CHAPTER 4

The Vegetation Removal Zone

Plains of Abraham (September 9, 1980). This image captures the stark beauty of this desolate plain. No plants were found over a wide area, and nine years later, during my first detailed survey, individuals were extremely rare.

How the landscape lost its vegetation

This chapter discusses the terrain from which all vegetation was removed, but which escaped the devastation caused by pyroclastic flows. The vegetation removal zone was devastated, yet remnants of vegetation remained and plants soon began to establish in spots. Although no lava flows were spawned by the 1980 eruption, I will discuss older lava surfaces. In order to place the events of 1980 in perspective, I will provide an overview of similar historic eruptions.

Denuding blasts in history

When the catastrophic eruption of Mount Mazama formed Crater Lake about 7700 years ago, a deep deposit of pumice from pyroclastic flows and tephra left a barren desert that persists to this day. The eruption must have been a pivotal point in the history of humans who witnessed (and survived) the spectacle. Such events testify that volcanism has lasting effects on the landscape.

The eruption of Krakatau in 1883 was a turning point in the history of communications. For the first time, a major event was described and communicated almost instantaneously around the world using the newly laid sub-marine telegraphic cables. Even before this fifth most powerful eruption in recorded history had turned sunsets red, the news of the cataclysm taking place in the remote Sunda Strait (between Java and Sumatra) was known in London. The eruption blasted away most of the island. The resultant landslide, the collapse of the northern part of Krakatau into the sea created a mammoth tsunami (Francis 1985) that peak at 40 m when it struck land. It destroyed many villages on nearby islands and killed more than 36,000 people.

Most of the pumice fell in the sea where it floated for months; some nearly sank ships that were unable to flee or that were trying to document the horrors. The force of the blast sterilized the remnant cones and many pyroclastic flows reached Sumatra. Pressure waves from the final, cataclysmic explosion were recorded everywhere and circled the globe seven times; ash was injected into the atmosphere to at least 80 km. A dense mass of tephra also fell on the Sumatran town of Kaitibung, killing about 1000 people. It is believed that it could only have been from a lateral blast that crossed the strait.

Biological recovery on the slopes of Krakatau and on those of the cone that emerged from its caldera ("Anak Krakatau", or Child of Krakatau) was rapid and the subject of several major expeditions (Whittaker and Fernández-Palacios 2007). The tropical conditions and dense forests on surrounding islands allowed vegetation to recover relatively rapidly, but colonization was selective and forests bear little resemblance to those of the surrounding islands. The number of plant species on the remnant of Krakatau, continues to increase and is far from an equilibrium between colonization and local extinction.

Against all expectations considering the utter devastation and isolation, scientific studies of Krakatau started within three years and have produced major insights into island biogeography and succession. Long-term studies on Krakatau set a very high bar indeed. However, Mount St. Helens has now become the "type" location for directed volcanic blasts. It is on land, near urban and research centers and surrounded by an existing road system. These factors helped to ensure that this volcano became the most intensely and extensively studied one on the planet. No place on earth has been subjected to such scrutiny from geologists of all kinds and by biologists of every persuasion.

Historical lava flows

Lava (from Italian, labes, a falling, coined by Francesco Serao upon observing an eruption of Vesuvius in 1737) forms hard rock that is difficult for plants to colonize. Studies of vegetation on lava are the source of the generality that succession on volcanoes starts with either lichens (dry) or mosses (wet). Smooth (Hawaiian, *pahoehoe*) lava is more difficult to colonize than rough (Hawaiian, *a'a*) lava. The surface differences mean that succession will proceed more rapidly in *a'a* lava because seeds can lodge in the cracks (Fig. 4.1).

Fig. 4.1. *Pahoehoe lava on Hawai'i, with vegetation in cracks.*

While many lava flows have affected recent human history, two distressed Europe greatly. Mount Etna, a nearly continuously erupting volcano forms the northeast corner of Sicily. It is the tallest active volcano in Europe (3329 m and growing; Fig. 4.2). Its eruptive history is well dated in church records, and it is a focus of Sicilian culture. Its lava weathers slowly to form fertile soil that sustains productive vineyards and citrus orchards. The most prominent of the flows occurring since Ionian Greeks founded *Magna Graecia* (8th century B.C.) occurred in 1669 when earthquakes proclaimed an eruption heard across the Strait of Messina in Calabria. A mass of lava over 3 km wide reached the Sicilian city of Catania where newly built 20-m-high walls diverted it into the harbor. Over 50 villages between Catania and the vents were destroyed, and many farms were buried. Today, this lava is mined to pave streets throughout eastern Sicily.

Fig. 4.2. *House buried in lava from 1983 eruption of Mt. Etna.*

The Icelandic fissure volcano Laki produced the deadliest eruption in history starting on June 8, 1783. Most fatalities were indirect, related to the crop failures caused by climatic cooling effects of the sulfuric and ash clouds in Iceland and northern Europe (Fig. 4.3). A 25 km long fissure opened to extrude 14 km^3 of lava that covered over 150 km^2 and melted vast quantities of Vatnajökull (River of Glaciers). The resultant massive jökulhlaup (glacial outburst flood) destroyed much of Iceland's agriculture. The lava filled a river valley to overflowing, and replaced a lake. It buried 20 villages and the land that sustained them. Nothing of this magnitude has occurred elsewhere in the recent human experience.

Fig. 4.3. Lava from one of many eruptions of Volcano Hekla on Iceland.

The vegetation removal zone

The blast zone of Mount St. Helens is complex and includes three regions based on the intensity of the effects: the blown-down zone, in which succession commenced quickly, the pyroclastic zone that was completely removed and hot deposits laid down and the vegetation removal zone, that region from which all vegetation was removed by the directed blast, but which escaped pyroclastic deposits. The force of the blast revealed old lavas in places, but most sites received tephra deposits that buried the older surfaces.

Fig. 4.4. July 27, 2001 was the first great year for prairie lupines in the pumice zone. This species needed about 20 years to become abundant in this area; it now fluctuates on a 3 to 4 year cycle due to life history characteristics, herbivory and parasitism.

The vegetation removal zone has three units that differ in the nature of the habitat, landscape effects and subsequent impacts. Below the cone, the gentle topography that extends to Spirit Lake and to abrupt lava ridges is the Pumice Plain. The central part of this plain, the pyroclastic zone, experienced many pyroclastic flows. To the east, terminating at Windy Ridge and Windy Pass, is the pumice zone, which includes all parts of the Pumice Plain unaffected by pyroclastic flows (Fig. 4.4). It did suffer the direct blast and received deep deposits of large pumice chunks. It became dissected by spring-fed streams and

Fig. 4.5. Thirty *years after the eruption, the vegetation on the Plains of Abraham remains barren. Scattered beardtongue and dune bentgrass dominate this vegetation. The topography is generally flat, but subtle differences in surface characteristics have allowed vegetation to differ subtly on this landscape (July 29, 2009).*

Fig. 4.6. *Along Studebaker Ridge, there is a sharp gradient of vegetation change.* Vegetation *developed slowly on this ridge, but the pace of succession was fastest at the lowest sites. Here, lava is exposed and 25 years of succession had produced only a few plants struggling to grow in favorable microsites (August 4, 2005).*

watercourses fed by snow melt. These stream beds are rocky and the feeble attempts by plants to colonize the unstable surfaces are often washed away. On steep, north-facing slopes, snow and aspect protected ground layer vegetation allowing survival in refugia.

