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Overview of Ecological Responses to the Eruption of Mount St. Helens: 1980–2005

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20.1 Introduction

The sensational 1980 eruption of Mount St. Helens and the subsequent ecological responses are the most thoroughly studied volcanic eruption in the world. The posteruption landscape was remarkable, and nearly a quarter century of study has provided a wealth of information and insight on a broad spectrum of ecological and physical responses to disturbance. The eruption and its effects on ecological and geophysical systems have many dimensions: a complex eruption affected an intricate landscape containing forests, meadows, lakes, and streams populated by diverse fauna and flora. This complexity created a rich environment and an exemplary living laboratory for study. Because the volcano is in close proximity to major metropolitan areas, scientists were able to perform reconnaissance trips and establish a network of permanent plots within days to months of the eruption. These early observations enabled scientists to assess the initial impacts of the eruption, which was important in understanding the subsequent quarter century of invasion and succession.

Suddenly, and almost beyond comprehension, at 8:32 a.m. on May 18, 1980, and lasting for little more than 12 hours, the eruption of Mount St. Helens transformed more than 600 km^2 of lush, green forest and meadows and clear, cold lakes and streams to a stark gray, ash- and pumice-covered landscape (see Figure 1.1; Swanson et al., Chapter 2, this volume; Swanson and Major, Chapter 3, this volume). The area influenced by the eruptive events will respond to them for hundreds or even thousands of years. However, even within the 24 years since the eruption, substantial change took place as hill slopes gradually turned from gray to green, opaque lakes cleared, and streams flushed sediment from their channels. Some of the initial ecological responses are well advanced; others have been set back by secondary disturbances; and yet others, such as soil development, will respond to the eruption over millennia.

The major 1980 eruption created distinctive disturbance zones that differed in the types and magnitudes of impacts on terrestrial and aquatic systems, including the types and amounts of surviving organisms and other legacies of the preeruption ecological systems (Figure 20.1). Thereafter, the natural system consisting of surviving and colonizing plants, fungi, animals, and microbes began responding to the new conditions. During the subsequent decades, species diversity, plant cover, and vegetation structure (the size and shape of plants) developed rapidly. Vegetation in 2005 ranged from herbs and scattered shrub cover in the severely disturbed pyroclastic-flow zone to the continuous canopy of young forest in tree plantations around the perimeter of the blast area. The story of this collective ecological response to the 1980 eruption of Mount St. Helens involves both successional change over time at individual sites and development of landscape patterns.

The 1980 eruption provided a special opportunity for scientists from a variety of disciplines to study ecological survival and establishment after a large disturbance, but several caveats challenge efforts to integrate this information. Developing a synthesis of ecological responses to the eruption is complicated by three factors:

- No ongoing, coordinated program integrated research efforts across taxa, research themes, disturbance zones, or time. Consequently, individuals and small groups of investigators operated relatively independently and focused narrowly on specific components of the overall story.
- Many studies initiated shortly after the eruption were terminated after a few years; others began many years after the eruption; and only a handful were maintained through the first 25 years after the eruption. Of the long-term studies, several have maintained regular measurements, producing outstanding long-term data sets.
- Most ecological studies at Mount St. Helens have sampled relatively small spatial scales, using different sampling designs, which further limit comparative analyses.

Even so, the collective work at Mount St. Helens provides a wealth of information and new insights on the responses of ecological composition, structure, and function to a large, catastrophic disturbance.

Relevant fields of science that might provide theoretical guidance in unraveling and communicating the complex

