

CHAPTER 6

Dispersal and the Effects of the Landscape



Early morning on the Pumice Plain (July 29, 2001). Seeds dispersed onto this surface from several sources, including Windy Ridge, above in the shadow, relict habitats and possibly survivors in the deeper gullies.

Introduction

Early succession is restricted either by the lack of seeds or by the inability of seeds to establish. On Mount St. Helens, both limitations apply. In this chapter, I focus on how dispersal limitations alter species composition. A major discovery from my work on Mount St. Helens was that plant dispersal abilities have been substantially overrated. I have described species composition changes in response only to distance from likely sources of colonists. Documenting the importance of landscape factors in early succession was a major accomplishment of this research. In this chapter, I will summarize central findings about dispersal and discuss the variety of dispersal mechanisms found on this volcano.

Studies discussed in this chapter explore how isolation from sources of potential colonists affects the seed rain. Could the composition of early vegetation be predicted with any accuracy? Once an individual became mature, does it begin to produce successful seedlings in its immediate vicinity? Answers to these questions emerged from several long-term studies and from considerations of the life history characteristics of the invading species.

Clearly, on sites devoid of vegetation after the eruptions, dispersal ability is paramount for colonists. It is more likely that wind-dispersed species will initiate succession in temperate land habitats, but such species may not be well adapted to stressful conditions. Most plants, including those generally regarded as having good dispersal ability, can disperse only a few meters, not kilometers as people might think (Clark et al. 2001). Plant ecologists traditionally believed that the first species to arrive at a site (the “pioneers”) did so because they were well adapted to the nasty conditions that occurred, but in fact, this is rarely true. In fact, there is a trade-off between dispersal ability, which favors small seeds, and establishment ability under harsh conditions, which favors larger seeds. As I will discuss at the end of the chapter, that readily dispersed species have poor stress tolerance is a fundamental reason that succession on barren sites at Mount St. Helens was impeded.

Dispersal mechanisms

Plants disperse by methods both simple and obscure. We have all seen a plumed dandelion seed wafting gently across a lawn, perhaps to land in a favorable gap in the

turf. For many years, observers on Mount St. Helens saw multitudes of plumes from composites drifting gently across the Pumice Plain. Backlit in the late afternoon, the view was inspiring. Happily for the future course of succession, nearly all of these plumes of exotic species lacked a viable seed, which, I suppose, explained why they so easily drifted across the landscape. However, the observation did emphasize that most of the early seed input resulted from just this sort of passive dispersal—seeds dispersed at the whim of physical processes.

In this section, I look at dispersal mechanisms in general, with an occasional reference to events on Mount St. Helens. Mechanisms may be passive or active. Passive mechanisms use the freely available physical forces of wind, water and gravity. Active dispersal mechanisms engage the transport ability of birds or mammals to effect dispersal, but the service comes with a steep price. Seeds may have otherwise superfluous appendages to cling to animals, or must produce tasty fruits to encourage ingestion. Animal dispersers may transport seeds externally (“hitchhiker” seeds) or by ingesting seeds or fruits. If the seed emerges intact from its journey through the digestive system, it has a chance of landing in a favorable site. Most plants have two or more dispersal mechanisms, often both passive and active.

Passive dispersal. Most plants use the pervasive physical forces to scatter seeds and spores across the landscape. This type of dispersal is not directed, so many seeds are dispersed to enhance probabilities that some will reach safe havens.

Dispersal by wind (anemochory), or as some of my colleagues like to say, aeolian forces, is the most common mechanism of dispersal in plants. Wind can transport seeds and spores across large bodies of water and inhospitable terrain. Adaptations to wind dispersal typically occur in species that frequent barren and often sterile habitats. These species are poorly adapted to conditions with strong competition (e.g., shade). The scattergun approach to dispersal can be cost-effective because no inducement is needed to bribe dispersal agents and the energy conserved translates into many more seed being produced. Plants with tiny seeds or those with seed appendages are usually wind-dispersed, but even when they successfully establish, they may be at a disadvantage compared to species with larger seeds. Wind dispersed species dominate the flora of early successional sites, whether the site be natural, as on Mount St. Helens or created by human activities such as mining. Wind offers a more likely avenue for a long-distance jump than animal dispersers do (Clark et al. 1999).

While wind can carry diaspores (which include seeds and spores) over long distances, the density of input is sparse. The statistical curve that describes fall out density as a function of distance from sources always shows a very steep decline. The nature of such curves can help predict the composition of the early colonists, but in the field, the spatial heterogeneity of the seed rain is highly variable. Often a single seed arrives safely to encounter a favorable site for germination. Champion long-distance dispersers include many ferns and temperate zone orchids. Over moderate distances, many composites have effective “parachutes” called the pappus: other species have various bits of “fluff” or membranous wings attached to their seeds that aids buoyancy (fireweed is a great example).

On Mount St. Helens, Roger Fuller and I (2003) described three basic forms of wind dispersal in seed plants: parachute (e.g., the “pappus” of a hawkweed; hairs of fireweed), gliders (e.g., wings found in pussypaws) and tumblers (seeds, fruits or entire plants that can blow across open territory, e.g., Davis’ knotweed). I will use this classification when discussing dispersal.

While dispersal success is vital, it does not guarantee establishment. Ferns, lycopods and mosses, to say nothing of orchids, would seem to have dispersal advantages, but when the site is barren, dry and infertile; these dispersal units can do little but add incrementally to the gradual buildup of organic matter. Thus, the establishment of spore-bearing species on dry substrates is often delayed for years or confined to favorable sites such as rock crevices in gullies.

On Mount St. Helens, dispersal by wind has particular advantages. Intense autumn storms can drive seeds uphill. Later, they can be washed down, or slide along snow to reach new habitats. Wind is a silent partner for many dispersal mechanisms.

Dispersal by water (hydrochory) on Mount St. Helens is confined to streamside plants and wetland species. Streamside species are more likely to be hard and to tumble along the surface, a process that facilitates germination. Species adapted to sedentary sites in wetlands are likely to demonstrate great abilities to float. The problem with dispersal by water is that it is a one-way process. Seeds cannot fight gravity to emerge either farther upstream or into the uplands. Upland species are rarely adapted to transport by water.

Biologists invoke gravity when there are no other obvious dispersal mechanisms. The seed (or fruit) just drops to the ground, perhaps to roll away. Gravity is often offset by other mechanisms to get a seed uphill, across a barrier

or into a suitable microsite. Sometimes, a species is categorized as a passive self-disperser, but gravity is involved, if only ensuring that the fruit eventually falls from the plant.

Self-dispersing plants (autochory) provide a link between passive and active dispersal. Those that simply release seeds from a fruit often open gradually as the fruit dries out. This is called dehiscence. What happens next is crucial. For species adapted to stable conditions, e.g., forest understory species, often the answer is “nothing.” As the fruits of false azalea mature, the seeds simply fall to the ground. Seeds persist in the soil until triggered to germinate. Wallflowers, found in very dry sites on the south side of the cone, also drop seeds from the gradually opening fruit onto suitable soil.