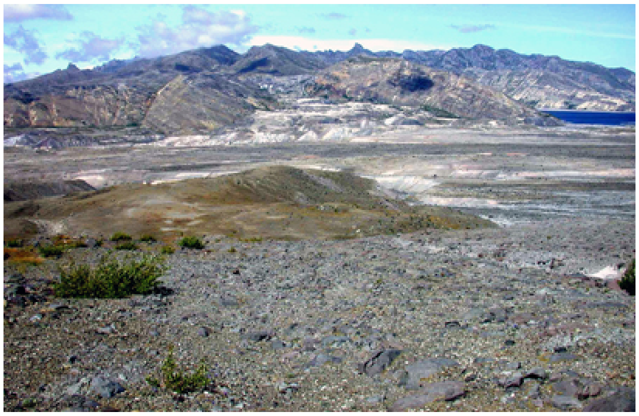

Fig. 4.7. *The view from Studebaker Ridge shows Coldwater Peak and the persistent remnants of the 1980 pyroclastic flow. Lower on the ridge, dense vegetation developed because some soil remained (July 30, 1998).*

On the east side of the cone, there is an extensive flat area that is called the Plains of Abraham (Fig. 4.8). It was denuded by the initial directed blast, scoured by lahars and buried by pumice. Subsequent erosion has created rills and channels.

Fig. 4.8. *The lava dome Studebaker Ridge shows Coldwater Peak and the persistent remnants of the 1980 pyroclastic flow. Lower on the ridge, dense vegetation developed because some soil remained (July 30, 1998).*

To the west, overlooking the pyroclastic zone and Spirit Lake, is Studebaker Ridge, where the blast exposed old andesitic lavas (Fig. 4.9). From the lower part of this ridge, the residue of the run-up of the debris avalanche on Coldwater Ridge remains clear (Fig. 4.10). Climbing further uphill, the crater of Mount St. Helens comes into view and lava becomes increasingly prominent (Fig. 4.11). Monitoring the vegetation in each barren area revealed a great deal about the dynamics of succession and has contributed much to our understanding how plant communities form.

Fig. 4.9. *While no lava was exuded in 1980, it is revealed in several places around the mountain: Top: this prominent mass of red* pahoehoe *lava is at the trailhead leading up to Butte Camp at Red Rock Pass (July 26, 1995). The rocks formed less than 1900 years ago and are covered with lichens, while most vascular plants are confined to cracks; Bottom the dark lava around Butte Camp and on ridges to the northeast remains scantily clad after centuries (July 30, 1998).*

Lava on Mount St. Helens

Most of the younger lava surfaces exposed on Mount St. Helens were produced by smooth flowing (pahoehoe) lavas. The steady erosion has exposed other types of rocks. Abrupt exposure of rock surfaces comes from such sudden events as landslides.

Lava from the 1980 eruption was confined to the new

Fig. 4.10. *We flew to the edge of the crater at the end of a long day (September 10, 1980). The dome was steaming.*

domes. Older lava is exposed around the mountain in several locations. Prominent among these are the old lava plug that forms the butte above Butte Camp and pahoehoe lava extending south from just below the cone to near the Swift reservoir. Older lava flows form much of the southeastern portion of the mountain that includes the Lava Canyon of the Muddy River. Studebaker Ridge is covered by andesite from the 1854 eruption. The Toutle River Trail that leads north from Red Rock Pass starts on a blocky, lichen encrusted lava flow that is 1900 years old (Fig. 4.9A, B). This flow underlies most of the forest area to the toe of the cone. The most visited lava feature on Mount St. Helens is, of course, Ape Cave, north of the Swift Reservoir. It is a long lava tube also formed about 1900 years ago and is composed of pahoehoe lava.

Fig. 4.11. *In more protected sites on Studebaker Ridge, vegetation developed relatively rapidly (August 12, 2008).*

The dome within the crater. The crater of Mount St. Helens is a dynamic and dangerous place. Rock falls are frequent, and landslides can be triggered by small earthquakes. Like earlier mount St. Helens cones (e.g., Goat Mountain), the crater walls partially surround a dacite lava dome emerging from the crater floor. After a few tentative starts that were terminated by explosive eruptions during the summer of 1980, the dome began to grow (Fig. 4.10). This dome-building episode continued from late 1980 to October 1986 as multiple lobes piled up into a jumble and fractured into a talus at the foot of the dome. A quiescent period was interrupted by an eruption that started in September 2004. This event deposited significant amounts of ash on nearby Studebaker Ridge, but the phase of dome growth continued for over four years.

Fig. 4.12. *High up on Studebaker Ridge, the blast removed vegetation and plants to reveal lava that is about 130 years old. Few plants could establish on this rugged terrain, even after 25 years (August 2, 2005). The newly active dome may be seen just above the crater wall.*

Against the odds, a snowfield started to form within the crater in 1980; eventually this structure became a glacier. The steep crater wall and north-facing aspect encouraged the birth of this glacier, easily the youngest in the world. Officially recognized as the Crater Glacier, it has continued to grow and has produced two lobes that encompass the crater and surround the new, larger (and hot) dome. While there is little vegetation in the crater, Jon Titus (pers. comm.) reported on six plots sampled just before the 2004 dome building. Three wetland sites had Sitka willow and wetland mosses, along with an assortment of wind-dispersed sedges, willow herbs, fireweed and even bentgrasses. Notable was the dense population of common horsetail in one plot, a single prairie lupine in another and Indian paintbrush in two plots. Although these plots were at high elevation, three species of lowland weeds, cattails and the willow were encountered. Due to the expansion of the glacier and the eruptive activity, these sites may have been destroyed. The glacier also feeds Loowit Falls (a direct drop of 57 m), which feeds a creek that has carved out Loowit Canyon, a steep, unstable feature that cuts across the pyroclastic zone, periodically flooding to create secondary disturbances.

Studebaker Ridge. The eruption blasted Studebaker Ridge, an isolated spine of lava that extends from the crater towards the northwest. It escaped pyroclastic flows and prevailing winds blew away most tephra. As a result, lava from 1854 flows was exposed. The Studebaker Ridge transect is within 2 km of the crater. Here there were no survivors and even in 1984 only a very few individuals had colonized. On the lower parts of this ridge, vegetation remained sparse for a decade before it began to develop (Fig. 4.11). Upper slope plots remain barren (Fig. 4.12).

I studied Studebaker Ridge from 1984 to 2010, describing 20 permanent plots arrayed along the ridge between 1218 and 1468 m (del Moral 2007). As you trudge up the slope, residual soil becomes a rocky lava surface and it gets steeper. The lower plots became well vegetated, while the highest plots had little plant life by 2010.

Seven plots show how richness and cover percentage changed (Fig. 4.13A, B). Lower elevation plots gathered species more quickly than did higher elevation plots, but all had stabilized by 2000. Fluctuation in richness was due to losses of short-lived species and secondary disturbances that included eruptions during 2004-2007 that produced thin deposits of fine tephra. Once a few species appeared, first prairie lupine and then wind-dispersed species, richness accumulated rapidly. As the more favorable sites were occupied, some species were excluded, and richness stabilized.

