CHAPTER 8

The Development of Communities

Lahar 1 was quickly invaded by conifers; by 2000, the site began to shift from meadow to woodland (July 10, 2008).

Introduction

Succession starts when a few hardy seedlings poke through an inimical surface and develop sturdy roots that must cling tenaciously to the substrate. It continues as *these* enduring pioneers grow and reproduce, eventually transforming barrens into meadows. During the transition, species less adept at dispersal, but better able to establish and grow, arrive and begin to assert dominance. On Mount St. Helens, development was affected by local stresses like drought and infertility, further disturbances and landscape factors that influence the numbers and kinds of colonists. In this chapter, I describe typical developmental pathways and explore factors that control rates of change and patterns of species development.

Understanding factors that control succession rates stimulates effective restoration of wastelands like mine tailings (Walker and del Moral 2009). It is essential to understanding how climate change will affect the biota (Kapfer et al. 2012). Appreciating how rates are governed also improves methods to effectively reach specific goals in rehabilitating damaged habitats (Engel and Abella 2011).

While succession rates can be measured by changes in species composition, vegetation development is also about the recovery of ecosystem functions like productivity. Succession rate measurements can involve cover development and floristic changes over time. Assessing rates is daunting because rates vary during succession and can be erratic. Unpredictable biotic factors, like the invasion of a dominant species, may either stop the process completely or accelerate it (Prach et al. 1993). The Mount St. Helens study provides alternative ways to assess succession rates, each of which providing valid perspectives.

Ways to assess succession rates

Classification. To promote an understanding of patterns, the matrix of permanent plots by years for each set of permanent plots was classified into communities. Classification just puts samples into floristically similar groups by successively lumping them (e.g., BCA-01, 1980 with BCA-01, 1981) until all are in a single group. How plots are grouped is described by a tree-like graph called a dendrogram. I used a method called flexible beta, which uses Euclidean distance between plots to form clusters. In each analysis, samples were in the same community if their similarity exceeded 50%. The plots within communities found at the end of a study were then monitored through time to assess succession rates.

Structure. The time needed to reach the maximum species richness and stable percentage cover are two ways to judge succession rates. Trajectories may be compared directly for structure changes.

Ecological similarity. The concept of similarity (or its complement, ecological distance) is widely used in vegetation science. In comparing two pairs of plots over time, that pair which experiences the least floristic change has the higher floristic similarity and hence the slower succession rate. Different successional tracks may be assessed by comparing similarity differences during a fixed time interval (Chaideftou et al. 2012). I used Percent Similarity (PS), calculated for each plot in the study, i.e., from each year in the study to all other years. The mean value of the similarity matrix measures how much change has occurred.

Floristic turnover. An excellent way to compare floristic turnover rates is detrended correspondence analysis; 100 DCA units approximate a 50% change in species composition (Bach and Gradstein 2011). Temporal changes in this space measure succession rate (del Moral and Jones 2002). However, because cover fluctuates with weather patterns, the course of change through this constructed space is rarely smooth. Therefore, I used a second multivariate method called principal components analysis (PCA) on the first three DCA scores to find the general direction and rate of change in the trajectories. Visualize a three dimensional space (the DCA axes) and locate a plot in this space over successive years. PCA finds that line through this space that best captures the variation (see McCune and Mefford 2006). The slope of the regression is a measure of succession rate.

Changes in structure

I followed percent cover in communities as they developed. Rates were assessed by the time it took to reach 90% of the maximum cover. Cover ceases to be a good measure of rates once vegetation *becomes* dense, but does offer an assessment of that first spurt. The development of cover in representative communities from each habitat demonstrates the contrasts in development patterns (Fig. 8.1); larger symbols mark the year that 90% of maximum cover was reached. "Increments" indicate annual cover changes to the peak year.

Tephra. Most tephra communities persisted and there was little floristic turnover. Cover peaked quickly, usually by 1981, and then fluctuated in response to summer weather. By this criterion, recovery was rapid, although some gradual changes did develop as mosses and conifers expanded. The enormous cover jump from 1980 to 1981 was due to a response to nutrients released by the decay of dead, buried plants. These meadows retained their characteristics, with grasses forming a matrix for lupines and prostrate shrubs.

Scoured edges of lahars. Communities on scoured edges of lahars at Butte Camp required two decades to stabilize. Erosion from snow melt runoff periodically caused retrogression, so incremental changes were lower than at other sites. These communities were dominated by fleeceflower, beardtongue, buckwheat and bentgrass. Sites scoured at Pine Creek were more stable and their vegetation recovered by the late 1990s. The open habitats were dominated by bentgrass, lupines and mosses, while where snow accumulated, sites developed partridgefoot with Cascade lupine or with buckwheat. Cover increments were moderate.

Lahar deposits. Both plots on Lahar 1, near intact woodland, continued to develop steadily. The increases were due to subalpine fir and lodgepole pine; both plots sustained four communities during development; conifers dominated from the early 1990s on. In contrast, the isolated plots of Lahar 2 stabilized a decade earlier, but at much lower cover values. Incremental accumulation was moderate. Here, a diverse, open meadow has developed after developing through several communities to form just one. This community was dominated by fleeceflower, lupine, rush, beardtongue, yarrow and scattered conifers. Succession near the woodland was steady, with rapid accumulation of cover; plots on the isolated lahar developed at half the rate.