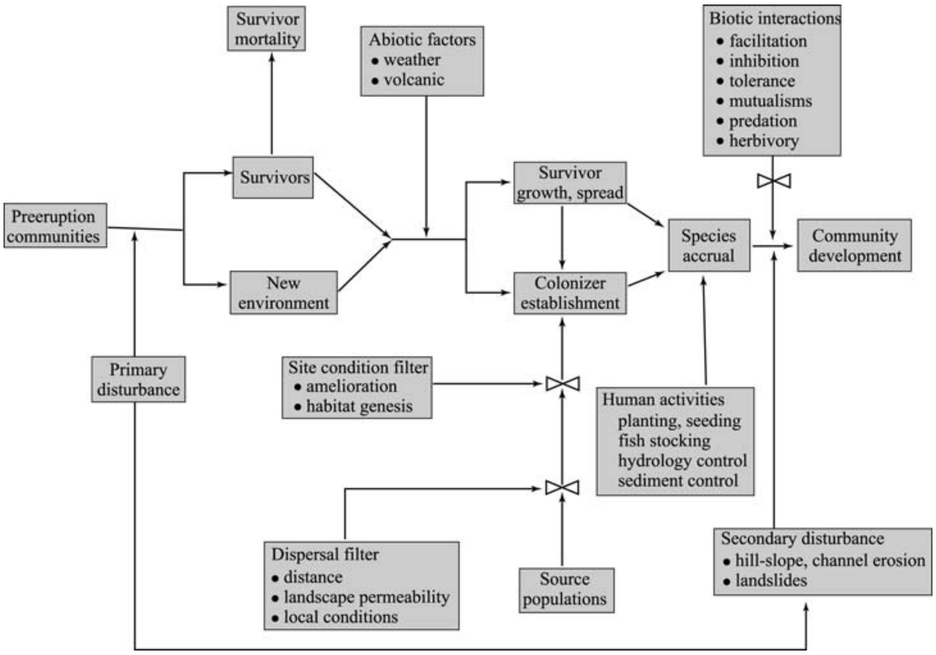

FIGURE 20.1. Generalized depiction of key biological, human, and physical factors and their flow paths influencing succession at Mount St. Helens after the 1980 eruption.

ecological responses to the 1980 eruption have themselves been seeking generality with only limited success [McIntosh (1999) reviewed succession, and White and Jentsch (2001) considered disturbance ecology]. Consequently, there was no unified theory from which to evaluate the ecological responses to the 1980 eruption. Studies at Mount St. Helens can provide information and insight for interpreting effects and responses to disturbances that may lead to the refinement of extant theory or the development of new constructs. Some of the lessons from Mount St. Helens have been consistent with findings from other disturbance studies, while others appear to be unique to the 1980 eruption of the volcano.

This closing chapter gives an overview and reflects on the physical and biological factors involved in survival and succession. First, we discuss the patterns and processes that were of prime importance for several taxonomic groups across the various disturbance zones. Perspectives on the development of landscape patterns are also discussed. Next, we describe the landscape of 2005 and the factors that have shaped its development. Then, we briefly place the Mount St. Helens experience of 1980 to 2005 in the context of the longer-term disturbance history of the area. The chapter concludes with key summary points from the Mount St. Helens experience.

20.2 Factors Influencing Survival

Surprisingly, numerous species survived the 1980 eruption in many locations throughout most of the disturbance zones (Table 20.1). Organisms survived by means of a wide variety of factors that were related either to characteristics of the disturbance and the species or to chance. The type, number, and extent of organisms that survived the eruption varied across the disturbed landscape, creating a complex mosaic of survival. We illustrate mechanisms of survival with the following examples.

20.2.1 Effects of Physical Disturbance and Topography on Survival

The specific disturbance types (e.g., directed blast), mechanisms (e.g., heating), and intensities (e.g., degree of heating) during the 1980 eruption strongly influenced survival of organisms (Swanson and Major, Chapter 3, this volume). The suite of physical processes operating during the eruption created a full spectrum of survival from nearly complete retention of biota, biotic structures, and abiotic features (such as soil, cliffs, and streams) to complete extirpation of life and loss (or gross reconfiguration) of landforms and drainage networks (see Table 20.1). Disturbance mechanisms of heating, burial, impact force, and abrasion damaged plants, fungi, and animals to varying degrees among the different volcanic processes and along the flow path of each process. The number of surviving species was inversely related to disturbance intensity (Table 20.1). In the case of the most extreme disturbance at Mount St. Helen, no multicellular organisms survived in the pyroclastic-flow zone (Means et al. 1982), where a new landscape was created by thick (greater than 10 m), 800°C pumice deposits (Table 20.1) in an area that was also profoundly altered by the debris avalanche and blast (Swanson and Major, Chapter 3, this volume). The much cooler debris avalanche transported a few living plant fragments that could establish (Adams et al. 1987), but the great thickness and high impact force of the debris-avalanche deposit precluded any in situ

Table 20.1. Survival of plant and animal taxa in several volcanic-disturbance zones following the May 18, 1980, eruption of Mount St. Helens.