Other species may employ animals to further their dispersal (zoochory; see below). Finally, there are the “bridge” plants. They actively thrust their seeds away into the harsh environment, but they do not depend on other forces. This behavior is called ballistic dispersal. On Mount St. Helens, violets of moist forest understories and trilliums (common in forests, rarely in refugia) typify this mechanism. However, it is the two lupine species are the most important. As a seedpod dries, it reaches a critical point where the least provocation will cause the pod to snap open and disperse most of the seeds contained within. This trait made seed collection a challenge because too soon, and the seeds were immature...too late and merely brushing them lightly causes their explosive dehiscence, allowing most seeds to escape. Expelled seeds can land over 1 m away. Ferns such as the alpine lady fern also forcibly expel spores, and then they drift away.

Active dispersal. Directly or indirectly, active dispersal involves animal vectors. This has been called zoochory and you will not be surprised to learn that there are many categories. I will stick to the fundamental ones that describe whether the seed (or fruit) is transported internally (endochory), externally (ectochoy, sometimes called epichory) or explicitly carried (e.g., myrmechory, carried by ants).

Plants that rely on endochory attract birds and mammals. These animals cannot be attracted for anything less than a big payoff. Plants that require endochory have, as a result, either big, nutritious seeds, like acorns, or seeds that are bundled into a tasty package, like strawberries. On Mount St. Helens, there is but a few plant species that effect dispersal by frugivores. These include several huckleberries, strawberries and pinemat manzanita. Only pine-mat manzanita can colonize barren sites. Other species,

not particularly adapted to endochory, are consumed incidentally to browsing or grazing by elk. Lupines, pussy-paws and the exotic sheep sorrel are commonly found in large clusters of seedlings in elk patties, evidence that while neither the plant nor the animal appears adapted to this form of dispersal, it occurs and it is important. Other species have been found in scat germinated under controlled conditions (e.g., white-flowered hawkweed, Sandberg’s bluegrass, mosses and spike trisetum).

Elk herds ramble across several habitats daily, indifferently redistributing the biota and creating favorable microsites. They also distribute spores of mycorrhizal fungi (Allen et al. 2005). Some plants suffer disproportionately from elk activities. The Cascade aster literally stands out above the ground layer and elk preferentially browse the flowers. Most browsing occurs before seeds are mature, so it appears that elk are seed predators, not dispersers (Morris and Wood 1989). Indeed, the aster has become increasingly rare where elk were common.

Several huckleberry species and the less common strawberry are actively sought by birds, coyotes and even black bears. Each of these animals moves substantial distances before defecating the surviving seeds into particularly fertile spots. Endochory has its limitations with regard to colonization of barren sites. Most animals, having eaten, rarely venture into barren, exposed sites. There is simply nothing to entice the prospective disperser into the new habitat. Coyotes are often overlooked as seed dispersal agents, yet they avidly seek huckleberries. Their scat often contains viable seeds (Yang et al. 2008). Birds rarely emerge from the forest, although some may flit out to exposed boulders.

While there are substantial disadvantages to being eaten, some species require passage through a gut to trigger germination. Seeds can remain dormant for long periods in an inappropriate habitat, but passage through the animal signals that conditions will soon be appropriate. Gut enzymes may breakdown seed dormancy or the seed coat is abraded in preparation for emergence.

Ectochoy simply involves movement of the fruit or seed by an animal. The animal may willingly participate in the transaction, but often the dispersal unit is a passive “hitch-hikers,” attached to the fur of a passing mammal by barbs, awns, fuzz or sticky surfaces, or clinging to mud on a bird’s foot. In most cases, ectochory is haphazard and dispersal is fortuitous. Grasses and some members of the sunflower family can lodge in the fur of elk, bear and coyotes, to be dispersed elsewhere.

Deer mice, generally seed predators, are often overlooked as seed dispersers, but on Mount St. Helens, they may cross wide barren swaths, from a refuge to a wetland for example, carrying seeds lodged in their fur (C. Crisafulli, pers. comm.). Elk also move quickly from one favorable habitat to another, and thus are likely to provide directed dispersal services, either internally or externally.

Some external seed transport is directed. In surviving old-growth habitats that occur around Mount St. Helens, flickers, Steller's jay and woodpeckers collect large seeds, either individually or in cones, and transport them in their beaks. Often they hide them away, and some of these treasures escape to germinate.

Douglas tree squirrels stuff their cheeks with seeds, scamper away and may cache the hoard in secure locations. However, these forest dwellers seldom seek the barrens, so their activities scarcely affect succession on Mount St. Helens. In contrast, the bold golden-mantle ground squirrel, seen often where visitors stop at scenic vistas, can and probably does transport conifer seeds in their mouths from forest margins into sparse vegetation. These creatures engage in the common rodent behavior called "scatter-hoarding," a very apt description. Seeds caches are generated at substantial distances from the source (see Sidebar 6.1). Out of sight for long periods, the cache may be forgotten, or the greedy squirrel stashed far more seeds than it could eat. Or, while the hoard survives, the squirrel does not. Lost hoards may be the focus of a new plant population, established well beyond the main population. Scatter hoarding works because at least in some years, the sheer quantity of seeds produced ensures that some will escape being a meal. A little appreciated aspect of scatter hording is that much of the dispersal is conducted by naïve animals that behave inappropriately, get lost, forget or succumb to predators. Neophyte dispersers are likely to be more effective from the perspective of a plant.

Wetland birds provide another exception to an aimless seed transport system. Canada geese occur on Pumice Plain wetlands and they pick up seeds of many wetland plants on their feet or in their feathers from the mud. The tiny seeds and spores of wetland species like rushes, sedges, horsetails and mosses, are transported in mud clinging to their feet. When the bird flies to another wetland, all the barren, inappropriate habitat is by-passed.

A final example of purposeful ectochory involves ants (as you recall, this is called myrmecochory). We rarely think that invertebrates are effective dispersers because they are so small compared to most seeds or fruits, and since they will not travel far. However, on Mount St. Helens ants do

drag lupine seeds that weigh more than they do to their nests, often many meters away. The seed is quite irrelevant to the ant, which is interested only in a tiny morsel called an elaiosome. This oily energy packet is irresistible to many ant species and it provides food that is chemically compatible with the needs of their larvae. Once at the nest, the ant clips the oily structure from the seed and carries it into the nest. The seed is discarded into a fertile midden that is guarded by patrolling ants. While many seeds are killed, a few survive. Dispersal distances rarely exceed 4 m, but this is sufficient to expand the lupine territory. Elaiosomes have evolved in over 70 plant families, so there must be advantage to the plants in question.