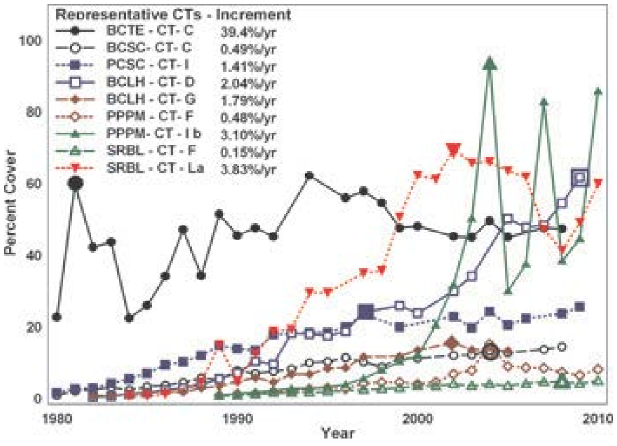

Fig. 8.1. *Cover percent in selected communities based on their final classification. Abbreviations: BC = Butte Camp; PC = Pine Creek; PZ = Pumice Zone; SR = Studebaker Ridge; TE = tephra; SC = scour; LH = lahar; PM = pumice surface; BL = blast. Large symbols indicate first occurrence of > 90% of maximum cover in that CT.*

Pumice zone. The pumice zone transect (Fig. 8.2; 8.3) had 12 plots that terminated in three communities. During succession, five other communities appeared and evaporated. These communities were dominated by pioneer species such as pearly everlasting. An immature community (F) persisted in the middle of the transect due to frequent by mud scours. It had low cover of graminoids, lupines, beardtongue and some pioneer species. At low elevation, vegetation (G) was dominated by graminoids and scattered prostrate shrubs. Cover and cover increment were low. The upper plots (I) had large cover variation due to lupines cycles. Cover increased slowly to 2000 and then accelerated. These plots developed as lupines, beardtongue, sedges, willows and mosses gained dominance. In low lupine years, community H was recognized.

Fig. 8.2. *Lower pumice zone permanent plot showed limited development after 30 years due to chronic stressful conditions. Prairie lupine was dominant, but sparse. Beardtongue, Parry's rush and bentgrass were common associates.*

Fig. 8.4. *The lowest plot on Studebaker Ridge occupies the most fertile, least stressful portion of this transect. The vegetation in 2010 was dense and dominated by prairie lupine and bentgrass.*

Studebaker Ridge. There were six communities on this high elevation, blasted ridge by the end of the study). There was a long delay before communities began to develop. The communities at lower elevation developed from immature ones. Peak cover was reached in 2002, after which the lupine bust reduced values. By 2010, cover was substantial (Fig. 8.4). Communities at high elevation developed slowly, reaching degrees of development that declined with elevation (Fig. 8.5). These communities were characterized by scattered grasses, lupines, pussypaws, rock moss and beardtongue, with low overall cover.

Community development

Once a data set was classified, the number of communities found in each plot over time was determined, and from this, the turnover rate of communities. If a plot experienced only one community, then its turnover is minimum, i.e., 1/number of years. If a plot had a new community each year, then the rate would be 1.

Butte Camp tephra. Six of 12 plots had only one community type. Three exhibited two CTs with one lasting one or two years; the remaining three lower plots changed gradually after 15 to 18 years, suggestive of a successional shift involving more conifers and denser grasses. Turnover ranged from 0.033 (no changes) to 0.089 community per year, with an average of 1.75 communities represented per plot over 29 years.

Butte Camp lahars. The plots near the woodland at Butte Camp each traversed four communities; both had been stable for well over a decade, dominated by conifers. Isolated plots also developed through four communities. Turnover was 0.178 community per year in each case. The woodland plots each developed four communities, diverging to form distinctive ones based on shifts in conifer

Fig. 8.3. *An upper pumice zone plot showed that succession has advanced to an interactive phase. Dominance was by prairie lupine, along with beardtongue and Merten's sedge.*

composition. Turnover was 0.15 community per year, similar to that of the isolated lahar.

Scoured edges of lahars. Plots on lahar edges had 2 to 4 communities. Turnover ranged from 0.033 to 0.112 community per year. The average plot experienced 2.46 communities. Surviving plants expanded and communities quickly stabilized.

Fig. 8.5. *At the upper end of the Studebaker Ridge transect, vegetation in 2010 was sparse. Only scattered pussypaws, Parry's rush and pearly everlasting characterized this plot.*

The pumice zone. The 12 pumice zone plots occupied sites subject to different subsequent disturbances and exposure. Floristic change was large, and although only nine communities were recognized, the plots changed through an average of 5.33 communities over 22 years; only three were recognized at the conclusion of the study. Less developed sites reached maximum cover by 2004, with mean turnover of 0.25 community per year. Better developed sites reached maximum cover either in 2004 or 2010, and had a mean turnover ratio of 0.307 community per year, the largest of any site.

Studebaker Ridge. The blasted Studebaker Ridge supported 20 plots that provided a gradient of impact intensity and elevation. Floristic change was gradual at first, with development correlated strongly to elevation. Development was dominated by the expansion of bentgrass and rock moss and the early establishment of lupines in less stressful sites. These plots traversed an average of 5.15 communities each. Turnover ranged from 0.162 community per year for high elevation plots to 0.292 community per year.

