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[CE1]

Proximity, Microsites, and Biotic Interactions During Early Succession

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7.1 Introduction

Our studies of succession on mudflows and pumice surfaces at Mount St. Helens support the view that plant succession is determined as much by chance and landscape context as by the characteristics of the site itself. Early primary succession is dominated by the probabilistic assembly of species, not by repeatable deterministic mechanisms. Before most plant immigrants can establish, some physical amelioration in the form of nutrient inputs or the creation of microsites may occur. As vegetation matures, there is a shift from amelioration to inhibition (Wilson 1999), but the magnitude of this shift varies in space and time. Species-establishment order is not preordained as stated by classic succession models (Clements 1916; Eriksson and Eriksson 1998). Life-history traits influence both arrival probability and establishment success, and the best dispersers are usually less adept at establishment. Therefore, interactions between site amelioration and proximity to colonists affect the arrival sequence and initial biodiversity. Unique disturbance events combine with usually low colonization probabilities to produce different species assemblages after each disturbance at a site. Early in primary succession, individuals just accumulate. However, over time, interactions begin that cause species to be replaced. Here we describe how a few struggling colonists slowly developed into pioneer communities (see Tsuyuzaki et al. 1997) and suggest how these communities may develop further.

7.1.1 Background

Until 1983, we focused on sites that had some survivors, for example, tephra-impacted and scoured sites at Butte Camp [CE2] and Pine Creek (del Moral 1983, 1998). Descriptive efforts were gradually supplemented with experiments (Wood and del Moral 1987; Wood and Morris 1990; del Moral 1993; del Moral and Wood 1993a,b; Tsuyuzaki and Titus 1996; Titus and del Moral 1998b) as primary succession became our focus. Our first studies of primary succession on Mount St. Helens documented plant establishment on mudflows at Butte Camp. Subsequently, we focused on the Pumice Plain to explore surface heterogeneity (Wood 1987; Titus and del Moral 1998a; Tsuyuzaki et al. 1997), spatial patterns (Wood and del Moral 1988; del Moral 1993, 1998, 1999a; del Moral and Jones 2002), wetlands (Titus et al. 1999), and system predictability after disturbance (del Moral 1999b). This chapter provides an overview of early vegetation development on mudflow and pumice surfaces after 23 growing seasons at Mount St. Helens. These studies have modified and illuminated our understanding of primary succession. [See Walker and del Moral (2003) for a broad discussion of primary succession.]

Our view of primary succession is summarized in Figure 7.1. This perspective can be explained by considering vegetation life histories and strategies in isolated, barren habitats that were common immediately north of Mount St. Helens. Isolation from vegetation that survived the worst of the eruption's effects implies that most immigrating species were those with able wind dispersal. Mudflows that were near habitats with limited disturbance received many stress-tolerant species with poor dispersal in addition to the wind-dispersed species. Thus, the degree of isolation affected the types of species found in the first wave of colonists. The first successful immigrants established because of physical amelioration of the substrate and the presence of especially favorable microsites [*safe sites* (Harper 1977; del Moral and Wood 1988a)]. At first, there were few safe sites, but physical processes such as rill formation, rock fracturing, and freeze-thawing created more. Colonists eventually produced seeds, so local dispersal became possible. As more species established and populations became denser, biological effects created other types of safe sites, modified existing ones, or caused them to disappear entirely. Biological amelioration (facilitation) permits other species to invade the primary-successional landscapes, for example, in the shade or in litter. Established individuals can grow more robust and reproduce because of improved substrate conditions (fertility and water-holding capacity) or decreased exposure. In the future, we expect some species to fail because they cannot reproduce in the emerging environment, whereas others will be eliminated by competition (Aarssen and Epp 1990; del Moral and

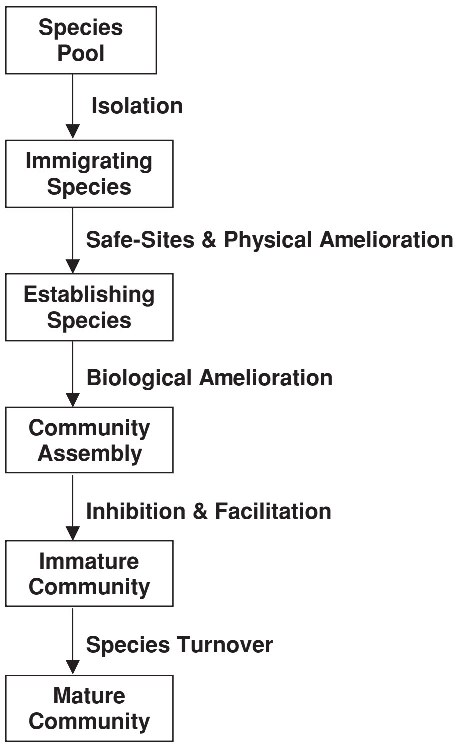

FIGURE 7.1. General model of primary succession at Mount St. Helens. Isolation is a sieve that permits only some species to reach a site. Of these immigrants, only those that find a particularly favorable safe site can establish; physical amelioration gradually improves the probability of seedling success, widens the spectrum of species able to establish, and improves the production of established plants; biological amelioration occurs as the biota modifies microhabitats; and a community of species gradually assembles. During assembly, individuals may inhibit others through competition or they may facilitate the success of other plants, thus leading to a dynamically changing community. Species turnover leads to a mature community that may have little in common with the initial vegetation on the site.

Grishin 1999). The net result is species *turnover*, one way to recognize succession. In our studies, we have observed little turnover, although shifts in the relative abundance of many species have occurred. Thus, as communities assemble, biotic interactions intensify, but only species well adapted to the new conditions thrive (Callaway and Walker 1997; Weiher and Keddy 1995). Notably, species that establish early by chance often persist even though they are not competitively superior. They can exclude seedlings of better-adapted species by control of the “space” resource [a *priority effect* (Drake 1991; Malanson and Butler 1991)]. For example, on wetland margins, where well-developed primary vegetation exists, upland species such as pearly everlasting (*Anaphalis margaritacea*) appear to exclude wetland species by virtue of the prior establishment. It will eventually be excluded, in all likelihood, only when tall shrubs dominate these margins. Thus, on mudflows and pumice surfaces at Mount St. Helens, as in many other primary-successional environments, vegetation heterogeneity was initiated by chance and may persist (Glenn-Lewin 1980; Mathews 1992; Savage et al. 2000).

7.1.2 Questions

Several questions sharpened the focus of our studies. Landscape ecologists suggest that the matrix within which a biota develops is crucial to early species accumulation (Kochy and Rydin 1997; Söderström et al. 2001). We first asked: How did isolation from propagule sources affect seed rain and seed availability and thereby the rate of vegetation development? Most early recruits did not flower, so further population growth (as distinguished from vegetative expansion) depended on continued long-distance seed dispersal from other populations. When did seedling recruitment switch from long-distance colonists to seedlings recruited from locally produced seeds?

Vegetation refugia on other volcanoes, such as *kipukas* (Hawaii) or *dagale* (Sicily) that are outcrops isolated by lava flows, can accelerate primary succession by providing adjacent propagule sources adapted to harsh environments. We were interested to determine if surviving vegetation on Mount St. Helens accelerated vegetation development and, if so, what were the mechanisms and extent of these effects?

We asked if the initial effects of chance colonization and of early arrival persist or if strong links between environmental factors and species composition were forged to created similar vegetation over space. We investigated changing statistical correlations between species composition and environmental factors in several habitats through time.

Most of the world is experiencing dramatic biological invasions, so recent disturbances have occurred in novel biological settings (Magnússon et al. 2001). Consequently, we asked if nonnative species could affect the trajectory of early primary succession to create species assemblages never previously observed.

7.1.3 Locations

Our main study sites focused on primary succession are on mudflows on the southwest and east flanks and on the pumice surfaces on the north side of Mount St. Helens (Table 7.1; Figure 7.2). Sites differed in their degree of isolation from potential sources of colonists. At Butte Camp, on the south side of the volcano, meadows and forests recovered quickly from thin tephra deposits (10 to 20 cm thick). However, several mudflows were deposited below the tree line when rapidly melting ice transported a jumble of rocks and mud that lacked any soil or seed bank. A large mudflow on the Muddy River was also studied. Mudflows are usually next to intact vegetation

TABLE 7.1. Study sites used for studies of primary succession.

Site	Disturbance type	Elevation range (m)	Isolation	Type of study	Sampling dates
Mudflow 1	Fine Pumice	1380	Very low	Monitoring: plots	1980–
	Mudflow	1415–	Low	Monitoring: plots	2002
	Mudflow	1430	Low	Monitoring: grid	1982–2002
	Mudflow	1415–1430	Low	Dispersal: seed traps	1987–2001
		1425			1989–1990
Mudflow 2	Mudflow	1430–1460	Low	Monitoring: plots	1982–2002
	Mudflow	1430–1460	Low	Monitoring: grid	1987–2002
	Mudflow	1430–1460	Low	Dispersal: seed traps	1989–1990
Muddy River	Mudflow	790–1140	Low	Survey: convergence	1996
Pumice Plain	Pyroclastic flow	1100–1180	Moderate	Monitoring: grid	1986–1999
	Pyroclastic flow	950–1500	Moderate	Survey: habitats	1993
	Pyroclastic flow	1125	Moderate	Dispersal: seed traps	1982–1986
	Pyroclastic flow	1100	Moderate	Dispersal: seed traps	1989–1990
	Pyroclastic flow	1095	Moderate	Dispersal: seed traps	1989–1990
	Wetlands	950–1350	Moderate	Wetland surveys	1993 & 1999
Eastern Pumice Plain	Coarse pumice	1200	High	Monitoring: grid	1989–2002
				Monitoring: plots	1989–2002
	Coarse pumice	1200–1320	High	Mycorrhizae	1991–1995
	Refugia	1100–1525	High	Landscape effects: relicts	1997–1999
	Depressions	1280–1320	High	Monitoring: similarity	1992–1994; 1997–1998
Studebaker Ridge	Blast on lava: low	1050–1250	High	Monitoring: plots	1984–2002
	Blast on lava: high	1255–1450			1989–2002
Plains of Abraham	Blast, mudflow	1320–1360	Very high	Dispersal: seed traps	1989–1990
				Permanent grid	1988–2001
				Monitoring: plots	1995–2002

