to offer suitable conditions to invading plants, weathering, erosion and nutrient inputs must first occur. The earliest colonists are usually confined to specific microsites that offer some physical protection and enhanced resources. Primary succession on Mount St. Helens has been very slow because most habitats are isolated and physically stressful. Well-dispersed species lack the ability to establish until physical processes ameliorate the site. Species capable of establishment lack suitable dispersal abilities. Subsequently, facilitation may occur, for example through symbiotic nitrogen fixation, but these effects are thus far of only local importance. *Lupinus lepidus* usually facilitates colonization of other species only after it dies, leaving behind enriched soil lacking any competitors. Experiments and fine-scale observations suggest that successional sequences on Mount St. Helens are not mechanistically necessary. Rather, they result from local circumstances, landscape effects and chance.

Keywords: Biogeography; Community structure; Competition; Facilitation; Lahar; Pumice; Safe-site; Spatial pattern.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

The 1980 eruptions of Mount St. Helens produced a huge devastated landscape devoid of plants. New landscapes were created by an initial avalanche, a massive lateral explosion, large pyroclastic flows and lahars (= mud flows) spawned by rapidly melting ice. Here, we

focus on primary succession in habitats formed on May 18, 1980, to explore mechanisms that control establishment of plants on new landforms.

The rate of early primary succession is generally believed to be slow (cf. Crocker & Major 1955; Shure & Ragsdale 1977; Houle & Phillips 1989), though rates can differ significantly. As conditions are ameliorated by weathering and nutrient accumulation, the rate of succession gradually accelerates. Recruitment patterns shift as populations establish and reproduce successfully. Community structure may change strongly once a few poorly dispersing species become established. Primary succession may take centuries to unfold, but events that shape the entire process occur within a decade.

Well-defined successional stages of primary succession on volcanoes have been described (Beardsley & Cannon 1930; Smathers & Mueller-Dombois 1974), but discrete stages have not been demonstrated in harsh arctic environments (Bliss & Peterson 1992). Successional stages may relate primarily to habitat differences. Early succession in stressful volcanic situations frequently involves only the gradual accumulation of species and incremental increases in biomass (Tagawa et al. 1985; Fridriksson 1987). Species numbers may plateau for many years while biomass continues to increase. Several abiotic processes must occur on bare substrates before biotic succession mechanisms can be initiated.

Until recently, most studies of primary succession have emphasized retrospective descriptions including historical records (Whittaker, Bush & Richards, 1989; van der Maarel et al. 1985; Rydin & Borgegård 1991) or transects in which space is substituted for time (Houle & Phillips 1989). Long-term studies using frequently recorded permanent plots are less common (cf. Roozen & Westhoff 1985). Here we explore succession mechanisms using repeated sampling on permanently marked grids, pattern descriptions and small-scale experiments.

Early succession on lahars at lower elevations has been described by Halpern & Harmon (1983), Frenzen, Krasney & Rigney (1988) and Dale (1989), whereas del Moral (1983; del Moral & Wood 1986; del Moral & Wood 1988) emphasized the development of species

richness and cover, and Pfitsch & Bliss (1988) the primary production of stable habitats.

Richness and cover have increased in all sites. Rates and patterns differ sharply depending on initial disturbance intensity and local conditions. Richness on lahars has increased steadily to average 17.1 species/250m² in 1991, while cover increased slowly to 5.8%. On the Pumice Plain mean richness reached 8.9 species per plot (1991), while cover is about 1.1%. On the Plains of Abraham, richness was only 3.7 species, and cover was much less than 0.1%. The rate of species accumulation is related to the degree of isolation. The rate of cover development appears related to environmental stress (del Moral & Bliss in press).

Study sites

Volcanic events

After a 130 yr dormancy, Mount St. Helens, Washington, USA (41° 12' N, 122° 11' W), burst into activity. On May 18, 1980, an earthquake triggered the collapse of the north face, resulting in a landslide unprecedented in recorded history. This was followed immediately by a cataclysmic juvenile pyroclastic event (= 'lateral blast') that levelled trees up to 20 km distant. This event became a Plinian eruption that spewed tephra (ash) over thousands of square km. Events near the crater were devastating and have had persistent consequences. Pyroclastic flows of incandescent gasses ejected from the cone were superimposed upon blast deposits immediately north of the crater. Lahars, spawned by rapidly melting glaciers and snow fields, created new landforms. The eruption reduced the cone from 2950 m to 2550 m. See further Rosenfeld (1980), Cummins (1981), Foxworthy & Hill (1982) and Bullard (1984).

Locations

Fig. 1 locates features mentioned in this paper. Climatic timberline in this region is about 1800 m, but due to active volcanism, local timberline was suppressed by more than 800 m (Lawrence 1938) prior to the eruption. Depressed timberlines are common on volcanoes (cf. Masuzawa 1985). All sites are on or near the cone, above 1150 m, at or above local timberline or deforested by the eruption; they differ in substrate type, fertility and isolation from potential colonizers. Studies continued from June 1980 - September 1991. We established permanent study sites on two lahars near Butte Camp and on adjacent less disturbed sites between 1300 and 1360 m. During the first two years, these lahars were unstable, with erosion forming small channels and removing some tephra.

The Pumice Plain occupies a large area immediately

north of the crater. The pyroclastic flow area was formed by the deposit of over 100 m of material from the debris avalanche and subsequent pyroclastic flows. This area has been dissected by many streams that flow from the crater. It has been impacted repeatedly by new lahars (Wood & del Moral 1988). This study focuses on the eastern portion of the Pumice Plain, which escaped the debris avalanche. It was devastated by the lateral blast and several subsequent pyroclastic flows. The study area ranges from 1150 to 1300 m. The Plains of Abraham, a single geomorphological feature on the east flank of the volcano, is between 1400 and 1450 m. It was sparsely vegetated prior to the eruption (Kruckeberg 1987), and dominated by scattered *Abies lasiocarpa*, *Polygonum newberryi* and *Penstemon cardwellii*. The plain was seared by the lateral blast, received several pyroclastic flows and was impacted by lahars driven by melting ice fields. Wind removed most fine material so that the surface now consists of coarse pumice.