Vegetation cover lagged except in SR-1, a plot situated on a gentle slope, with some protection from the eruption. The abrupt jumps and crashes in cover were the result of the population dynamics of prairie lupine. After an initial population boom, it crashed in the face of insect herbivory. There was a significant lag in most plots between the establishment of species and their expansion. By the end of the study, there was a strong correlation between plot position (elevation) and the development of cover; all plots had increased over time, but elevation was the best predictor of vegetation development (Fig. 4.10B). Local conditions modified development patterns, so the progression is irregular. For example, SR-5 is near a small ridge with unstable, porous soil. It barely developed for many years, then unexpectedly developed swiftly. While all plots had some prairie lupine, it was a small part of the vegetation in the upper eight plots.

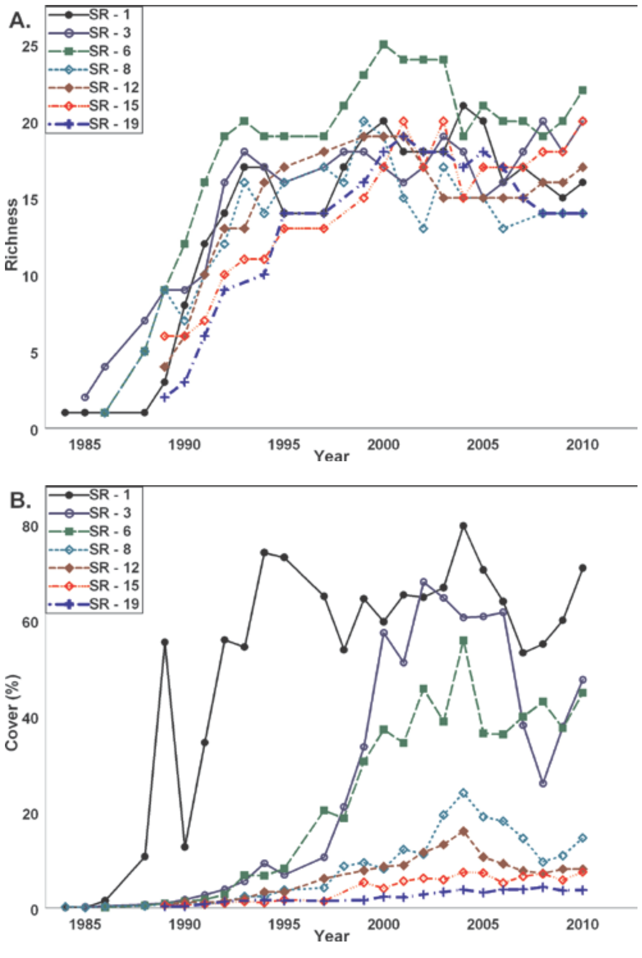

Fig. 4.13. *Vegetation structure on selected permanent plots on Studebaker Ridge: A. richness; B. cover percent. Plot numbers increase with elevation.*

Species composition changed with elevation. SR-1 started with a few scattered prairie lupines in 1984. By 2010, it was diverse, still dominated by lupines but with substantial quantities of rock moss, beardtongue, bent grasses, rushes, yarrow, strawberry and other common species. SR-8, mid-way up the slope, was barren until 1986. Initially, it had just a few scattered plants, mostly lupines and bent grass. By 2010, it had an assortment of species at low cover, with strong dominance by rock moss and willows. SR-12 quickly accumulated a diverse assemblage, but became dominated by grasses and mosses by 2010. The sparsest plot, SR-20, remained barren until 1990, when only a few wind-dispersed species were found. By 2010, it had accumulated species that included western needle grass, ferns, mosses, pussypaws, beardtongue, prairie lupine, pearly everlasting and wind-dispersed species, but none was common.

The Studebaker Ridge transect offered a way to visualize changes in space and time simultaneously (Fig.

4.14A, B). It is apparent from the graphs that vegetation structure developed more slowly as elevation increased and that species richness accumulated more rapidly than did vegetation cover. It is as if there was a wave of vegetation development progressing up the ridge.

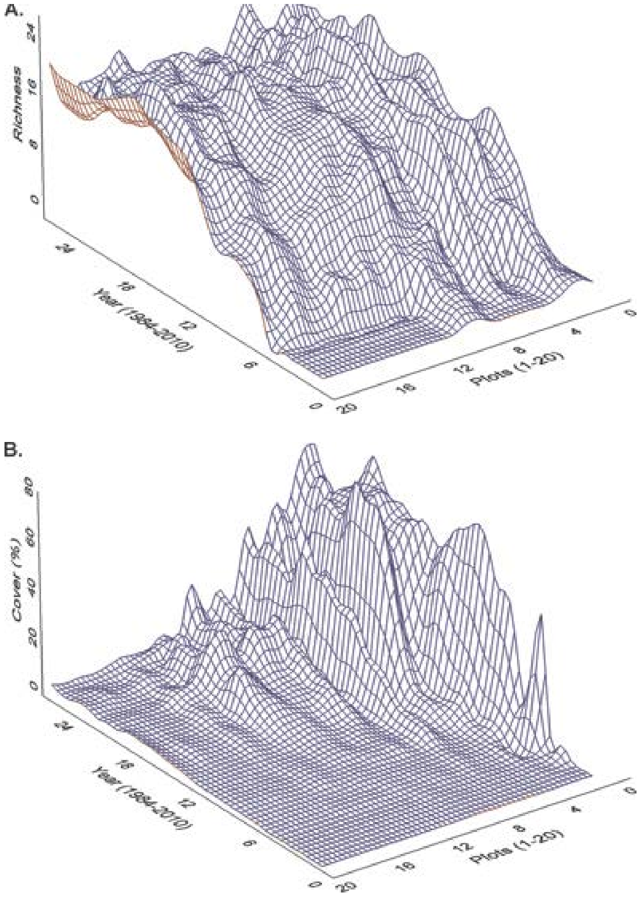

Fig. 4.14. *Space-time map of the vegetation structure of all plots on Studebaker Ridge. Each row represents one of the 20 plots while each column represents a year. Values are shown in the third dimension: A. species richness; B. percent cover.*

Composition also changed at different rates with elevation gain. In order to develop a general picture of these patterns, I classified plots in all years into communities. The method puts each sample (i.e., a plot sampled in a year) into a group of similar samples regardless of year. I expected that each plot would progress through several communities as succession proceeded. The 11 communities indeed showed a pronounced temporal developmental pattern. Most communities were ephemeral, rapidly changing into better-developed ones, while only three persisted in 2010 (Fig. 4.15). The first communities were "pioneer" types, characterized by tiny amounts of either prairie lupine or bentgrass. These communities developed into others as pioneer species became more common and when they were joined by persistent species. Later community development was driven by moss invasion. Eventually, pioneers species began to decline as late-arriving, persistent species expanded, driving conversion still further. Beardtongue and rough bentgrass developed gradually in some cases, while pussypaws became common in others. When beardtongue became dominant, it marked a community that is likely to persist until conifers become established. Stable communities found in 2010 were dominated by grasses, lupines, beardtongue and mosses. At low elevation, cover was high. At high elevation, cover was low and no species was either common or dominant.