Similarity

The similarity between samples of a plot undergoing succession decreases with time between observations. For each plot, the mean similarity between each pair of years was determined. Plots were then grouped by their community type to determine mean similarity. Finally, the means were compared using analysis of variation to detect differences. There were three patterns (Fig. 8.6). Communities on tephra averaged 50.6% similarity, indicating little change. Lower similarities with low minimum values occurred on the all pumice zone communities and most Studebaker Ridge communities. The sites scoured by lahars at Pine Creek, lahars near woodland and low elevation sites on Studebaker Ridge had low mean similarities and very low minimum values. These results indicate that similarities had reached minimum values early in succession and indicate rapid early succession. The similarity matrices were examined to determine how long it took to reach 20%, 10% and 5% similarity (Table 8.1). The lower the proportion, the more rapidly did communities develop away from the baseline. Tephra communities each remained more than 20% similar throughout the study demonstrating little change. Communities scoured by lahars became very different from their starting point by the mid-point of the study. Only those with persistent mat forming species (e.g., partridgefoot) in late snow melt microsites remained similar to their initial conditions. Lahars deposits developed rapidly next to woodlands, more slowly beyond 100 m from the edge. The most stressful

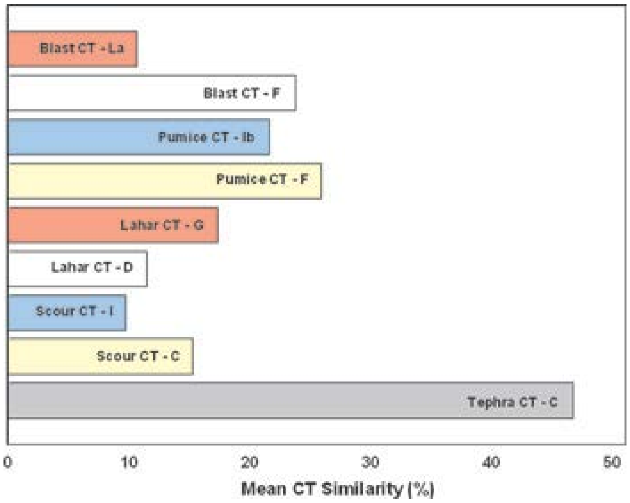

Fig. 8.6. *Mean percent similarity in representative communities. For each plot, the mean of cover similarity for all pair-wise comparisons was determined; the average for all plots in the community listed is shown.*

Table 8.1. Time required by developing vegetation to reach thresholds of similarity indicated. Data are proportion of available time to reach 20%, 10% and 5% similarity. In some cases, the community had not changed sufficiently from first measurement to reach a criterion (i.e., never). Where a community includes more than one plot, time to reach a criterion was averaged.

Community	20%	10%	5%
Butte Camp Tephra	never	never	never
BC Scours-C	0.40	0.56	0.60
BC Scours-D	0.36	0.46	0.50
PC Scours-F	0.06	0.13	0.30
PC Scours-H	never	never	never
PC Scours-I	0.10	0.27	0.36
PC Scours-J	0.23	0.50	never
Butte Camp Lahar-D	0.26	0.30	0.40
Butte Camp Lahar-E	0.28	0.37	0.47
Butte Camp Lahar-G	0.33	0.43	0.53
Pumice Zone-F	0.50	0.80	never
Pumice Zone-G	0.45	0.52	0.72
Pumice Zone-Ia	0.36	0.54	0.59
Pumice Zone-Ib	0.41	0.59	0.64
Studebaker Ridge-F	0.59	0.73	never
Studebaker Ridge-G	0.33	0.48	0.67
Studebaker Ridge –Ha	0.45	0.59	never
Studebaker Ridge -Hb	0.59	never	never
Studebaker Ridge -I	0.36	0.45	0.54
Studebaker Ridge -J	0.25	0.33	0.37
Studebaker Ridge -K	0.50	0.68	never
Studebaker Ridge -La	0.18	0.22	0.32
Studebaker Ridge -Lb	0.32	0.41	0.68

pumice zone community developed most slowly as is consistent with its chronic disturbance. The other pumice zone communities developed at rates similar to each other. High elevation communities on Studebaker Ridge rarely achieved less than 5% similarity. Lower elevation plots reached 20% similarity within the first decade of development; the most rapid development occurred in the lowest community.

Floristic turnover

Indirect ordination using DCA. The detrended correspondence analysis of all plots was conducted. Then, to determine overall changes, principal components analysis (PCA) of this DCA analysis was calculated. I plotted the regression lines of PCA scores of the representative communities (Fig. 8.7A). Steeper lines indicate more rapid change. Of the 24 analyses, 17 showed significant changes, the remaining indicted little directional change or large variation. These seven exceptions included four tephra communities, not expected to change, Lahar-G, which fluctuated significantly and the lupine-dominated Studebaker Ridge-L, which also fluctuated greatly due to lupine pulses. The lack of significant change in the regression in these cases does not mean little change. It appears from the direction of the regressions, that the primary sites are becoming floristically more similar despite occurring in different habitats.

Euclidean distance of DCA scores. These patterns become clear when the net Euclidean distance in DCA space was plotted (Fig. 8.7B). Tephra and Butte Camp scour communities changed little. Pine Creek communities, well