Climate

Persistently cloudy, wet weather characterizes the regional climate from October to April. Snow depths vary with elevation and topography. Snow may persist into July, but most sites are free of snow in April or May. Precipitation is episodic between May and September; summer rainfall has varied from 3 - 400 mm during 1980 - 1986 (Reynolds & Bliss 1986). Though established plants rarely experience drought stress, surface soil temperatures, often exceeding 50 °C (Braatne 1989), cause high mortality among seedlings.

Local environmental conditions

Soils created prior to the eruption are poorly developed. New substrates lack significant structure, have almost no clay, have a low bulk density, are friable, and contain few nutrients (LaManna & Ugolini 1987; Ugolini et al. 1992). On lahars, surfaces dry rapidly during the summer dry period, making seedling establishment difficult. However, below 5 cm soil water potentials are moderate (Chapin & Bliss 1988, 1989; Braatne 1989) and once established, most adults appear insulated from impacts of drought. Soil nutrients are very low. Phosphates averaged 400 µg/g, potassium 1100 µg/g and total nitrogen is at or below the range of detection (25 µg/g).

Soil moisture on the Pumice Plain was highly variable between microsites. Silt contained more moisture than sand; erosion channels were wetter than other sites. Surface soil moisture during July was very low. As elsewhere, substrate nutrients are very low. Phosphorus averaged 380 µg/g, potassium 1380 µg/g and total nitrogen was rarely detectable, though a few swales had values up to 36 µg/g.

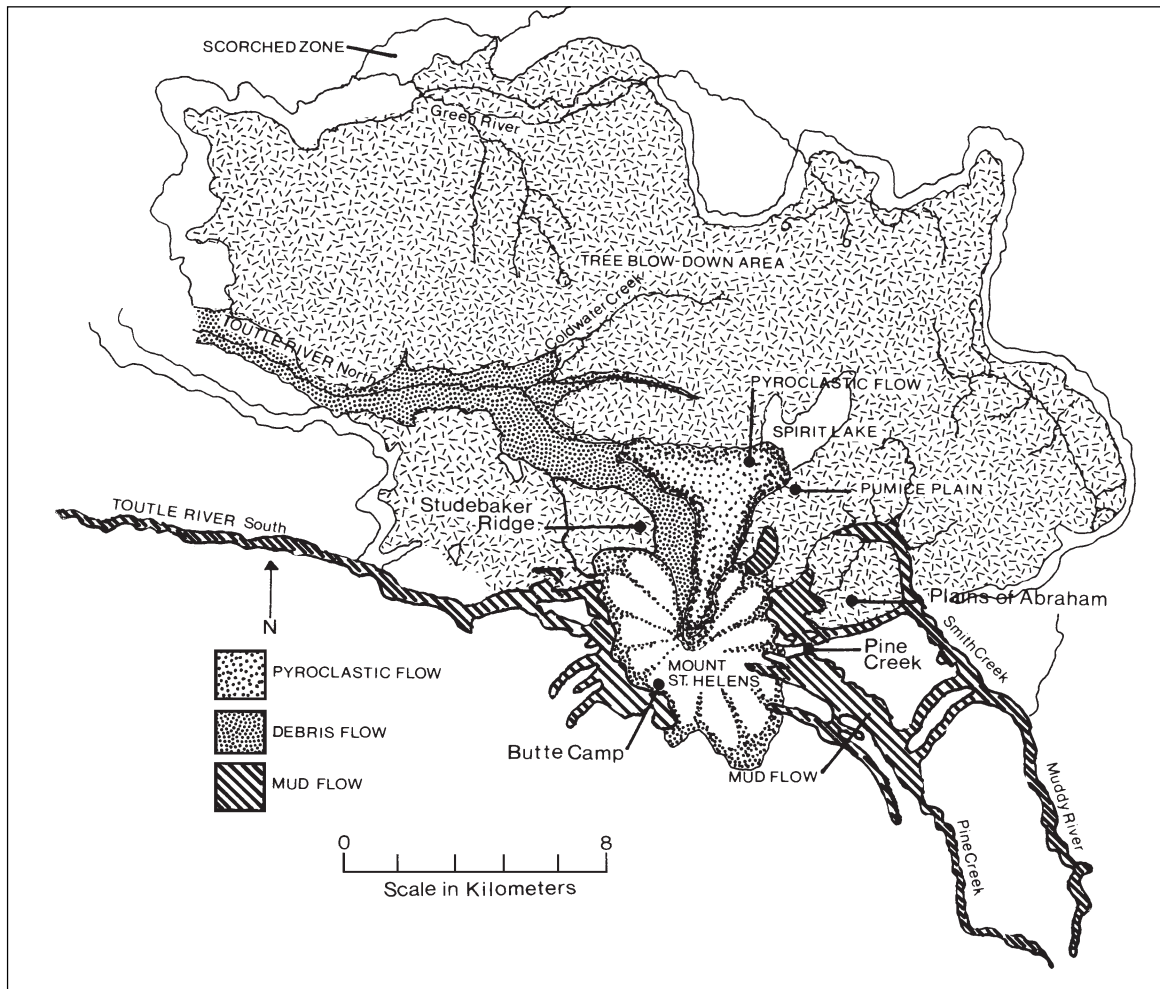


Fig. 1. Mount St. Helens volcanic impact area.

