# CHAPTER 7

# Establishment in Barren Sites

*A meandering rill, formed by gentle water erosion on nearly flat surfaces, has been colonized by species that include bent grass and beardtongue. Note that surface erosion by wind has created a densely packed layer of pumice similar to desert pavement (Abraham Plain, August 17, 2011).*

## Introduction

Having reached a barren site, the propagule is far from secure. It still must germinate, grow and mature if it is to contribute to the successional development of the site. While dispersal ability and landscape effects determine which species reach a site and in what numbers, site characteristics constitute a filter that determines which seeds will prosper. Initially, there is strong environmental resistance to seedling establishment and most seedlings perish. Eventually, erosion, importation of organic material and other factors permit the pioneering seedlings to establish. In this chapter, I describe how sites become more suitable to seedling establishment.

*Fig. 7.1. By late summer, 1980, erosion had formed small channels in the fresh silt deposit on Pine Creek Ridge. Plants relieved on the silt cover survived to a much greater degree than did those that remained covered until mid-1981.*

## Amelioration of harsh conditions

Physical changes. Erosion often delays succession, but on Mount St. Helens (Antos and Zobel 2005) and other active volcanoes (Tsuyuzaki and Hauki 2008), it can

*Fig. 7.2. Natural weathering fractured rocks to provide suitable habitat for seed germination: a. fracture lava with pearly everlasting seedling (1989).*

be the crucial first step on the path to recovery. Wind removed sterile, unstable layers of ash, leaving behind stable pebbles and a few cracks on the Plains of Abraham. Water removed silt from on Pine Creek Ridge to expose original surfaces and a few distressed plants (del Moral 1981; Fig. 7.1). Pumice rocks absorbed water that expanded as it froze in the winter. This freeze-thaw cycle fractured rocks into ever-smaller chunks, eventually to form material suitable for plant growth (Fig. 7.2). Water removed unstable surfaces to create topography where seeds might be trapped. One stable feature is a rill (small erosion channel). Such sites soon supported successful seedlings. As a seed germinates, it is protected from wind and experiences better moisture conditions. Roots can establish and are unlikely to be torn away. Because dispersal favors small, buoyant seeds that cannot survive in harsh conditions, these physical types of site improvement are critical during the early stages of succession.

*Biological input*. Conditions on newly created surfaces were remarkably harsh, so other forms of amelioration were vital for colonization to succeed. Winds usually blow from the southwest across the new landscapes of Mount St. Helens. Before reaching the devastated areas, air masses flowed over forests and clear-cuts to entrain arthropods, spiders, plant fragments and pollen as well as seeds and spores of potential colonists. Much of this flotsam reached desolate sites to enhance their fertility. If a seed happens to germinate, only to soon perish, it has at least augmented the carbon in the soil. Edwards and Sugg (1993, Sugg and Edwards 1998) estimated that 40 mg $m^{-2}$ $day^{-1}$ of dry organic matter were deposited during summer in the years after the eruption (Fig. 7.3); this is a not an inconsiderable amount.

*Fig. 7.3. Dead insect contributes essential organic matter to the barren soil (1981).*

A macabre form of nutrient accumulation occurs when carcasses decay. Parmenter (2005) studied decomposition rates of small mammals in several habitats by observing how long it took for a mouse remains to disappear. In the pyroclastic zone, rates were the least of any on the mountain; 80% of a mouse remained intact after 3 months. Eventually, the soil surrounding a carcass becomes fertile as nutrients (e.g., carbon, nitrogen and phosphorus) are released gradually. When an elk dies, the effect is, of course, much greater than when a mouse perishes and the surrounding areas bloom (Fig. 7.4).

### Amelioration of harsh initial conditions

*Physical changes*. Erosion usually has a *negative* connotation, but on Mount St. Helens and on other recently active volcanoes (Tsuyuzaki and Hauki 2008), it often was a crucial step on the path to developing vegetation. Wind removed sterile, unstable layers of fine ash, leaving behind stable pebbles and some cracks. Water removed silt deposited on Pine Creek Ridge to expose original surfaces and permit the survival of a few plants (Fig. 7.1). Large rocks absorbed water that, during the winter, expanded as it froze. This freeze-that cycle fractured pumice into ever-smaller chunks, eventually forming material suitable for plant growth (Fig. 7.2). Water also removed unstable surfaces and created topography where seeds might be trapped. One such feature is called a rill (small erosion features) and such sites soon attracted successful seedlings. Seeds are protected from wind along rill edges and experience better moisture conditions. Because dispersal favors small, buoyant seeds that cannot survive in harsh conditions, these physical forms of site improvement are critical to starting succession.

