

LESSONS FOR RESTORATION OF PROTECTED LANDS

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ABSTRACT

Primary succession requires amelioration, dispersal, establishment and development. Biotic interactions, landscape effects, changing safe-site qualities and chance all affect succession. Studies on many volcanoes (e.g. Etna, Fuji, St. Helens, Ksudach, Tarawera and Kilauea) reveal lessons to improve restoration of damaged habitats within protected areas. Successional trajectories develop at different rates due to stress and in alternative directions due to priority effects and dispersal limitations. Natural mosaics are the result. Recovery from major disturbances can be hastened by alleviating stress through appropriate fertilization, while taking care to avoid competitive effects. Even very short distances limit dispersal of most species, so managers must continually facilitated dispersal. Competition and herbivory can retard and deflect succession, so active management may be needed. Natural processes can produce several alternative, stable, but still natural, plant communities, so a mosaic of vegetation in protected natural areas should be encouraged. Monitoring through permanent plots is required to detect invasions by alien species and responses to climatic changes. The information from long-term monitoring has deepened the understanding of succession processes and can lead to more effective vegetation management.

KEYWORDS: Mount St. Helens, Plant dispersal, Primary succession, Volcanoes.

INTRODUCTION

Volcanoes occur throughout the world, at all latitudes and in most climates. They are concentrated on islands associated with spreading seafloors (Iceland; Rift Valley of Africa), where continental plates meet (the Sunda Arc near Indonesia; west coast of South America) and over geological hotspots (Galapagos Islands, Réunion, Yellowstone Park). Volcanoes are very diverse in

their environments. Mt. Etna, formed by the collision of Africa and Europe is in a Mediterranean climate (POLI MARCHESE & GRILLO, 2000). Mt. Kilauea, a young hot spot volcano is tropical at its base, alpine at its summit and supports rainforests and deserts (KITAYAMA *et al.*, 1995). Mt. Tarawera occurs in a populated warm temperate zone (CLARKSON & CLARKSON, 1995). Japan's Mt. Fuji reaches to permanent snows from a subtropical habitat (MASUZAWA, 1985) and is climbed by thousands of pilgrims each year. Mt. Ksudach, at the tip of the Kamchatka Peninsula is in a harsh, remote continental, sub-boreal zone (GRISHIN *et al.*, 1996) and is rarely visited. Mount St. Helens, in a cool temperate coniferous zone is the most studied volcano on the planet (DEL MORAL *et al.*, 2005). The biota of many volcanoes is protected by regulations, while others are protected by their isolation. Most have no legal or practical protection.

Volcanoes are important to biological complexity because they can provide refugia for many species, and their environments contrast with the surroundings. They also offer recreation and tourism values. Studies on many volcanoes have led to greater understanding of primary succession (cf. WALKER & DEL MORAL, 2003; DEL MORAL & WALKER, 2007), but more importantly, such studies are leading to greater understanding of restoration (WALKER *et al.*, 2006; DEL MORAL *et al.*, 2006). Without fundamental research into the

mechanisms of succession, restoration efforts will be inefficient and often unsuccessful.

This paper summarizes lessons learned during 26 years of study on Mount St. Helens. I will describe how some of these lessons can be applied to returning derelict lands to productive and efficient ecosystems.

SUCCESSIONAL MECHANISMS

The outline of primary succession mechanisms (Fig. 1) shows critical points, sometimes called bottlenecks, where community assembly may be delayed by natural processes or assisted by management efforts. Plant establishment after a major disturbance normally requires physical amelioration before colonizing seeds can survive. Nutrients may arrive as dust, pollen, non-viable seeds, excreta of passing birds or large animals and even in the form of insects and spiders who soon perish after descending into an inhospitable landscape. Erosion may remove unstable substrates to reveal suitable terrain, while cracks may develop to trap seeds. Such safe-sites are crucial in the early stages of community assembly.

Dispersal mechanisms continually feed the new landscape. At first, seeds are rare, and their main effect is to add nutrients to the substrate. The species pool is more limited than is usually appreciated (cf. DEL MORAL & ECKERT,