Nitrogen fixation is crucial in pumice and pyroclastic habitats that have very low levels of most nutrients. Symbiotic nitrogen fixation requires bacteria (e.g., *Rhizobium* in lupines and *Frankia* in alders). Many other plant species form mycorrhizae (see Chapter 7) that require symbiotic fungi such as the widespread *Glomus* species (Titus and del Moral 1998A, B) and several *Diversispora* species. It is likely that rodents, elk and possibly birds assist in the dispersal both of fungal spores and bacteria. This colonization of spores has been quite slow. Local refugia have more species than the barrens and a few of these have yet to invade plants on barren sites (Titus et al. 2007).

Diplochory. Many species depend on multiple dispersal mechanisms. Wafting dandelion seeds may get a few meters, but if they become trapped in socks or fur, they may travel long distances. With luck, they will land in a favorable microsite. Species with two common dispersal modes are said to be diplochorous. Ecologists have underestimated the frequency and importance of diplochory. Wind-blown conifer seeds that reached the forest edge might be collected by a ground squirrel, then moved an additional 50 m onto a lahar and finally, buried.

Ants discussed above form the second part of a complex dispersal mechanism for lupines. Those seeds dropped by a wetland plant into moving water, only to be picked up by a water bird form another example. Pussy-paws also has two dispersal mechanisms. Its winged fruits are adapted for buoyancy, but their weight and the plant's low stature suggest that wind is only a local factor. However, elk avidly eat these fruits and transport the seeds for a substantial distance before defecating.

In each of these examples of diplochory, the first stage of dispersal is not directed. Seeds are cast away from the parent. The second phase often results in the seed landing in a more favorable micro-site (See Appendix 1 for dispersal mechanism). It is likely that succession is slowed by the absence of the second dispersal partner, although this

has not been studied on Mount St. Helens. On Krakatau, which erupted violently in 1883, the shoreline of the newly barren land quickly received water dispersed species. However, in the absence of mammalian dispersers, there they stayed. The developing upland forests remain very poor in species and very different from those on surrounding islands (Whittaker and Fernández-Palacios 2007).

Using a simulation study, we showed that nearly all spatial patterns that had developed between 1989 and 1998 on the Pumice Plain were consistent with the following. Seeds that travelled long distance by wind were the founders. They then expanded into the local area using dispersal by gravity, water or tumbling (del Moral and Jones 2002). Initially sparse species with poor dispersal mechanisms that expanded quickly included beardtongue, saxifrage, Merten's rush and woodrush. This pattern is common when the invaded habitat is isolated and inhospitable and was likely the way in which most species invaded primary surfaces on Mount St. Helens.

Dispersal patterns

Regardless of the mechanism, species can colonize in one of two ways. A population can move forward along a broad front or individuals may establish far from the core population and expand outward.

Dispersal by diffusion. Most plants have little difficulty expanding from a colony when there are no barriers. Dispersal by diffusion results in a gradual, but steady, advance. This has been compared to the tactics of a crack Roman phalanx in conquering the field. Unlike a legion, however, this advance has young plants at the leading edge, older ones in the rear. Usually, as on Mount St. Helens, diffusion is by seedling establishment, but sometimes plants simply grow by rhizomes into the unstable, barren habitat. This process results in establishment in habitats unsuited for seedlings until substantial changes can occur. Because various members of a donor community may disperse at different rates, we expect there to be sharp gradients in measures of community structure at increasing distances from intact vegetation. If diffusion were the sole means of dispersal, we could not explain the observed rates of recolonization observed in the fossil record. Following glaciation in North America, members of the eastern deciduous forest migrated north rapidly. The observed dispersal rates for large-seeded species such as oaks, beeches, the now nearly extinct American chestnut and even maples are far slower than the rates of recolonization observed in the fossil record. However, we know that rare long-distance events, such as suggested above, can produce rates comparable to those estimated

from the fossil record.

Jump dispersal. If diffusion is like an advancing legion, jump dispersal is like a parachute division occupying a small landing zone, then expanding in all directions. Because water poses a clear barrier to most species, biogeographers have long-studied its filtering effects on islands. Only recently have we realized that similar, although more subtle, filters occur on land. These effects have been shown most clearly on Mount St. Helens, and will be discussed below. Diffusion on Mount St. Helens is slow and relatively ineffective and must be aided by long-distance, often seemingly miraculous, events. Jump dispersal is crucial for the reestablishment of species on barren sites.

The best example of jump dispersal on Mount St. Helens is the prairie lupine. Despite its apparently poor long-distance dispersal, this species cropped up in very some very isolated pyroclastic zone sites in 1981 and 1982 (Bishop et al. 2005). We are unsure of the mechanisms of the first, crucial, long-distance step, but because we occasionally found lupine seeds in seed traps (Wood and del Moral 2000), there may be a yet undocumented aerial mechanism. Senescent plants that retained their pods may have been blown onto snowfields in the winter of 1981, then washed down to the plains below. Since lupines were not found near stream courses, a subsequent dispersal may have occurred. It has also been suggested, with as much evidence, that a bird dropped a pod near Willow Spring where the first lupine plant was encountered (Allen et al. 2005). Whatever unlikely events combined, small confined colonies were soon formed by explosive dehiscence and ant dispersal as described above. Although it took nearly two decades for this species to become widespread, it was the first species to be found in most habitats of the barrens and locally abundant. Because it is a nitrogen-fixing species (see Chapter 8), it plays a central role across the Mount St. Helens landscape.

The seed rain

Which seeds find their way to a site determines the course of primary succession, yet it is very hard to quantify. No method can capture all types of seeds, and many species, particularly bird-dispersed species, avoid capture in most traps. Each method of trapping is biased in one or more ways. Together with John Edwards (see Edwards 1986), I developed a method to gather what we believed would be the most common early colonists, those species capable of long-distance wind dispersal (see Sidebar 6.2). Bird dispersed seeds were unlikely to appear since there was nothing in the barren zones that might attract birds. We assumed that we would find seedlings associated with scat. We also gathered seeds from pitfall traps designed to

catch crawling insects. The most successful trap was 0.1-m² in area and set so that its surface was level with the ground (Fig. 6.1). The wooden frame was stabilized by hardware cloth over which fine mesh netting was placed. Then, I filled the frame with 50 golf balls in an array and sprayed the color of the adjacent soil. After a summer in the field, the balls were carefully removed and the mesh collected and stored in a plastic bag. Trapped seeds were counted and identified in the lab. Golf balls were intended to mimic the coarse pumice surface common in the sampled habitats in the first decade after the eruption. Traps were placed on pumice barrens at Abraham Plain, the Pumice Plain, on lahars at Butte Camp, on Willow Spring wetlands and on pyroclastic materials near Spirit Lake (Wood and del Moral 2000).