*Fig. 7.4. Remains of an elk amidst a bloom of lupines (Courtesy of Tara F. Ramsey; August, 2004).*

*Biological input.* Conditions on newly created surfaces were remarkably harsh, so other forms of amelioration were vital for colonization to succeed. Winds usually blow from the southwest across the new landscapes of Mount St. Helens. Before reaching the devastated areas, air masses flowed over forests and clear-cuts to entrain arthropods, spiders, plant fragments and pollen as well as seeds and spores of potential colonists. Much of this flotsam reached desolate sites to enhance their fertility. If a seed happens to germinate, only to soon perish, it has at least augmented the carbon in the soil. Edwards and Sugg (1993, Sugg and Edwards 1998) estimated that 40 mg $m^{-2}$ $day^{-1}$ of dry organic matter were deposited during summer in the years after the eruption (Fig. 7.3); this is a not an inconsiderable amount.

A macabre form of nutrient addition results when carcasses decay. Parmenter (2005) studied decomposition rates of small mammals in several habitats. In the Pyroclastic zone, rates were the slowest of any on the mountain, with 80% of a mouse still intact on the surface after 3 months. Eventually, the region surrounding a carcass becomes more fertile from the slow release of nutrients that include carbon, nitrogen, phosphorus and other nutrients that were almost non-existent. When an elk dies, the surrounding areas eventually bloom (Fig. 7.4).

*Input from disseminules themselves.* Seeds and spores dispersed by the wind will be deposited on landscapes in accordance with physical processes associated with wind velocity and direction. The suitability of the landing site plays no role in dispersal, and most seeds die, usually without germinating. However, the mere act of dispersal also ameliorates the site by adding significant organic matter, and in the case of plants, any germination, no matter how ill fated, results in even more carbon addition to the soil.

*Fig. 7. 5. Pumice Plain elk herd at their leisure (August 18, 2011).*

*Direct nutrient inputs by animals.* Other forms of organic matter also reach isolated barren sites. Rodents, birds and other small animals produce feces and urine. Where they survived, gophers were particularly energetic in bringing up soil buried by tephra to the surface, thus accelerating secondary succession (Anderson and MacMahon 1985). However, the resident elk are responsible for most nutrient transport and addition to the landscape. There are about 600 elk within the blast zone and they deposit copious and conspicuous chunks of concentrated organic matter and deposit it widely across the landscape (Fig. 7.5). Despite high variability of both the background conditions and the species response to fertility, Fleming (2011) showed significant responses to site amelioration by elk. Working on sites that had already developed, he found that the addition of "scat" (general term for animal feces) produced positive responses comparable to those of experimental nutrient additions. On both the Muddy River and on the Pumice Plain, the biomass response to scat was muted, and due primarily to lupines and mosses, which dominated the communities. However, species composition changed significantly in response to scat in both places, with lupines, grasses and sedges increasing drastically.

Under controlled greenhouse conditions, the effects of elk scat were more prominent. Several species experienced greater germination rates (e.g., several sedges) and all species grew bigger. These included alder, fireweed, Merten's sedge, squirreltail, cat's ear, Sandberg's bluegrass and beardtongue. Clearly, elk, and undoubtedly other animals, provided useful amelioration of the habitat for many plant species. They continue to graze or browse, increase local soil disturbance, disperse seeds and redistribute nutrients.

### Biotic facilitation

*Direct nutrient inputs by plants.* Plants can favorably affect other species in many ways. Nurse plants, discussed below, trap seeds and organic matter and then provide physical protection from herbivory and harsh conditions. Biological facilitation improves fertility directly though nitrogen fixation, indirectly by carbon addition to the soil, and by mutual interactions with soil microbes (e.g., mycorrhizae). Nurse plants facilitate other plants in many ways, but here I consider effects that do not require the continued living presence of the facilitator.

On Mount St. Helens, facilitation through nitrogen fixation by lupines and alder is complex. While soil fertility is improved, competitive effects can suppress beneficiaries. Prairie lupines were often the pioneers although they had limited long-range dispersal. Barren landscapes developed a few dense colonies of prairie lupine as early as 1981, and by 2000, there were many colonies. Because this species is short lived and susceptible to multiple forms of herbivore attack, the colonies expanded slowly and experienced large abundance fluctuations. After several cycles, species that can establish during lupine "down" years become abundant.

Halvorson et al. (2005) found that pyroclastic materials lacking prairie lupines were infertile, low in carbon, phosphate and especially nitrogen. The soil biota was sparse. Conditions in lupine patches in 1987 were similar to patches without lupines in 2000. By 2000, soil beneath lupines had 20 times more carbon and nitrogen as barren pyroclastic material in 1990. Barren soil in 2000 had only 25% as much carbon and nitrogen as the adjacent lupine soil. Lupines were clearly changing soils and altering the course of succession.