Location information is for the center of the study referenced. Sampling date ranges are annual. See Figure 7.2 for map of these locations.

and, therefore, normally have a low degree of isolation. The north face of the cone collapsed spawning a directed blast and searing pyroclastic flows (see Chapter 3, this volume) and forming deep deposits of pulverized materials that have since been eroded (Wood and del Moral 1988). This area, termed the Pumice Plain, was substantially isolated from potential colonists. All plants were killed, except in a few refugia on steep terrain (concentrated in the eastern part of the north slope) that escaped pyroclastic flows. We continue to monitor pumice habitats north and northeast of the crater. On the eastern Pumice Plain, many sites are less exposed to physical stress and are closer to surviving vegetation found in refugia. Wetlands are also developing rapidly across the Pumice Plain. Typical sites were only moderately isolated from potential colonists, usually 1 km. Isolated from intact vegetation on the eastern Pumice Plains are depressions we call "potholes," which formed when snow melted beneath thick pumice deposits to create a few hundred small self-contained depressions (del Moral 1999a). Wetlands and pyroclastic flows have been studied in a variety of ways since the mid-1980s (del Moral et al. 1995; Titus et al. 1999). Studebaker Ridge, on the northwest flank of the cone, received an intense blast during the early stages of the eruption that removed all plants and most soil to reveal old lava rocks. It is exposed and at a higher elevation than the Pumice Plain sites and, therefore, received a limited seed rain. East of the crater, the blast, a massive mudflow, and pumice deposits impacted the Plains of Abraham, and that area continues to be isolated from colonists by a ridge and the prevailing winds.

7.2 Methods

7.2.1 Permanent Plots

Permanent plots are located in four areas and provide the opportunity to nondestructively monitor vegetation through time (Table 7.1). Starting in 1980, these 250-m^2 circular plots (18 m in diameter) were sampled. The area of the vertical projection of the canopy of each species within a subplot is called percent cover. Percent cover was determined at the same 24 places each year with 0.25-m^2 subplots (del Moral 2000b). From these data, the total number of species (richness), mean percent cover of the plot, and other structural features were calculated (McCune and Mefford 1999). We compared changes in species richness in the same plot over time by employing repeated-measures analysis of variance with Bonferroni comparisons of the means (Analytical Software 2000).

We also sampled species richness, cover, evenness, diversity, and vegetation pattern in permanent grids formed of contiguous

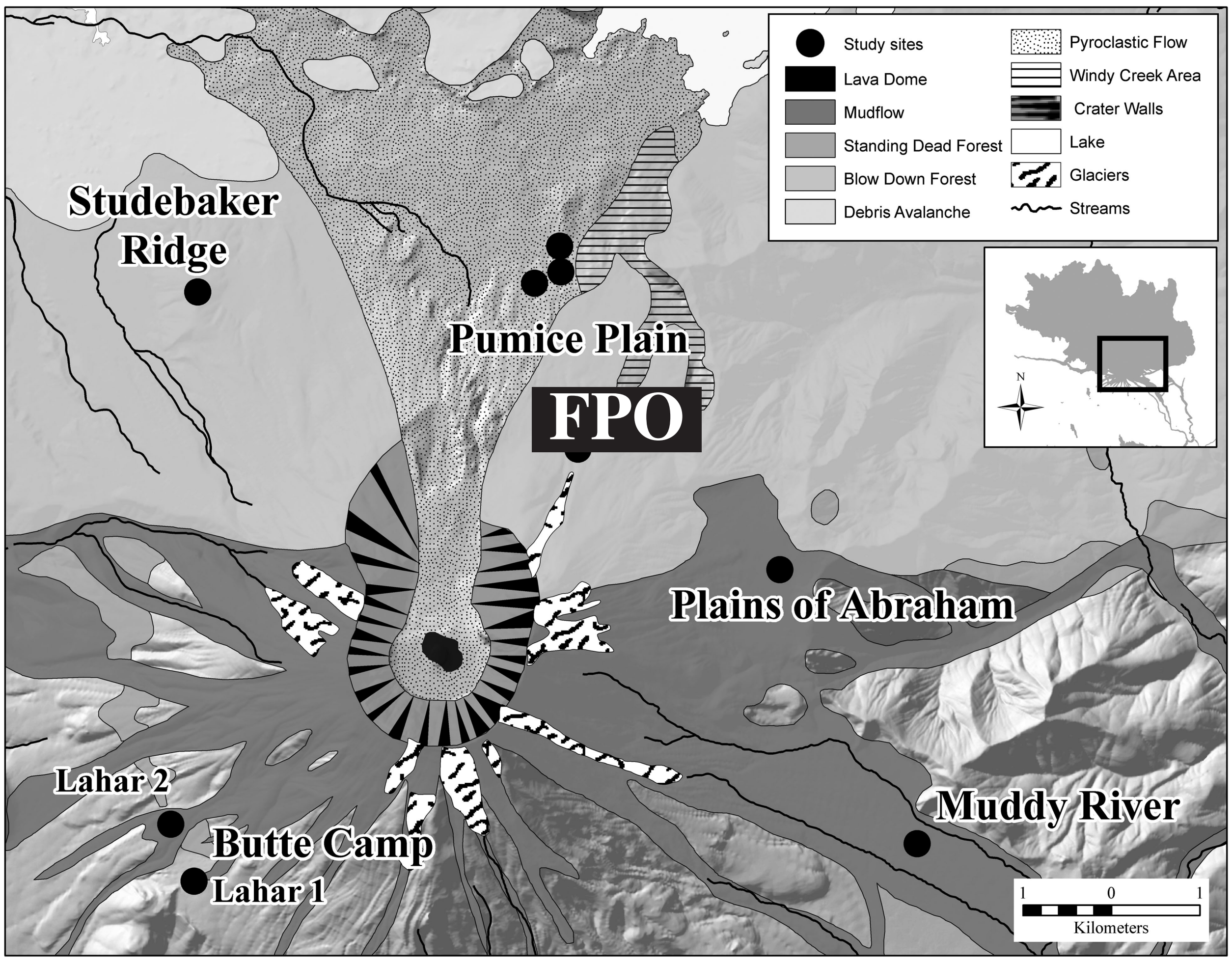

FIGURE 7.2. Location of study sites on north side of Mount St. Helens.

10- by 10-m plots sampled with this cover-unit scale (Wood and del Moral 1988):

1. 1 to 5 plants
2. 6 to 20 plants
3. More than 20 plants *or* 0.25% to 0.5% cover
4. More than 0.5% to 1% cover
5. More than 1% to 2% cover
6. More than 2% to 4% cover
7. More than 4% to 8% cover
8. More than 8% to 16% cover
9. More than 16% to 32% cover
10. More than 32% cover

The index sacrifices precision for generality and provides reliable estimates of relative vegetation change. Grids document plant establishment and species expansion. The grids were established in 1986 in the pyroclastic zone (Pyroclastic, $n = 400$), on two mudflows at Butte Camp in 1987 (Mudflow 1, $n = 175$; Mudflow 2, $n = 317$), on pumice at the Plains of Abraham in 1988 (Plains of Abraham, $n = 400$), and on the eastern Pumice Plain in 1989 (Coarse Pumice, $n = 200$). Figure 7.2 shows their locations.

7.2.2 Colonization Patterns

We compared observed patterns of distribution on the Coarse Pumice Grid with the null hypothesis of random colonization using a simulation model. Input data were maps of each species distribution at 3-year intervals (with an empty grid used as the basis for predicting initial patterns) and N, the number of plots colonized between intervals. The model filled N quadrats randomly. The number of clusters (composed of contiguous plots containing the species) and the ratio of clusters to occupied plots were calculated. The simulation was repeated 100 times for each suitable species. The mean ratio and standard deviation of ratios were calculated and compared to the observed ratio with a t test (see del Moral and Jones 2002).

7.2.3 Relict Effects

The effects of relict sites, small patches of vegetation that survived the eruption within the eastern Pumice Plain region, were determined along a series of belt transects radiating from each of 37 refuges and from control plots located more than 100 m from any refuge (Fuller and del Moral 2003). Each relict site

TABLE 7.2. Community structure in permanent plots on Mount St. Helens after 20 years (1999).

Impact type	Richness [R] (species/plot)	Mean cover (%)	Evenness (H′/ ln R)
Recovered:			
Tephra ($n = 10$)	20.9	48.3	0.651
Primary succession:			
Mudflow ($n = 7$)	21.0	15.5	0.652
Blasted ridge ($n = 6$)	20.0	32.1	0.610
Coarse pumice[a] ($n = 11$)	19.3	7.1	0.777
Blast–mudflow[b] ($n = 10$)	17.0	5.0	0.796

[a] Eastern Pumice Plain.

[b] The Plains of Abraham.

was carefully searched to establish a complete species list. Then the percent cover of species found within the relicts in 1997 and 1998 were sampled by 1-m^2 quadrats until at least 90% of the species were encountered. The plant cover surrounding each relict was sampled along four transects consisting of 20 contiguous 1-m^2 quadrats each. Quadrats were oriented uphill, downhill, and along the contours in both directions from the relict.