The Plains of Abraham consist of pumice that weathers to a fine sand. Wind removes fine material to form a 'desert pavement'. Areas not eroded by water are nearly smooth, lack sites where seeds might lodge, and dry quickly. July soil moisture is low. Early in the growing season, protected microsites were relatively wet, while exposed ones were much drier. Substrate nutrients were higher than at other sites. Phosphorus averaged 540 $\mu\text{g/g}$, potassium averaged 1750 $\mu\text{g/g}$ and total nitrogen averaged 68 $\mu\text{g/g}$.

Methods

Grids

Several permanent grids were established using protocols to provide a spatially based method to describe developing vegetation (Wood & del Moral 1988). In 1987, a grid of 175 quadrats was established on Lahar

1 and a grid of 317 quadrats on Lahar 2. On the Pumice Plain a grid of 200 quadrats was established in 1989 and on the Plains of Abraham a grid of 400 quadrats. Each grid consists of contiguous, permanently marked 10 m \times 10 m quadrats so that repeated cover estimates can be made. Species cover/abundance was estimated as follows: Class 1 = 1 - 5 plants; 2 = 6 - 20 plants; 3 = > 20 plants, or 0.25 - 0.5 % cover; 4 = < 1 % cover; 5 = 1 - < 2%; 6 = 2 - 4 %; 7 = 5 - 8 %; 8 = 9 - 16 %; 9 = > 16%. Classes 1 - 3 were converted to cover values; class 1 to from 0.063 - 0.153% (depending on species size), class 2 to from 0.09 - 0.20%, and, for smaller species, class 3 to 0.15 % or 0.20%. Higher index scores were converted to the mid-range of the cover value. We analyzed maps of individual species distributions to determine the number of plot clusters, their mean size and the standard error.

Seed traps

Seed traps, 0.1 m² in size, with mesh bottoms over

which fine netting was placed were filled with golf balls to simulate pumice (Edwards 1986a). They were placed in July and collected in October. Seeds were identified and counted.

Microsites

We conducted studies to relate the types and abundance of microsites to the presence of established plants at Plains of Abraham ($n = 1041$), Pumice Plain ($n = 690$) and Lahar 2 ($n = 292$). Quadrats, $1/4 \text{ m}^2$, were placed at 0.5 m intervals along transects within a grid. Each quadrat was scored for its microsite as follows: smooth, rocks twice the size of local pumice, rill edges, drainage courses, and local undulations. If a plant was present, the habitat scored was that of the plant. Otherwise, the least common microsite within the quadrat was recorded. This procedure under-estimates the proportion of smooth habitats and therefore increases the expected frequency in all other types. On the lahars, species microsites were determined in these quadrats. On the Pumice Plain and the Plains of Abraham, the microsites of individual species in the grids were determined.

We used χ^2 tests to determine if any species showed departures from random (Fienberg 1977); the assumption was that species were distributed into the several classes in the same proportion as the habitats occur.

Lupine patch studies

On the Pumice Plain, where lupines form dense, but isolated colonies, we sampled five patches. Randomly located $1/4\text{-m}^2$ quadrats were scored as being barren, containing living lupines, or containing lupine mounds resulting from soil accumulation during the several years that a lupine, now dead, once grew. Simultaneously, each quadrat was scored for the presence of any seedling. Departures from an expectation of random association between seedlings and habitat type were evaluated by χ^2 tests using Pearson's r (Diggle 1983).

Results

Vegetation development on grids

There is a large overlap in species composition between lahars and the adjacent tephra, but vegetation structure differs greatly (Table 1). In 1990, there were 34 species on tephra and 35 on Lahar 2. Eight species from the lahar did not appear in tephra samples, though each of them occurs near the lahar. Spearman's rank correlation between species ranks on tephra and lahar is $r = 0.27$ (n.s.), indicating that structure differed clearly.

Species absent or slow to arrive to the lahar include large-seeded species (*Juniperus communis*), grasses with

Table 1. Species ranks on Butte Camp tephra and an adjacent lahar in 1988 and 1990. Species are in order of their 1988 rank on tephra. RC = relative cover of each species. Lahar data are from a 3.17-ha grid of 100-m^2 plots; tephra data are from ten 250-m^2 permanent plots.

Species	Tephra		Lahar 2	
	1990 RC	Rank	1988 RC	1990 Rank RC
<i>Agrostis diegoensis</i>	30.68	11	2.56	11 2.11
<i>Lupinus lepidus</i>	22.59	2	13.56	2 10.57
<i>Phlox diffusa</i>	7.05			
<i>Polygonum newberryi</i>	5.24	1	31.10	1 49.00
<i>Phyllodoce empetriformis</i>	4.54			30 0.02
<i>Eriogonum pyrolifolium</i>	3.75	5	5.44	5 3.61
<i>Fragaria virginiana</i>	3.69			33 0.01
<i>Achillea millefolium</i>	2.89	24	0.17	23 0.16
<i>Juniperus communis</i>	2.64			
<i>Aster ledophyllus</i>	2.48	4	7.60	6 3.50
<i>Penstemon cardwellii</i>	2.10	3	10.00	3 5.76
<i>Luetkea pectinata</i>	2.01	9	3.43	8 2.93
<i>Juncus parryi</i>	1.83	7	3.65	12 2.00
<i>Pinus contorta</i>	1.52	13	2.07	16 1.01
<i>Carex rossii</i>	1.19	10	2.61	14 1.70
<i>Lomatium martindalei</i>	1.14	17	0.82	21 0.52
<i>Danthonia intermedia</i>	0.98			32 0.01
<i>Sitanion jubatum</i>	0.83	21	0.27	9 2.84
<i>Stipa occidentalis</i>	0.51	18	0.54	18 0.79
<i>Spraguea umbellatum</i>	0.45	14	1.52	13 1.72
<i>Antennaria microphylla</i>	0.40			
<i>Carex phaeocephala</i>	0.31	29	0.11	24 0.16
<i>Castelleja miniata</i>	0.29			
<i>Poa incurva</i>	0.29	28	0.11	27 0.04
<i>Trisetum spicatum</i>	0.17			31 0.01
<i>Agoseris aureus</i>	0.12	25	0.15	29 0.02
<i>Lupinus latifolius</i>	0.11	16	0.92	20 0.56
<i>Hieracium gracile</i>	0.07	12	2.29	17 0.98
<i>Hieracium albiflorum</i>	0.05	15	1.47	15 1.07
<i>Abies lasiocarpa</i>	0.03	6	4.41	7 3.40
<i>Sibbaldia procumbens</i>	0.02			
<i>Festuca occidentalis</i>	0.01			
<i>Vaccinium membranaceum</i>	0.01	30	0.03	35 0.01
<i>Anaphalis margaritacea</i>		8	3.48	10 2.75
<i>Hypochaeris radicata</i>		19	0.43	4 4.01
<i>Epilobium angustifolium</i>		20	0.36	19 0.59
<i>Arnica cordifolia</i>		22	0.24	22 0.16
<i>Salix commutata</i>		23	0.22	25 0.12
<i>Epilobium alpinum</i>		26	0.15	28 0.03
<i>Luzula piperi</i>		27	0.12	26 0.08
<i>Juncus mertensiana</i>				34 0.01
Mean absolute cover	46.88		1.83	3.88