*Dead nannies.* In the late 1980s, I was entranced by the observation that there were no seedlings in close associations with prairie lupines, but that seedlings of fireweed and cat's ear were common in mounds left when a large lupine died (Fig. 7.6). Over the early years, I studied the impact of lupines on seedling establishment, along with several colleagues. On the Pumice Plain, where lupines often acted as a locus to trap blowing sand, I conducted a set of simple observations concerning lupine effects on seedling establishment (see del Moral and Wood 1993a, b). The most common seedlings at that time were the pioneering parachute species. In three habitats (barren, living prairie lupine and dead prairie lupine), we determined the presence of pearly everlasting, fireweed or cat's ear seedlings. Using a $\chi^2$ test, I found that seedlings were present in the dead lupines much more often than in either the living lupines or the barren sites (Fig. 7.7). In this graph, the expected frequency is set to 1.0, bars above the line indicate observations greater than expected and bars below the line indicate observations less than expected. I found more seedlings in mounds that were formed by lupines that had died. There were many fewer than expected seedlings among living lupines and in barren areas. While living, lupines enhance the fertility of surface soil. During the first decade in pumice and pyroclastic areas, fine pumice dust was trapped by isolated individuals of the first generation of lupines. Thus, soil fertility and moisture status improved, but the competitive effects of living plants lupines died, mounds degenerated. Lupine seeds were so plentiful that a second generation formed dense colonies and such sites became poorly suited for most species until excluded seedling establishment. Once the founding lupine died, the mini-mound was ideal for seedlings. After this colony collapsed. That a vigorous population of lupines would create a nearly impenetrable situation can be inferred from the broad expanses of lupine found

*Fig. 7. 6. Prairie lupine was a major facilitator in the first decade of succession on the Pumice Plain. During this time, lupines collected drifting sand to form small mounds. When the lupine died, the mounds became ideal sites for other species to establish: a. cat's ear and haircap moss are major beneficiaries (July 1990).*

periodically over much of the Pumice Plain (Fig. 7.8).

Tsuyuzaki et al. (1997) also found that microsites with dead lupines had significantly more seedlings than those *lacking* lupine carcasses, although seedling plots also had more microsites suitable for growth. Plots with and without seedlings did not differ in their overall cover, suggesting that lupine effects were crucial. Lupine remains and soil movement were the main predictors of density and cover of seedlings.

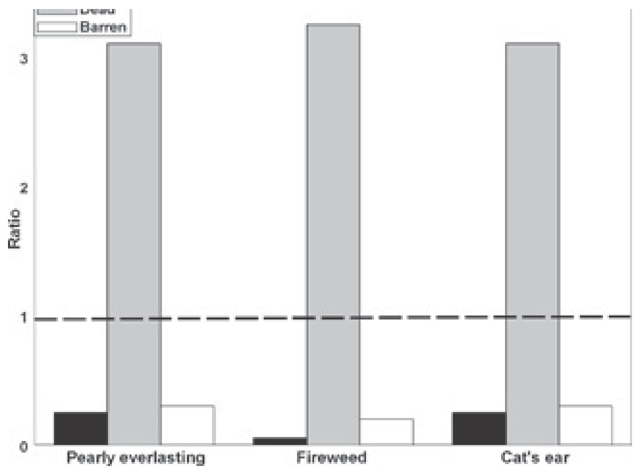

*Fig. 7. 7. Dense field of prairie lupine (July 18, 2010) with only the occasional sedge, bentgrass, rush and fireweed present.*

*Mycorrhizae*. One mutualistic relationship between plants and microbes is called "mycorrhizae," literally fungus root. The fungus partner facilitates the ability of the plant to absorb soil nutrients and the fungal component obtains organic nutrients. Many species do not require mycorrhizae, while others must form a relationship to survive. Most species on Mount St. Helens are facultative with respect to mycorrhizae, so they will form the relationship if available but they function well without the interaction.

Jon Titus studied what are called arbuscular mycorrhizae fungi (AMF) during the early 1990s, when vegetation on the Pumice Plain was sparse and mycorrhizae sparse. In one series of experiments, the interaction between microsites and mycorrhizae was investigated (Titus and del Moral 1998a). In general, mycorrhizae had little effect in these studies (see below for site effects). Ten years later, these sites were resurveyed (Titus et al. 2007) and at least 15 species of AMF were found, in contrast to the single species in 1993. In contrast to the earlier study, microsites all had a significant potential to exhibit relationships with species present, and a wide variety of dominant species were colonized in barren and rill sites (as well as in lupine patches). Titus concluded that the growth of facultative mycotrophic species is facilitated by mycorrhizae, which have become widespread on the Pumice Plain due to dispersal by mammals.