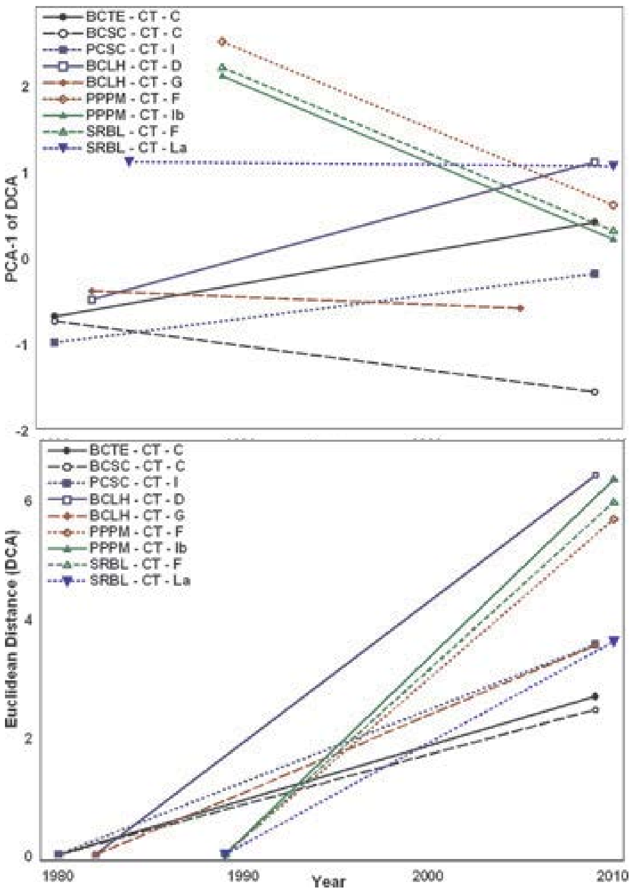

Fig. 8.7. *Floristic change of all communities in permanent plot data: Above, General Pattern of successional development based on a principal components analysis (PCA) of the detrended correspondence analysis. Lines indicate the regression of PCA axis 1 over time. Nearly level lines are not significant, either because there is little directional change (BCT-C) or because annual variation is large (SRBL-La); Below, Changes in Euclidean distance (DCA space). Each community starts at 0, and terminates in the 3 dimensional distance from that point.*

developed communities on Studebaker Ridge and the isolated lahar plots changed moderately. Stressed communities (PP-F and SR-F) changed to a large degree. Invasion of new species (e.g. conifers) caused the greatest changes.

How stress affects succession

An alternative to overall statistical analyses is to frame specific hypotheses and seek observations that test them. One hypothesis is that the length of the growing season affects the time available for species to develop competitive interactions, and hence affects the rate of succession. Plots at higher elevations, where the growing season is short due to lower temperatures, late snow melt and early frosts should develop more slowly than similar plots at lower elevations. This prediction was tested in several ways by comparing plots along elevation gradients in the pumice zone, at Studebaker Ridge and on the Muddy River lahar deposit.

Cover comparisons on permanent plots. Cover values in plots with different levels of stress show the degree to which vegetation has developed. Stress was determined in the 12 pumice zone plots based on surface and exposure factors (del Moral et al. 2012). The linear relationship between stress cover on the pumice zone transect in 2010 was strong (r^2 = 0.92). Their rate of recovery, based on cover accumulation, had been influenced by exposure to wind and the resulting drought. This transect shows that several factors can affect the growing season by altering stress levels, so indirectly affect the rate of succession.

On Studebaker Ridge, the 20 plots extended for 1 km along the ridge (from 1212 m to 1447 m). Cover of vascular plants in 2010 was substantial at lower elevation and declined sharply moving up slope. The relationship of total cover to elevation was significant (r^2 = 0.80). When only vascular plants were included, the relationship was weaker, but significant. Vegetation development on Studebaker Ridge supports the idea that the succession rate is related to elevation, which determines the growing season. Other factors, including soil development and aspect modify this response slightly.

From 2006 to 2010, I monitored vegetation of 10 plots established at 200 m intervals between 987 m and 1140 m on the Muddy River lahar deposit (Fig. 8.8; Fig. 8.9). The cover of these plots in 2010 declined substantially. This implies that vegetation development was retarded by environmental stresses associated with an elevation gain of just 260 m. The surfaces were similar along this part of the lahar. A comparison of cover in 2006 with that in the same plot in 2010, suggested that development was retarded by one year for every 25 vertical meters of elevation. The effects of increasing elevation were similar to effects of a shorter successional time.

Fig. 8.8. *Permanent plot on the lower Muddy River Transect, 2010. Several conifer saplings, including white pine and noble fir were among the rocks, while prairie lupine, beardtongue and rock moss dominated the open areas.*

Fig. 8.9. *Permanent plot on the upper Muddy River transect, 2010. Parry's rush and rock moss dominated, and, while conifer saplings occur, they have remained small and infrequent.*

Permanent plots established in 2006 on a ridge 450 m east south east of the pumice zone transect gave evidence for the direct effects of stress. Five plots in more protected sites had substantial lupine and beardtongue cover (Fig. 8.10), while five exposed plots were barren (Fig. 8.11). These were compared to the best developed vegetation on the pumice zone transect. Exposed plots had 11.8% cover (11.0 species), moderately protected plots had 34.3% cover (14.4 species) and the best protected community on the pumice transect had 71.5% cover (20.8 species). These results show the negative effects of exposure on vegetation development.

Fig. 8.10. *Protected permanent plots east of the pumice zone transect (July 20, 2010). The dense vegetation is dominated by beardtongue and bentgrass, with some prairie lupine.*

Fig. 8.11. *Permanent plots on exposed ridge east of the pumice zone transect (July 20, 2010). The sparse vegetation was dominated by prairie lupine with some beardtongue and bentgrass.*

Structure comparisons on grids. While elevation is one indicator of growing season, rates may be compared among local habitats that reflect different levels of stress. Four grids were established to provide a large number of contiguous 100 m² plots (see Del Moral and Wood 2012). They were located: on the Plains of Abraham, in the pumice zone and on both lahars at Butte Camp.

The vegetation structure of these grids suggested different levels of stress. Each site is the same age, so differences in the vegetation must be due to habitat factors and dispersal. Although the sites were isolated to different degrees from sources of colonists, all species accumulation curves all became flat by the year 2000 in each site, so that all species able to establish on a particular grid have had the opportunity.