Seed rains in barren sites were low, substantially less than 100 seeds per 0.1 m² per year. In contrast, plots near established vegetation, i.e. dense lupine patches and willow thickets, had ten to 100 times as many seeds. From 1982 to 1986 in the pyroclastic area, all collected species were wind-dispersed and dominated by parachute species such as pearly everlasting and fireweed. The woodland ragwort (also a parachute-disperser), was rarely encountered in the barrens, but common in clear-cuts to the southwest. It was abundant in the first two years, but was scarce by 1986. Over the study, we collected 33 species. Nearly all were parachutists, but gliders (e.g., maples) and tumblers (e.g., sedges) were encountered. However, among the rarely collected species were maples and (with winged seeds), sedges with membranous seeds, and rushes with tiny seeds. Traps during the early 1980s reflected the long distance seed rain and no lupines were encountered.

Over 1989 and 1990, seeds were trapped in nine sites, some of which had developed significant vegetation. The four “usual suspects” are all parachutists (pearly everlasting, fireweed, cat’s ear and white-flowered hawkweed) were always among the top five species collected except on the lahars at Butte Camp. The prairie lupine was captured, although it was quite rare, in some years on exposed (hence windy) pumice sites. It was, not surprisingly, common in traps placed in a lupine patch. The lahar plots offered a different perspective. Pearly everlasting was not captured, nor was it present on either grid in 1989. The prairie lupine was relatively abundant. Species with less inefficient wind-dispersed seeds, e.g., the tumblers Davis’s knotweed and desert parsley and the glider pussypaws, were common, and were common in the vegetation. By 1989, the seed traps were reflecting the local seed rain.

Sidebar 6.1. *The mystery of the missing key*

“And **NEVER** leave the car key hidden on top of the wheel” was the last instruction I left my research team before I left for a short conference. The seven-person team was ably led by two senior graduate students and a research technician. Their mission was to conduct several sets of observations on the Pumice Plain.

The crew arrived in two vehicles at the start of the Truman Trail in a mist. This was the expected weather in July, most years. Since the team would be separating, and members of the team might return at different times, the crew decided (and I will not name names) to leave the key to the UW van on the tire. It was unlikely that anyone would come by, and even less likely that he or she would want to steal the car. The van had most of the camping gear since the team had driven up from the Silver Springs Camp ground, and would be camping near Bean Creek.

Upon their return, the team found that the van was safe and sound, but the key was missing. Each person riffled through his or her gear to no avail. Using the other van, the team ferried to the camp area where the two small tents and extra clothes were shared out, and the van became a makeshift hotel. Before trying to sleep, one team member phoned a friend in Seattle to explain the situation and ask for help. He said he would go to the Motor Pool to get another key, and then bring it to them. Cold, wet and hungry, the team traveled to Windy Ridge, where cell phones were known to work, occasionally. The friend was contacted at the motor pool. They would not release a key to this stranger, particularly based on his dubious story. Eventually, after a long conversation with the team leaders, they agreed to give out a key, and to make sure that I was responsible for repaying the University for any Losses. Well, the heroic friend made the five-hour trip to Windy Ridge and he was treated with cheers and hugs. The remainder of the excursion went smoothly, but the mystery of the missing key remained.

The following year, I had just finished dinner at our newly established camp when John Bishop sauntered over. After a while, and with a mischievous grin, he pulled out a badly chewed key holder, complete with bent credit card and asked if I knew whose it was. Of course, it was the missing UW key holder and the tooth marks exposed the mystery. A golden-mantled ground squirrel had purloined the shiny object and dragged it to its burrow. John reported that he found it in plain view where we all park, and not 10 m from where the key had been “hidden.” I can only deduce that the key was ejected during spring burrow cleaning. Never again was a key left behind.

Direct measurements of seedlings from 1983 to 1985, by Wood and del Moral (1987) on lahars at Butte Camp suggested that dispersal was extremely limited and that most individuals in an isolated population were produced by a few lucky early invaders. Nearly all seedlings found were within 3 m of an adult that had produced seeds in the previous year. They also found that barren sites were

unlikely to have any seedlings and that most seedlings occurred in sparse vegetation. Del Moral and Jones (2002) inferred that most seedlings were produced by colonists that had arrived at least one year earlier.

The results from these laborious seed trap studies suggested that early colonization was quite haphazard and that later colonization was dominated by the species already present. Later studies supported the inference that the dispersal curves were very steep and that only a few seeds read a sight and even fewer establish and reproduce. These lucky few dictate the direction of successional trajectories. Studies by Mandy Tu in the mid-1990s (Tu et al. 1998) confirmed that the species in the soil seed bank reflect the existing vegetation or species that recently grew on the site, and does not represent the sparse long-distance seed rain.

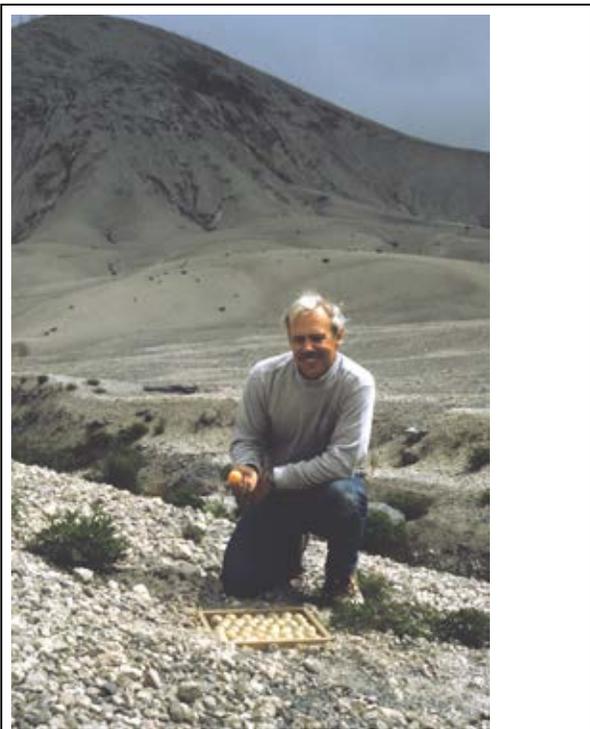


Fig. 6.1. The author triumphantly places the last ball into this trap near Abraham Plain. The balls are about the size of the surrounding pumice; very little vegetation

Disharmony

A common result of isolation of any kind is that the biota is disproportionately represented by species more capable of crossing the barriers and under-represented by poorly dispersing groups. The bias is the result of isolation by true barriers, like mountains, or of distance. In either case, some species are better fit to reach a newly exposed site

quickly. Therefore, we expect that pioneer communities will be dominated by species that excel in reaching distant sites. I expect that a few seeds of species without long distance dispersal will somehow reach isolated sites in low numbers. Because these species typically are more stress tolerant and longer lived, they will come to dominate the vegetation (Wood and del Moral 1987).