7.3 Results

7.3.1 Patterns of Vegetation Development

Permanent plots and grids documented the development of species richness and cover after 20 years (Table 7.2). These plots include mildly impacted fine-tephra sites at Butte Camp for comparison and primary-succession sites on mudflows (Butte Camp), a blasted ridge (Studebaker Ridge), coarse tephra on the eastern Pumice Plain, and coarse tephra situated over the remains of a devastating mudflow on the Plains of Abraham. The mildly impacted tephra plots at Butte Camp returned to preeruption conditions of 48% cover within 5 years (del Moral 2000b). Richness fluctuated at about 20 species per plot since 1984 but has declined slightly since 2000. During this time, subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), hawkweed (*Hieracium* spp.), orange agoseris (*Agoseris aurantiaca*), and mosses were among those accumulated. A few uncommon species disappeared, and other species were sporadic.

Richness of plots on the adjacent mudflows has approached that of tephra sites. However, species composition of mudflows differs from that of tephra sites, reflecting the difference between mature meadow vegetation and early primary succession. We expect richness to remain stable or to decline on mudflows. Pioneer species are beginning to be lost, and conifer density increases may exclude other species. Richness in all primary plots appears to be converging to a level of about 18 species per plot.

Species richness and percent cover in permanent plots (see Figure 7.2) are shown in Figure 7.3 for two mudflows near Butte Camp, two sites on (upper and lower) Studebaker Ridge, the eastern Pumice Plain, and the Plains of Abraham. The Butte Camp tephra plots are shown for comparison. Figure 7.3a shows species richness. All sites showed increased species richness during the monitoring period. Statistical analyses showed that even annual increments were often significant. The richness of the mudflow plots began to increase before that of the other plots, probably because of proximity to available seed sources (cf. Wood and del Moral 2000). Richness gradients extending from intact vegetation were pronounced for several years of monitoring. Mudflow 1 appears to be declining because of the exclusion of pioneer species by conifers, and Mudflow 2 also may be in decline. On Studebaker Ridge, richness continued to increase, but was reduced in the lower-elevation plots when prairie lupine (*Lupinus lepidus*) achieved strong dominance during the late 1980s. The upper plots lacked vegetation for 8 years, but after 20 growing seasons, they had achieved richness similar to that of the lower-ridge plots. Many of the Pumice Plain sites are windswept, which may contribute to their low mean richness. However, the less-stressful plots had relatively high richness values. The Plains of Abraham plots are more than 1 km from surviving vegetation, but achieved richness similar to that of the other sites after 17 growing season. These plots remain open, and richness continues to increase.

Mean plant percent cover (Figure 7.3b) contrasts with species richness. Vegetation cover on fine tephra fluctuated in response to summer precipitation (del Moral and Wood 1993a), a pattern similar to that of small-mammal abundances on Mount St. Helens (MacMahon et al. 1989; Crisafulli et al., Chapter 14, this volume). Cover development began significantly later on primary-succession sites than on other sites. The mudflows were the first primary sites to develop significant vegetation, and Mudflow 1 approached cover values found on tephra in 1983. Much of this cover was caused by conifers. Cover on the lower Studebaker Ridge fluctuated in response to variations in prairie lupine, but cover was comparable to that of tephra after 23 years. Cover of other species accumulated slowly. In 2001 and 2002, lupines exploded in cover on the eastern Pumice Plain to increase cover significantly. However, cover remained less than that on the mudflows and for lower-ridge vegetation.

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The grids provide both species-composition and spatial data because we can determine where and when a species originated and how it expanded. Here we only address structure (Figure 7.4a,b). On the two mudflows at Butte Camp, richness increases were similar and had not increased appreciably during the last 5 years of the study. However, Mudflow 1 experienced a dense invasion of subalpine fir and lodgepole pine that sampling in 2002 suggested may eliminate pioneer species. Mudflow 2 had less tree invasion, but pioneer species such as fireweed (*Chamerion angustifolium*) and hairy catsear (*Hypochaeris radicata*) were declining. Field surveys in

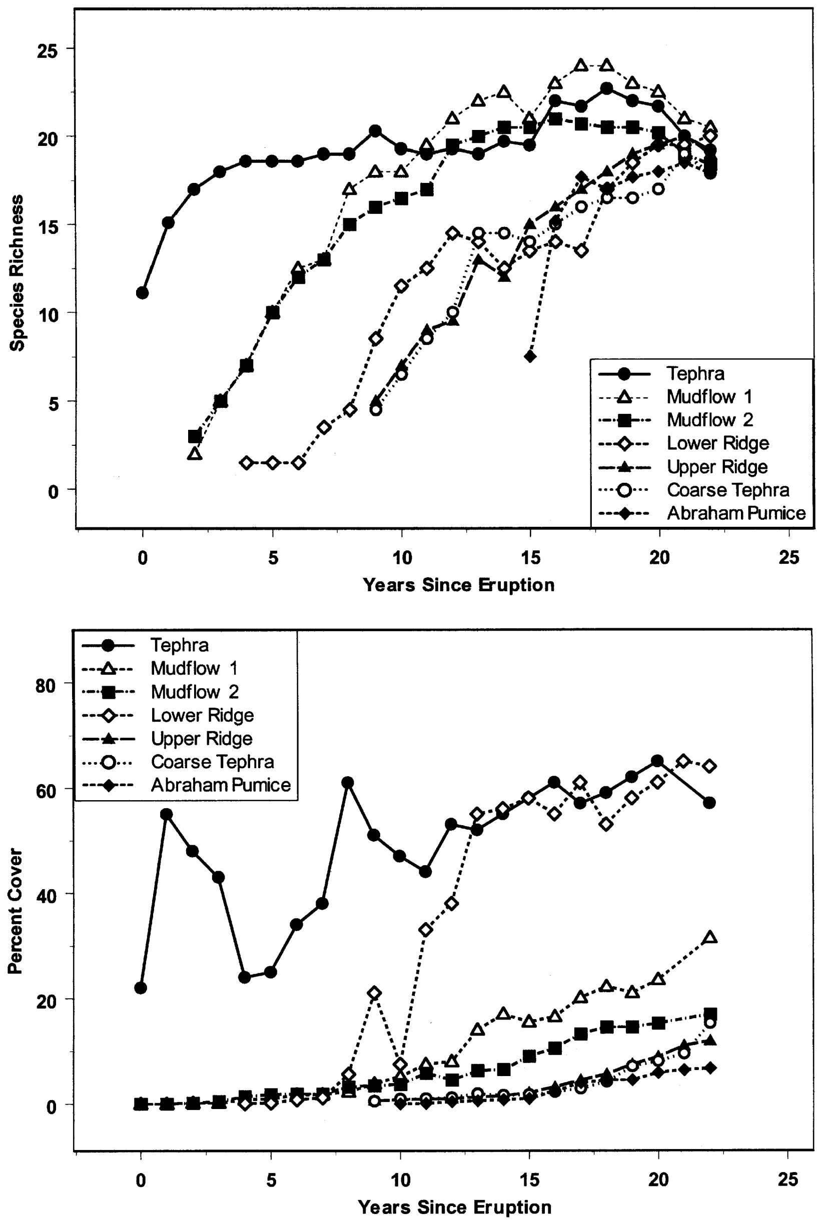

FIGURE 7.3. Structural changes in permanent plots on Mount St. Helens. (a) Richness; (b) total-cover percentage. Tephra ($n = 6$) represents recovered plots at Butte Camp and is shown for comparison to the other sites, all of which are primary-successional sites; Mudflow 1 ($n = 2$) and Mudflow 2 ($n = 5$) are near Butte Camp; Lower Ridge ($n = 4$) and Upper Ridge ($n = 4$) are on the blasted Studebaker Ridge on the northwest flank of the volcano; Coarse Pumice ($n = 11$) is on the eastern side of the Pumice Plain; and Abraham Pumice ($n = 10$) is on the eastern flank of the volcano.

1986 indicated that the eastern Coarse Pumice Grid lacked plants at that time, except in a gully. By 1989, the 10th growing season posteruption, vegetation was sufficiently developed to merit detailed sampling. The mean richness became similar to that of the mudflows, although richness may decline when prairie lupine becomes dominant in swales and other protected sites. In several more exposed parts of this grid, mosses formed mats that also may restrict seedling establishment. Mean plot richness increased substantially on the Pyroclastic Grid, although there was a slight reduction during the mid-1990s. Jumps in mean richness between other sample years were produced primarily by the expansion of existing species. Only on the Plains of Abraham do we expect further substantial increases in mean species richness. The site remains sparsely vegetated, and common genera [such as lupines (*Lupinus*), rush (*Juncus*), and pussypaws (*Cistanthe*)] are absent from many plots.