*Nurse plants*. Plants that do establish dramatically alter the rules of establishment. When altered conditions favor other species, the adult is called a nurse plant. Such plants ameliorate conditions and foster succession in several ways. As noted above, the negative effects of an adult may overwhelm positive effects, but often more shade, less wind and generally more favorable moisture conditions foster germination and survival of other species. Growing beneath a young conifer or a dense alder may provide protection from grazing, but in both cases, the potential nurse is a strong competitor. Broadleaf lupine creates dark conditions under its canopy. However, it dies back in the autumn and sprouts late in the spring, so there is a window during which pioneers can establish in the fertile soil found in this lupine's rhizosphere (Fig. 7.9).

*Fig. 7. 8. Dense field of prairie lupine (July 18, 2010) with only the occasional sedge, bentgrass, rush and fireweed present.*

Often, conditions beneath the canopies of large species are unfavorable. On the Muddy River, I compared vegetation was considerably sparser than that immediately beyond the canopy. It was obviously much shadier beneath the canopies, and conifer litter altered soil properties. In some cases, it was clear that the vegetation of open sites with that beneath conifers. This ground layer species had established before the conifer had, yet it persisted. For example, beardtongue was relatively abundant beneath canopies but with a high variation. Understory beardtongue were rarely in flower and looked stressed, while those growing in full sunlight were vigorous and reproductive. Only broadleaf lupine, rare in barren lahars in this vicinity, was common and healthy beneath conifers, and it was no more abundant than in the open. A few species performed consistently better beneath the canopy than in the open. These included strawberry (common in forest openings, rare on barrens) and Parry's rush. Manzanita was common in this area and equally abundant beneath and beyond canopies. This was the result of the shrub invading conifer canopies and from conifers growing through the mass of manzanita, a case of a nurse plant interaction. Haircap moss was common beneath conifers, but was also common in the surroundings

The forest will continue to expand as conifers disperse into currently barren areas and spaces between trees will shrink as trees mature. As these processes occur, most of the currently dominant species, *including* prairie lupine and rock moss, will be replaced by species more tolerant of shade and conifer litter. Thus, the conifers will inhibit the meadow species and facilitate the establishment and further development of forest species such as bear grass.

*Fig. 7. 9. Broadleaf lupine is a harsh facilitator, providing soil amelioration and dense shade. Its leaves die back each year, and are tardy to develop the following year. Species like cat's ear can benefit from the physical protection and enhanced fertility by growing rapidly before the lupine fully develops (Courtesy David M. Wood, August 1987).*

**Safe-sites**

For germinating seeds to have any chance of success, they must land in particularly favorable sites. Scattered unpredictably in each landscape were special places that somehow mitigated conditions for germinants. These micro-sites are called safe-sites. They may be tiny and be occupied by only one plant, but sometimes a veritable garden can develop (Fig. 7.10).

**Sidebar 7.1.** *Boomer herds the crew*

In late July 1997, the weather on Abraham Plain was quite iffy. You know, if the wind died down it would be pleasant…if the rain stopped and if it warmed up. Roger Fuller, Brian Witte and I struggled through a long day, helped out by my Australian shepherd Boomer. I was recording the thin vegetation on the grid. Boomer loved herding and spent much of the day trying to convince Brian, 300 m to the west, or Roger, 200 m to the south, to join me. His method of persuasion involved running over to the offender, barking at his heals and nudging his knees. This soon became annoying and Boomer was put on "guard duty," tied to the packs, but he still occasionally issued barking orders for his charges to coalesce. We camped in a designated place, still having a few hours' work to do the next day. The morning dawned, according to our clocks and not the sun, with a persistent drizzle. As Roger and I tried to finish recording the grid data, Brian started to pack away the tents and gear. As the new front moved in, the wind picked up. Roger and I nearly died laughing as Brian refused to let go of the tent, which had become a parasail. Boomer, showing all of his considerable talent, realized that herding was not useful, and to stay dry he had to stay immediately behind either Roger or me. Brian, 300 m away, could look out for himself. Once we started to leave, wind at our backs and rain on our shoulders, Boomer again got us organized and headed up a very rapid return to the 99 road.