Disturbance zone	Mean % vegetation cover	Average number of herbaceous species per square meter	Species of small mammals	Species of large mammals	Species of birds	Species of lake fish	Species of amphibians	Species of reptiles	References[a]
Pyroclastic-flow zone	0.0	0.0	0	0	0	0	0	0	1,2,3,6,7,9
Debris-avalanche deposit	0.0	0.0	0	0	0	0	0	0	1,2
Mudflow central flow path	0.0	0.0	0	0	0	na	0	0	5
Blowdown zone			8	0	0	4	11	1	3,7,8,9
Preeruption clear-cut	3.8	0.0050							1
Forest without snow	0.06	0.0021							1
Forest with snow	3.3	0.0064							1
Scorch zone	0.4	0.0038		0	0	2	12	1	1,7,8,9
Tephra-fall zone outside of blast			11	4	21	3	12	3	3,7,8,9
Tephra depth:									
23 mm	27.0	3.1							4
45 mm	28.2	2.0							4
75 mm	34.3	2.4							4
150 mm	10.5	0.2							4

Data are based on surveys within the first few years after the eruption.

[a] See the references listed below for details.

1. Means et al. (1982).
2. Adams and Adams (1982).
3. Andersen and MacMahon (1985b).
4. Antos and Zobel (1985b).
5. Frenzen et al., Chapter 6, this volume.
6. Crisafulli et al., Chapter 13, this volume.
7. Crisafulli et al., Chapter 14, this volume.
8. Bisson et al., Chapter 12, this volume.
9. Crisafulli and MacMahon, unpublished data.

survival of plants or animals (Table 20.1). At the other extreme of disturbance intensity, survival was exceedingly high for many taxonomic groups in the tephra-fall zone because deposits were emplaced with low impact force and temperature and thickness was generally quite limited (e.g., less than 20 cm) (Table 20.1). In zones of intermediate disturbance intensity, where deposit thickness was typically less than 1 m, many organisms survived in a great variety of refuges, such as under snow and within the soil and decaying logs. In these disturbance zones where biological legacies were very important, local topography created fine-scale heterogeneity in deposit thickness, which affected survival of plants and animals. Some topographic settings (e.g., rock outcroppings, cliffs, and ridges) protected sites from the brunt of the blast, while elsewhere landforms caused deposition of thick deposits (e.g., valley floors and benches), which smothered the life beneath.

20.2.2 Effects of Biological Attributes on Survival

Life history, habitat associations, life form, and organism size, among other biological attributes, influenced the survival of species during the 1980 eruption. Of primary importance were species characteristics that provided ways for organisms to avoid the brunt of disturbance events by being either temporarily away from the area or in protected habitats. Life-history traits, for example, aided the survival of anadromous fish that had a portion of their populations at sea during the period of greatest disturbance impacts (Bisson et al., Chapter 12, this volume) and the survival of many migratory birds that had yet to return to their summer breeding grounds when the spring eruption occurred. Zooplankton have eggs and resting stages that settle to the bottom of lakes and can remain viable for decades; those eggs provided a source of stored propagules (Vogel et al. 2000).

Cryptic habits of organisms, habitat preferences, and life forms contributed to the survival of some organisms but doomed others. Animals that live beneath the ground, such as the northern pocket gopher (*Thomomys talpoides*) and numerous invertebrate species, survived in soil or in large, decaying logs. Likewise, entire aquatic communities survived in many lakes, where they were buffered from the eruption by cold water and a protective layer of ice and snow. In contrast, species living in exposed habitats, such as resident birds and arboreal rodents, perished in the blast area. Amphibians associated with water had higher survival rates than did entirely terrestrial species (Crisafulli et al., Chapter 13, this volume). The most common plant survivors in the blast area were plants with buds located belowground, where soil provided protection (Adams et al. 1987). Mosses and low-stature herbs sustained heavy mortality in the tephra-fall zone, whereas erect shrubs and tree saplings experienced widespread survival (Antos and Zobel, Chapter 4, this volume).