Disharmony has been documented on many islands. Studies on Surtsey (Magnusson and Magnusson 2008) and

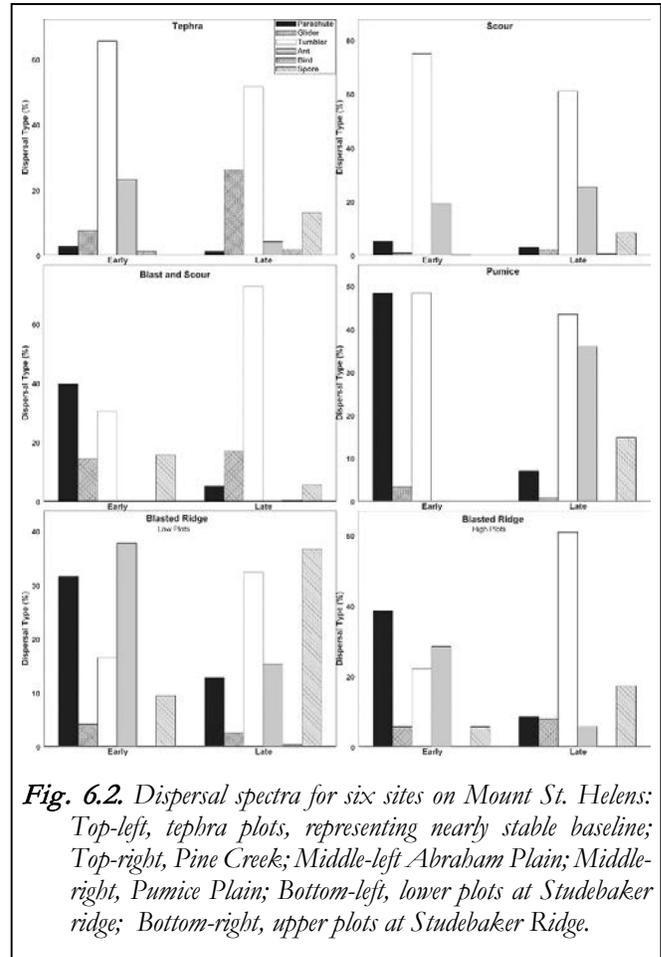


Fig. 6.2. Dispersal spectra for six sites on Mount St. Helens: Top-left, tephra plots, representing nearly stable baseline; Top-right, Pine Creek; Middle-left Abraham Plain; Middle-right, Pumice Plain; Bottom-left, lower plots at Studebaker ridge; Bottom-right, upper plots at Studebaker Ridge.

on Krakatau (Tagawa 1992, Whittaker et al. 1997, 1999) documented initially disharmonious floras. However, in these cases of truly isolated, young volcanic islands, disharmony continues. On Surtsey, the system is young with new species being recorded annually. On Krakatau, significant secondary dispersers such as monkeys have yet to arrive, so upland forests have few species and remain dominated by small-seeded species. In the case of Mount St. Helens, there are two aspects to consider. First, vegetation early in succession should be strongly dominated by wind-dispersed species and second, that over time, the vegetation should become more harmonious.

Six sets of permanent plot data were used to demonstrate differences in spectra with isolation and changes over time (Fig. 6.2). Six categories of dispersal were used. Wind dispersers were seed plants that were disperse over long distances (parachute), moderate distances (glider) or short distances (tumblers). Spore-bearing plants (mosses and ferns) can float for long distances, but those in this sample require either moist or stable surfaces to grow. Lupines were categorized as ant-dispersed, which only slightly augments their explosive dehiscence. Finally, bird-dispersed species lacking other mechanisms formed a small category. Most of these species have supplementary means of dispersal, but a species was categorized according to the more usual and effective mechanism.

Tephra plots form one baseline for mid-elevation relatively stable meadow vegetation of Mount St. Helens. Tumblers (e.g., grasses, knotweed, phlox, buckwheat and Ross’s sedge) were abundant after the eruption and maintained their dominance. Ant dispersed species (i.e., prairie lupine) thrived in the aftermath of the eruption (see Chapter 1), but declined as a proportion of the vegetation. Parachute species remained rare, and unlike other sites, this category was dominated by the Cascade aster, a persistent species. Bird dispersed species (e.g., strawberry) were uncommon. The biggest change was the development of mosses. The tephra burial eliminated this group (although buried spores probably survived). After three decades, mosses had reasserted themselves and provided about 10% of the cover. A second baseline is available from a recovering dry meadow at Sunrise, Mount Rainier (Frank and del Moral 1986). Here, 35-year-old meadows were dominated by tumblers (59%) and ant dispersed species (29%; lupines and violets). Parachute species still represented 9% of the total, while gliders were rare (1%). This spectrum is similar to mature sites on Studebaker Ridge and Pumice Plain (when mosses are removed from consideration). The two baselines suggest that most species capable of reaching devastated sites on Mount St. Helens have done so, and have established well. Further successional changes on the Pumice Plain and similar sites will require the development of “game-changing” species, particularly conifers.

The scours at Pine Creek were virtually barren in 1980, but some plants survived. Again, tumblers were predominant (e.g., bentgrass, partridgefoot, buckwheat, knotweed and beardtongue). Both lupines were common and they increased over the study. Parachute species were slightly more common than on tephra, but the species were not those considered pioneers or weeds (e.g., yarrow, aster and yellow hawkweed).

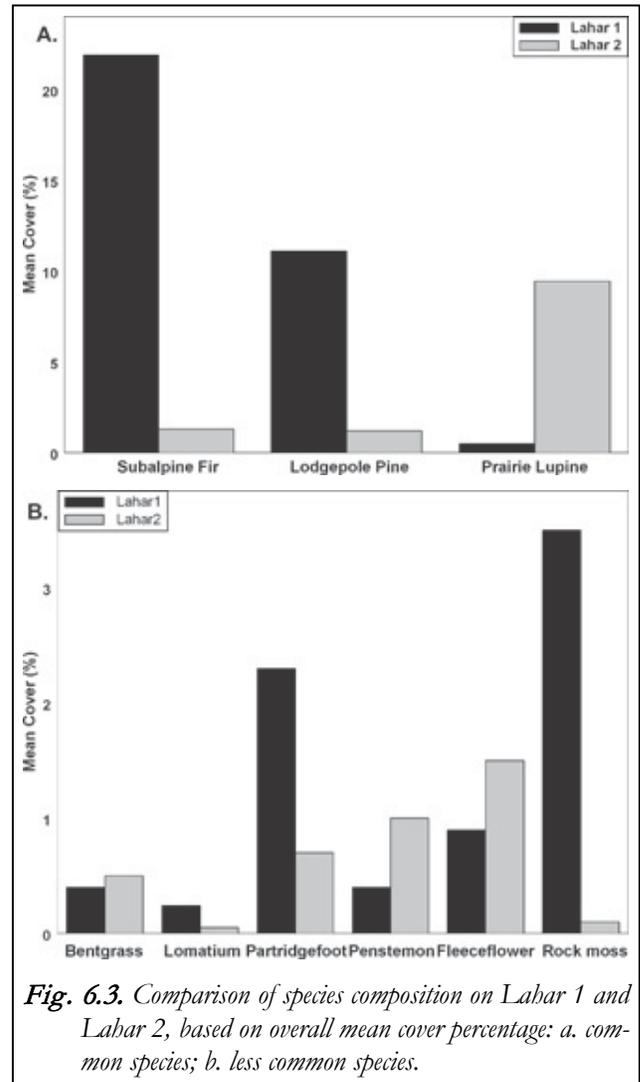


Fig. 6.3. Comparison of species composition on Lahar 1 and Lahar 2, based on overall mean cover percentage: a. common species; b. less common species.