poor dispersal (*Festuca occidentalis*, *Danthonia intermedia*, *Trisetum spicatum*), the hemiparasite *Castelleja miniata*, and species that lack specialized dispersal mechanisms (*Phlox diffusa*, *Phyllodoce empetriformis*, *Sibbaldia procumbens*). *Fragaria virginiana*, a bird-dispersed species of open, dry sites, occurred only once.

Between 1988 and 1990, major changes on lahars include the expansion of *Hypochaeris radicata*, *Sitanion jubatum* and *Epilobium angustifolium*, and the decline

Table 2. Five leading dominants in each study area.

Species	Tephra	Lahar	Pumice	Abraham
<i>Agrostis diegoensis</i>	1			5
<i>Anaphalis margaritacea</i>			1	1
<i>Epilobium angustifolium</i>			2	2
<i>Eriogonum pyrolifolium</i>		5		
<i>Hieracium albiflorum</i>			3	4
<i>Hypochaeris radicata</i>		4	4	3
<i>Lupinus lepidus</i>	2	2		
<i>Penstemon cardwellii</i>		3		
<i>Phlox diffusa</i>	3			
<i>Polygonum newberryi</i>	4	1		
<i>Phyllodoce empetriformis</i>	5			
<i>Saxifraga ferruginea</i>			5	

of *Juncus parryi* and *Carex rossii*. *Hypochaeris* and *Epilobium* are major invaders of barren substrates elsewhere on Mount St. Helens. Here, they invaded only after physical amelioration and facilitation by species such as *Lupinus lepidus*, *Luetkea pectinata*, *Penstemon cardwellii* and *Polygonum newberryi*.

Table 2 compares the leading dominants on each substrate. Lahar vegetation differs from tephra vegetation, yet it is clearly derived from it. *Lupinus lepidus* is lacking in the other sites, dominated by wind-dispersed species. Species abundant in seed traps, notably *Epilobium* spp., *Anaphalis margaritacea* and *Hypochaeris radicata*, are most abundant in isolated habitats.

Community characteristics

Table 3 summarizes structural characteristics on the grids between 1987 and 1991. Richness continues to increase on Lahar 1, but appears to be more stable on other sites. Of greater interest is that the mean species richness has increased significantly between each sample date on all grids. Species already on a grid expand ($P < 0.001$, paired t -tests). Expansion of established species accounts for most species richness increases on the grids since completely new species are always very rare.

The cover conversions permit a better comparison among the grids and to the permanent plots than does the index. Lahar 1 has the highest cover of any primary surface. It is surrounded by intact herbaceous vegetation. Small, intact areas of *Abies lasiocarpa* and *Pinus contorta* are common adjacent to this lahar and the seed rain is large. The substrate is composed of reworked material. Lahar 2 is more isolated than Lahar 1, but its mean cover is only slightly lower.

Plant cover on the Pumice Plain and the Plains of Abraham is scant, though now increasing appreciably. On the Pumice Plain, mean cover tripled in three years and its increase is accelerating. On the Plains of Abraham, cover has increased significantly. For example, only 28.5 % of the plots on the Plains of Abraham had any

Table 3. Mean richness and calculated cover in grids. Lahar 1 is adjacent to intact vegetation; Lahar 2 is more isolated. The Pumice Plain and Plains of Abraham grids are isolated.

	1987	1988	1989	1990	1991
Lahar 1 (n = 175)					
Total richness	31	35	35	-	43
Mean cover (%)	0.95	1.86*	1.97	2.69*	-
Mean richness	8.40	9.75*	11.27*	-	12.86*
Mean cover (%)	1.57	2.69*	3.22*	-	4.05*
Lahar 2 (n = 317)					
Total richness	31	33	35	37	-
Mean richness	7.23	10.05*	11.91*	12.58*	-
Mean cover (%)	0.95	1.86*	1.97	2.69*	-
Plains of Abraham (n = 400)					
Total richness	-	24	29	33	33
Mean richness	-	0.44	1.25*	2.35*	3.67*
Mean cover (%)	-	0.04	0.12*	0.23*	0.34*
Pumice Plain (n = 200)					
Total richness	-	-	38	35	38
Mean richness	-	-	4.45	6.09*	6.84*
Mean cover (%)	-	-	0.54	0.71*	1.44*
Tephra (10 250-m² permanent plots)					
Total richness	34	34	34	34	34
Mean richness	18.9	18.0	21.5	20.0	20.5
Mean cover (%)	38.9	35.8	44.6	46.4	40.1

* = significantly different from previous year (Paired t -test, $P < 0.05$).

plants in 1988. By 1991, 98.75 % had been colonized.