Total richness on each grid increased rapidly at first but then stabilized. No new species were encountered after 1999. Most species, and all that were dominant at the end of the century, had invaded by 1990. The Coarse Pumice Grid is more than 1 km from intact vegetation, as is the Plains of Abraham Grid (see Figure 7.2). After 10 years, these grids had received only 60% (30 of 50 species) and 70% (33 of 47), respectively, of their total after 22 years since disturbance. In contrast, after the same 10 years, Mudflow 1, within 100 m of intact vegetation, had received 84% (41 of 50) of its 20-year total; and Mudflow 2, which is 0.1 to 0.3 km from intact vegetation, had 76% (35 of 49) of its ultimate total. These data tend to indicate that the greater the isolation, the lower the percentage of

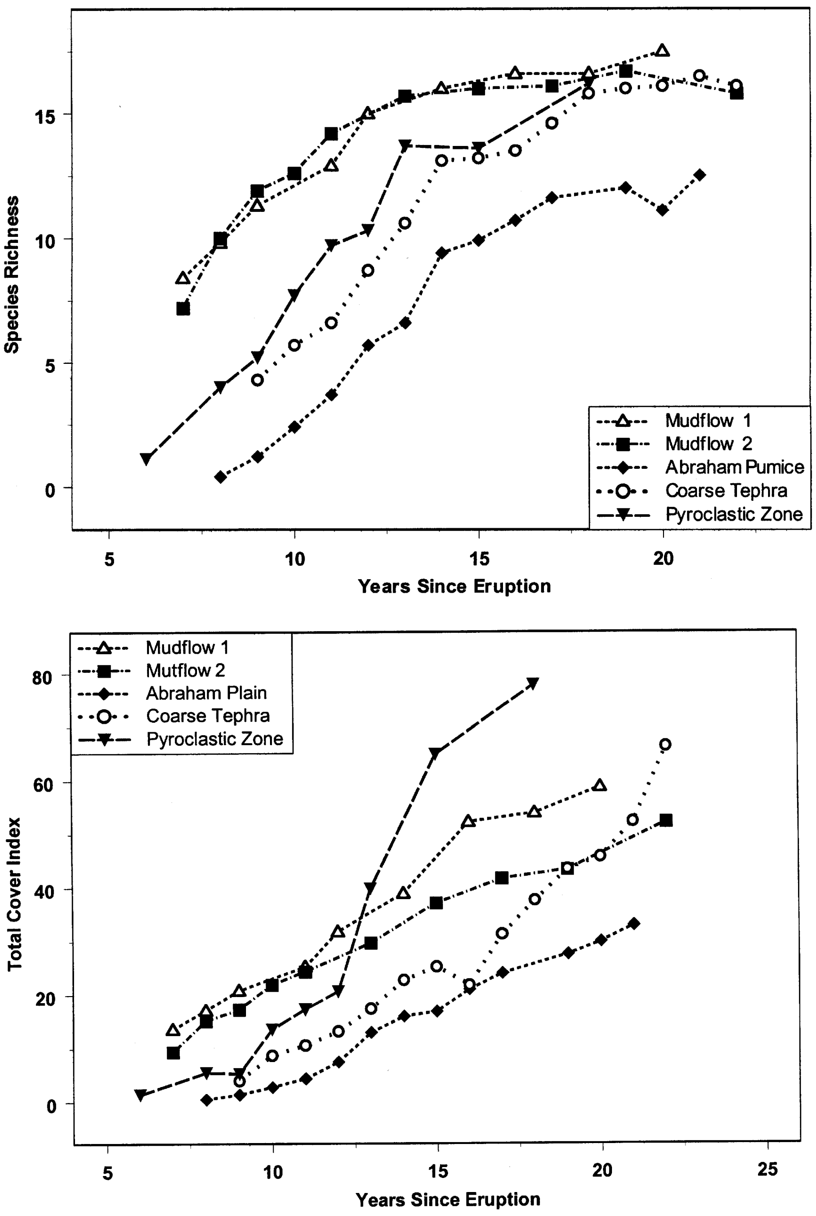

FIGURE 7.4. Structural changes on grids on Mount St. Helens. (a) Richness; (b) total-cover index. Mudflow 1 ($n = 175$ plots) and Mudflow 2 (317 plots) are near Butte Camp; Abraham Pumice ($n = 400$) is east of the mountain; Coarse Pumice ($n = 200$) is on the eastern edge of the Pumice Plain; and Pyroclastic ($n = 400$) is on the pyroclastic flow north of the crater.

species hboxencountered within the first 10 years. The Pyroclastic Flow Grid is an exception in that it received 80% (58 of 72) of its species within 10 years despite being isolated to the same degree as the Plains of Abraham Grid. This difference may result from its more western location, where it more readily received input from logged sites. The abundance of wind-dispersed exotic species in this sample supports this suggestion. Thus, while dispersal was a major limiting factor with respect to the rate of primary succession (see Wood and del Moral 2000), most species entered the system within 12 years of the eruption and subsequently expanded from these centers of establishment.

Grid cover continued to increase in all cases through 2002 (see Figure 7.4b). Differences between successive samples greater than 4 cover units were significant. Because species richness was nearly constant in most cases since 1996, this change reflects the increase in cover of many taxa. On Mudflow 1, cover increases were dominated by firs (*Abies*) and pines (*Pinus*), while on Mudflow 2 alpine buckwheat (*Eriogonum pyrolifolium*) and lupines were major increasers. On the eastern Pumice Plain, lupines, rock mosses (*Racomitrium*), hair-cap mosses (*Polytrichum*), and sedges (*Carex* spp.) all increased significantly, while on the Pyroclastic Grid, cover increased exponentially during the mid-1990s because of the expansion of the lupine and willow populations. On the Plains of Abraham Grid, cover increased in most taxa, although early dominants (e.g., pearly everlasting and fireweed) declined during the last several years.

Species proportions changed dramatically during our studies. Most notable was a reduction in initial colonizers on the

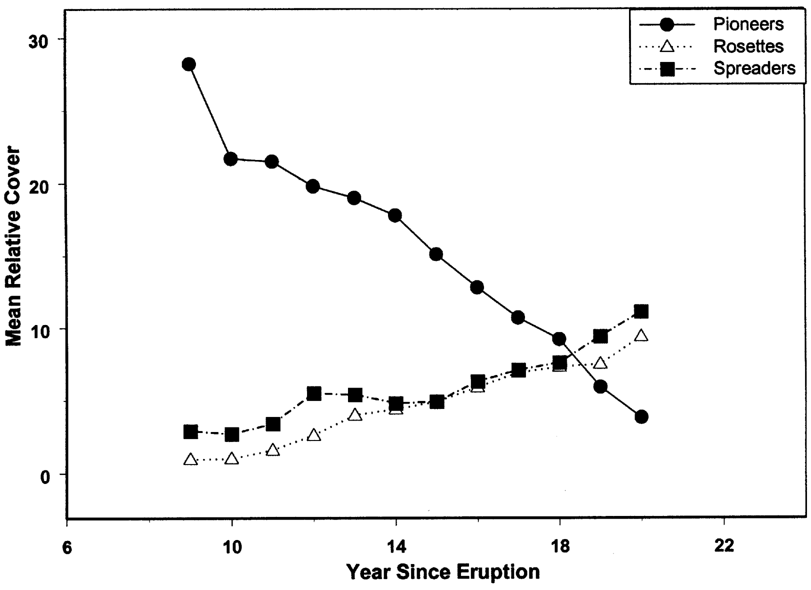

FIGURE 7.5. Relative cover of three types of species from the Plains of Abraham: the most common pioneers (pearly everlasting, fireweed, and hairy cats-ear); clumping rosette species that reproduce abundantly and become locally dominant (umbellate pussypaws, Parry's rush, and russethair saxifrage); and persistent, spreading species that were initially rare (seashore bentgrass, partridgefoot, and Cardwell's penstemon).

more-isolated grids, combined with an expansion of spreading and prolific species. On the Pyroclastic Grid, grasses expanded from trace in 1986 to 12.5% of the cover by 1999, whereas pearly everlasting declined from 22% to 4% by 2000. We suggest that grass expansion results because evapotranspiration is greater from the graminoid species because of their more expansive root systems, which results in a reduction of water for forb species. In addition, slide alder (*Alnus viridis* spp. *sinuata*) has expanded since 2000 in the pyroclastic zone, suggesting that it may dominate in less stressful habitats in this area. Figure 7.5 shows the shift from pioneers to dominance by later-colonizing species on the Plains of Abraham. Each curve is the mean relative cover of three species sampled between 1988 and 2000. (Relative cover is the proportion of the total represented by a species. Mean relative cover is the average relative cover of the three species in each category.) Pioneers (pearly everlasting, fireweed, and hairy cats-ear) were a declining proportion of the total, while less well dispersed rosette species [umbellate pussypaws (*Cistanthe umbellata*), Parry's rush (*Juncus parryi*), and russethair saxifrage (*Saxifraga ferruginea*)] and spreading species [seashore bentgrass (*Agrostis pallens*), partridgefoot (*Luetkea pectinata*), and Cardwell's penstemon (*Penstemon cardwellii*)] increased consistently. In 2000, the six rosette and spreading species accounted for more than 60% of the cover, while the three pioneers accounted for less than 12%.

7.3.2 Isolation

Isolation from sources of colonists can affect the species composition of a site because of differential seed rain. We noted repeatedly that similar sites have different species composition and that the species present differ in their dispersal mechanisms. Sites near intact or partially recovered vegetation are dominated by species with large seeds and poor dispersal, while those in isolated sites were initially dominated by species with good dispersal (see Fuller and del Moral 2003). Next, we examine isolation from several perspectives.

7.3.2.1 Seed Rain

Even distances as short as 100 m can restrict the species pool to wind-dispersed invaders soon after site creation. Therefore, isolated sites initially will be both depauperate and sparse. All our long-term data indicate that species richness increases more rapidly than cover. Eventually, less-adept species do arrive, and occasionally one may establish before wind-dispersed species do (e.g., prairie lupine on pyroclastic materials by 1981). Isolation also creates a stochastic effect that has been poorly appreciated. The chance that *any* seed would reach a particular, favorable, isolated microsite is very low; thus, the chance that two adjacent sites would receive the same seed rain is even lower. Therefore, species composition in two different isolated sites may initially be quite different and bear little relationship to the environment (del Moral 1993). Much unexplained variation on the landscape might have its origin in stochastic establishment in isolated habitats.

We sampled the seed rain when there was little onsite seed production (1982 to 1986) and when vegetation had recovered slightly (1989 to 1990; Table 7.3). Except where traps were located immediately adjacent to vegetation, seed densities were low, and variation among traps was high. The seed rain during the early years was dominated by "parachutists," species with excellent wind dispersal. Species with poor dispersal were rarely trapped, even if seeds were produced within 5 m (Wood and del Moral 2000).

7.3.2.2 Dispersal Ability

We investigated the nature of establishing species under different degrees of isolation. Grids were analyzed to determine the distribution of species grouped into five degrees of dispersal ability (from poor, with no obvious dispersal mechanism, to

TABLE 7.3. Seed rain in distinct habitats and years expressed as the rank of each species in the sample.