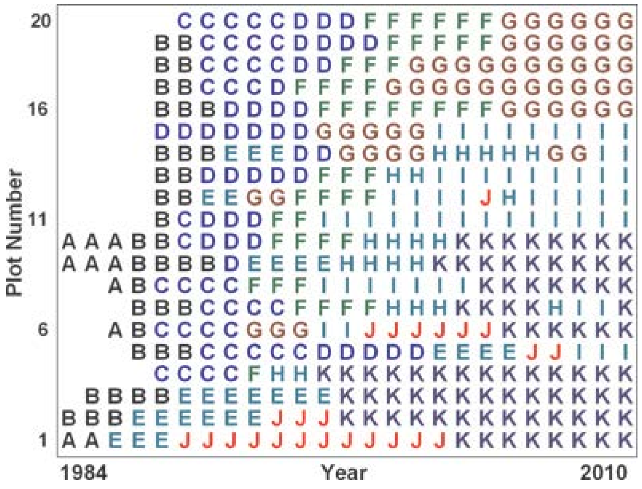

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Fig. 4.15 *Space-time map of the communities on Studebaker Ridge. Each letter designates a different community. Rows are the 20 plots, columns represents a sample year, 1984 to 2010. Communities do not change in unison; rather there is a lag moving up slope. While 11 communities were described since 1984, only three persisted to 2010.*

Each plot developed progressively through from three to seven communities, but at different rates and with different trajectories. Habitat differences associated with elevation precluded any plot from transitioning through all 11 communities. Trajectories of the plots on Studebaker Ridge, determined by detrended correspondence analysis, reflected their unique patterns (Fig. 4.16) and confirmed the degree of species composition change. The vectors of species composition change are described by the geometric (Euclidean) distance between the first and last year of this study (value in parentheses). SR-12 and SR-15 changed little. They merely accumulated a few species and increased cover slightly. SR-20 accumulated several species and developed some cover, which produced a substantial change over the study. The remaining plots had moderately long trajectories indicating a traditional successional development of gradual species accumulation and vegetative cover expansion.

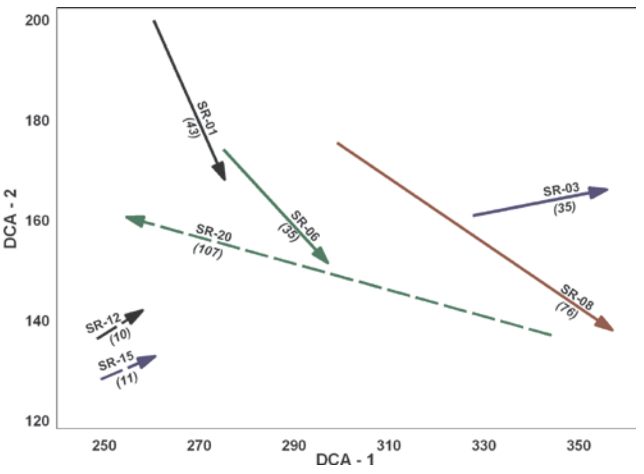

Fig. 4.16. Individual *plots on Studebaker Ridge changed as reflected by this analysis using DCA. Net trajectories for representative plots are shown here. Values in parentheses by each arrow are estimates of the distance in floristic space traversed by the represented plot.*

The results from Studebaker Ridge demonstrated the effects of initial impact intensity on the rates of recovery, superimposed on the elevation gradient. The lower plots with some residual soil recovered quickly (Fig. 17A, B). Plots lacking soil or any surviving species depended on the wind to ameliorate the surface and to introduce colonists. This produced a long and continuing assembly phase (Fig. 17C, D). Once plants established, local wind erosion slowed, wind-blown seeds were trapped and safe havens for seedlings were created. The vegetation of the high elevation plots is becoming more like that achieved in lower elevation plots. Lupines and grasses expand are expanding, which suggests that these plots eventually will become similar to lower elevation plots. However, that time is decades distant and due to environmental differences, vegetation gradients will persist.

Pumice on Mount St. Helens

Pumice across the Pumice Plain of Mount St. Helens was deposited during and after the explosive eruptions. Because heavy pieces fell to the ground quickly, the Pumice Plain and the Plains of Abraham received pumice in pieces ranging from the size of golf balls down to coarse gravel on top of any other deposit. Therefore, I distinguish the pumice fall from ash fall zones (Chapter 1). Pumice is a frothy, porous, volcanic glass that can occur as boulders, rocks, gravel or sand. It floats in water and it is highly abrasive. Pumice on Mount St. Helens was brilliantly white when formed, but over the decades, it turned cream colored and all forms gradually decomposed into sand and silt. The name comes from Latin, *pumex*, a foam or froth. Pumice mines give us "lava" soap actually formed from fine pumice as well as commercial abrasives. Pumice is mined from thick tephra deposits in volcanic areas like the Aeolian Islands of north of Sicily. If you take your dog out onto pumice, put booties on his paws.

Fig. 4.17 *Vegetation changes on Studebaker Ridge: A. Low elevation, 1984; B. Low elevation, 2008); C. High elevation, 1989; D. High elevation, 2010.*

Pumice zone. The pumice zone occupies a swath of land northeast of the crater (Fig. 4.18) not impacted by pyroclastic flows. This pumice is frothy dacite lava produced during eruptions when lava and water mix during simultaneous cooling and depressurization. After a few decades of exposure, pumice has eroded to sand, become rounded and pitted and fractured into small lumps (Fig. 4.19). The pumice zone has been more stable and resistant to erosion than the pyroclastic zone to the west. It does contain streams, deep channels and refugia (where vegetation survived the eruption). It took 20 years for significant vegetation to develop as shown by comparison of images taken in 1994 and 2010 (Fig. 4.20A, B).

A grid of 200 100 m² plots was sampled from 1989 to 2010 according to the method described in Chapter 3 (Del Moral et al. (2012). In order to grasp patterns enmeshed within this large data set, I grouped plots of the grid measured in 2010 into five communities by their species composition. One community represented relict vegetation that had survived in a deep channel. The others were on surfaces barren new pumice deposits.

The community dominated by prairie lupine and by

***Fig. 4.18**. The pumice zone lost most plant life in 1980, but by 2000 many sites were well vegetated. Here, lupines, willows and paintbrushes dominate a relatively protected site overlooking Spirit Lake (July 21, 2004).*

***Fig. 4.19**. Pumice rocks have become rounded and pitted; they have lost all their sharp edges and weathered from white to a dull cream color (August 7, 2004).*

mosses occurred in protected sites below a small ridge (A). Closely related was a community with proportionately more Cardwell's beardtongue found primarily in sites more exposed to wind (B). Grasses characterized the third community (C), which had little lupine cover and greater diversity. The fourth community (D) was next to gullies and had more amounts of fireweed and higher species richness due to invasion from the surviving vegetation. The relict community (E) was confined to gullies and was dominated by shrubs including willows, blackberries and gooseberries.

Because I sampled this 2-ha patch of pumice annually since 1989, I could track vegetation development (del Moral and Jones 2002). The vegetation was initially sparse even in relict sites (Fig. 4.21A). Richness increased through 1995, and then increased slowly. By 2004, the grid was nearly covered with plants, although some plots remained sparse. Richness in relict plots has continued to increase as barren zone species invaded along their margins. Richness began to decline after 2004 in the other communities because persistent species expanded at the expense rarer species.