The blasted, scoured plots on the Abraham Plain were initially dominated by parachute dispersers (pearly everlasting, fireweed, cat’s ear and white-flowered hawkweed). By 2010, tumblers (e.g., beardtongue, partridgefoot, grasses, rushes and sedges) dominated the vegetation. Gliders like pussypaws, woodrush and conifers were relatively common, while parachutists had been relegated to holdover status. While mosses were a smaller share, they had expanded in absolute cover.

The pumice sample contained sites that developed strongly and had significant quantities of prairie lupine by 2010. Initially, the plots lacked mosses, lupines and bird-distributed plants. Dominance was from exclusively by wind-dispersed species. The usual parachute dispersed species and tumblers (e.g., grasses and sedges) dominated the early flora. Over time, lupines and mosses became

dominant, and tumblers such as beardtongue and partridgefoot became abundant.

Sidebar 6.2. *Golf balls seemed a good idea*

But in retrospect, Ping-Pong balls were a much better choice. However, I was enticed by an offer of 10,000 slightly defective golf balls, gratis, and my budget was non-existent. The idea was to make seed traps that mimicked the pumice surface. The 32 by 32 cm wooden frames had a wire bottom and a mesh cloth, over which 49 balls were positioned. Golf balls weigh 46 g (17 times more than a Ping-Pong ball); a trap weighed 2.5 kg and a trap line weighed 25 kg (55 lbs.).

To get the traps to the Abraham Plain involved carting them in my fully loaded 1979 Toyota Corolla, which ordinarily had little difficulty with the Road of Terror. Except that when fully loaded, it did not clear the tilted pumice terror spot, and there I was, hung up and alone. Before I analyzed that I would have to unload, drive and load up again, a small marvel occurred. Briskly forging up the trail were four young men who turned out to be German exchange students taking a tour of natural wonders before returning home. In no time, they unloaded, I drove and they reloaded the car. While I did explain what the golf balls were for, I had a very distinct impression that either they thought me crazy, or that something was lost in translation.

The traps worked well, but every so often, I would return to a trap line to find a few balls scattered around. My knowledge of bird behavior is limited, or else I might have guessed the cause. None in my group could fathom the reason...was it frost heaving? Did snow somehow eject the balls from the traps? Midway through the second season, enlightenment happened. Trudging back to Abraham Plain to collect any seeds in the traps, I was annoyed by a conspiracy of ravens. As I topped a ridge, there they were, playing with MY golf balls. Well, I suppose that they thought that they had found particularly tough eggs, and they were methodically taking a ball, flying high and dropping it. Golf balls just don't break. Ravens do learn quickly, so it was rare that more and a few "eggs" were disturbed.

Studebaker Ridge provides two examples, from lower and higher plots respectively. In the lower plots, the usual parachute species and tumblers (grasses) were common, but both were exceeded by the unusual dominance of prairie lupine. It was usually the first and for several years the only species in some plots. Pussypaws was the only common glider and this species, being dispersed also by elk, had an erratic pattern. Mosses were common in the early years. As these plots developed, tumblers became dominant and lupines became better integrated. Mosses filled in across most surfaces. In the upper plots, tumblers (e.g., grasses, partridgefoot and beardtongue) came to dominant and lupines were still common.

Overall, it is clear that the normal vegetation in open meadows is dominated by persistent, spreading species, primarily tumblers. Tumblers increased their proportion

in each example other than pumice, where lupines were extraordinarily abundant. In years when lupines were rare, tumblers dominated. Over longer periods, most of these meadows will be invaded by conifers. This will generate a further rearrangement of dispersal types. While dispersal spectra develop towards similarity with donor vegetation, the species composition may differ if it is largely a matter of chance as to which of two tumbler species (for example) reach a site.

Evidence for the effects of isolation

Lahars at Butte Camp. Studies of island biogeography clearly demonstrate that the species composition of sites developing in isolation differs greatly from the norm. There are no native terrestrial mammals in the Galapagos Islands, and, owing to the effects of adaptive radiation, there are far too many finch and tortoise species compared to the mainland. The studies of Mount St. Helens have demonstrated that physical barriers are not required and that distance alone can offer resistance to dispersal and produce similar results.

To demonstrate this point, I compared the species composition on the two Butte Camp lahars in 2004 and 2005 (the last year of study for each lahar; Fig. 6.3). Total cover was 43.7% on Lahar 1 and 18.3% on Lahar 2. The percent similarity between the two lahars based on average cover of each was only 12.1%. Lahar 1 had over 33% cover of conifers compared to 2.6% for Lahar 2. On Lahar 1, dominants with greater than 1% cover included rock moss (3.4%), Parry's rush (2.33%, not shown) and partridgefoot (2.31%). On Lahar 2, prairie lupine was experiencing a boom year and had 9.45% cover. Subalpine fir (1.33%) and lodgepole pine (1.25%) were scattered, small plants. Davis's knotweed (1.5%), beardtongue (0.9%), buckwheat (0.81%, not shown) and partridgefoot (0.67%) were other common species. Dune bentgrass was similar on the two lahars, while desert parsley was substantially more common on Lahar 1. The vegetation and flora of these two sites were so remarkably different that it is hard to believe that they are developing on lahars spawned from the same location with the same composition at precisely the same time.

The differences also can be demonstrated by a comparison of their dispersal spectra at the end of the study. Data from Lahar 1 were divided into plots with more or less than 25% conifer cover. Lahar 2 was a single group. Again, the species were divided into six dispersal types. On Lahar 1, dispersal was dominated by species with seeds that can glide. All other groups had low abundance. On Lahar 1 plots with less conifer dominance, gliders re-

mained dominant, but mosses and tumblers were common. On Lahar 2, where conifers represented about 2.6% cover, ant-dispersed species, the two lupine species, were dominant and tumblers were common. Thus, the effects of isolation may be seen in two ways. On Lahar 1, conifers advanced slowly across the lahar and the plots most distant from the forest were very sparse, while those adjacent to the forest were dense. Lahar 2 is an island, so colonization by conifers was restricted. Isolation, combined with the pulse of lupines gives a distinctive dispersal spectrum.