On each grid, an analysis of individual plots in a time series shows either stable or increasing values. In each case, pair-wise comparisons of richness and cover have shown highly significant increases between years. There is no significant local loss from individual plots. Once a species becomes established, it remains, though its spread and reproduction may be delayed. Plots with plants in the previous year tend to develop more rapidly than those with no plants in the initial sampling year. This is particularly true of the Plains of Abraham.

Geography of population expansion

An important measure of population dynamics is spatial expansion. For species with limited dispersal, it is likely that expansion within a grid results from seeds produced by plants in the immediate neighborhood rather than from outside the grid. Even for readily dispersed species, a few local flowering individuals can contribute more seeds within 10 m than large but distant populations. To quantify expansion characteristics, we determined spatial clusters for each species. In theory, the number of clusters for a species that is expanding due to immigration from external sources will increase, but the mean cluster size will not increase significantly. In contrast, the number of clusters of a species that is growing from a few founder individuals should increase slowly, but the mean cluster size should increase rapidly.

Table 4 shows mean cluster size for moderately common species on Lahar 2 and the Plains of Abraham. Cluster size on Lahar 2 increased greatly. This condition holds both for well-dispersed species and for relatively poorly dispersed ones. All species growing on the Plains of Abraham, except *Anaphalis margaritacea*, show a pattern of geographic spread that is consistent with population dynamics being controlled from outside the grid.

Several species serve to exemplify patterns of geographic expansion and the likely sources of recruits. On Lahar 2, *Anaphalis* has spread rapidly to increase its relative share of cover, but fewer than 10% of the plots have flowering individuals. It has behaved similarly on the Plains of Abraham where it is both the leading dominant and a true pioneer. The few flowering plants of this species are unlikely to account for much recruitment in either location.

In contrast, *Spraguea umbellata* is a species with limited dispersal ability. On both substrates its expansion appears to be from local seed sources, though its development has barely begun on the Plains of Abraham. *Hieracium albiflorum* on the lahar has established a reproductive population that occurs in a few large clusters. Most new plants probably derived from individuals on the lahar. In contrast, at the Plains of Abraham, *Hieracium* occurs as many very small clusters, probably derived from well beyond the grid.

Epilobium angustifolium remains uncommon on the lahar, possibly due to competition. On the Plains of Abraham, it is widespread, forming many small clusters. This pattern and the fact that only four plants of this species have ever flowered on the grid, imply that most new recruits were produced elsewhere. Considering its high dispersal ability, the colonization of *Hypochaeris* was significantly delayed on the Plains of Abraham. Cluster size remained small in 1991, and few plants had flowered. However, due to its wide-spread distribution and because 60% of its occurrences include some flowering individuals, this species appears to be in transition. It appears that most recruitment soon will be from plants growing on or near the grid.

Populations begin a colonization in a microsite capable of trapping a seed. In a few species, such as *Lupinus lepidus*, initial colonists mature rapidly and produce viable seeds. The colony grows quickly and expands into surrounding quadrats. Such a pattern is common on the Butte Camp lahars where a variety of species soon invaded. On barren and isolated habitats, that pattern is rare. Species such as *Epilobium angustifolium*, *Anaphalis margaritacea* and *Hypochaeris radicata* establish only in extraordinarily favorable microsites after several years of failure. Conditions near most reproductively successful individuals remain unsuitable to colonization. As a result, few seeds are produced locally and most new

Table 4. Cluster statistics for Lahar 2, 1987 and 1990; and the Plains of Abraham, 1988 and 1990. Mean = average number of 100-m² plots in the cluster; SD = standard deviation of cluster size; N = number of clusters.

Species	Lahar 2					
	1988			1990		
	Mean	SD	N	Mean	SD	N
<i>Agrostis diegoensis</i>	3.09	4.48	34	29.54	33.89	7
<i>Anaphalis margaritacea</i>	5.00	11.24	26	82.67	140.60	3
<i>Aster ledophyllus</i>	4.30	9.48	30	78.00	129.00	3
<i>Carex rossii</i>	4.41	6.44	27	24.50	63.26	8
<i>Hieracium albiflorum</i>	2.39	1.89	36	36.17	69.54	6
<i>Hieracium gracile</i>	1.41	0.83	42	15.25	35.00	12
<i>Lomatium martindalei</i>	1.70	1.06	10	3.38	5.75	16
<i>Spraguea umbellata</i>	2.00	2.53	25	16.23	31.79	13

Species	Plains of Abraham					
	1988			1990		
	Mean	SD	N	Mean	SD	N
<i>Abies lasiocarpa</i>	1.41	0.87	17	1.67	1.94	21
<i>Agrostis diegoensis</i>	1.00	-	1	1.83	1.37	29
<i>Anaphalis margaritacea</i>	4.54	3.93	13	81.7	160.2	4
<i>Epilobium angustifolium</i>	1.00	0.00	7	2.76	3.99	36
<i>Hieracium albiflorum</i>	1.20	0.45	5	2.04	2.43	50
<i>Hypochaeris radicata</i>	-	-	-	2.47	2.97	45
<i>Juncus parryi</i>	-	-	-	1.20	0.41	15
<i>Penstemon cardwellii</i>	1.00	-	1	1.58	1.71	18
<i>Spraguea umbellata</i>	1.00	-	1	1.50	1.10	16

colonists of isolated habitats continue to be derived from the general seed rain.