*Fig. 7. 10. Log from tree killed in 1980 persists in creating a large safe-site. The log traps wind-blown seeds and protects from the wind. Over the decades, it has also added organic matter to the soil. Here, an island of lush vegetation in an otherwise barren site consists of wind-blown species. Prominent in this view are fireweed, yarrow, Indian paintbrush, pearly everlasting and white-flowered hawkweed. 1987).*

The safe-site concept originated with John Harper (1977) who proposed that only certain portions of any landscape were suitable for the germination, growth and establishment of seedlings. He was concerned with scales of about 1 cm. Surfaces are rarely homogeneous at this scale and some *microsites* have more resources or are less stressful than are others. These sites are destined to harbor the first fortuitous colonists. Such mini-sites may be physically obvious, being in stark contrast from the surroundings, or subtle and not perceptible by direct observation. For example, a site may be otherwise suitable, but is lacking in enough phosphorus to sustain a seedling. The importance of safe-sites was recognized by those struggling to understand how very similar species could coexist. One answer is that coexisting species may have different requirements for seedling success although all other requirements are similar. This idea recognizes the importance of what has been called the regeneration niche (Grubb 1977).

Once spatial heterogeneity forms, opportunities for establishment arise. Over time, as site amelioration occurs, a greater fraction of the landscape becomes suitable for seedling establishment. Eventually, biotic interactions like competition begin to reduce the number of safe-sites. Safe-sites improve the prospect of seedling success in many ways. They may collect water and *thus* reduce drought stress (Wood and Morris 1990). Early in succession on Mount St. Helens, most seeds reaching a site merely became part of the biotic rain, acting to improve site quality gradually. Several studies provided estimates of seedling mortality. Each of these studies produced underestimates of mortality because they start with seedlings, not seeds. Wood and del Moral (1987) found that no more than 4% of any of 22 cohorts survived for 3 years, and most of these had very few survivors. Titus and del Moral (1998c) found that less than 10% of the planted seeds of four pioneer species survived to maturity. However, those that did survive grew much better in particular habitats that ameliorated conditions. Some species, such as Parry's rush and Cardwell's beardtongue, each with small seeds, had very low survivorship in another study (Titus and del Moral 1998a), but Chapin and Bliss (1989) showed that up to 40% of buckwheat and knotweed survived for three years.

In my studies on Mount St. Helens, physically obvious microsites suggested themselves as safe-sites, and these were pursued in a variety of studies. Safe-sites can develop from physical or biological processes, as discussed above, and they may disappear as well. Each species has a set of unique requirements and what serves one species may tax another. Fireweed seeds, floating across the barren landscape, may survive in crevices that offer sufficient protection and thrive near wetlands, while pearly everlasting may perish in a wet depression.

Among the many observations that have documented safe-sites were those in depressions I have called potholes. These structures have flat, fine-textured bottoms and moderate, sandy, steep slopes. Seedling establishment during the first 15 years was confined to the lower slope where protection and soil heterogeneity provided a suitable combination of conditions. Higher on the slope, exposure and erosion killed most seedlings. In the center, snow persisted and then water accumulations produced anaerobic conditions that limited seedling establishment. However, over time, silt and sand drifted over the central area and elk, through trampling and bedding down in the pothole, made the central flat suitable for seedlings.

Below, I summarize several studies that explored the importance of safe-sites to seedling establishment. These studies focused on physical manifestations of safe-sites, but also sometimes *included* lupines.

*Establishment patterns*. Simple observations can often reveal much about processes, although care is needed to avoid the pitfall of confusing a subsequent event with a *caused* event. That seedlings of a species always establish after those of another does not demonstrate the causal relationship *between* the two (*cf*., Wood and del Moral 1987). However, finding that a particular species occurs far more often in one site suggests that site qualities are causally involved.

I conducted several studies to determine how seedlings were associated with microtopography on Abraham Plain in 1990 (del Moral and Wood 1993a). In order to highlight the results, I converted their table to a figure (Fig. 7.11). Five habitats were sampled with 0.1 m$^2$ quadrats. We *then* determined the habitat type and if any seedlings were present. For each species, a table of five habitats (smooth, rocky, rill edge, undulation and drainage bottom) and presence or absence was constructed. Rills are persistent indentations that contrast with the surrounding smooth sites (Fig. 7.12). Rill edges offer protection from wind and crevices, but there is some erosion and surface temperatures may be higher than the *barrens*. Undulations are depressed areas that do not show evidence of water erosion. Drainages erode during snowmelt and are dry during much of the growing season.