Grids were subdivided either by their internal habitat conditions or by proximity to a forest in order to explore the effects of stress. The Plains of Abraham grid consisted of gully plots and smooth surfaces (del Moral et al. 2010). Lahar 1 was divided into plots within 70 m of the nearest forest, and those more distant. Lahar 2 was relatively homogeneous and isolated, and thus it was not subdivided. Pumice zone plots consisted of gullies, protected plots and exposed plots. For each measure of structure, I used a statistical procedure that compares the means and determines which means fall into the same group.

By any measure (e.g., infertile soils, exposed position, impact intensity), the grid on the Plains of Abraham is the most stressful. The lahars and exposed pumice are moderately stressful. They are each drought stressed and infertile. Protected pumice sites are the least stressful, having developed greater fertility and are moister. Richness is highest in pumice and pumice gullies, and moderate on lahars. The low richness value of Lahar 1 plots near the woodland is due to competitive effects of conifers, not to stress. The similarly low value of Pumice-high plots is due to their exposed habitat (Fig. 8.12A).

The mean cover index complements this interpretation (Fig. 8.12B). Clearly, vegetation on the Plains of Abraham, having achieved only half the cover of other sites, is stressed. Lahar 1 is least stressed, and has benefited from colonization by conifers. Plots that are more distant have less cover, and the exposed plots of Lahar 2 have much less cover than does Lahar 1. The pumice plots are similar to one another, but the protected plots (Pum-low) are more developed.

Isolation affects succession rates. The rate of vegetation development decelerates as distance from established vegetation increases. For example, in 2003 I described ground layer vegetation in several transects on the Muddy River lahar deposit. Ten transects were arrayed up its southeastern edge and cover was measured in five 25 m² plots placed at 50 m intervals increasingly distant from the forest edge. Cover declined regularly from 42% near the forest to 8% 250 m away. Floristic variation among the subplots of each plot increased with distance and composition shifted towards species with better dispersal. Thus, isolation alone reduced cover, allowed greater heterogeneity and altered species composition.

Another example involves potholes located in the pumice zone. Pothole vegetation developed as the sum of many discrete long-distance dispersal events, but contributions from one pothole to another were restricted. Isolation affected initial composition, which showed little pattern or repeatability, while the physical characteristics of

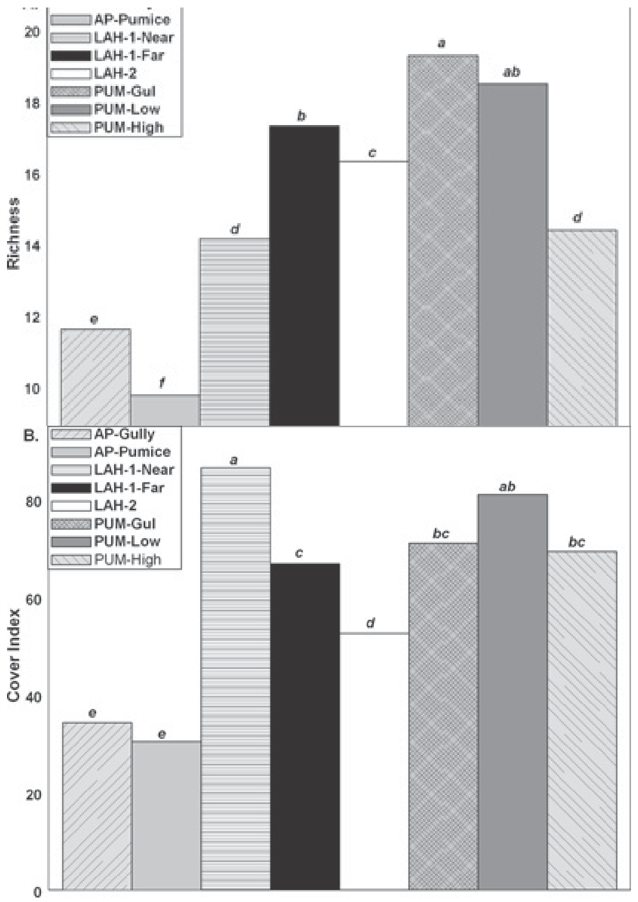

Fig. 8.12. Structural features on four grids; data segregated as follows: Plains of Abraham (AP) divided into gullies and smooth pumice sites; Lahar 1 (LAH-1), divided into plots within 70 m of the forest and those more distant; Lahar 2 (LAH-2) was not divided as plots are similar in characteristics and distance from potential colonists; pumiced zone (PUM) was divided into lower, protected sites and higher, exposed sites: A. mean species richness; B. mean cover index.

the potholes suggested that they were less stressful than the surroundings. Although variation in nearby plots of the pumice zone grid decreased, between-pothole variation remained high and changed little. The mean number of species per plot increased gradually from 1992 through 2004 when richness stabilized (Fig. 8.13A). That was the first major lupine surge in this area and it produced a decline in species richness. The richness of the pumice zone grid was typically 3 to 7 species more than that of the potholes. On the grid, once established, a species could readily spread to the surrounding grid cell, whereas the dispersal between potholes was restricted. Cover in potholes was always greater than on the pumice zone plains, presumably due to reduced stress (Fig. 8.13B).