		Habitats						
		1982–1986				1989–1990		
Species	Dispersal	PZ 1	PZ 2	WS	MUD 1	MUD 2	PA 1	PA 2
Fireweed	Excellent	1	5	3	2	3	1	2
Pearly everlasting	Excellent	2	3	2			2	3
Fringed willowherb[a]	Excellent	3	1	1			3	5
Hairy cats-ear	Excellent	4	4	4	3	7	4	1
White flowered hawkweed	Moderate	5	6	5	6	6	5	4
Woodland groundsel[b]	Excellent	6				8		
Prairie lupine	Modest	7	2	6	1		6	
Canada thistle[c]	Excellent		7			9		
Umbellate pussypaws	Modest		8		4	2		
Newberry's knotweed	Moderate				5	1		
Cascade aster[d]	Moderate				8	5		
Slender hawkweed[e]	Moderate				9	4		
Few-fruited lomatium[f]	Poor				10			

Dispersal ability from del Moral (1998). Footnotes provide scientific names of species not mentioned in text.

PZ 1, pyroclastic zone; PZ 2, pyroclastic zone with high-density vegetation dominated by lupines; WS, pyroclastic-zone wetland area dominated by *Salix*; MUD, mudflow; PA, Plains of Abraham.

[a] *Epilobium ciliatum*.

[b] *Senecio sylvaticus*.

[c] *Cirsium arvense*.

[d] *Aster ledophyllus*.

[e] *Hieracium gracile*.

[f] *Lomatium martindalei*.

Source: Derived from Wood and del Moral (2000).

excellent wind dispersal). Each type was common at all sites, but there was a shift from poor to excellent dispersal with increasing site isolation (Table 7.4). This simple observation demonstrates the importance of the landscape context and emphasizes that early primary succession will be affected by the available colonist pool as well as by the physical characteristics of the site.

Wood and del Moral (1987) demonstrated that, although wind-dispersed species were most likely to reach a site, large-seeded, poorly dispersed species were more likely to establish *if* they reached the site. Larger seeds also tend to produce more vegetatively spreading plants, so we predicted that these species would eventually come to dominate a site. We analyzed the Coarse Pumice Grid data from 1989 to 1999 (del Moral and Jones 2002) to test this prediction. Early dominants were those with good dispersal. In 1989, the 8 good dispersers accounted for more than 65% of the cover, while the 21 poor dispersers accounted for 31% and the 4 moderate dispersers accounted for 4%. Relative cover of poor dispersers increased to 68% by 1999 whereas that of good dispersers declined to 25%. Absolute cover of poor dispersers increased from a mean of 2 to a mean of 27 cover units; moderate dispersers increased from 0.2 to 3.3 units; and good dispersers increased from only 3.8 to 9.8 cover units.

TABLE 7.4. Relative percent cover in each of five dispersal categories on four grids at Mount St. Helens.

Dispersal category	Adjacent mudflow	Isolated mudflow	Isolated pumice	Very isolated pumice
Poor	6.8	6.8	5.1	8.8
Modest	**58.5**	**27.2**	19.5	20.7
Moderate	7.4	18.0	14.8	6.7
Good	16.0	**32.1**	**23.9**	13.8
Excellent	11.5	16.6	**33.7**	**50.0**

Largest values in bold.

Source: From del Moral (1998); used by permission.

7.3.2.3 Floristic Effects

Isolation affects which dispersal types reach a site, so that the vegetation of similar sites often differs floristically. Samples on mudflows at Butte Camp (adjacent to forests and meadows) and on Coarse Pumice, Studebaker Ridge, and the Plains of Abraham documented the dispersal processes. We compared species composition among grids and among permanent plots with the Spearman rank-order test. Mudflow grids were strongly correlated with each other ($r = 0.81$) but had low to negative correlations with the other grids. The Plains of Abraham Grid had low correlations with mudflow grids ($r = 0.37$; 0.22) and with the Coarse Pumice Grid ($r = 0.23$). The Coarse Pumice Grid was negatively correlated with the mudflow grids, indicating that the flora was drawn from different populations. Permanent plots on Studebaker Ridge were strongly correlated with plots on Coarse Pumice and moderately were correlated with those on mudflows.

Isolation also affects the rate of vegetation development. We demonstrated this effect using plant cover as a development index and comparing plots in comparable habitats across elevational gradients at several locations in 2000. At Studebaker Ridge, cover was negatively correlated with elevation, even though substrates, slopes, and aspects were similar. Cover at 1220 m was more than 70%. At 1285 m, cover dropped to 4%, whereas at 1340 m it was less than 2%. Above 1450 m, vegetation was sparse, and cover was less than 1%. Similarity also declined with distance between plots. Similarity of composition declined with distance between samples. Mean similarity of samples that are within 50 m, 200 m, 500 m, and 1 km declined from 54% to 42% to 31% to 26%, respectively. Thus, isolation can affect both species composition by filtering potential species and cover by reducing the frequency of colonization events by any species. [CE4]

7.3.3 Seedling-Recruitment Patterns

For some species, we could determine when species recruitment shifted from dominance by seeds from long-distance dispersal to dominance by seeds from resident plants. This change is important because cover increases dramatically when seeds are produced locally, although the pace of species turnover may slow because recruitment is dominated by resident species that may inhibit invaders. The shift from donor-maintained species composition to locally controlled species composition was inferred by Wood and del Moral (1988) and elaborated by del Moral and Wood (1993a). del Moral and Jones (2002) modeled the invasion patterns and found that, when invasion is dominated by long-distance dispersal, the spatial pattern of invaders is random. If local plants produced seedlings, aggregation should occur. This simulation provided a conservative test of whether the observed pattern was consistent with a random invasion rather than expansion from local seed sources. The observed ratios of infrequent species were random, suggesting that rare species continue to invade from a distance.

Twenty-one species were analyzed on the Coarse Pumice Grid. Nearly all species with intermediate frequencies were clustered more than would be expected from long-distance dispersal. Species with random patterns included those for which only long-distance dispersal could provide seeds [e.g., firs and Douglas-fir (*Pseudotsuga menziesii*)]. However, willow species, which had not produced seeds on the site by 2001, were more clustered than random. Seashore bentgrass and Cardwell's penstemon, two common species of moderate dispersal ability, were not clustered more than would be expected of a random pattern, but species with good to moderate dispersal did demonstrate significant clustering. These species included hair bentgrass (*Agrostis scabra*), hawkweed, hairy cats-ear, Parry's rush, and russethair saxifrage. Three species of sedges, prairie lupine, small-flowered wood-rush (*Luzula parviflora*), and Sandberg's bluegrass (*Poa secunda* J. Presl.) also displayed clustering that suggested founder effects. We have observed similar patterns developing on the other grids, suggesting that the shift from donor to local control of species demographics is widespread, but occurs for each species at a unique rate. The process also occurs at different times for different species, depending on site isolation and the availability of safe sites for the species in question.

7.3.4 Microsites

7.3.4.1 Observations

On mudflows and pumice surfaces at Mount St. Helens, favorable microsites were crucial to early plant colonization in many cases (Wood and Morris 1990; del Moral and Bliss 1993; del Moral and Wood 1993a; Tsuyuzaki and Titus 1996). The phenomenon of initial establishment being localized in especially favorable sites is widespread (Oner and Oflas 1977; Tsuyuzaki 1989; Walker and del Moral 2001, 2003). Safe sites differ in environmental characteristics and provide relief from stress. For example, rills may be wetter than ridges because of longer snow retention, and near-rock microsites offer shade. The specific microclimate of a microsite within which a propagule is trapped may be critical for plant germination and growth. However, some microsites may permit dense colonization, leading to intense competition and low survival (see Lamont et al. 1993; Titus and del Moral 1998a), although greater biomass of a few individuals may result.

On a fine scale, initial colonization patterns were related to safe-site distributions (del Moral and Wood 1993a). Pioneers establish nonrandomly on pumice because favorable safe sites are strongly preferred by colonists. The stress of dry, hot, posteruption surfaces was emphasized by the observations that, although most seedlings were associated with safe sites, most safe sites lacked seedlings (del Moral 1993). These patterns have decayed on coarse tephra as plants expand from initial loci and as amelioration proceeds. Amelioration gradually improves all sites and blurs distinctions among microsites.

Eleven years after the eruption, we studied the distribution of seedlings with respect to rocks, rill edges, undulations, drainages, and flats on the Plains of Abraham. Pearly everlasting, fireweed, hawkweed, hairy cats-ear, seashore bentgrass, and pussypaws were all associated with rocks and negatively associated with drainages and flats. Rills and depressions supported the first three species disproportionately. These patterns became muted during the second decade as safe sites became more rare because of the breakdown of pumice and erosion within rills (del Moral 1999a) and were virtually nonexistent by 2001. Established species expand, preventing new seedlings from establishing. The habitat has ameliorated because of weathering, soil development, and continued inputs of organic matter from surrounding forests (Edwards and Sugg 1993; Sugg and Edwards 1998).

7.3.4.2 Experimental Studies

For several years, we manufactured safe sites on mudflows near Butte Camp, on the Plains of Abraham, on the eastern Pumice Plain, and in the pyroclastic zone to test the hypothesis that safe sites were indeed crucial to establishment success. Treatments were designed to mimic the effects of both abiotic and biotic amelioration. We showed that the addition of mulch, which lowers surface temperature, improves moisture, and traps seeds, produced at least 10 times more seedlings than when only rocks were provided. Creating shade, making rills, cultivating the surface, and adding nutrients all increased natural seedling recruitment (Wood and del Moral 1987).

Several aspects of plant colonization must be assessed when considering safe sites. We examined establishment and growth with native seeds sown in six microsites (flat, ridge, near rock, rill, dense vegetation, and dead lupines) on pumice (Titus and del Moral 1998a). We also studied colonization into constructed microsites. Maximum natural colonization did not occur in the same microsites as maximum establishment and growth from sown seeds. Colonization patterns also differed from year to year. This year-to-year shift in microsite colonization patterns illustrates the dynamic nature of the landscape and the important influences of climate, amelioration, and seed rain on plant establishment and community development.