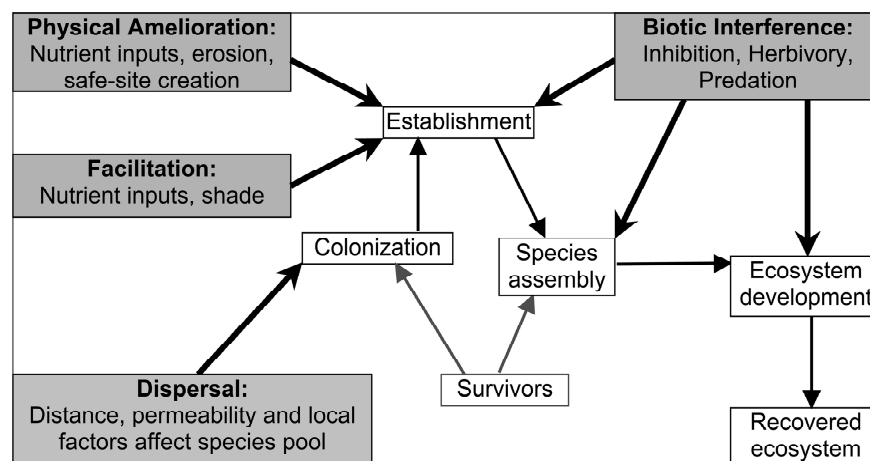


Fig. 1 - Mechanisms of primary succession, determined from studies on Mount St. Helens.

2004). A few tens of meters is sufficient to isolate a site from most invaders and distance alone leads to substantial heterogeneity in early communities because the seed rain is sparse and capricious (DEL MORAL & ELLIS, 2004). Landscapes differ in the degree to which they resist dispersal (called permeability). If favorable microsites dot the site, then dispersal will be more efficient (JONES & DEL MORAL, 2005). Wind direction, animal vectors and the local presence of species adapted to stressful conditions are among factors that affect dispersal rates and hence colonization.

In some sites, patches of survivors occur in refugia. On volcanoes, refugia occur on high ground that does not receive lava flows or on slopes protected from eruptive blasts. Survivors may contribute disproportionately to early colonization (FRANKLIN & MACMAHON, 2000), but this effect is restricted where surviving species are poorly adapted to the stressful conditions found after a major disturbance.

Once physical amelioration and dispersal have set the stage, seedlings can begin to establish. Survival may be enhanced by other species (facilitation), but the balance between positive and negative effects of neighbors is complex (WALKER, 1993; CALLAWAY & WALKER, 1997; BELLINGHAM *et al.*, 2001). Nutrient status, drought stress, plant density and substrate age are a few factors that determine this balance (DEL MORAL & ROZZELL, 2005). As the first colonists mature, they alter conditions so that additional colonists can estab-

lish. In addition, competitive inhibition, herbivory and seed predation (BISHOP, 2002) affect survivorship and the relative composition of the assembling community.

The rate of succession is normally determined by environmental stress (DEL MORAL, 2006), so even when the vegetation trajectory tends towards a stable equilibrium, a mosaic develops on the landscape. The mosaic represents the same community at different stages of successional development. On Mount St. Helens, permanent plots have recorded species composition changes on a ridge near the crater since 1984. Twenty plots are arrayed between 1218 and 1468 m. While the plots suffered the same devastation, differences in elevation and residual soils have led to different rates of development. DCA was applied to the matrix of plots by years and I aggregated the plots by their composition in 2005 into four categories that were strongly correlated with elevation. During the 22 years of development, individual plots developed through several associations. Early in the process, groups were sparse and poor in species. Through time, plots underwent transitions so that by 2005, they were in three groups, and seven groups were no longer present. Group H was the least developed and occurred at the highest elevations. Group I occurred in ten intermediate sites, while Group J, containing the best developed, most diverse plots was at the lowest elevations. DCA-1 scores are a good indicator of vegetation cover and composition. The mean

scores declined most rapidly in Group J, least in Group H (Fig. 2). A linear regression of plot age with DCA was significant in each case. The relationship was strongest in the two samples of Group I in which change was greatest. Group H changes only moderately, while most of the changes in Group J occurred by 1999. Other studies on Mount St. Helens have demonstrated similar differences in development rates based on environmental stress.

The mature vegetation that forms after major disturbances is often similar to that which once occupied the site, but this is not a requirement of succession. The degree to which there are survivors from before the disturbance may reduce initial variation and increases the similarities between pre- and post-disturbance vegetation. However, many factors can cause vegetation to form a stable community distinct from its surroundings and from earlier vegetation on the site (McCUNE & ALLEN, 1985). These factors include different available species pools (due to changes in surrounding land use, invasions by exotic species, etc.), changes in climate compared to the last establishment window, differences in the intensity of the initiating disturbance, patches of surviving plants, seeds or soil, and various stochastic factors. Development rates, trajectories and stable species composition after primary succession are less predictable than after secondary succession (TURNER & DALE, 1998). The main cause of this phenomenon is that surviving organisms are a signal from the previous community that conditions development and limits developmental options.

FACTORS THAT AFFECT TRAJECTORIES

On Mount St. Helens, similar sites have not necessarily developed towards similar composition (DEL MORAL & JONES, 2002). Two physically similar sites may retain dissimilar vegetation due to priority effects related to stochastic dispersal events, small differences in distance from colonists and subsequent unusual events that are not uniformly distributed on the landscape.