***Fig. 4.20**. The pumice zone: A. sparsely vegetated (July 21, 1994); B. dense lupine population (July 16, 2010).*

The sum of the cover index also increased over time, and shows the strong effect of prairie lupine (Fig. 4.18B). Due to its short life span and to herbivory, this species is prone to periodic booms and bust. Boom years occurred in 2004, 2007 and, to a degree, 2010. Until 2002, relict plots always had greater species cover than did the others, but thereafter the patterns became more complex. Relict species suffered from browsing and frost, and did not continue to become denser after 2003. Cover in all primary sites increased. By 2010, protected sites had developed strong vegetative cover, while exposed ones remained sparse. The development of prairie lupine in most

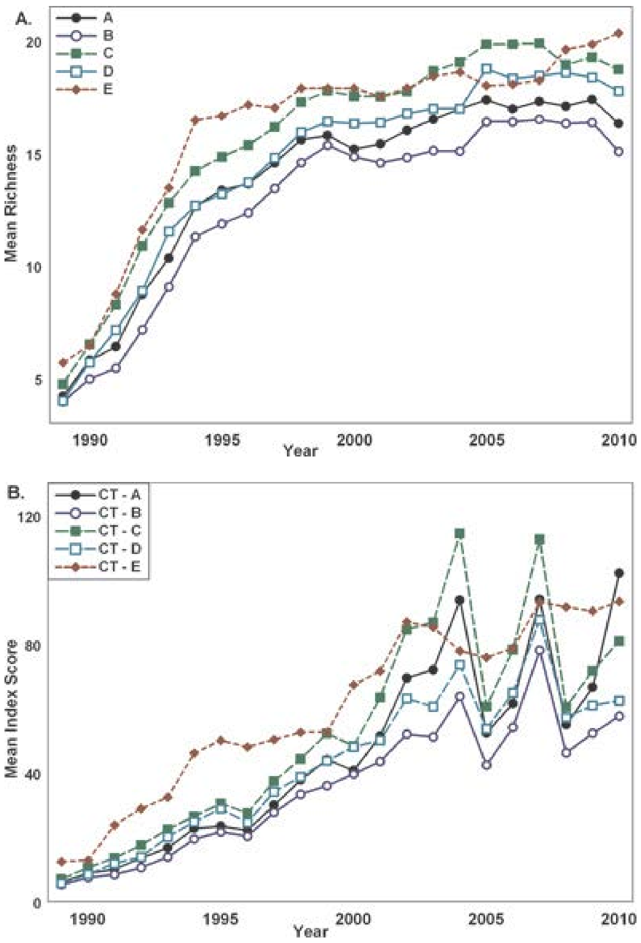

Fig. 4.21. *Development of structure on the pumice zone grid, classified into five communities based on their species composition in 2010. A. Richness; B. Sum of the cover index. (Plots in earlier years were not necessarily similar in composition to their composition in 2010.)*

plots suggested that vegetation will develop more fully and that species that require greater soil fertility will colonize. As of 2010, the stage was for colonization by several species of conifers. However, they also will require mycorrhizal spores, which remain rare.

In order to track succession changes, the entire data set, excluding the relict sites, was classified using percent cover. Seven communities resulted, but only four occurred in 2010. These communities differ from those based only on 2010 data, in part because relict sites were excluded. The plots were analyzed using DCA, and mean values of plots within a community were plotted. Each community changed significantly in DCA space over time (Fig. 4.22) indicating that species composition within a community was variable. Pioneer communities (A, B, C) were composed of sparse populations of pearly everlasting, fireweed, white-flowered hawkweed and hairy cat's ear. A plot could develop by the addition of Merten's sedge, bentgrass, beardtongue and, eventually, prairie lupine to form persistent communities. Prairie lupine was dominant in many communities (E, F, G), while willows characterized others (F). By the end of the study, community G was the most common, dominated by lupines, mosses, beardtongue grasses and scattered willows.

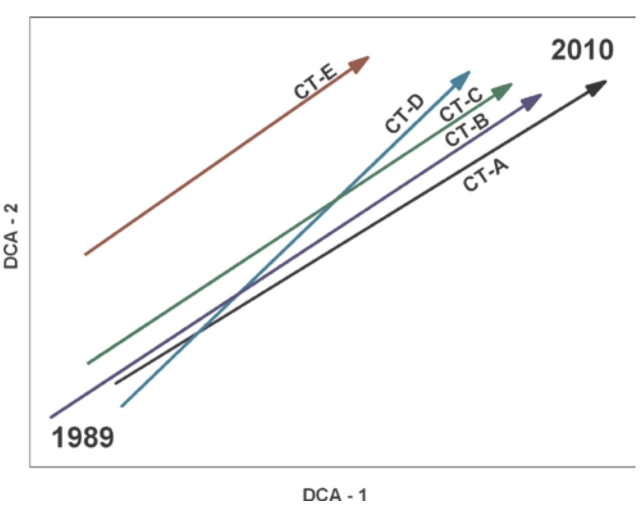

Fig. 4.22. *Trajectories of seven communities ever to occur on the pumice zone grid. Communities were determined by an analysis of each plot in each year. The length of each arrow is proportionate to the degree of change.*

While there was a trend from dominance by pioneer species to dominance by persistent ones, the trajectories did not follow predictable patterns. Each of the early communities could end as any of the persistent communities. Thus, the trajectory pattern was netlike. However, by 2010, the communities were distributed in a few contiguous blocks (Fig. 4.23), which did suggest some convergence. Although the habitat was uniform over much of the grid, different communities still appeared to occupy similar habitats. This suggested that factors other than habitat conditions were affecting species composition and permitting alternative types to occupy similar habitats.

Despite significant habitat variation and relative floristic similarity among the four persistent communities early in this study, succession trajectories suggested floristic convergence. This may be seen by comparing the position of the tails of the persistent communities with the location of their heads. This convergence was due primarily to the expansion of Parry's rush, beardtongue, prairie lupine and partridgefoot. Analyses of floristic similarity directly

2008-2010

E	E	E	E	D	D	F	G	G	G
F	F	F	D	D	G	G	G	G	G
F	F	F	E	F	G	F	F	F	F
E	F	E	F	D	F	F	F	F	F
E	F	F	D	D	F	F	F	F	F
D	F	F	F	F	E	F	E	F	F
G	F	D	G	G	F	F	F	F	F
G	G	F	G	G	G	G	E	F	F
G	G	G	F	G			F	F	F
F	G	G	F	E	F		G	F	E
G	G	G	G	F	E			G	G
G	F	F	G	G	G	G			G
E	D	G	G	G	G	G			
E	D	D	G	G	G	G			
G	G	D	G	G	G	G			
G	G	G	G	G	D	G	G		
G	G	G	G	G	G	G	G		
G	G	G	G	G	G	G	G	G	G
G	G	G	G	G	G	G	F	G	F
G	F	F	G	F	F	G	F	F	F

Fig. 4.23. *Map of communities on the pumice zone grid in 2010, excluding the relict sites, based on the analysis of mean cover in three-year increments. Although the habitat is relatively homogeneous and each community was heterogeneous, four communities persisted. Often, different communities occupied adjacent plots that appeared to share identical habitat qualities.*

demonstrated convergence in most cases whether plots were grouped by habitat or space.