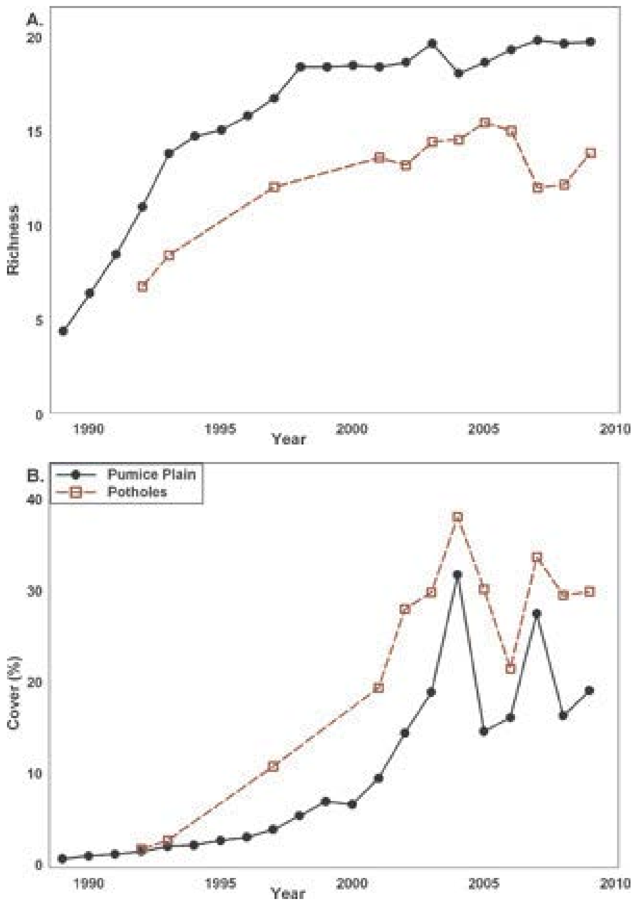

Fig. 8.13. Vegetation structure of grids (no barriers to internal migration) and (topographically isolated) potholes: A. richness; B. percent cover.

Rate assessment is conditional

The rate of succession on Mount St. Helens is controlled by stress related either to temperature or to soil infertility. It is also affected by isolation from potential colonists. Different ways to assess succession rates give different results, but each view offer insight into vegetation dynamics.

The vegetation cover and the time needed to reach stable cover are direct methods of assessment. Tephra sites quickly stabilized. These sites are not developing in response to the 1980 eruption; rather, they are merely recovering from a disturbance and perhaps resuming slow a long-term development. Plots scoured by lahars at Butte Camp continued to gain vegetation, albeit slowly by the end of the study; their rate is inhibited by repeated disturbance by water erosion. The sites scoured by the lahars overtopping Pine Creek ridge are physically stable and have not experienced recurrent disturbance; they developed more quickly and stabilized within 18 to 20 years.

Lahars at Butte Camp developed at distinctive rates. Adjacent to the woodland, recovery produced relatively dense vegetation that has yet to stabilize. The rate of succession accelerated when the shade of conifers began to influence the site. In contrast, the plots on the isolated Lahar 2 developed slowly. Sites on newly deposited pumice or newly revealed rocks demonstrated a range of patterns. On repeated erosion sites on pumice naturally arrested recovery, and after 30 years plots remained barren. Development was slow and cover was stuck at very low values on upper Studebaker Ridge plots. In contrast, the protected, higher elevation communities in the pumice zone developed quickly, with the highest ground layer cover in the study. Cover development was also rapid on the lower Studebaker Ridge plots, principally because prairie lupine developed quickly.

Similarity values give an excellent indication of succession rate. For example, slopes at Butte Camp that were scoured by lahars have higher similarities than do those at Pine Creek. Butte Camp scoured plots have experienced repeated disturbance that has suppressed development, while plots at Pine Creek developed and differentiated for many years. The high elevation plots on Studebaker Ridge have higher similarities than do those at low elevation, suggesting that they are less developed. These evaluations are mirrored by the detailed analyses of time needed to reach bench mark levels of similarity.

Principal components analysis of DCA scores, combined with the Euclidean distance traversed in this floristic space, showed that tephra sites and plots scoured by lahars at Butte Camp changed relatively little, while other scours changed to a moderate degree and lahars changed even more. Pumice zone and upper Studebaker Ridge communities all changed dramatically, indicating rapid succession.

Each approach to the evaluation of succession rates revealed different aspects of recovery on Mount St. Helens. Succession rates generally slow with elevation because growing seasons become shorter. Infertile sites lacking much soil have slower rates than rates obtained on soil. Stresses associated with exposure to wind also reduce succession rates.

The rate of succession was reduced by the isolation. The impacts of most wind-driven amelioration processes and of the density of the seed rain both decline with distance. Thus, the ability of a site far from intact vegetation to support seedlings is substantially lower than that of sites right next to intact vegetation. Distance also checks the ability of persistent, spreading species that are more poorly dispersed to encroach onto a site. The combined effects of poor amelioration, limited seed rain and slow phalanx dispersal combine to produce succession that is retarded with increasing distance from intact vegetation.

Biotic facilitation

Shifts in dominance from easily dispersed, short-lived species to those that eventually reach the site but spread primarily by vegetative means were documented previously. Perennials like beardtongue and partridgefoot can blanket the ground, but they will be replaced by taller shrubs or by conifers. These transitions are governed by many species interactions. The most easily observed involve biotic facilitation, inhibition and herbivory. These processes can occur simultaneously and form complex webs of interaction. A conifer may facilitate one herb, adapted to shade and acid soils, while inhibiting a species adapted to meadow conditions.

Facilitation often involves only physical effects such as producing shade, trapping seeds or reducing wind velocities. These create favorable moisture and enhance chances that a seedling of another species will survive. It can involve soil changes from nutrient additions, especially nitrogen. Litter can add carbon to the soil, which may subsequently improve nutrient holding and moisture trapping abilities. If these processes occur when the adverse effects of the facilitator are weak, other species will exploit the opportunity.