PRIORITY EFFECTS

To illustrate some of these processes, I selected data from a grid of contiguous 100 m² plots that have been sampled annually since 1989 (Fig. 3). The

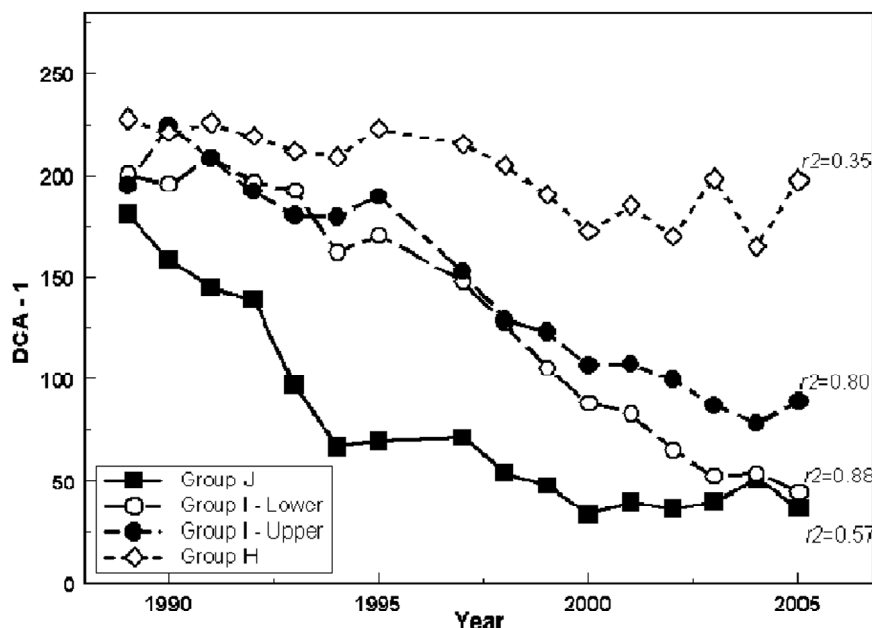


Fig. 2 - Changes in mean DCA-1 scores in four composite samples of vegetation on Studebaker Ridge, Mount St. Helens. Low elevation plots (J) changes most dramatically and stabilized by 2000; high elevation plots (H) changed little, and remain sparse. Intermediate plots (I, two samples) continue to develop; lower samples have progressed more quickly and may be converging with association J.

first five plots in each of 20 rows were analyzed in the years shown. Clearly, succession has occurred, as the strong decline in DCA-I between 1989 and 2003; then, while DCA-1 changed little, DCA-2 increased strongly. There was a decline in standard deviations consistent with convergence from 1989 to 1995, but there was an increase in 1999 as mosses began to invade. The shift in DCA-2 was due to the unexpected crash of *Lupinus lepidus*. This was the result of an unusual climatic event and to the resumption of volcanic activity in late 2004 that has inhibited mosses. These unforeseen results also led to a reduction in the SD. These data illustrate that long-term monitoring is required and that stochastic geological and climatic events can influence the trajectory of recovering vegetation.

A particular site will develop in different directions if the first colonists differ. One indication of such effects comes from comparisons of lupine colonies with adjacent sites with only sparse lupines. The colonies were stratified by age, based on work by DEL MORAL & ROZZELL (2005), who compared structural differences in lupine colonies with the adjacent sites (Tab. 1). The data for one site were frequency determinations in 500 20 by 20 cm quadrats per site. Dominance (1 - Simpson's index) and diversity (H_p) were calculated from these data. To assess the effects on other species, calculations were also made after excluding lupines.

All sparse sites had significantly lower frequencies when lupines were included; but even excepting lupines, vegetation was denser in lupine colonies. Dominance was greater only in mature sites with lupines, while excluding lupines showed only stronger dominance in young, sparse sites. Diversity was greater in mature sparse sites when lupines were included. When lupines were excluded, diversity was greater in old and young colonies. These results demonstrate that the presence of lupines facilitates vegetation development and that this effect increases with age. However, the effect is complex because mosses are the major beneficiaries of lupine presence, and they tend to restrict the development of other species.