Species composition over time suggests which kinds of species are better adapted to developing changes. During this grid study, percent cover in pumice plots increased from 0.9 to 24.9%, having peaked at 39.8 in 2004 due to the large jump in prairie lupine cover. The relative cover (which makes the total cover of each time-period

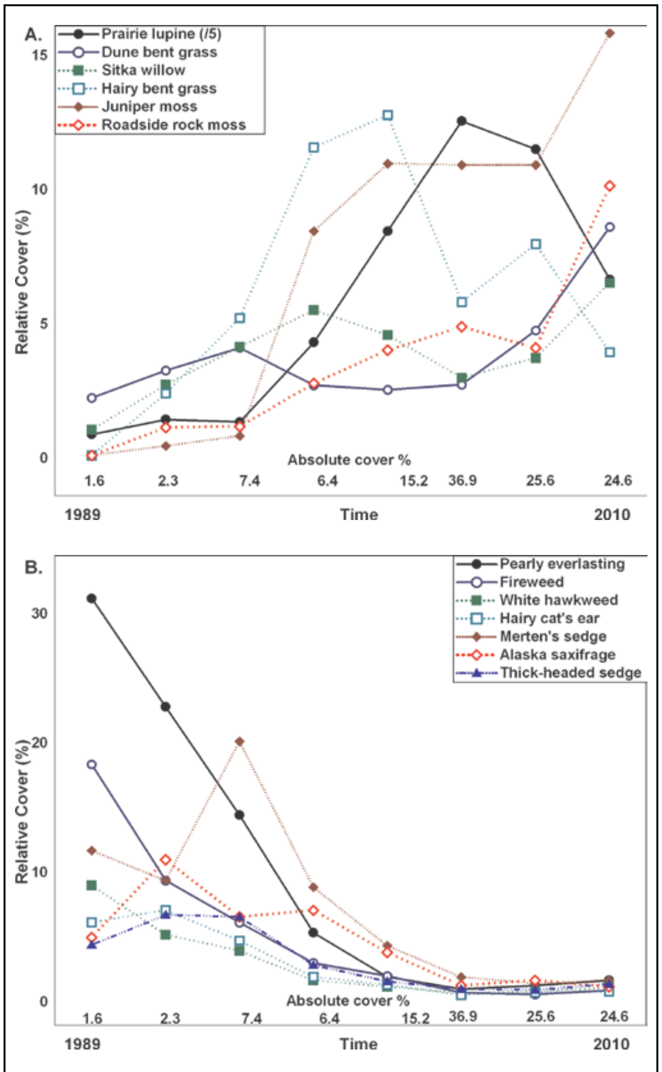

Fig. 4.24. *Changes in relative species composition on the pumice zone grid. A. Persistent species; (B) pioneer species.*

the same) of characteristic demonstrates how dominant vegetation changed from pioneer species to persistent ones. The graphs use mean values for three-year increments to reduce variation. Persistent species (Fig. 4.24A) started slowly and then accelerated. Two moss species became dominant in most plots. (Note that the values for prairie lupine were reduced by a factor of five, so that less common species could be distinguished.) All of these species also increased in absolute cover except hairy bent grass. The relative cover of pioneer species declined over time although they also increased in absolute cover for several years before they commenced a decline (Fig. 4.24B). Hawkweed and cat's ear remain prominent among the pioneer species.

Similar patterns of development were noted on the permanently marked sites arrayed on the transect of 12 plots that started above the grid and was arrayed uphill towards the cone. The plots range from 1247 to 1307 m and were monitored from 1989 to 2010. All received the blast and some pumice deposits. The lower seven plots are more exposed than the upper five plots, and PP-5 and PP-6 were also disturbed by surface water erosion. These plots demonstrate the typical pattern for relatively rapid increase in species richness (Fig. 4.25A). Richness was reduced by several repeated disturbances in PP-1 and PP-5. Richness declined slightly in PP-12 after a peak, but this may be due to rare species being masked by the dense cover of prairie lupine. Cover in all plots was low until 2000; then most plots gradually began to increase (Fig. 4.25B). Note that nearly all species had already assembled before the cover increases began. The prairie lupine began to increase in the upper plots and demonstrated its characteristic boom and bust cycle (Fig. 4.26 A, B). Species composition shifted from pioneer species to persistent ones in a pattern similar to that of the adjacent grid.

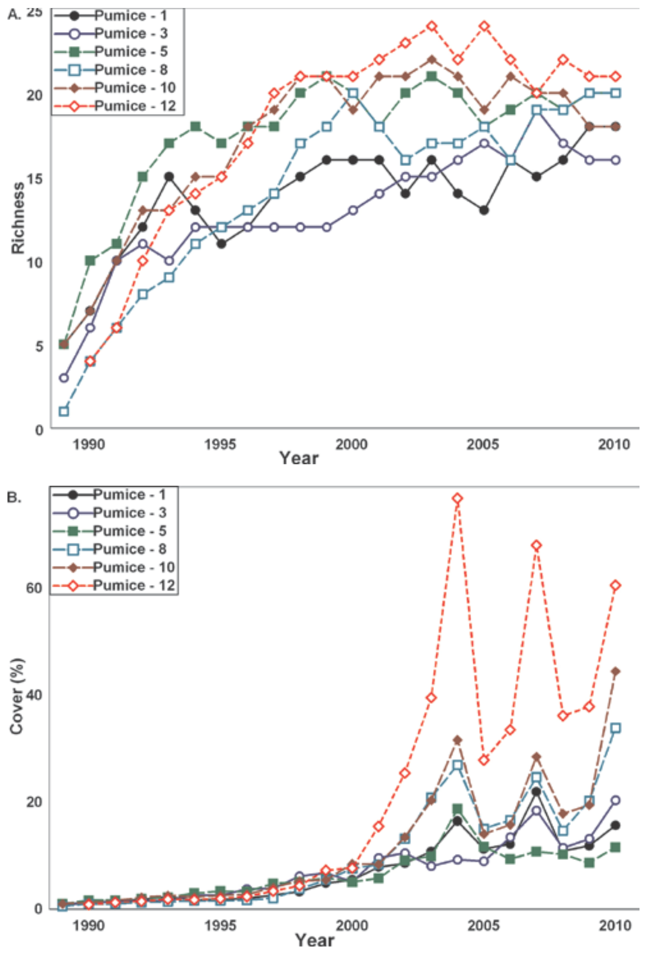

Fig. 4.25. *Vegetation structure on plots of the pumice zone: A. richness; B. cover index.*

Fig. 4.26. *Vegetation change in the upper pumice zone: A. 1989; B. 2010.*

Development on pumice reflected a universally slow initial phase. Plots had little or no vegetation after a decade, and in took several additional years for external processes to import nutrients. Gradually, as species established in better habitats, the number of species and the occupancy of space increased. Two factors accelerated the process in these isolated habitats. Adjacent to relict vegetation, species diversity was enhanced, but this factor was limited to only a few meters. Of much greater importance was the development of episodically dense prairie lupine populations that added greatly to soil fertility and offered protection for seedling establishment. Two factors served to dampen succession. Locally, secondary disturbance due to surface water erosion periodically removed some vegetation. Across the pumice zone, herbivory on willows and on lupines reduced their ability to promote further successional development.

Plains of Abraham. This exposed plateau was first as glaciers and ice fields on the adjacent slopes melted, it was scoured by hot mud slurries. This mass swept south, blasted by the scathing force of the directed blast. Then, and merged with the Muddy River Lahar. Finally, coarse pumice, having been shot high into the air, dropped relatively fine ash on to this landscape. Soon, shallow water channels formed. These multiple impacts created a flat expanse of slowly regenerating vegetation. The gullies are scoured annually, so vegetation is confined to the margins. Change over the years has been gradual (Fig. 4.27).

Fig. 4.27. *The Plains of Abraham remains barren after more than thirty years (August 17, 2011). Beardtongue, partridgefoot and Parry's rush are the dominants across the plain.*

I began studies of the Plains of Abraham in 1988 by establishing a grid of 400 plots. It was then that conditions on the eastern slope had become stable. At that time, only 121 plots had any plants whatsoever (del Moral et al. 2010). Here I add two additional years of data, but conclusions remain similar.