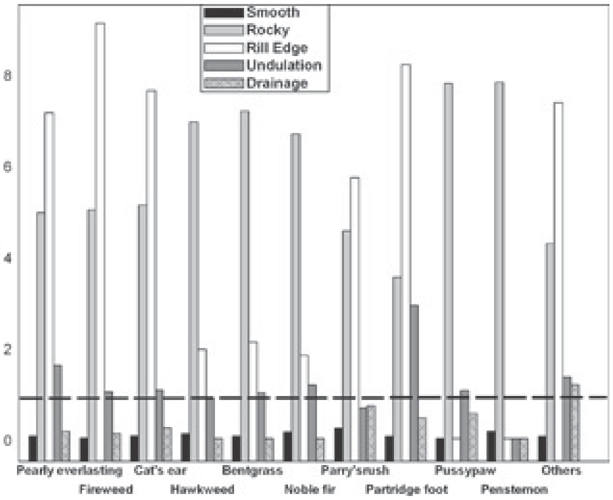

*Fig. 7. 11. Species distribution in five microsites on the Abraham Plain. The horizontal line is the frequency expected if the distribution was random. Bars well above the line indicate an affinity for the microsite; bars below the line are either indifferent or shun the microsite.*

A $\chi^2$ test assessed departures from a random expectation. The expected value is the proportion of each habitat for the number of observed presence values for that species. The dashed line indicates the *expected* number of occurrences and the observed values were adjusted so that a value of 1.0 indicates that the expected and observed values were identical. Values > 1 indicate observed values that were more common than chance would suggest. For the ten species and the aggregate of rare species, the observed pattern differed strongly from random ($P << 0.0001$). No species was likely to occur on smooth, barren surfaces. For example, pearly everlasting occurred 16 times on smooth surfaces, but it should have occurred at random over 300 times. In contrast, this species occurred 247 times in rocky habitats, while it would be expected to occur only 50 times if chance were the only factor involved.

All taxa preferred rocky *habitats*, where seeds and organic matter were trapped, crevices existed and there was protection from desiccation. Most species also demonstrated a preference for the edges of rills. White hawkweed, dune bentgrass and noble fir displayed only modest preferences. Species tend to occur in undulations about as would be expected by chance, except for partridgefoot, which has a slight preference. Erosion precludes most species from occurring in drainages.

*Fig. 7.12. Rill on the Abraham Plain (August 18, 2011). The rill edges host bentgrass and beardtongue. Only a few pussypaws were found in the barren sites.*

Tsuyuzaki et al. (1997) monitored seedlings on the Pumice Plain over two years and discovered that seedling establishment was much more common in plots where the substrate had moved slightly during the season. This suggests that slight movement permits seeds to be redistributed into better microsites. Greenhouse studies showed that pioneer species grew better in moist, gravelly sites that corresponded to rills in the field, where most seedlings occurred. Seedling survival was not guaranteed by germination. Most surviving seedlings occurred in rills and within dead lupine sites. Here moisture and fertility conditions were a little better.

Titus conducted several experiments with mycorrhizae and microsites (Titus and del Moral 1998). In 1993, we found that microsites had little effect on the rate of mycorrhizal infections of four pioneers and beardtongue. Natural rates of colonization in these species were low, while when he added innoculum, the rates were uniformly high. We also found that the presence of mycorrhizae had little effect on the growth of seedlings in the field, while plants grew much better in dead lupine patches and other favorable microsites. Seedlings appeared to be indifferent to the presence of mycorrhizae, in contrast to the standard view that they are beneficial. Beneficial interactions may develop as overall site fertility improves.

Favorable microsites produced more biomass in all pioneers, especially beardtongue and Merten's sedge (non-mycorrhizal; Titus and del Moral 1998c). The numbers of seedlings that emerged from standard plantings differed little among sites, but the size of these species differed greatly (Fig. 7.13). Three of four pioneer species grew better in rills or among lupines than in flat or ridge habitats. Pearly everlasting, fireweed and cat's ear also appeared spontaneously in rills and in dead lupine patches. Cat's ear, when sown, did reasonably well in flat surfaces. This suggests that a major component to being a safe-site is the ability to trap seeds (e.g., rills and behind rocks) rather than enhanced fertility. White hawkweed did very poorly in this study, perhaps due to poor quality seed used. Sites near rocks were not particularly effective in promoting growth of these pioneer species, suggesting that the effects noted in other studies were due primarily to seed trapping abilities of this habitat.