Taxa found in seed traps were the major colonists on pumice (e.g., pearly everlasting, fireweed, and hairy cats-ear). These colonists also had greater biomass in dead lupine patches than in other sites, confirming that facilitation effects by lupines are delayed until most lupines have died (Morris and Wood 1989). Our studies also unexpectedly revealed that those microsites supporting the most seedlings were not always the most favorable for subsequent growth. Some sites (rills) trapped many seeds but did not support the best growth. As more vegetation developed, many seedlings colonized once-hostile sites because their seeds were trapped by previous colonists.

An overlooked aspect of sites lacking vegetation is that they are dynamic, with chronic erosion. Tsuyuzaki et al. (1997) examined erosion and tracked seedling survival on eroded pyroclastic sites. More seedlings established where eroded material accumulated and on coarse-textured surfaces, even though finer-grained surfaces had more organic matter and were moister. In addition, sites with higher cover of dead lupines, more rock and gravel substrate, and more rills had more seedlings.

Safe sites have been demonstrated to be crucial to the establishment of plants on exposed primary sites. The nature and frequency of safe sites has changed, and the competitive environment has undergone a profound shift. Future colonization will require species with different characteristics, and the next phase of succession will require species to compete effectively and to utilize biological facilitation by established individuals.

7.3.4.3 Mycorrhizae

Mycorrhizae, normally occurring as a root–fungus mutualism, are often important determinants of plant succession (Boerner et al. 1996). However, knowledge of their role during early primary succession is scant. During primary succession on volcanic substrates, it is unlikely that pioneer species would depend on mycorrhizae because nonmycotrophic and facultatively mycotrophic species could readily invade these sites. Species that require mycorrhizae cannot establish until a population of arbuscular mycorrhizal (AM) fungi is present (Allen 1991, chapter 14). Because mycorrhizal mutualism is a major investment for a plant, AM effects during early primary succession on infertile soils may be weak.

Mycorrhizal plants and AM fungal propagules (spores, hyphae, and AM-colonized roots) were common in sites with thick vegetation in the blowdown area but were extremely rare on pumice (Titus et al. 1998a). Only three AM fungal species were detected by Titus et al. (1998a). The vegetation of the Pumice Plain is composed primarily of facultatively mycotrophic species that remained nonmycorrhizal. On pumice, created microsites were inoculated with AM propagules, but these locations were no more favorable for the growth of six pioneer species than were uninoculated microsites (Titus and del Moral 1998b). There was, in fact, a trend for greater biomass in the nonmycorrhizal treatments, suggesting that AM were parasitic in this infertile environment (see Fitter 1986). Thus, the infertility of volcanic successional sites and the facultative nature of invading species preclude an early role for mycorrhizae. With substrate amelioration, increased plant density, and the invasion of species with greater AM dependency, AM may assume greater importance.

We conducted two greenhouse studies to examine the role of AM in pioneer species under three nutrient treatments and four competitive scenarios (Titus and del Moral 1998c). Nutrient treatments were either: **[CE5]**

- Complete
- Complete but lacking phosphorus (−P)
- Tap water

Phosphorus is the principal nutritive benefit plants receive from mycorrhizae. A negative effect from AM colonization was observed in tap water, perhaps because of a parasitic action of the AM fungi. A weak benefit from AM occurred in the −P treatment, where plants were similar in biomass to those in the complete nutrient treatment and where AM colonization levels were greater. AM did not significantly influence competitive outcomes between facultatively mycotrophic species. However, the performance of the facultatively mycotrophic hairy cats-ear in competition with the nonmycotrophic Merten's sedge (*Carex mertensii*) was significantly improved with AM compared to its growth in the absence of AM. Under field conditions at Mount St. Helens, it is unlikely that competitive dominance is affected solely by mycorrhizal associations. AM is only one of several interacting factors that, at best, only slightly alters plant-species composition.

Several conifer species, which are ectomycorrhizal, occur at low densities throughout the Pumice Plain, but rarely have they reproduced. Conifers may be limited by substrate infertility and elk browsing, but because ectomycorrhizal spores are well dispersed, the lack of mycorrhizae is not a likely source of population restriction. Conifers such as Douglas-fir, western white pine (*Pinus monticola*), and lodgepole pine grow very well and frequently produce cones on the slightly more fertile mudflows of Butte Camp and the Muddy River.

7.3.5 Relict Vegetation

Refugia (sites with surviving vegetation) are considered sources of colonists to disturbed landscapes (Cousins and Eriksson 2001). They contribute to ecosystem responses after disturbances in agricultural (Zanaboni and Lorenzoni 1989), industrial (Labus et al. 1999), and natural (Danin 1999) landscapes. They can contribute colonists after glaciation (Stehlik 2000) and lava flows.

In the eastern Pumice Plain, snow and northeast-facing slopes combined to permit survival of some species and soil. It was soon clear that refugia were vegetationally distinct from their surroundings (del Moral et al. 1995). Because refugia occur on steep slopes that are more shaded, cooler, and moister than coarse tephra, surviving species were not well adapted to colonizing coarse tephra. To assess the extent to which refugia

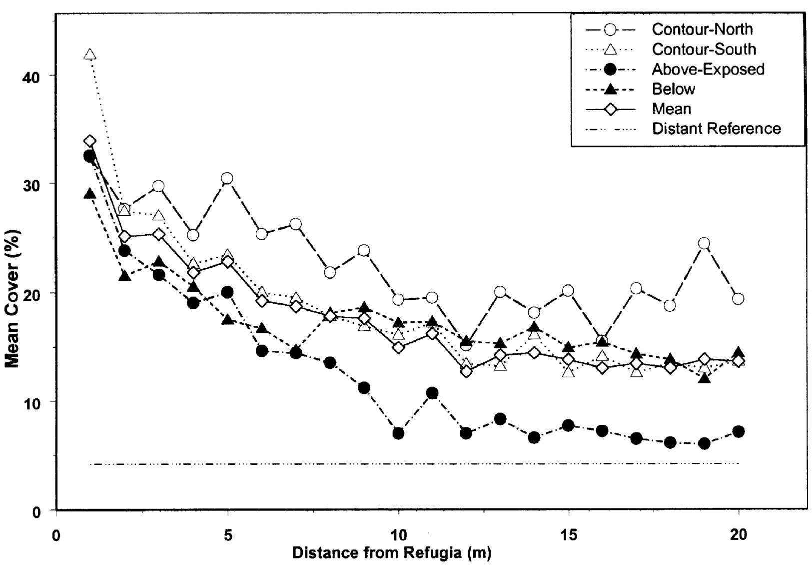

FIGURE 7.6. Changes in plant-cover percentage along transects from refugia. [From Fuller and del Moral (2003).]

and the coarse-pumice matrix are similar, we sampled each habitat type. There were 122 species (mean = 28.8 species) in refugia. Cover (mean = 82%) was dominated by 18 species, primarily shrubs and forest understory species. There were 25 species in the coarse pumice samples that were more than 100 m from any refuge. Of these, 23 reproduced abundantly in refugia, but few were refugia survivors. Nine species accounted for 90% of the coarse pumice cover (mean, 4.2%). These species included wind-dispersed taxa (e.g., pearly everlasting, fireweed, hawkweed, hairy cats-ear, and willow) and taxa that exhibit tumble dispersal (e.g., penstemon, bentgrass, and rush). Cover adjacent to a refuge was high but declined sharply with distance (Figure 7.6). At 20 m, cover above refugia was only slightly greater than the values for distant coarse tephra. Transects below refugia had the highest cover, and those above refugia had the lowest. Refuge effects will continue to expand as the habitat is ameliorated, but on coarse tephra, as of 2002, their present effects are constrained to no more than 50 m (Fuller and del Moral 2003).

Most species that survived in refugia have poor dispersal in the absence of animal vectors and a limited ability to establish in seasonally hot, dry, windswept sites. Refugia were invaded by the common wind-dispersed colonizing species, which found reduced competition and adequate soil fertility to reproduce abundantly. These species use refugia as "mega safe sites" and then contribute many more seeds to adjacent pumice than reach these sites from a long distance. These wind-dispersed species have three variants:

- *Parachute* species have plumes or other buoyancy mechanisms and routinely travel long distances.
- *Parasail* species have wings that permit some aerial movement.
- *Tumbler* species are adapted for movement along the ground.

Wind-dispersed species were disproportionately abundant in the Mount St. Helens refugia because large numbers of their seeds arrived. In 1989, they were also much more abundant on pumice, but by 1998 species with limited dispersal were more abundant than the wind-dispersed species (del Moral and Jones 2002) on pumice. The superior establishment ability and greater persistence of more poorly dispersed species (usually with larger seeds) compensates for their limited dispersal ability.

We investigated the effects of one refuge on its immediate surroundings (del Moral and Jones 2002). By analysis of the Coarse Pumice Grid, which includes a small refuge, we detected subtle effects of the refuge on local vegetation. The 100-m^2 plots were divided into those immediately adjacent to the refuge ($N = 17$) and those at least 10 m distant from the refuge ($N = 164$). The latter group was subdivided into plots that had less than 3% cover of prairie lupine ($N = 120$) because the cover of this species exploded and could swamp any relict effects. Richness, the cover index, and percent cover were calculated. Adjacent plots had significantly more species, 25% larger cover index, and 60% more cover than did distant plots with limited lupines.

Seedlings of bird-dispersed species such as black huckleberry (*Vaccinium membranaceum*) are increasingly becoming established downslope of refugia. Because refugia attract birds and rodents, vertebrates may be enhancing the rate of nutrient accumulation near refugia and therefore may accelerate the growth and dispersal of existing species. Ameliorated soils may become invasible for additional species, thus promoting succession. However, through 2002, refugia had rarely donated their own species to the surroundings. As coarse-tephra sites are ameliorated, for example, by the rapid expansion of prairie lupine, refugia should become more important.