Lupine facilitation of seedling establishment was discussed in Chapter 7. This species facilitates growth by improving local fertility and by reducing drought. The root system stabilizes the soil and traps flowing fine dust. Even dense lupine populations facilitate mosses; other species expand when lupine populations crash. Facilitation takes precedence in young, sparse lupine colonies and in the year or two following a population crash. Overall, the longer a colony of lupines persists, the greater are the community's floristic and structural differences from the surroundings, thus marking a deflection of the succession trajectory.

Biotic interference (competition)

As species assemble and individuals mature, they must begin to interact directly. These interactions are usually antagonistic (but see Callaway and Walker 1997). Larger, more persistent individuals prevail. The results of these interactions are obvious when trees invade meadows, change the environment and exclude meadow species. Such invasions also usurp resources. While meadow species decline, forest understory species may invade the developing forest. A forest with a typical understory eventually develops.

Recovery in meadows. Interference increases in those habitats that are developing dense conifer canopies. In 2002, we compared Lahar 2 vegetation to that of nearby meadows at Butte Camp (del Moral and Ellis 2004). These meadows were present before the eruption and received limited coarse tephra deposits. Recovery from this disturbance was rapid. These comparisons provided insight into changes mediated by competition. There were 33 meadow plots and 61 Lahar plots.

In each 100-m^2 plot, we sampled 25 1-m^2 subplots. There was a high degree of overlap in species present and richness was similar in the two samples. However, total cover was 50% greater in the meadows (35.1%) than on the lahar (21.5%). Species were locally more frequent in the meadow (8.3 species per m$^{2)}$ than on the lahar (5.5 species per m^2). The lahar vegetation was more variable (42% similarity) than the meadow (57% similarity).

The bentgrass represented over 50% of the vegetation in the meadow, but only 3% on the lahar. The most abundant lahar species were prairie lupine and fleeceflower that represented only 22% and 17% of the total, respectively. Species that appear to have gained ascendancy over time included desert parsley, Ross's sedge, Parry's rush and needlegrass, all persistent species. Species that were reduced in the meadow included pioneer species such as hawkweed, cat's ear, pearly everlasting and less persistent species such as pussypaws. This comparison suggests that there is a competitive rearrangement over time.

Effects of lupines. Prairie lupines not only facilitate, they can out-compete species by denying nutrients and moisture and by casting dense shade. Lara Rozzell and I (2005) studied lupine colonies that had established at different times in the pumice zone. We identified lupine colonies that were old (Fig. 8.14), middle aged and young. For each colony, we sampled vegetation along transects within the dense colonies and in a parallel transect outside the colony. The effects of prairie lupine colonies on vegetation were complex (Gill et al. 2006). Within each age class, the similarity of species composition between colonies and adjacent barrens was relatively low and less than the internal similarity within these colonies.

Similarity within a sample increased from 40% in old colonies to 53% in young ones, suggesting that the lupines change the trajectory of succession. Mosses were denser in older colonies and rare in sparse habitats. Cat's ear persisted in old colonies, but was infrequent in young ones. This suggested that infertility in younger sites restricted some pioneer species. The mean species richness increased with colony age and was always greater than the adjacent barrens. Over time lupines constituted a declining share of cover in the barrens, suggesting that other species gain dominance if lupines remain scattered.

Fig. 8.14. *Lupine patch in the lower pumice zone transect (2007).*

The lupine patch data were analyzed using DCA. Floristic differences between dense and sparse lupine colonies in an age group were small, but significant (Table 8.2). Age class floristics differed greatly, a result of the long-term lupine effects. Old dense plots differed from mature dense plots by nearly 1 HC and from dense young plots by even more. The abundance of cat's ear, rough bentgrass, mosses, Parry's rush and squirreltail were greatest in old plots, while that of dune bentgrass and pussypaws declined with age. These differences are the drivers of successional development associated with lupines and show that they can both facilitate and alter with succession trajectories, while suppression some species.

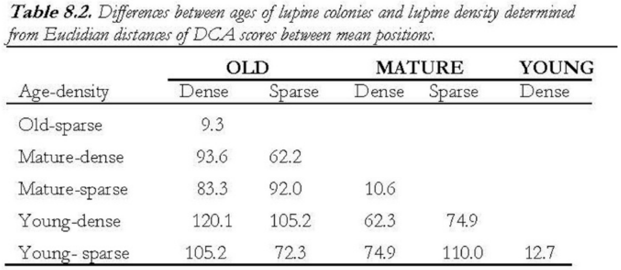

Table 8.2. *Differences between ages of lupine colonies and lupine density determined from Euclidian distances of DCA scores between mean positions.*

	OLD		MATURE		YOUNG
Age-density	Dense	Sparse	Dense	Sparse	Dense
Old-sparse	9.3				
Mature-dense	93.6	62.2			
Mature-sparse	83.3	92.0	10.6		
Young-dense	120.1	105.2	62.3	74.9	
Young- sparse	105.2	72.3	74.9	110.0	12.7

Effects of invasive species. Before the eruption, there were few invasive species at higher elevations on Mount St. Helens. Most invasive species grew along roadsides, in clear cuts and at lower elevations. Various members of the sunflower family occur sporadically in the pyroclastic zone and on low elevation lahar deposits. Without question, the most common invasive species is the nearly ubiquitous cat's ear. This species has excellent dispersal ability, is tolerant of infertile sites (but thrives with enhanced fertility) and endures competition. Sheep sorrel occurs sporadically, but when it is found, there is usually a lot of it. It is dispersed by elk. It does not persist in developing meadows or in forests. Only cat's ear appears to be able to combine with native species to form recognizable plant communities. It shares traits with white-flowered hawkweed with which it is often found. The long-term effects of this invader are unclear.