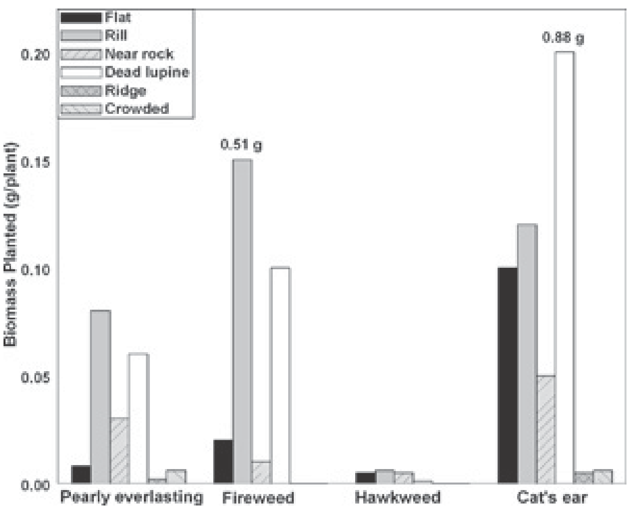

*Fig. 7. 13. The four common pioneer species were planted in several microsites, including crowded conditions and dead lupines. Rills and dead lupines were generally beneficial, conditions crowded with living plants and barren sites were generally adverse to seedling growth.*

*Safe-site creation studies*. In a series of manipulations of the environment, Dave Wood and I (1986) found that the response of bentgrass and broadleaf lupine varied with the habitat at Butte Camp and on Pine Creek ridge. The treatments were the application of fertilizer, cultivation (to create safe-sites), removal of existing vegetation (no competition) and seeding of the two species. In dense vegetation, the lupine responded only to cultivation and removal, while bentgrass responded to removal. In barren vegetation, adding seed was significant for both species, while bentgrass also responded to fertilization and cultivation.

In a second study, conducted in 1989, we added mulch (to improve soil moisture status), nutrients and rocks to sites that were either cultivated or left smooth. Only seedlings that occurred naturally were counted. On the Pumice Plain, only mulch improved the number and size of seedlings. Mulch trapped seeds and ameliorated stress. Nutrients improved the growth of seedlings that did reach the site.

These studies confirm the inferences derived from direct observations. Conditions on volcanic barrens were initially so harsh that amelioration of drought stress was required. Infertility alone does not impede establishment, but the combination of drought and slow growth was deadly to most seedlings. Safe-sites that both ameliorate conditions and collect seeds have the most seedlings.

*Safe-site stability*. Safe-sites appear to have been an ephemeral phenomenon on Mount St. Helens. They form as a direct or indirect result of physical processes and function for several years, but as plants established in safe-sites mature, the site becomes less favorable to seedling establishment. Early establishing species such as pearly everlasting usually form dense, relatively long-lived clones that created dense shade and can usurp water and other soil resources. Further, weathering and the general improvement of all sites results in a blurring of spatial patterns of seedling establishment. By 2002, when I conducted a detailed set of observations on the Abraham Plain, no species demonstrated any significant pattern with respect to microsite heterogeneity. This was in stark contrast to the results of studies in the same area conducted in 1990. When we explored changes on the Pumice Plain grid from the perspective of colony establishment (del Moral and Jones 2002), it was clear that after initial establishment in the relatively few safe-sites and the resultant flood of second generation seedlings, safe-sites disappeared as plants expanded by vegetative means.

I conclude from these and other similar studies that safe-sites offer a window for establishment that is narrow in both in space and time. That safe-sites are mutable has been observed in other habitats. Older sites on a glacial foreland had few safe-sites compared to sites close to the receding glacier (Stöcklin and Bäumler 1996). In deserts, it is common for adult plants to eradicate the effectiveness of safe-sites (Walker and Powell 1999). As nitrogen and organic matter accumulate beneath alders and conifers, safe-sites were eliminated for most species in Alaska floodplains (Fastie 1995). When Tsuyuzaki and Titus (1996) studied large gullies that had formed in pumice uplands with more stable sites on the Pumice Plain, they found sparse vegetation in the gulley. The erosion that formed these gullies clearly removed any safe-sites that had been present.

*The paradox of primary succession.* As early as 1985, I became aware of what I call the paradox of primary succession (cf., Wood and del Moral 1987). Pioneer species were, with the notable exception of prairie lupine, able dispersers. However, they could not tolerate stress well. In this, they were more closely aligned with what Grime (2001) had called "ruderal" species, those adapted to disturbed sites, but generally unable to establish in dry or infertile sites. In contrast, species that had survived the eruption and dominated stable subalpine communities were tolerant of stressful conditions but had limited powers to disperse. Species such as pussypaws, knotweed and beardtongue are "stress-tolerant." Typically, they are slow growing, large seeded and slow to mature. No species can combine the two sets of traits; succession is slowed because pioneers cannot survive and stress tolerant species cannot arrive. It is only because safe-sites are created that succession can commence.