7.3.6 Predictability and Determinism

Do environmental factors predict plant species patterns during succession? Most seres become more homogeneous through time, if only because the site fills in with vegetation. A more important question is whether the trajectory of succession (direction of change) leads to one community (convergence) or to multiple communities (divergence). The elapsed time has been insufficient to fully assess convergence on Mount St. Helens, but our work provides the groundwork for future studies. Next, we explore changes in vegetation heterogeneity to suggest how trajectories may develop.

7.3.6.1 Variation

Dlugosch and del Moral (1999) measured floristic heterogeneity along a short elevational transect on the Muddy River mudflow. The gradient mimicked a successional gradient because plant succession is slowed by the shorter growing season found at higher elevations. Species composition, measured in plots 100 m^2 in size, was similar over the gradient, but heterogeneity, measured by comparing variation within a plot, was lower at lower elevations because the vegetation sampled was more mature. This result suggests that species assembly in primary succession has a large element of chance. At higher elevations, chance effects are more prominent than in lower elevations because there have been fewer successful colonizations relative to the available area.

When first sampled, the pyroclastic-zone grids were nearly empty. Over more than 10 years, they filled in, and the variation among plots decreased. However, reduction in variation per se means neither that plots are becoming one homogeneous community nor that they are converging upon some mature vegetation type. Later dominance shifts may reverse the initial trend toward homogenization. These grids demonstrated a typical homogenization from their inception (1986) through 1993 as plot cover increased, and many species occurred in most plots. However, after 1993, some plots became dominated by grasses, others by lupines, and still others by other forbs or by low shrubs. As of 2000, heterogeneity was again substantial with cover ranging from less than 10% to nearly 100%. This result suggests that different portions of the pyroclastic zone are revealing alternative accumulation and expansion patterns that could lead to different successional trajectories when the vegetation matures. Even when (if) conifers dominate, significant compositional differences may result from events early in the process rather than from environmental differences.

The Coarse Pumice Grid provides an example of the complexity of vegetation development. Eleven samples each composed of 15 contiguous plots were formed. Detrended correspondence analysis (DCA) was used to analyze floristic changes at 3-year intervals between 1989 and 1998, plus 1999. Most variation occurred along Axis 1 as composition changed with time. The variation within each group, measured by mean similarity of the plots and by standard deviation of the DCA scores, declined significantly after 1989, indicating increasing homogeneity. However, while some groups converged as might be expected, others did not. Convergence occurred where the more-persistent or longer-lived taxa (lupines, penstemons, willow, and bentgrass species) increased at the expense of pioneer taxa (pearly everlasting, hawkweed species, fireweed, and hairy cats-ear). Two groups that were initially similar to each other developed in parallel, but each diverged from the other groups. Their divergence is based on increased dominance by roadside rock moss (*Racomitrium canescens*) and juniper hair-cap moss (*Polytrichum juniperinum*) where erosion has removed fine material.

7.3.6.2 Early Community Assembly

The shifts in plant species composition found in all our studies imply that several factors mold the vegetation populations. These factors could be environmental, such as moisture and nutrients, or they could be biological, such as competition and seed predation. We have explored the degree to which species patterns can be predicted by environmental variables under several circumstances.

In 1993, statistical correlations between measured environmental factors and species composition across the eastern Pumice Plain were very weak. The most important predictors of species composition were spatial, not moisture, fertility, or edaphic factors. This result indicated that landscape effects and dispersal limitations were more important than site factors (del Moral et al. 1995).

A unique situation occurred on the eastern Pumice Plain, where several hundred "potholes" formed soon after the first eruption. They provided an opportunity to study the relationships between species composition and the local environment. Potholes are environmentally similar to one another. They share a common internal slope, general aspect, and soil. They are of similar depth and were formed essentially simultaneously. However, their vegetation composition was very heterogeneous when first sampled, 13 years after the eruption (del Moral 1999a).

Between 1993 and 1999, percent similarity in species composition among potholes did not change significantly. We divided the potholes into seven spatial groups (to limit spatial effects) and found that, even though the vegetation cover increased substantially, species composition did not change appreciably. Richness increased by 3.2 species per plot and cover increased by a factor of 4. Each pothole appears to have developed along its own trajectory in which priority effects (see Section 7.4.2), the consequences of chance initial establishment, have dictated local succession.

The location (determined from a map based on field distance measures) and soil properties of these potholes were used to predict species composition and to determine if deterministic factors were coming into play. Using canonical correspondence analysis (ter Braak 1986), we tested for significant correlations. In 1993, the overall correlation between species patterns and environmental variables was not significant ($r = 0.62$ for the first axis). In 1998, the first axis was significant ($r = 0.72$, $p < 0.02$) with moisture (determined gravimetrically from three soil samples) and location variables being the leading predictors. By 2001, the relationship had

TABLE 7.5. Structure of community types.

Type	Dominants	Richness	Cover %	H?	E	% Hydrophytic
A	Willow/yellow willowherb[a]/mosses	10.0^{CD}	157.6^{A}	1.09^{AB}	0.484	97.9
B	Willow/goatsbeard[b]–Merten's sedge	13.7^{BCD}	83.7^{BC}	1.34^{AB}	0.508	80.9
C	Willow/fringed willowherb–bluejoint[c]/mosses	$13.0b^{CD}$	67.5^{CD}	1.42^{AB}	0.596	96.4
D	Willow/mixed herbs/mosses	20.5^{A}	28.9^{D}	1.68^{A}	0.562	91.5
E	Willow/Lewis's monkey flower[d]–fringed willowherb/swamp moss	19.6^{AB}	117.6^{AB}	1.61^{A}	0.540	92.6
F	Willow/rushes/golden short-capsuled moss	12.0^{CD}	85.5^{BC}	1.18^{AB}	0.481	99.9
G	Willow/rushes–fringed willowherb/golden short-capsuled moss	16.0^{ABC}	57.2^{CD}	1.70^{A}	0.613	99.1
H	Willow/field horsetail–rushes	14.2^{BCD}	72.9^{BC}	1.67^{A}	0.633	99.2
I	Willow/field horsetail	8.3^{D}	73.0^{C}	0.79^{B}	0.387	99.7
J	Cattail–toad rush[f]	12.8^{BCD}	52.6^{CD}	1.52^{AB}	0.603	97.2

Column values with different alphabetic (ABCD) superscripts are significantly different ($p < 0.05$, Bonferroni comparison). Richness is the mean number of species per sample; Cover % is the total percentage found in the sample, H? (diversity statistic) and E (evenness) are defined in text; and "% Hydrophytic" is the cover of species considered to be hydrophytes (e.g., obligate, facultative wetland, or facultative species). Footnotes a–f provide scientific names of species not mentioned in text.

[a] *Epilobium luteum.*

[b] *Aruncus dioicus.*

[c] *Calamagrostis canadensis.*

[d] *Mimulus lewisii.*

[e] *Brachythecium frigidum.*

[f] *Juncus bufonius.*

Source: From del Moral (1999b); used by permission.

strengthened slightly ($r = 0.74$, $p < 0.01$), with total nitrogen and location being significant factors. The increase in nitrogen as a predictor may have resulted in the large increase of lupines relative to other species. Thus, the relationship between the physical environment and species composition increased slightly. That the spatial dimensions were important implied that priority effects were important. Priority effects continue to influence development in these potholes, and trajectories have not converged.

To test if chance played a large role in determining the vegetation of these potholes, we developed a stochastic model to predict composition from initial species compositions (del Moral 1999a). This model accurately predicts mean richness, cover, frequency, and rank order of the potholes, a result that suggests that species assembly in such sites as these potholes is largely caused by chance. However, there was spatial homogeneity for several species, which implied that subsequent dispersal from adjacent potholes helps to structure vegetation.

7.3.7 Wetlands

Wetlands are a natural focus for studies of early primary succession because they develop rapidly, attract fauna, and may export materials to adjacent sites. New wetlands on primary surfaces north of the crater occur in depressions, on the new margins of Spirit Lake, along new springs, and along snow-fed streams. The first wave of colonists was dominated by wind-dispersed species (del Moral and Bliss 1993). Primary wetland vegetation remains variable, probably because of the combined effects of chance and the availability of several species that are able to dominate a site. For example, spike bentgrass (*Agrostis exarata*), field horsetail (*Equisetum arvense*), and toad rush (*Juncus bufonius*) can each dominate early in succession. As willows develop, a more consistent array of species adapted to shade may occur. Some upland species (e.g., pearly everlasting, fireweed, and hairy cats-ear) are common on wetland margins because of their broad ecological amplitudes in the absence of competition. As shrubs expand, the upland species should decline sharply.

Several community types described on the primary surfaces of Mount St. Helens have regional analogues (Titus et al. 1996, 1999; Table 7.5), although they differ because of their immaturity. These communities include a sitka willow (*Salix sitchensis*)/field horsetail (*Equisetum arvense*)–sweet coltsfoot (*Petasites frigidus*) association in northern Oregon similar to community type A and a lung liverwort (*Marchantia polymorpha*)–swamp moss (*Philonotis fontana*) association, similar to community type E, both described by Christy (2000).

Deterministic mechanisms that structure vegetation in wetlands on the Pumice Plain are increasing in strength. The principal structuring mechanisms on these wetlands are the moisture regime, which permits rapid development of plant biomass, and the competitive effects of willows. Developing wetlands demonstrated increasingly tight connection between vegetation and aspects of the environment. Titus et al. (1999) studied wetlands on the Pumice Plain after 14 growing seasons, and del Moral (1999b) sampled 78 new wetlands 6 years later to assess changes in vegetation and environmental relationships. Geographic, topographic, physiographic, moisture, and soil data were analyzed to determine which environmental features were correlated with vegetation patterns. During this interval, explained variation increased from 19% to 31%, when location, soil pH, and habitat type were the best predictors of species patterns. During the sampling interval, willow cover increased from 10% to 28%, resulting in reduced diversity and heterogeneity of understory vegetation. The understories of wetlands with more than 70% willow cover were significantly more similar to each other than were the understories of wetlands with less than 10% willow cover. These data suggest that the wetlands have begun to demonstrate deterministic effects because of greater competition and stronger coupling to moisture regimes.