Herbivory

Mammals. The recovering vegetation suffers from significant herbivory that slows the pace of succession. Elk are abundant in most years and as they travel across the landscape, they consume much of what they see (Fleming 2011). This slows, but does not arrest the pace of development. In the winter and early spring, they browse heavily on willows, adding to the already heavy strain placed on this species by insects. Wood and Anderson (1990) noted that elk also are seed predators, particularly on aster and other species with tall inflorescences.

Small mammals, including deer mice and voles, are quite abundant, particularly in wetlands and the adjacent sites. These species consume large quantities of seeds. They also appear to browse conifer seedlings and may be one reason that conifers have had difficulty becoming established in pumice and pyroclastic zones.

Insects. Most work on herbivory in succession on Mount St. Helens has involved prairie lupine. Studies of the Sitka willow have been conducted, but remain unpublished. Most of this work has been organized by John Bishop (see Fagan and Bishop 2000, Bishop et al. 2005). The prairie lupine attracts many consumers. These include root-boring larvae of two moth species, aphids, cutworms, leaf-mining caterpillars and several kinds of seed predators (Bishop 2002, Fagan et al. 2004, Bishop et al. 2005). The effects on lupines vary by type of consumer, year and, surprisingly, the density of the lupine colony. Plants in young colonies or in sparse densities suffered dramatically more than those in older, denser colonies. Although individual prairie lupines rarely survive for more than seven years, it appears that the suite of consumers radically alter mortality patterns. To the extent that lupines facilitate succession by improving the soil, the consumers of lupines retard, but do not stop succession. Prairie lupines achieved landscape dominance despite the adverse effects of consumers. They continue to play a pivotal role in succession across most of the pumice zone.

The *Sitka* willow, dominant in wetlands, also spreads vigorously by seeds into uplands (Fig. 8.15). Some think that were it not for the introduced stem-borer (*Cryptorhynchus lapathi*); willows would be abundant across the Pumice Plain. Instead, while widespread, it is rarely large or reproductive. Plants only a few years old are attacked by the stem borer and killed. Thus, willows appear to persist in the uplands by virtue of a continuous rescue effect. Plants struggle to establish and rarely produce seeds before they succumb to the stem borer. It is because willows thrive in nearby wetlands and have exceptional powers of dispersal that they remain common across the Pumice Plain.

Fig. 8.15. *One of many struggling Sitka willows surviving in the pumice zone. Note the several dead shoots, a result of herbivory.*

Summary

Many factors affect succession rates on primary surfaces of Mount St. Helens. Some act by affecting the growth rates. Succession occurs more rapidly at lower elevations than at higher ones and in protected sites than in exposed ones. Soil infertility restricts development. When lupines invade, the pace of succession accelerates and its course changes. Similar habitats can develop differently if they occupy different landscape situations. Once the vegetation becomes dense, plants can interact. Plants can alter their surroundings to create less hostile microsites and facilitate seedling growth. The most important facilitator is prairie lupine, but its effects are complex; lupines alter species composition and the rate of succession.

Sidebar 8.1. *The trail of terror* (2002)

The narrow dirt road (Truman Trail, or the 99-road extension) down from Windy Ridge once provided access to the western side of Spirit Lake. It was maintained by the Corps of Engineers and extended across the pyroclastic zone near the western edge of Spirit Lake. Due to the danger that the dam formed of debris might collapse to produce another massive lahar, the lake had to be lowered. The Corps first started to pump water out of Spirit Lake and then burrowed a tunnel through a bedrock ridge to permanently lower its level. Once the drilling was complete, the road was left to disintegrate, so that today vehicles cannot go beyond the small parking lot at the start of the Truman Trail. Closed to public vehicular traffic, it is used by researchers and Monument personnel. The 3.5 km from Windy Ridge was scarcely maintained due to budget constraints. Each season was different, depending on erosion, ad hoc repairs and the good will of maintenance personnel. This led to recognition of what I called the Five Terror spots. Each presented a unique driving challenge going in and coming out. One had a chronic pumice slide that meant that the vehicle moved through soft gravel and about a 15-degree angle (which seemed like more). Another combined a short radius hairpin turn with a gully on a steep grade. A third was just a water hazard, spawned by a spring, which sustained a developing wetland (Fig. S8.1). I had driven this road many times each season and really had stopped thinking about the sheer, eroding, slope on one side and the absence of any safety barrier whatsoever. In 2002, after a long day in the pumice zone, six of us crawled into our SUV. I drove, with two next to me and three in the back. As we started up, there were simultaneous wails from the back seat and person next to me. Two of my assistants were suffering acrophobic panic attacks. Steep slope on the right, wetland and cliff on the left, no problem, all is under control. Suddenly, my seatmate grabbed the wheel and tried to swing it away from the steep slope…and into wetland and cliff wall. I regained control, stopped the car to let everyone calm down. It turned out that if you are singing you are unlikely to realize your situation, so the SUV was filled with raucous opera songs until we passed the five terror spots and reached Windy Ridge. Acrophobia means a fear of the edge, or peak. It is irrational and leads to panic. Only about 3% of the population is affected. What are the odds that 33% in the SUV would be afflicted?

***Fig. S8.1**. The trail of terror occupies the last km of the road from the road from Windy Ridge to the Pumice Plain. This spot is the water hazard, a wetland developing in a seep.*