The effect of lupines clearly influenced vegetation trajectories (Fig. 4). Lupine colony composition changed with age, as did the adjacent sparse sites. Colonies differed moderately from adjacent sites, which is an effect that was due primarily to lupines, but also to changes in species composition among

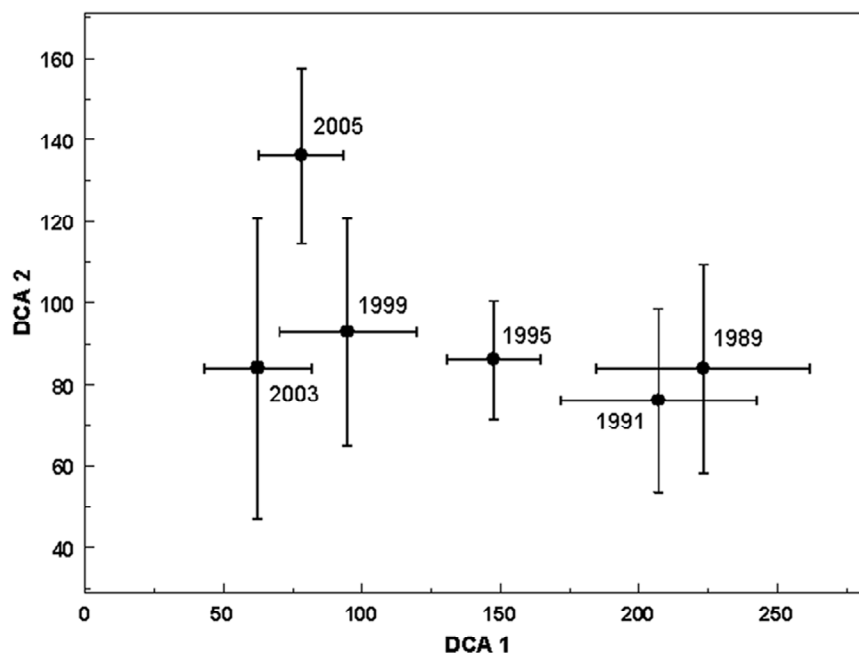


Fig. 3 - Changes in mean DCA ordination scores among contiguous plots on a sample grid, Mount St. Helens. Samples changed progressively from 1989 to 2003, then an unexpected, dramatic decline in the dominant species (*Lupinus lepidus*) resulted in a sharp deviation in the trajectory. Standard deviations remain large, indicating that convergence has not occurred.

the other species. Variation among the colonies was less than among sparse sites (note the very large SD in each set of sparse sites).

These and several other long-term studies on Mount St. Helens clearly demonstrate the importance of the species that first colonize a site. Pioneers alter the subsequent rules of establishment and affect the rate at which biomass and nutrients accumulate.

GRADIENT EFFECTS

The distance from a source of vegetation affects species composition. Based on an earlier study (FULLER & DEL MORAL, 2003), we showed that the effects of dense surviving vegetation attenuate sharply with distance (DEL MORAL & ECKERT, 2005). Beyond 8 m of surviving vegetation, there was little effect on percent cover or richness (Fig. 5) as both measures reached the background level. However, in that study, few surviving species were capable of invading the bare pumice, and the limited effect was due to pioneer species first establishing in the refugia, then dispersing copious seeds into the surroundings. The floristics changed significantly with distance from refugia, as demonstrated by DCA (Fig. 6). Sites adjacent to the refugia were diverse, but all occur on the right side of the graph, while those more distant occur scattered on the left side of the graph.

DEL MORAL & ELLIS (2004) also demonstrated the gradient effects of

distance in a different way. Four transects consisting of 100 m² plots were established at regular distances from the edge of intact vegetation on a large lahar deposited 23 years prior to the study. Transects were at increasing elevation, and thus each was more stressful than the previous. Species richness and plot cover declined with distance and with elevation. Heterogeneity (measured by percent similarity among 25 sub-samples and by standard deviations of these values) also declined significantly. Within plot similarity declined from 57.4% to 30% with elevation, while similarity between plots declined significantly (from 71.2% to 45.4%) and the SD doubled. There is no question that

Tab. 1 - Structural features within and outside of lupine patches established for over 20 years (Old), 12 to 15 years (Mature) and 5 to 10 years (Young). Data are shown for all species and without *Lupinus lepidus*. Frequency is the sum of individual percent frequency in the sample; dominance is the complement of Simpson's index and diversity is the Shannon-Wiener function.

Site	Frequency	Dominance	Diversity
All Species			
Old lupine patch	270	0.78	1.76
Old sparse site	159	0.75	1.78
Mature lupine patch	195	0.67	1.49
Mature sparse site	116	0.76	1.80
Young lupine patch	228	0.66	1.42
Young sparse site	137	0.64	1.34
No Lupines			
Old lupine patch	174	0.76	1.89
Old sparse site	121	0.70	1.67
Mature lupine patch	100	0.69	1.67
Mature sparse site	82	0.70	1.66
Young lupine patch	130	0.62	1.39
Young sparse site	87	0.50	1.14

distance alone contributes to landscape variation and to differences in successional trajectories.