We recognized 10 primary wetland vegetation types on Pumice Plain sites after 19 years (see Table 7.5; from del Moral 1999b). Richness, diversity, and evenness are inversely correlated with cover percentage, suggesting that, as willow dominance increases, fewer species will persist. However, common species that colonized wetlands by chance persist and seem to be resisting exclusion. If many species occur because of early stochastic events, then a strong, deterministic relationship between species patterns and the environment cannot develop. Eventually, these wetlands should continue to mature and develop tighter ties to the environment as competitive pressures from canopy dominants and from better-adapted understory species are exerted.

Willow thickets may eventually resemble communities observed elsewhere. However, herbaceous wetlands may change in less predictable ways. Clonal species, such as field horsetail and cattails, can persist indefinitely (Keddy 1989; Tsuyuzaki 1989; Prach and Pyšek 1994). It is likely that cattails (*Typha*) will continue to dominate some habitats while being excluded by willows in other, similar habitats (Tu et al. 1998). Physically unstable sites may continue to be dominated by horsetails or rushes. As of 2002, several primary wetland assemblages are not developing toward mature wetland communities.

7.3.8 Nonnative Species

Species that only appeared with Europeans are a part of the recolonization process. Most exotics are not adapted to higher elevations, having evolved in European cultivated land. Titus et al. (1998b) listed native and exotic species found around Mount St. Helens and found 341 vascular plant species in primary-successional habitats in 1995. Of these, 57 were exotic. The exotic flora is dominated by composites. On the Pumice Plain, 151 natives and 20 exotics occurred, but only 4 were common. On the Plains of Abraham, 65 natives and 4 exotics occurred. Primary wetlands had 110 natives and 11 exotics. The western Pumice Plain was positioned to receive many species from the clear-cuts to the west. As the vegetation of this area has developed, the number and dominance of exotic species [e.g., tansy ragwort (*Senecio jacobaea*), wild lettuce (*Lactuca serriola*), Canada thistle (*Cirsium arvense*), and velvetgrass (*Holcus lanatus*)] declined. The exception is hairy cats-ear, which appears to have become "naturalized" in many habitats. It is common where lupine has become abundant. We predict that hairy cats-ear will remain an integral part of the flora, although its importance will decline as shrubs and conifers come to dominate.

7.4 Implications and Conclusions

7.4.1 Dispersal Limitations

Our studies of succession on mudflows and coarse pumice at Mount St. Helens have offered valuable lessons and altered the traditional view of primary succession. Primary succession is usually slow (Walker and del Moral 2003), but its rate is strongly affected by proximity to sources of colonists as well as to resource availability. Mudflows at Butte Camp and on the Muddy River were invaded rapidly from adjacent, intact forests. However, these field studies, as well as the analyses of vegetation gradients surrounding refugia and remote sensing results (see Lawrence, Chapter 8, this volume), show that the effects of adjacent mature vegetation is limited. Beyond a surprisingly short distance, all sites are similarly isolated. Vegetation more than 100 m from forest margins or refugia is sparse and less diverse than vegetation within 20 m. The size and density of conifers also decline with distance, suggesting strong dispersal limitations. Exposed, sparsely vegetated sites have experienced little species turnover, the hallmark of succession. Species continue to assemble slowly, and only some pioneer species have shown relative declines. When a dense canopy of shrubs or conifers develops, species turnover can be expected. As the ground-layer vegetation becomes dense, as has occurred since 2000 in much of the eastern Pumice Plain as a result of lupine expansion, local extinction and colonization of different species may be expected. The development of forest vegetation on newly deposited pumice will take decades. In isolated wetlands formed on pyroclastic materials, species accumulation and growth has been rapid because seedling establishment was not greatly influenced by summer drought and because the dominant species have excellent wind dispersal. Biomass has developed quickly, dominated by tall shrubs that attract birds and mammals that can introduce additional species (see Crisafulli et al., Chapter 14, this volume). These **[CE6]** results imply that dispersal, context, and vegetation structure are more important determinants of succession than is commonly thought and that rehabilitation projects should devote more effort to introducing species rather than depending upon natural dispersal.

7.4.2 Priority Effects

The term "succession," in the original, extreme sense, implied that a series of communities (or species) occupies a site sequentially and that there is a predictable trajectory toward a single stable community (but see the discussion in Dale et al., Chapter 1, this volume). The more recent term "assembly" describes a more stochastic case in which the course of species change is affected by the initial colonists, historical events, and landscape context (Belyea and Lancaster 1999). Many alternative communities that can persist indefinitely may result (see Young et al. 2001). The reality on successional surfaces that we have studied appears to be intermediate. Successional trajectories are not strongly deterministic. There appear to be a few, not many, communities during the first two decades of reestablishment. It will be many decades before the situation in profoundly disturbed, isolated sites on Mount St. Helens can be assessed fully. For now, we offer some preliminary comments about community convergence.

As succession unfolds, species fill in the landscape, and spatial variation in vegetation typically declines. Heterogeneity persists, although gradually becoming reduced, because there are only weak links among patches in a vegetation mosaic and local differences can persist because of inhibitory effects of the founding species. Local environmental conditions (such as the moisture regime) eventually exert their effects to reduce heterogeneity. In most cases, as seen in our wetland examples on the Pumice Plain, vegetation will tend to become more homogeneous, if only because few dominant species exist there. However, trajectories may not converge, and they may even diverge to form persisting novel assemblages. Mature communities will retain a residual of unexplainable variation linked to historical accidents (contingencies), stochastic invasion patterns, and landscape effects. Apparently, several alternative, equally "natural" communities can develop after an intense disturbance, and the one that ultimately results is initially poorly predictable. Restoration ecologists should acknowledge several potential alternatives rather than aiming for one sequence of species replacements. Restoration should be cast in more general plant functional types and conditions of the ecosystem (e.g., plant biomass, cover, and soil organic matter) and not specify particular target community types.

7.4.3 Phases of Primary Succession

Although recovery in response to disturbance forms a continuum from primary succession through secondary succession to mere damage repair, we have focused on several kinds of primary succession sites and compared them to secondary succession sites. Community development has three fundamental phases: assembly, interaction, and maturation. At some point after initial assembly, the processes cease to be unique to primary succession and occur also in secondary succession because of minor disturbances or senescence. In most primary habitats we have studied, the initial assembly phase appears to be nearly complete. Additional species, best adapted to forest understories, likely will wait until significant structural changes result from the maturation of tall woody species. Others, such as Newberry's knotweed (*Polygonum davisiae*), are common on some primary surfaces but remain absent from others. Eventually, they may colonize such habitats as the eastern Pumice Plain. Physical amelioration and biotic facilitation (e.g., nurse-plant effects) dominate, although negative interactions also occur. While species come and go on a microscale (van der Maarel and Sykes 1997), most survive in a larger study area, and other species invade.

The interaction phase has scarcely begun in most sites we have studied, although on mudflows near intact vegetation, in lupine patches, and in wetlands interactions have intensified. As a community shifts from assembly to interaction, the relative importance of facilitation and inhibition also shifts. Where woody species are gaining dominance, competition for light and other resources should exclude many pioneer species and should permit the invasion of species adapted to shade. Early in the interaction phase, diversity increases because pioneers persist in the gaps between woody plants. In our ongoing studies of invasions on mudflows, we note that virtually none of the invading species remained beneath alders or conifers, but they persisted in the gaps. The invasion of woody species appears to foretell reduced species diversity, but it is premature to determine whether subsequent invasions by forest herbs will replace lost diversity and lead to more or less heterogeneity. It may be possible to find general rules of establishment during this phase. The maturation phase involves strengthening dominance by large woody species. These species reduce environmental heterogeneity by casting more-uniform shade and by depositing litter that minimizes surface variations. Although diversity in nonvascular plants, arbuscular and ectomycorrhizal fungi, and saprophytes increases, the overall diversity of vascular herbs and low shrubs will decline, if adjacent forests are a guide.

7.4.4 Significance of These Studies

Long-term ecological studies are invaluable in fostering our understanding of how ecosystems assemble. Primary succession is stochastic and controlled initially by chance, contingency, and context. Prediction of trajectories is problematic and will be influenced both by the initial conditions (priority or founder effects) and by subsequent events, such as herbivore damage or minor disturbances. While our studies help to illuminate restoration guidelines being developed from studies of succession (see Walker and del Moral 2003), several implicit problems remain. Thoroughly degraded habitats, such as toxic mine wastes, will not recover without intense intervention, at least to alter the substrate and to introduce appropriate species. Appropriate intervention to rehabilitate human-disturbed habitats requires the scientific knowledge of basic succession mechanisms, appropriate trajectories, and management techniques. These attributes are all constrained by local social and fiscal factors. Studies on Mount St. Helens have done much to provide the scientific knowledge to effectively enhance restoration projects in this region. We have demonstrated that dispersal limitations alone often determine the course of early succession. Soil amelioration in the form of nitrogen fixation and inputs from outside the system accelerate the invasion process. The presence of resource oases, such as refugia and springs, clearly alters local succession, but they also may affect their surroundings.

The eruption of Mount St. Helens profoundly altered the lives of the present authors. We each followed professional trajectories remarkably different from what we could foresee in 1979. We hope that this chapter has conveyed some of the reasons why we were compelled to return consistently to document how recovery is unfolding on this unique volcano and to learn more about one of nature's most fascinating processes—primary succession.

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