Succession on the very harsh Plains of Abraham has been sluggish. We should not be surprised because the eruption devastated this site in at least three intense ways, any one of which was sufficient to have removed all vegetation. Once the blast, lahars and pumice deposits subsided, wind erosion removed most of the fine tephra and water erosion carved channels across the plain. The height of the lahar across the plain can be seen on the toe of Pumice Butte and the foot of the cone where surviving vegetation, protected by snow and above the lahar line, recovered quickly. Both lupines and sedges are common on these slopes. Recovery over 30 years has left a plain more poorly vegetated than is the Pumice Plain despite similar elevations.

Unlike other sites, richness and cover on the Plains of Abraham increased at about the same pace (Fig. 4.28), primarily because most species occurred at very low density. Mean plot richness peaked in 1999 at 12 species. At that time, cover increases leveled out, although they increased slightly throughout the study. Richness declined slightly after 2000 as pioneer species began to decline, rare species were lost and new species did not invade.

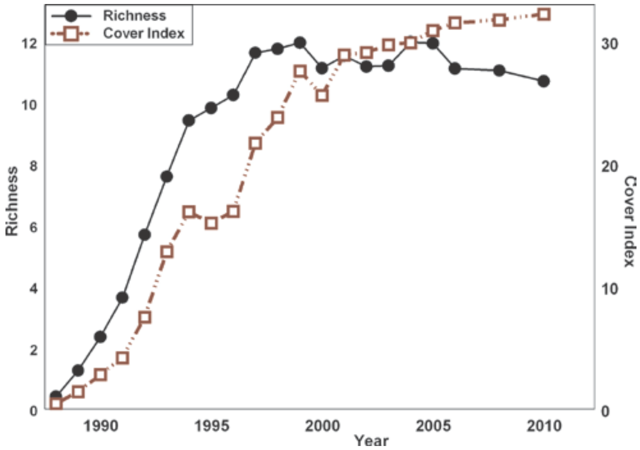

Fig. 4.28. *Vegetation structure on the Plains of Abraham grid. For many years, most species did not exceed the minimum index value, so the richness and cover index were similar until some species become more abundant.*

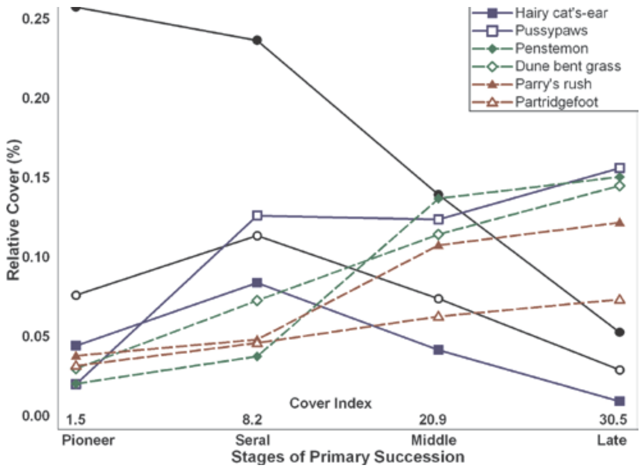

Fig. 4.29. *Changes in the relative cover of common species on the Plains of Abraham grid. Although the relative cover of some species declined, the cover index of most species increased as the vegetation developed.*

The Plains of Abraham has few lupines, unusual for recovering meadows on Mount St. Helens. Thus, patterns of invasion are clearer and not confounded by a periodically abundant species. The four pioneer species were nearly always the only plants on the Plains of Abraham during the first few years. Eventually, species that are more persistent became dominant. These species included beardtongue, Parry's rush, partridgefoot, bentgrass and pussypaws.

Sidebar 4.1. *Forced landing*

The forecast was for strong winds and clear weather all day. We roused ourselves, had a great breakfast and prepared to head for Pine Creek by helicopter. Once we got to our study site, all would be well. My team was low on the priority list, and we were assigned to a contract pilot not a Forest Service pilot. Flight rules were relaxed compared to those of the government and the pilot appeared a bit shaky. While my crew and I had turned in early at Cispus Center, along with most of the 60 other investigators, our pilot had been in Randal, the nearest town. We headed east, towards the rising sun and Mount Adams, buffeted by strong easterly winds. As we turned south to circle the crater, the winds came gusting from the side, creating a very bumpy ride. We hung on. Below, we traversed blown-down forests of Smith Creek and started to cross the Plains of Abraham. Suddenly, the pilot, fighting for control, shouted into the headphones "Hang on!", as if we were not already doing so. He turned into the wind, dropped precipitously to the barren surface and cut the engine. After a pause to let the blades stop whirling, we exited the cabin happily and relieved. We were near the southern edge of the Plain, with a spectacular view of the harsh, absolutely desolate terrain (see Frontispiece). Our nerves settled down, the wind settled down and we eventually resumed our journey. Years later, I realized that this site would be an excellent place to explore species invasions, and by then, the trail from Windy Ridge had been restored. So, in 1988 we started the grid study discussed in this chapter. I realized that had I not experienced the trauma of a forced landing, I might never have thought about this site. As it was once said about the sampling methods of the pioneering ecologist Fredrick Clements, the most important decision was where to stop the car.

Fig. S4.1. Landing on isolated ridge, September 10, 1980. RdM is resting, field assistant Nancy Weidman is working in background.

In Fig. 4.29, the developing relative cover of eight common species on the Plains of Abraham is shown. The pioneers all declined while persistent species such as Cardwell's beardtongue, dune bentgrass, Parry's rush, partridgefoot and pussypaws increased. Throughout succession to date, wind dispersed species dominated strongly. In 2010, nearly all species were wind-dispersed (a mean of 10.5 species per plot) and as of 2011, there was no evidence that bird dispersed species were colonizing. Only 0.12 species per plot was dispersed by vertebrates.

All Plains of Abraham data were classified to form ten communities, five of which persisted. Communities dominated by pioneers (fireweed and cat's ear) disappeared as persistent species slowly invaded and became dominant. These persistent plots remained relatively sparse. They all had combinations of beardtongue, bentgrass, pussypaws and rush. Sedges, partridgefoot and willows were scattered in most plots. Mosses developed slowly, in contrast to conventional theory about the role of non-vascular plants, were characteristic in some communities (e.g., H). By 2010, the grid demonstrated some spatial pattern, with plots of particular communities tending to cluster together (Fig. 4.30).

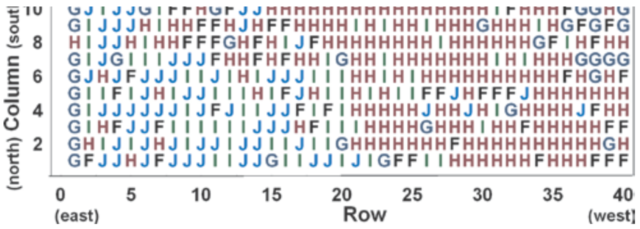

***Fig. 4.30**. Community map for the Plains of Abraham grid (2010). Five communities persist and show some relationship to habitat conditions, but several cases of distinct communities occurring surrounded by others occur, suggesting imperfect habitat to vegetation control.*

The transitions among these communities followed alternative pathways (del Moral et al. 2010). Rather than being predictable, successional trajectories developed in a complex, braided stream. Species composition in adjacent plots could change in different ways. Neither habitat factors nor species composition provided strong filters on species composition.