Dispersal mechanisms

Inferences about colonization mechanisms derived from grids

Primary succession on isolated sites is dominated by wind-dispersed species. On the lahars, a wider variety of species are early pioneers. Of 24 species growing in lahar permanent plots, 15 are clearly wind-dispersed and the four grasses are probably wind-dispersed. However, five large-seeded species account for a disproportionate share of cover. This suggests that once large-seeded species do arrive, their survivorship is higher than wind-dispersed species and they quickly dominate a site. Grasses and these large-seeded species dominate stable herbaceous vegetation on adjacent tephra sites. Cover on the Plains of Abraham includes from 92-94% wind-dispersed species, compared to 70-72% on this lahar. The Plains of Abraham lack significant contributions of *Lupinus* spp., *Lomatium martindalei* and *Eriogonum pyrolifolium*. Vegetation development on the Plains of Abraham will necessarily differ from that of the lahars as a result of variable distances to sources of colonists. On the lahars, wind-dispersed species form a

smaller portion of the vegetation than they do in more isolated sites. Many relatively poorly dispersed species reached the lahars and, being better able to tolerate early stressful conditions, became dominant. It is uncertain whether these differences will persist or whether the vegetation of these sites will converge as a result of the eventual colonization of poorly dispersed species.

Seed traps

From 1983 to 1986, seed trap data were collected and analyzed by Wood (1987; Wood & Morris 1990; Wood et al. unpubl.). Subsequently, 125 traps were installed on the lahars, Pumice Plain and Plains of Abraham. The proportions of seeds collected in 1989 confirm that wind-dispersed species are the major invaders of isolated sites (Table 5). Nearly all seeds trapped in isolated sites were composites or *Epilobium* species. These species are poorly adapted to establishment in the early phases of succession at higher elevation, and they serve as prime examples of the fact that the best dispersing species do not colonize effectively under stressful conditions (Wood & del Moral 1987). On the lahars, there was a wider assortment of seeds collected, including several unknowns. This reflects the presence on lahars of many seed-bearing species and the proximity of mature vegetation (cf. Table 1).

Facilitation

Site manipulation

Direct evidence about amelioration requirements is available from surface manipulation studies. In 1989, we established factorial experiments in four locations. Surface cultivation, nutrients, the addition of an inert, organic mulch and seed trapping ability (by adding small rocks) were altered. This study will be described fully elsewhere. Preliminary results for the Pumice Plain

are typical. Mulch is the single most important factor. It increased the number of naturally occurring seedlings to 37/m², compared to fewer than 1/m² in controls. Nutrient addition had limited effects on numbers, but surviving seedlings were robust. Results on lahars, pyroclastic surfaces and the Plains of Abraham were similar.

Safe-sites

Harper (1977) described the safe-site concept, which is well exemplified on Mount St. Helens. Initially, no site can harbor successful seedlings. Seedlings were lacking on lahars in 1980 and 1981. None was observed on the Pumice Plain until 1983 and the Plains of Abraham was virtually devoid of plants in 1987. Physical amelioration must occur (del Moral & Clappitt 1985; del Moral & Wood 1986; Edwards 1986b, 1988) before colonization can commence. The landscape slowly differentiates as some microsites become more favorable due to erosion, weathering and nutrient inputs via wind and rain. Seedling survival is determined by those surface characteristics that affect moisture.

The relationship between seedling establishment and microsite types was determined by describing the pattern of joint occurrences between seedlings and microsite types. Patterns are most pronounced on the Plains of Abraham. All species avoid smooth surfaces and favor rocks to varying degrees. Seedlings are also disproportionately common in undulations and generally absent from drainages. Rill edges are favored by most species, particularly by *Hypochaeris*. Those few seedlings found in smooth, exposed habitats are invariably young or stunted.

On the Pumice Plain, the pattern is similar, but less pronounced. Rocks, rill edges and undulations support nearly all seedlings.

The patterns on Lahar 2 are weak. Species occur only slightly less frequently in smooth habitats than would be expected by chance, and only slightly more often in rocky sites. Drainages are avoided by all species. After ten years, the relationship between individuals and microsites has been weakened and most available surfaces are now suitable for seedling establishment.

Lupine patch effects

Lupines on the Pumice Plain are either very rare or occur sporadically in dense patches. Individuals may live up to five years. When they die, they leave behind a legacy of accumulated fine soil particles. Such mounds are enriched in organic matter, nitrogen and water-holding capacity. Table 6 shows the relationship between seedling colonizations of exposed habitats and living or dead lupines in one of five similar trials. Each species was much more likely to establish on a mound formerly occupied by a lupine than either exposed loca-

Table 5. Seed trap data for selected sites, 1989.

Species	Percent of Sample			
	Lahar (n = 32)	Pumice Plain (n = 37)	Plains of Abraham (n = 32)	Lupine Patch (n = 16)
<i>Anaphalis margaritacea</i>	18.53	36.67	7.21	18.05
<i>Carex</i> spp.	-	0.10	0.90	0.07
<i>Epilobium</i> spp.	44.87	30.99	60.81	41.61
<i>Hieracium albiflorum</i>	1.92	2.02	1.35	1.13
<i>H. gracile</i>	1.92	-	-	0.07
<i>Hypochaeris radicata</i>	3.21	11.45	16.67	8.23
<i>Lupinus lepidus</i>	4.49	4.33	-	28.60
<i>Polygonum newberryi</i>	7.69	-	-	-
<i>Spraguea umbellata</i>	8.33	-	-	-
Other Asteraceae	3.21	2.02	3.15	-

tions or beneath a living lupine. For example, of the 42 *Anaphalis*, 34 occurred near mounds lacking lupines and only five were near living lupines. Put another way, 52% of mounds, but only 4.3% of lupines had associated *Anaphalis*. A primary beneficiary of facilitation is the introduced species *Hypochoeris radicata*. Several former lupine patches are now dominated by this weed.

Though locally abundant on the Pumice Plain, lupines play little role in the development of vegetation in the devastated habitats of this region. They are most abundant on the pyroclastic surfaces and lahars and only scattered where pumice prevails. Where lupines are abundant, their facilitative role is frequently delayed until the individual dies.