UNUSUAL EVENTS

Superimposed on the effects of arrival order (priority) and landscape effects (gradually increasing isolation with disturbance size) are unpredictable and unique events. Studies by many individuals have demonstrated the wide array of these contingent events. They range from the date of the eruption at a time when much of this landscape was covered in snow and the unexplained

early arrival of *Lupinus lepidus* at a few severe, isolated sites within one year of the event. *Lupinus* has a large seed and is dispersed locally by explosive dehiscence and by ants, but the first seeds to establish on pyroclastic material crossed at least 4 km of inhospitable terrain. Many cases of unusual, even novel, and unforeseen joint occurrences of species rarely found together have been very common. The occurrence of *Lupinus latifolius* (a species of forest margins and lush meadows) with *L. lepidus*, a species of dry, subalpine habitats is most notable. These species continue to coexist at lower, drier elevations than either normally occupies and in expo-

sed habitats at higher elevations.

Most recently, an unusual climatic event occurred. Severe cold occurred above 900 m on Mount St. Helens before snow blanketed the terrain in 2004. Throughout its range, *Lupinus lepidus* (an herbaceous perennial) suffered nearly total dieback causing it to be sparse until mid-summer in 2005. The consequences of this event are still being investigated, but it appears that species suppressed by lupines expanded substantially.

LESSONS FROM LONG TERM STUDIES

THE VEGETATION MOSAIC IS NORMAL

Most mature vegetation exists as a variable mosaic. The mosaic is established early in primary succession by landscape factors that provide a heterogeneous propagule rain. Favorable microsites (safe-sites) are initially rare, so that colonization is not uniform, nor is it random. Spatial heterogeneity that affects levels of productivity and stress also contribute to the mosaic. Species composition varies and the rate of development is not synchronized on the terrain. A large suite of contingent factors enhances this mosaic. Subsequently, habitats become further differentiated by the actions of key species, of introduced herbivores and the nomadic behavior of herbivores such as elk. These large ungulates affect vegetation at Mount St. Helens in many ways, including, but not limited to, differential browsing, seed predation, internal and external seed predation, trampling, wallowing and creating safe-sites in their hoof prints.

Managers of protected landscapes should recognize that the mosaic is not only natural, but also desirable if biodiversity is to be preserved and augmented. A corollary is that there is rarely a single desirable stable end-point for vegetation. Multiple stable vegetation states have now been demonstrated in several habitats, and may well be the rule, not the exception.

DEL MORAL & LACHER (2005) reported on the vegetation pattern on Mount St. Helens after 23 years. It remains variable both between habitats and within habitats. There was substantial variation even within each of seven community types. The vegetation pattern was only loosely tied to environmental factors and these were all spatial. This result supports the hypothesis that at least during early succession, site

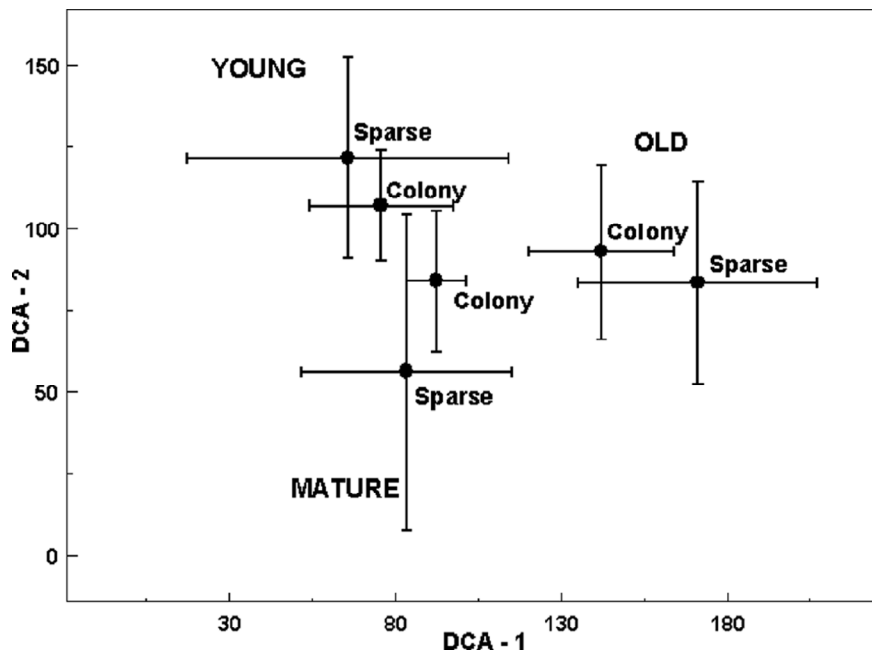


Fig. 4 - *Lupinus lepidus* affects trajectories both by the length of time it is present and by its density. Colonies and adjacent sparse sites differ strongly. Colonies are relatively similar, while adjacent sites differ from one other to a much greater degree. Sparse sites are much more variable.