The effects of diffusion were quantified by a regression analysis of cover of both conifers on the grid. Subalpine fir cover decreased strongly with distance from the edge, while lodgepole pine decreased with distance, but increased with elevation. These results demonstrate that distances less than 100 m can restrict the dispersal of species with restricted dispersal.

Muddy River Lahar. The large lahar on the upper Muddy River offers another chance to investigate diffusion in conifers. Parachute species were able to disperse into most areas of the lahar within a few years. Tumblers can establish readily and lupines can quickly occupy an area by diffusion and jump dispersal. Only the conifers, which have short dispersal distances regardless of whether dispersal results from wind or from rodents, can provide a useful exploration of diffusion. Data from the 2007 study of this lahar (del Moral et al. 2009) were used to determine if conifers were in fact dispersed as is predicted by a diffusion model.

The prevailing winds are from the southwest, and we had noted that dispersal of conifers extends farther from the southwest boundary than from the northeast one (del Moral and Ellis 2004). For this exploration, plots near the northeast edge were excluded. The distance away from the southwest edge and the west to east location (strongly correlated with distance) were used. When all conifers were used (dominated by Douglas fir, noble fir and lodgepole pine), the regression showed lower cover with distance from the edge ($r^2 = 0.25$). Each of these conifers responded similarly, while the others were too infrequent to yield significant results.

Most of the upper Muddy River Lahar remained open (Fig. 6.4), but the surface has stabilized. Therefore, over time, coniferous forests will reclaim most of the former river valley. However, it is obvious that this process is much slower than that described for the lower Muddy River Lahar (Chapter 3). Here, the lahar is quite broad and conditions above 1000 m are more stressful. Significant facilitator species such as red alder cannot grow at this

elevation.

Evidence for stochastic dispersal

Muddy River Lahar. When access restrictions were relaxed in 1982, opportunities to examine the boundaries between forest and lahar on foot developed. It was evident that despite an effective seed rain, there was a strong gradient of tree size and density as you walked out on to the lahar.



Fig. 6.4. The upper Muddy River lahar, with the remains of the resilient Shoestring Glacier in distance. The higher plots of the 2007 survey were located in this area, where the vegetation remained sparse.

This was an early suggestion that distance alone filtered species composition.

In 2002, we explored vegetation variation as a function of distance from the edge of the lahar and with elevation (del Moral and Ellis 2004). Plots were arrayed at increasing distances from both edges of the lahar, and along transects at several elevations. Each plot was 10 m by 10 m in size and was sampled with 25 1-m² plots arrayed in a regular fashion, so that there was 1 m separating each. The cover of each species was recorded in each quadrat. There were several analyses conducted in this study and the original data have been re-interpreted as well.

Many of the species more abundant near the forest were dispersed by birds (Table 6.1, at end of chapter). Frugivorous birds were sparse on the lahar compared to the forest, so such birds do not venture far on to the lahar. The conifers were indeed more abundant and larger (indicating earlier establishment) near the forest margin. These species are dispersed by squirrels and by wind. The distance-dispersal curves for both vectors rapidly approach zero and the “seed shadows,” the area where seeds may land with a measurable probability, are hard to predict; arrival of most species beyond a few meters is largely

a matter of chance. Most shrub species were confined to the lahar margins. Huckleberry (bird) and slide alder (wind and water) became increasingly sparse with distance and rarely occurred beyond 100 m from the edge. In contrast, pinemat manzanita was highly variable. Large clones were found at great distances from the forest edge margins. The occurrence of this species did not reflect any measured environmental or landscape factor

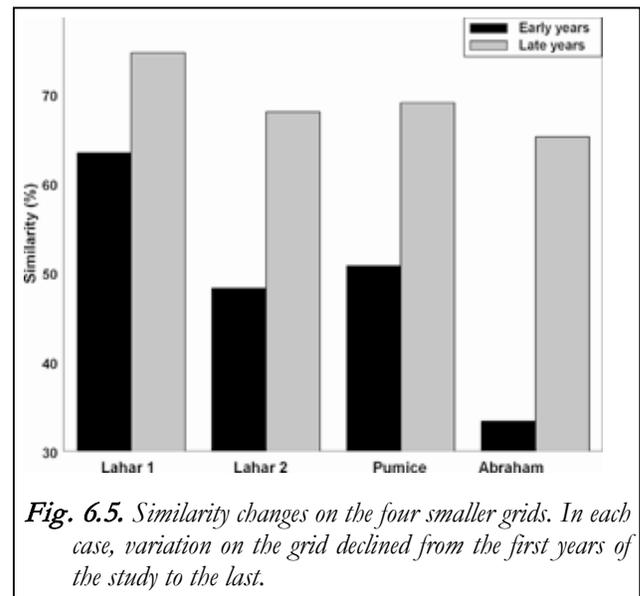
The herbaceous species with parachute or glider dispersal were pioneers and either showed no pattern or increased with distance. Tumblers, except for the tiny seeded Parry's rush, declined, as did the bird-dispersed strawberry. Broadleaf lupine, common in the forest, declined with distance. Pussy paws, a tumbler, also lacks a pattern, but unlike other species that have colonized from the adjacent forests, it dispersed from higher elevations by water and by elk.

Community structure also changed with distance. The cover of the plots declined sharply with distance from both edges and with elevation up the lahar. In addition, species diversity increased with elevation on each side of the lahar. This indicates more even distribution of the species, a characteristic of a less developed plot. These results simply demonstrate that succession is retarded by distance and by elevation.

The stochastic nature of the development of vegetation was demonstrated when the variation among quadrats of a plot was explored. Plots became increasingly variable with elevation on both sides of the lahar. Since plots at higher elevation represent a relatively early stage of succession, this result is consistent with the hypothesis that early dispersal is random.

Similarity changes. Initial dispersal into habitats distant from donor populations was highly variable. One way to demonstrate this is to compare floristic similarity among plots of a homogeneous sample early and late in the process. The value of long-term studies was again demonstrated because it was possible to compare similarity directly among plots as they developed across two decades. For this study, plots on four grids were grouped by their position and the mean similarity among the plots in a group was calculated. The greater the similarity between plots, the more homogeneous is the vegetation, and the closer to an equilibrium it is likely to be. Groups were separated by at least one empty plot. The Lahar 1 and Pumice Plain grids were grouped into six clusters of 16 plots each. The larger Lahar 2 grid was grouped into six clusters of 25 plots, while the homogeneous Abraham Plain grid was grouped into four clusters of 25 plots. Similarity was cal-

culated for each cluster for two early years, two intermediate years and two years at the end of the study. The mean similarity of each cluster was averaged for the grid. In each case, similarity increased with between early, middle and last samples (Fig. 6.5, showing only early and late year similarity; middle years were intermediate). Changes in similarity on the grids reflect several conditions peculiar to each, but the clear conclusion is that early plots have much more variation in composition than plots that have accumulated species, developed vegetation and that have responded to biotic and environmental factors.