Discussion

On barren substrates, where facilitation has been postulated to be significant, most seedlings establish only in favorable microsites, not under the influence of pioneers. Chance and amelioration strongly influence early successional patterns (cf. Walker & Chapin 1987).

Chance

Chance influenced primary succession in many ways. The eruption occurred when the study area was buried by snow. This simple fact was a major determinant of survival for both plants and animals (Halpern et al. 1990). A summer eruption would have been far more devastating. Del Moral & Bliss (in press) discuss numerous other instances of unpredictable events that have influenced vegetation recovery. These include unusually wet, followed by unusually dry summers, the fortuitous establishment of lupines on the Pumice Plain and the creation of literal oases by snow blocks entrained in the pyroclastic deposit.

Dispersal

On Mount St. Helens, colonization is diffuse because initial colonists are confined to scattered safe-sites (Wood & del Moral 1987) and the seed rain is sparse. The initial population density of any species is very low and the odds against establishment by a particular seed are staggering. Nonetheless, species richness increases relatively rapidly, even if cover remains low. Most safe-sites appear empty despite more than a decade of seed rain.

In isolated habitats, succession is qualitatively distinct from habitats near intact vegetation. Once a plant sets seed, it eventually becomes the greatest contributor to the local seed rain. As a result, new individuals on

Table 6. Seedling recruitment in a lupine patch on the Pumice Plains. ($N = 250$ 1/4-m² quadrats.)

Species	Microsites		
	Lupine-Alive	Lupine-Dead	Barren
<i>Anaphalis margaritacea</i>	$(\chi^2 = 66; P < 0.0001)$		
Observed	5	34	3
Expected	20	11	10
<i>Epilobium angustifolium</i>	$(\chi^2 = 88; P < 0.0001)$		
Observed	1	39	2
Expected	19	11	12
<i>Hypochoeris radicata</i>	$(\chi^2 = 100; P < 0.0001)$		
Observed	5	34	3
Expected	20	11	10

lahars tend to cluster around mature plants (Wood & del Moral 1987). Tendencies towards clustering on the Plains of Abraham and Pumice Plain are weak. Population expansion patterns on grids imply that establishment is most likely to occur near adults if most of them have produced seeds. On Lahar 2, cluster size has increased for most species and cover on previously occupied sites has increased significantly, consistent with a model of local regeneration. On the Plains of Abraham, clusters of most species remain small and there has been little annual cover increments within each quadrat. This is consistent with a model of continued recruitment from beyond the grid.

Amelioration

Amelioration begins to condition newly created substrates well before the first seed lands. Timmins (1983) reported that erosion on Mount Tarawera (New Zealand) formed gullies within which vegetation first established. Kadomura, Imkagawa & Yamamoto (1983) demonstrated how erosion enhanced recovery rates on Mount Usu (Japan). On Mount St. Helens, wind, then water, removed enormous quantities of loose material from unstable surfaces. Small rills were formed on gentle slopes even by light summer rain. Heavier erosion by snow-melt water and heavy rains in many places removed all newly deposited material to expose the original substrate. The resurgence of residual plants resulted in relatively rapid recovery, as for example on Pine Creek Ridge (del Moral & Wood 1988).

Frost-induced cracking of rocks creates a mosaic of microhabitats with differential capabilities to support seedlings. Wind concentrates fine particles in cracks, enhancing these sites. Seeds are trapped beneath rocks where shade and reduced wind significantly reduce drought stress.

Frequently overlooked is the dry deposition of dust, insects, pollen and seeds that are incorporated into a barren substrate (Edwards 1986b). Significant amounts of carbon and nitrogen accumulate, eventually providing sufficient nutrients to support seedlings.

Pioneers and climax species

We have shown that seed size was directly related to establishment ability and inversely related to dispersal ability in these subalpine species (Wood & del Moral 1987). Where intact vegetation is near and dispersal barriers minor, tolerant climax species behave like pioneers. We also concluded that primary succession is retarded by the paucity of species reaching and tolerating severe conditions.

Under stressful conditions, pioneers need not be 'ruderal' (Grime 1977) or *r*-selected (MacArthur & Wilson 1967). Stress-tolerant species can be effective pioneers. They have relatively large seeds and therefore rarely are the first to reach newly created habitats. Typical pioneers effectively exploit newly created habitats if resources are relatively abundant. Conditions on new volcanic substrates are infertile and often xeric. Where tolerant species are precluded by dispersal barriers, lengthy periods of amelioration (cf. Finegan 1984) must occur before vagrant species can establish.

Facilitation

Facilitation includes symbiotic nitrogen fixation, trapping soil and seeds and organic matter accumulation. Facilitation by nurse plants is recognized to be an important controlling factor in primary succession (Harris et al. 1984). Less well recognized is that established plants often inhibit immigrants (Morris & Wood 1989; Franco & Nobel 1989).

Nurse plants are typically considered to be beneficial to seedling establishment (Day & Wright 1989; Garcia-Moya & McKell 1970). Others noted explicitly that nurse plants also may have negative effects (Yeaton 1978; Yeaton & Romero-Manzanares 1986; Franco & Nobel 1989; Valiente-Banuet, Vite & Zavala-Hurtado 1991). Vitousek et al. (1987) and Walker & Vitousek (1991) demonstrate that the nitrogen-fixing *Myrica faya* deflects and inhibits succession and does not facilitate other woody species.

Intergenerational effects help to determine the spatial mosaic (Louda & Renaud 1991). Under experimental conditions, Bergelson (1990) found that *Poa annua* inhibited seedlings of *Senecio vulgaris* and *Capsella bursa-pastoris* after *Poa* had died. Our field study may be the first to show between-generation spatial effects of one species on another and on its own seedlings.