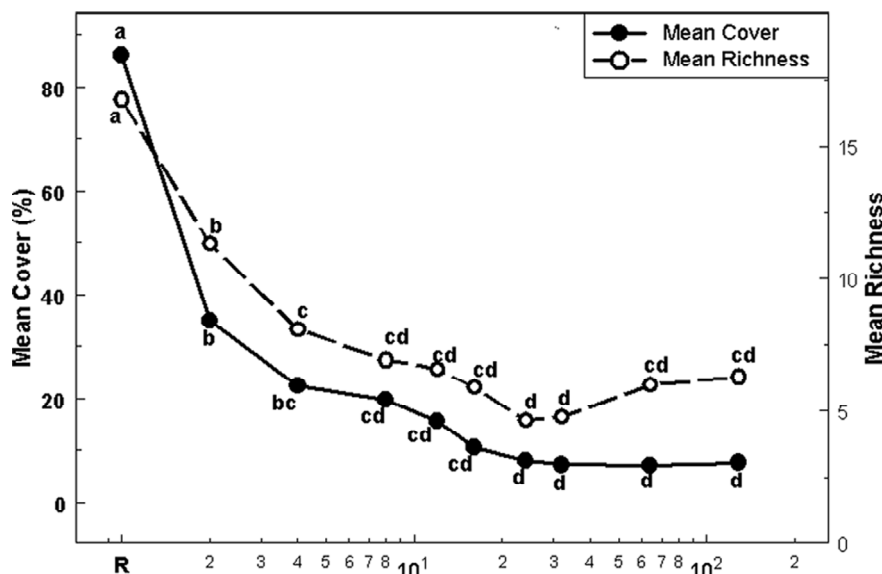


Fig. 5 - The effects of refugia on surrounding vegetation decline strongly with distance. Within 8 m of a dense colony of vegetation that survived the eruption, both cover and species richness reached a level similar to that at much larger distances. For each line, letters indicate membership in groups not distinguishable after analysis of variance, followed by a Bonferroni test.

location is the most important factor that determines species composition. Though it is too early to draw conclusions, there was no evidence that vegetation in similar habitats would converge to a relatively homogeneous state.

STRESS REDUCTION IS REQUIRED FOR INITIAL ESTABLISHMENT

Early in primary succession, nothing can occur until stress and infertility are reduced to levels where seedlings can establish. This process is initially dominated by physical processes (deposition of nutrients from outside the system, minor erosion) and usually includes a rain of such unlikely colonists as spiders. These predatory organisms soon perish, but add valuable carbon and nitrogen to the system. Restoration ecologists know that fertility must be managed for a successful outcome. However, as demonstrated where *Lupinus* achieves strong dominance, too much fertility can impede development and reduce diversity.

The conditions for establishment change as vegetation develops and the environment becomes less stressful. Where at first only a very few, particularly favorable, sites could support a successful seedling, a greater portion of the substrate becomes open to colonization as amelioration proceeds. As soon as plants establish and mature, the potential for biotic stresses to develop also increases. Not only do competitive interactions (see below) become prominent, but also herbivores begin to thrive (BISHOP, 2002), with complex implications for succession (FAGAN & BISHOP, 2000; FAGAN *et al.*, 2005). Long-term management of developing vegetation in protected areas must account for this fluctuating biotic environment.

COMPETITION AND FACILITATION OCCUR THROUGHOUT SUCCESSION

One standard concept of primary succession is that biological facilitation is crucial during the early stages and that competition is limited or balanced by other factors (KLANDERUB & TOTLAND, 2004). However, there is an increasing literature that indicates that competition is common in early succession and in stressful environments (FRANKS, 2003; TOTLAND *et al.*, 2004). The relative mix of positive and negative biotic forces changes space and time.

In the case of *Lupinus lepidus*, the accumulation of diversity and biomass

of other species may be retarded in dense patches, but promoted in adjacent sparse patches. Superimposed on this pattern is that of herbivory, which can be intense on the dense, vibrant margins of lupines, but restricted both in sparse populations and in dense, senescent colonies.

Herbivores can arrest succession by restricting facilitation effects. *Salix* spp. could develop moderately dense colonies on pumice at Mount St. Helens, but a stem borer kills most shrubs before they can produce significant facilitation for less stress-tolerant plant species. When variations in competition, facilitation and herbivory occur in both space and time, a vegetation mosaic is likely to develop and persist. A major challenge for maintaining vegetation in protected lands is to manage the biotic environment to preserve biodiversity and the vegetation mosaic.