Potholes. There is a small, peculiar region with several hundred small depressions (Fig. 6.6A, B). I discovered these potholes in 1992 and was struck by how similar was their form and by how variable was their vegetation (del Moral 1999a). How they formed is uncertain, but their compact distribution suggests that a combination of unique events led to their formation. One suggestion is that a massive chunk of glacial ice, blasted to the northeast, was large enough that it did not completely melt. Right after the ice was emplaced, it was covered by the pumice that rained down. Insulated, it melted unevenly, creating these small depressions. Depressions, albeit on a grander scale, occur in Iceland when huge chunks of glacial ice are blasted away by volcanoes smothered in ice, and then entrained by the subsequent lahars. Once they come to rest, they melt to produce “kettle holes” that are 4 to 10 m deep and 50 m across (Maarteinsdottir et al. 2010). The hypothesis for the formation of potholes on Mount St. Helens is not outlandish.

Very little *variation* in species composition was related to environmental factors. A few species, particularly those lacking effective wind dispersal (e.g., saxifrage), tended to cluster in potholes of one area, and the composition was chaotic. Even the largest potholes had fewer than half of the species present in all potholes. There was little competitive dominance until 2002, and secondary dispersal among these potholes was limited. In 1993, the similarity among potholes was $48.4\% \pm 15.38$. By 2008, it still was only 51.1 ± 13.5 , indicating little compositional change,

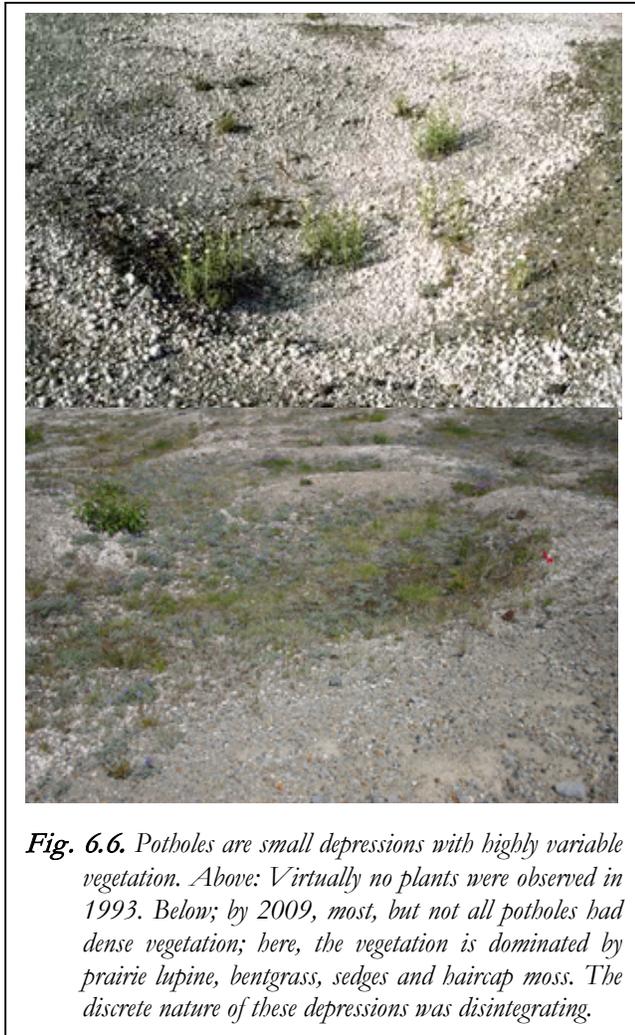


Fig. 6.6. Potholes are small depressions with highly variable vegetation. Above: Virtually no plants were observed in 1993. Below; by 2009, most, but not all potholes had dense vegetation; here, the vegetation is dominated by prairie lupine, bentgrass, sedges and haircap moss. The discrete nature of these depressions was disintegrating.

just development of cover (del Moral 2009). The initial composition of these potholes strongly indicated that dispersal into a homogenous environment might be described as a series of rare, random events. The establishment of one species in a pothole appeared to have little effect on the probability of establishment of another species. Potholes are discussed in more detail in Chapter 8.

Summary

Dispersal is crucial to primary succession, but its importance in dictating early species assembly has been underrated. Short distances filter the potential species pool. Founder individuals can produce most of the next generation because one plant in the neighborhood can provide many more seeds to the vicinity than thousands of plants a kilometer away.

Plants have several dispersal mechanisms. Pioneers do tend to be wind dispersed species capable of wafting long distances. Other wind-dispersed species contribute when dispersal barriers are modest. Occasionally, chance intervenes and a species like prairie lupine makes a seemingly miraculous jump. Over time, the spectrum of dispersal mechanisms shifts to include species with active and animal-mediated mechanisms and tumbling species.

Disharmony is measured in species composition or by some set of traits. Early in succession of isolated sites, the spectrum of dispersal types is asymmetric. Over time, the spectrum becomes more similar to the donor pool because slower dispersers tend to be superior competitors and exclude the first colonists. However, species composition may remain variable.

Isolation alone strongly affects species composition. Comparisons between the two Butte Camp lahars clearly showed that isolation leads to contrasting dispersal spectra. Studies on the Muddy River lahar demonstrated that the effect is gradational, but also that there was strong stochastic element. Samples at the same distance from the forest could differ significantly.

Over time, plots between which there were no dispersal barriers, as on the Pumice Plain grid, became increasingly similar. Where there were strong barriers to secondary dispersal, as in the potholes, between-plot similarity did not increase. Again, the importance of dispersal in determining species composition is revealed.

Table 6.1. Distribution determined to be near, intermediate or distant from the forest edge.

Species	Dispersal type	Pattern
<i>Trees</i>		
Douglas fir	Squirrel/wind dispersed	Steep decline with distance
Lodge pole pine	Squirrel/wind dispersed	Decline with distance
Noble fir	Squirrel/wind dispersed	Slight decline over distance
Western Hemlock	Primarily wind dispersed	Steep decline with distance
<i>Shrubs</i>		
Huckleberry	Bird, large mammal dispersed	Steep decline with distance
Kinnikinnick	Bird dispersed	Variable
Cardwell's penstemon	Tumbler	Decline with distance
Slide alder	Tumbler-cone	Decline with distance
Willow	Parachute-plumed seeds	Increases with distance
<i>Herbs</i>		
Bent grass	Tumbler	No pattern
False dandelion	Parachute-light seeds	No pattern
Hawkweed	Parachute-light seeds	Increases with distance
Pearly everlasting	Parachute-light seeds	No pattern
Broadleaf lupine	Self/ants	Decline with distance
Prairie lupine	Self/ants	No pattern
Pussy paws	Glider; water, elk	No pattern
Ross's sedge	Tumbler	Decline with distance
Parry's rush	Tumbler; water	Increases with distance
Strawberry	Bird dispersed	Decline sharply with distance