Lupinus lepidus plays a dramatic role on Mount St. Helens. Early observations of lupine colonies on the Pumice Plain emphasized the facilitative effects of lupines. Halvorson et al. (1991, 1992) studied nitrification in these lupine populations and determined that they only made significant local contributions to soil nitrogen. Morris & Wood (1989) demonstrated that locally improved growing conditions were outweighed by the competitive effects of lupines. Our studies have demonstrated that where lupines occur, they significantly influence the pattern of subsequent generations.

Factors that influence primary succession are many and complex. They cannot easily be categorized into the three Connell & Slayter (1977) models, facilitation, tolerance and inhibition, because each consists of numerous and overlapping specific mechanisms (Walker & Chapin 1987). The relative importance succession mechanisms in different communities at various successional stages has been studied intensively since 1977 (e.g. Hils & Vankat 1982; del Moral 1985; Walker & Chapin 1986). Our findings generally agree with the framework proposed by Walker & Chapin (1987), though details differ. They suggest that primary succession in severe environments should be dominated by seed arrival, stochastic events, facilitation and mycorrhizae. On Mount St. Helens facilitation has as yet only been locally important. Its usual role is replaced by amelioration processes. Mycorrhizae are also of limited and, at most, local importance (Allen 1987; J. H. Titus unpubl.). In accordance the Walker & Chapin framework, competition, rapid growth rates and herbivory are minor factors that control primary succession on Mount St. Helens.

Succession rate

Primary succession on barren, high elevation substrates on Mount St. Helens has been slow due to a combination of these factors: chronic erosion, the low stress-tolerance of well-dispersed species, the poor dispersal of stress-tolerant species, limited soil nutrients and chronic soil surface drought. On Surtsey, colonization was even slower (Fridriksson 1987). After ten years, only 10 species and 1319 vascular plants occupied 2.7 km², and after over 20 yr, only 13 species occurred, though *Honkenya peploides* was common. Total cover was about 1% of the island. On Surtsey, dispersal barriers are large, the growing season is short, the substrate is unstable, nutrient poor and xeric and erosion severe.

Less severe colonization conditions were described by Rejmánek, Haagerova & Haager (1982, based in part on Egger 1963) for El Parícutin, Mexico. After 25 yr, they found 39 vascular plant species and distinctive

stages of succession on different substrates. Based on species accumulation, succession has been relatively rapid. The cinder cone was neither large nor isolated. Environmental conditions are far less severe on Parícutin than on Surtsey. Tsuyuzaki (1989, 1991) followed recovery on Mount Usu under conditions similar to Mount St. Helens. Species turn-over has been relatively high, but species richness after a decade had equilibrated in the studied plots. Cover is developing relatively rapidly. There were some survivors on Mount Usu and the situation there most closely resembles the situation on the scoured ridge at Pine Creek (del Moral & Bliss 1993). Richness is increasing slowly, cover is increasing relatively quickly.

Invasion rates on the tropical Krakatau Islands are considerably higher than on Mount St. Helens in absolute terms, but probably not when considered in terms of the locally available flora (Whittaker, Bush & Richards 1989). The rate of succession on primary substrates on Mount St. Helens varies with the landscape situation of each site and generally fall between the extremes demonstrated by Surtsey and Parícutin. Total species richness on lahars, composed of reworked substrates and adjacent to intact vegetation, has increased to 43 vascular plant species by 1991, with cover of about 4%. In contrast, the Plains of Abraham had 33 species (of which 14 occurred $< 4 \times$ in 400 100-m² quadrats) and cover was estimated at 0.3 % (del Moral & Bliss in press). As conditions are ameliorated by physical processes and as biomass increases, the development vegetation will accelerate on each substrate.

Conclusions

Traditional succession concepts relate primarily to what occurs. Our observations and experiments emphasize that what occurs is not mandatory and that succession mechanisms cannot be inferred solely from observations of species replacements. Landscape context and differing amelioration rates are two determinants of primary succession that are frequently overlooked. Direct studies of plant colonizations on volcanoes have contributed substantially to both specific and general understanding of primary succession. As detailed mechanistic understanding of primary succession is accumulated by direct field and laboratory studies, general principles derived either from transect studies or from descriptions of arrival sequences often have been shown to be too simple.

Stochastic and rare events play a greater role in determining the initial development of devastated landscapes than has been generally realized. We find no evidence that biological events (e.g. competition) will

overcome early serendipity. Chance and history reduce the degree to which species patterns can be interpreted by descriptive methods.

Isolation restricts the species pool. Several lines of evidence indicate that even short distances combined with hostile substrates are barriers to establishment. Most established plants exist as a result of the sequential occurrence of low-probability events. Thus the initial distribution of individuals on the landscape may appear chaotic, even where most plants are associated with discrete microsites. Seedlings of each species combine a unique combination of tolerances and abilities that permit them to establish only under restricted conditions. Since characteristics of each species overlap, a given microsite might suite several species and the one that actually occurs could well be determined by arrival priority (cf. Shmida & Ellner 1984). There are many suitable empty microsites, from which we conclude that there is a paucity of immigrants, that their chance of encountering a favorable microsite is low and that few of those seeds that do encounter favorable microsites become established.

The literature says little about the importance of amelioration, though examples are common. On Mount St. Helens, amelioration must occur before any pioneer becomes established. In this system, physical processes may have substituted for functions such as surface stabilization and nitrification frequently attributed to lower plants in other systems (cf. Rayburn, Mack & Metting 1982).

Facilitation is restricted during early primary succession on Mount St. Helens. The effects of a potential nurse plant are usually out-weighted by its competitive effects. The balance between facilitation and inhibition by a single species is delicate and varies by species combination, relative densities and resource levels. We believe that delayed nurse plant effects may be more common than previously realized and that population structures frequently have strong historical components.

Primary succession remains relatively slow in isolated habitats of Mount St. Helens. This results from limited dispersal, low tolerance of colonizing species, severe environmental conditions and a balance between facilitation and inhibition that rarely promotes seedling establishment.

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