MOSAICS PERSIST

Once formed, vegetation mosaics tend to persist through time. The effects of priority can be profound. On lahars at Mount St. Helens, mosaics have developed that appear to be stable. An open woodland consisting of several species of conifers has invaded where exposed rocks facilitated seedling establishment. The diversity of conifers, many of them already reproductive after less than 20 years, exceeds that in adjacent mature forests. Vegetation beneath the canopies is sparse and distinct from open surroundings. Where conifers have not become established, a carpet of *Raco-*

mitrium, punctuated by *Lupinus* and the prostrate shrub *Penstemon* dominate large areas. In addition, there are patches of *Populus* with a distinct understory, thickets of the nitrogen-fixing shrub *Alnus viridus* and large patches of *Arctostaphylos nevadensis* (related to *A. uva-ursi*) that cover many square meters. While some of these elements may not persist, they will alter the local course of succession. While the mosaic may or may not be permanent, it will be an important feature of the vegetation for centuries. It is neither reasonable nor desirable to suppress this heterogeneity in an attempt to hasten the development of "climax" vegetation.

Based on an exploration of montane meadows on 400 year-old lahars on Mount St. Helens, mosaics may indeed persist. Consider that conifers may invade and establish rapidly close to sources of seeds, but in many places, no seed source occurs. In these places, open meadows develop. Meadows can resist the invasion of conifers on Mount St. Helens because summers are dry and soils infertile. Conifer seeds arrive in small numbers and a few germinate. Seedlings have been noted to persist for a few years, but slow growth due to nitrogen deficient (GILL *et al.*, 2006) soils pre-dispose seedlings to death from the inevitable extreme drought. The meadows also become differentiated into patches dominated by grasses and those dominated by low woody shrubs.

MONITORING IS REQUIRED

A major lesson for proper manage-

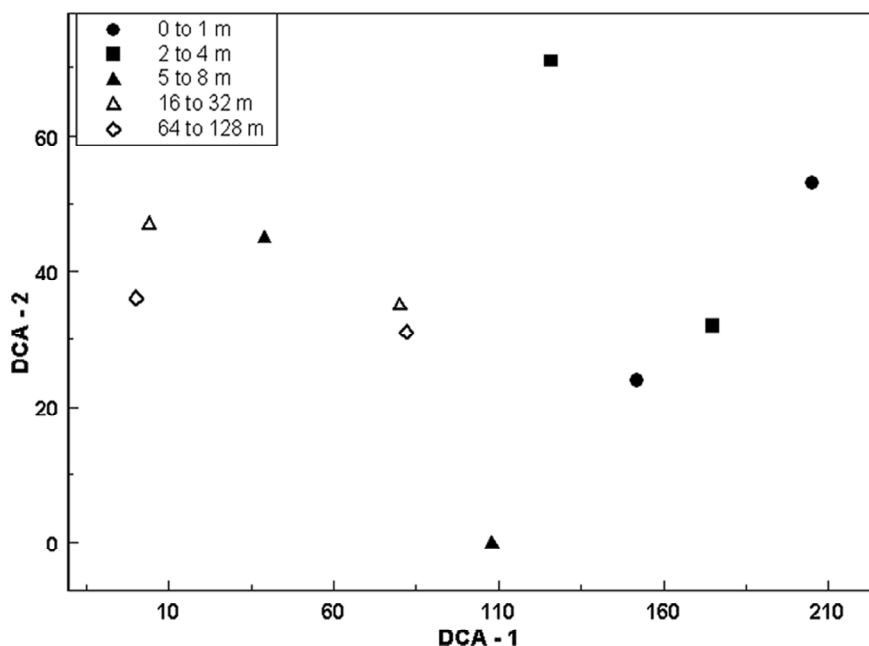


Fig. 6 - The composition of plots changed significantly with distance as shown by DCA of the mean composition. Sites 64 to 128 m distant share less than 50% of the species with those adjacent to the refugia.

ment of protected lands is that conditions must be continually monitored. Short-term fluctuations in climate, unusual disturbances (e.g., volcanic eruptions, insect plagues) can adversely affect vegetation. In some cases, remedial action may limit the damage. Monitoring can also provide crucial knowledge for restoration of damaged habitats and to curtail mechanisms that may generate undesirable deflection of succession trajectories.

Long-term monitoring also permits testing hypotheses. Short-term studies conducted under a particular set of conditions can lead to one conclusion. This conclusion may not be valid over the range of conditions to be expected over many years on a site. For example, it appeared that vegetation on a lahar at Mount St. Helens had reached a stage of very slow development and minimum heterogeneity after 20 years. However, subsequently (years 2002 and 2004 in Fig. 7), a major shift in the trajectory direction and sample heterogeneity occurred (cf. 1993 to 1999 with 2002 and 2004). In this case, an unexpected explosion in *Lupinus lepidus* in many, but not all, plots of the sample led to dramatic increases in biomass in several species. The result was dramatic. Had the study terminated in 1999, the conclusion would have been that a stable meadow community had been established and that further significant change would require the invasion of conifers.