Relict sites in the pumice zone

A striking feature of the pumice zone is the presence of densely covered vegetation on steep north-facing slopes (Fig. 4.31A, B). This vegetation survived the direct blast and much of the tephra deposited during the early eruptions eroded down slope. Among the earliest observations across the Pumice Plain was that there were small upland islands of survivors close to Windy Pass. Much was made of these relicts and they formed a basis for developing the "legacy concept" (Franklin et al. 1985).

However, predictions that these refuge islands would be the sources for rapid colonization of the surroundings did not come true. As was later realized, the refuge contrasted dramatically with the exposed pumice. Refuges were moist, cooler, retained snow longer and receive less direct solar radiation. The surviving flora had been adapted to conditions that were shadier, cooler and wetter than conditions outside the refuge. Furthermore, conditions within the refuges changed sufficiently that, while many species persisted, they suffered, grew poorly and considerable terrain became available to invasion by species tolerant of open conditions. Therefore, refuges developed a strange and novel mixture of forest understory species and invading pioneers. The pioneers found the fertile soil a place where they could establish and produce seeds quickly, putting far more seeds into the adjacent habitats than could get there directly from distant sources. Surviving species that thrive in moist conditions, but which tolerate open, sunny environments, also became common. Prominent among these were broadleaf lupine and Indian paintbrush.

Fig. 4.31. *Relict sites escaped some effects of the 1980 eruption as soil and some vegetation survived. Top: relicts retain distinct characteristics and abundant forest understory composition, but have been invaded by barren site species (August 19, 2002); Bottom: open site dominated by beardtongue, Cascade lupine, Indian paintbrush and sedges (July 19, 2010).*

Nineteen years after the eruption, Roger Fuller and I (Fuller and del Moral 2003) sampled 37 refugia, comparing the protected vegetation with that found in nearby slopes. Many shrubs (e.g., thin-leaf huckleberry, salmonberry and red elderberry), broadleaf lupine, partridgefoot, goat's beard, willows and sedges were common survivors. In addition, beardtongue, prairie lupine, pearly everlasting, fireweed, cat's ear, Indian paintbrush and bentgrasses were common. These latter were post-eruption invaders. While refugia supported vegetation cover in excess of 80% at that time, the adjacent barrens had only 4% cover. Species that had survived in the refugia remained confined to the refugia. The proportion of wind-dispersed species increased dramatically with distance and other-dispersed species scarcely registered beyond 100 m of any refugia.

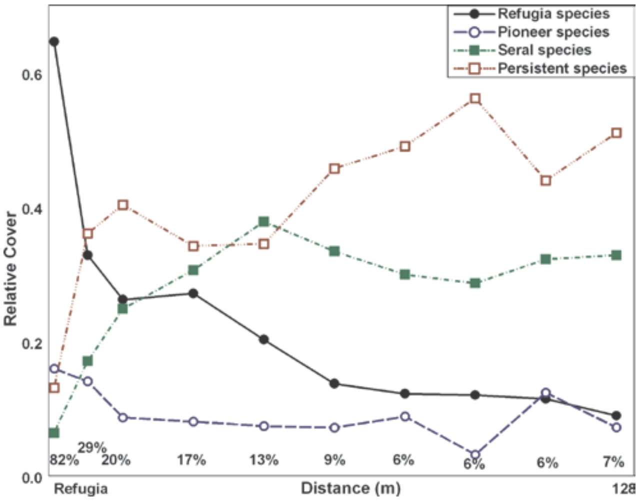

Fig. 4.32. *The effect of distance from a relict site on species composition. Plots were placed in the refuge, and at 2, 4, 8, 12, 16, 24, 32, 64 and 128 m distant. Relict species become uncommon within 2 m of a relict; seral and persistent species become more relatively more common. Cover declined from 82% in the relict to 7% over 100 m away.*

Several years later (2003), the refuges were investigated with an improved experimental design (del Moral and Eckert 2005), but the patterns and conclusions were similar. Plots were 4 m² in size and spaced to avoid statistical problems. While cover remained constant in the refugia, it had increased somewhat in the surrounding barren sites. The mean cover 4 m from refugia was a respectable 20%, but after 16 m, there were no differences in the transect.

When species were categorized by their ecological properties, another insight was revealed. The relative cover in species categorized as either pioneer, seral, persistent or relict species changed dramatically over space (Fig. 4.32), and total richness declined from 16 to 11 species per plot, then 6 within 4 m. Beyond 8 m, the number of species remained at about 3 per plot. The cover of refuge species declined to a baseline within 16 m and remained at less than 1% of the total absolute cover. By the time of the study, pioneer species had become relatively common in refugia (14% absolute cover). Beyond 4 m, their share of the community was low, less than 10%. This decline from dominance in barren sites to such low values was reflected in all long-term studies in the blast zone. The proportion of seral and persistent species increased dramatically within 8 to 16 m, and then remained constant.

Relicts do serve as a source for colonization into barrens, but the effect is restricted because the refuge harbors species poorly adapted to the stresses of the adjacent pumice barrens. Distance in general appears to limit the species composition of an isolated site.

Where to see recovering sites in the vegetation removal zone

The denuded sites are among the most interesting and widespread on Mount St. Helens. They have provided a rare glimpse of how vegetation recovers from complete destruction. The sites described in this chapter are located on ridges that bound the crater, front of the cone and on the eastern flank to the east.

Johnston Ridge Observatory: Denuded sites are accessed by hiking from the Boundary Trail #1. This joins the Hummock Trail #229, and eventually brings you across the pyroclastic zone to the pumice zone. A side trip from Willow Spring on Trial #207A takes you to the Loowit Trail #216, from which you can reach Studebaker Ridge by climbing towards the crater.

Truman Trail #207: You can reach denuded sites more easily from the east side of the Monument. Drive west from FR-25 on FR-99 26 km to Windy Ridge. The Truman Trail starts at the locked gate. Hike down the extension to the small parking area. Relict sites may be seen within 200 m. The Truman Trail travels northwest towards Spirit Lake. To reach Studebaker Ridge, continue to Willow Spring, then take the connector (Trail #207A) and follow the Loowit Trail #216 to the west. An alternative route it to ascent from the parking area via Trail #216E, which takes you through the potholes area and connects to the Loowit Trail #216. Turning west takes you below the crater and, eventually to Loowit Falls (Trail #216F). Turning right takes you over Windy Pass (not recommended for novices or the infirm) to the Plains of Abraham.

Abraham Trail #216D: To reach the Plains of Abraham, hike this trail, which joins #207 just uphill from the parking lot. This is a 3.5 km hike through interesting terrain, which rejoins Trail #216 near the edge of the Abraham grid.

Summary

Vegetation invading in the denuded zone has suggested the importance of survivors and of their being even a few particularly favorable microsites, which we called safesites (See Chapter 7). Most of the sites investigated were quite isolated, so recovery started slowly. The presence of refugia enhanced colonization slightly, but less so than was initially predicted. Proximity is only one factor that governs the rate of succession and these studies suggested several others, prominently the relative length of the growing season. On Studebaker Ridge, lower plots developed far more quickly than those at higher elevation. Even a few meters elevation gain, over which soil factors changed little, led to different succession rates. Vegetation changes gradually in time, but trajectories in similar sites do not necessarily develop in a similar fashion. These considerations will be discussed in Section II.