## Establishment heterogeneity

Early collections of species within one habitat remain heterogeneous. Their composition is affected by distance to pools of potential colonizers and, because the seed rain is sparse, adjacent sites may differ strongly. One way to demonstrate this effect is to explore the similarity between adjacent permanent plots over time. I calculated percent similarity among a sample of adjacent plots on the five grids. The greater the similarity, the more homogeneous is the vegetation, and the closer to an equilibrium it is likely to be. Typically, well-developed plots in similar habitats will approach 80% similarity as a limit because of sampling errors, annual fluctuations and the residual effects of earlier random colonization and disturbance.

*Similarity on grids.* Changes in similarity between plots on the several grids reveal a *consistent* pattern (Fig. 7.14). In each set of bars, the first three are the percent similarity in the first three years of the study; the last bar is the similarity in the last year. Abraham Plain was sparsely populated and had the lowest similarity among plots because in the early years, there were many plots lacking species in common. The grid became more homogeneous after 2002. By 2010, similarity was higher than the other grids except Lahar 2. Willow Springs was initially barren, but developed moderate similarity considering that it included eroded and wetland sites. Vegetation on the Pumice Plain grid was sparse when sampling started, but no plots were bare. It was quite variable, so all similarity values were relatively low. Lahar 1 and Lahar 2 had some vegetation when sampling started. Lahar 1 already had many conifer saplings, which raised the similarity index. Lahar 2 was initially more variable than Lahar 1, but developed greater similarity when the lupine population exploded. On each grid, plots became more similar because there were no dispersal barriers among adjacent plots. If two plots had started with different colonists, each could readily provide seeds to the other. The variance of the similarity measure also declined over time, strongly indicating greater homogeneity. However, none of the similarities yet exceeds 70%, indicating substantial differences between adjacent plots that were in most cases environmentally similar.

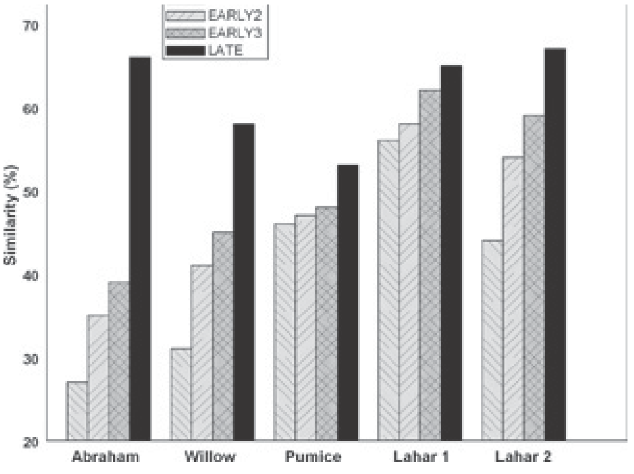

*Fig. 7. 14. The percent similarity among plots on a grid increased over time in every case. This suggests that initial species heterogeneity, established by random long-distance dispersal, is being overridden to some degree by competitive dominance.*

*Heterogeneity on lahars.* On the Muddy River Lahar, we explored variation as a function of distance directly. In this study, plot variation was estimated using the similarity among 25 1-m$^2$ quadrats located within 25 by 25 m plots arrayed at increasing distances from the forest margin.

Both mean cover and mean numbers of species per plot declined as distance from the forest increased. Plots were less developed at higher elevations than lower ones (Dlugosch and del Moral 1999). These plots had fewer species, lower cover and more internal variation, all suggesting that early dispersal was stochastic and that subsequent development by secondary dispersal and vegetative spread reduced, but did not eliminate the variation produced by the chaotic establishment (fel Moral and Ellis 2004).

On Lahar 1, near forested vegetation at Butte Camp, species richness declined with both elevation and distance from the forest, and variation among quadrats in these plots increased in each case. This is to be expected because some plots were "near" and others "far" from colonist pools. In contrast, while species richness was lower on the isolated lahar, there were neither distance nor elevation patterns. All plots are effectively "far" from pools of potential colonizers. The early patterns of seedling establishment are not easily expunged by the passage of time.

## Summary

While dispersal is stochastic, establishment can produce results with a degree of predictability. Initially variable species distributions become less variable within homogeneous habitats, but the rate at which this occurs is governed by habitat stress. On Mount St. Helens, stress includes drought and infertility. Herbivory and disease also can retard succession in many locations. Usually, a viable population is built by successful on-site reproduction. Successful early colonists will expand both by vegetative means and by seed to colonize the site rapidly. However, the pioneering individual often serves only to ameliorate the site and fail to survive. Successful early colonists will expand both by vegetative means and by seed to colonize the site rapidly.