A more important reason for monitoring is to be alerted to events triggered by global warming. Global climate

change associated with anthropogenic factors may lead to average temperature increases of 2-3 °C by 2100 (WESTOBY & BURGMAN, 2006). Such dramatic changes will require many species to migrate away from the pole or upwards (if possible). It is unlikely that species linked through facilitation, pollination or mycorrhizal association will be able to migrate at the same rates, so disruptions are inevitable. Monitoring may permit early warnings of impending disassociations so that intervention may occur. For example, species complexes could be translocated into more favorable habitats, after due considerations for rainfall patterns as well. The target species would require their associates (e.g. mycorrhizae, soil bacteria, pollinators) and would require assistance against competitors. While this is a daunting challenge, it would be impossible without long-term monitoring. The most effective method to preserve species in protected habitats is, however, not biological. Every social and political effort must be undertaken to reduce CO₂ dramatically... and soon.

CONCLUSION

The study of recovery from the effects of Mount St. Helens has many lessons for the restoration of damaged protected lands. Some lessons are cautionary, while others provide lessons for the kinds of proactive. Succession trajectories are unlikely to follow paths similar to those that previously occur-

red. Climatic factors are changing, landscape conditions differ, the biota may be different due to recent introductions and chance events may create unusual initial conditions. Thus, managers of protected lands should not attempt to force trajectories into predetermined, arbitrary paths.

Intrinsic habitat heterogeneity should be welcomed and preserved. This allows for variations in the vegetation that support biodiversity and offer a buffer to climate variation and change. Competition favors established plants, so the importance of arrival order cannot be overemphasized. The biotic variation imposed by strong competitors persists until life history events or disturbance permits transitions to other species (CONNELL & SLATYER, 1977). Initially sites are quite variable, with patterns dictated in large part by stochastic events (DEL MORAL, 1999). Eventually, deterministic processes lead to stronger relationships among species and between species and their environment. For example, in the early stages, many species can establish on a barren site, but after many years, only those that are more efficient under the developing regime can survive competition and herbivory. These processes result in associations that are more predictable, yet heterogeneity, once established, appears to persist.

Rehabilitation, restoration and protection of vegetation all require subtle and profound understanding of how communities assemble, where the bottlenecks occur and how trajectories can be modified to meet specific goals. Monitoring natural recovery from devastating disturbances has provided some of this understanding.

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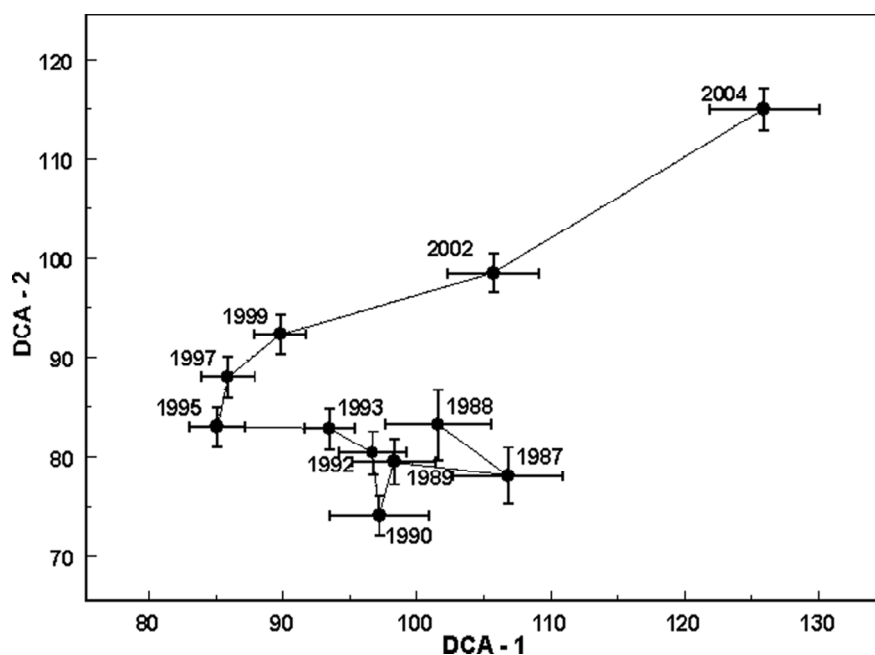


Fig. 7 - Long term monitoring can provide surprises. Repeat sampling of 64 plots on a lahar demonstrated moderate, consistent change from 1987 to 1999. Variation (standard error) decreased. However, the trajectory abruptly shifted direction and rate in 2002, and by 2004, variation was large. The years 2001 to 2004 saw more change than in all the previous changes.

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