Organism size was critical to survival, and small organisms experienced higher survival rates than did large organisms.

Small organisms were more likely to have been in protected locations, such as belowground or in decaying logs, whereas large organisms were typically exposed to volcanic forces. However, the effect of size had to be considered in relation to the scale of the disturbance process. In the area affected by the towering, hot cloud of the lateral blast, large-stature individuals experienced greater mortality than did smaller ones. Tall, mature conifers, for example, were toppled, while small saplings and shrubs survived under snow cover. In contrast, on the margins of mudflows, commonly only a few meters thick, tall trees survived because they were able to resist the force of the flow and hold their unaffected crowns above the flow (Frenzen et al., Chapter 6, this volume). Similarly, large mammals, such as elk (*Cervus elaphus*) and black bear (*Ursus americanus*), experienced complete mortality in the blast area, but many small mammalian species survived in subsurface refuges (Crisafulli et al., Chapter 14, this volume).

20.2.3 Effects of Timing of the Eruption on Survival

Effects of the 1980 eruption were strongly influenced by timing of the event at scales ranging from the time of day to the successional status of the ecological systems affected by the disturbance. The 8:32 a.m. beginning of the eruption, for example, occurred when many nocturnal mammals, such as mice and voles, had returned to their subterranean daytime retreats, where they were protected from the blast and tephra fall. The season of the eruption was significant in terms of the status of snow and ice in terrestrial and aquatic systems, the migratory status of seasonally transient visitors to the area (e.g., migratory birds and salmon), and the phenology of plants. Bud break, for example, had not yet occurred in many upper-elevation areas, so plants avoided damage to foliage that might have occurred if the eruption had been just a few weeks later. The status of succession across the Mount St. Helens landscape before the eruption influenced the ability of species present to survive. In the first few years after 1980, for example, preeruption clear-cuts supported more surviving species because early-successional communities were dominated by herb species with the ability to sprout vigorously from belowground, perennating structures, unlike most understory species of mature forests (Means et al. 1982). Had the eruption occurred at another time, the ecological consequences would have been markedly different. These sensitivities of ecological response to the timing of disturbance highlight the importance of chance in determining effects of disturbance, both in the near term and long term.

20.3 Factors Influencing Succession

Ecological succession at Mount St. Helens was influenced by

- Survivors of the eruption;
- Physical conditions, including secondary disturbances;
- New colonists that dispersed into the disturbed area, established, grew, spread, and interacted with other species and their environment; and
- Human activities.

These elements of succession provide a conceptual framework for discussing succession at Mount St. Helens (see Figure 20.1). Briefly, following the eruption, a subset of the organisms and structures survived, some of which later perished because of their inability to tolerate the new conditions, and the remaining survivors grew and spread, and were joined by colonizing species. The colonizing species were determined by source populations, species vagility, and a series of dispersal and site-condition filters. Species accrued to the point where biological communities developed and a myriad of biotic interactions commenced. Climate, human activities, and secondary disturbances strongly influenced the rate and pattern of succession.

The many processes of succession are highly complex and inextricably intertwined, which makes a discussion of each of the elements of succession in isolation somewhat artificial. Nonetheless, to discuss key aspects of succession, each is presented separately next. During the first quarter century after the 1980 eruption, all mechanisms of succession, for example, facilitation, inhibition, and nearly all forms of species–species interactions, have occurred in the Mount St. Helens landscape. Frequently, these successional processes and species interactions operate at the same time and place, and alternative sequences are common.

20.3.1 Influence of Survivors on Succession

Surviving fungi, plants, and animals played numerous important roles in many of the disturbance zones following the 1980 eruption. Survivors were source populations for adjacent areas, ameliorated site conditions, established important ecological linkages among biota, and served as habitat and food resources, permitting or promoting the persistence of other survivors and the colonization of new species. Survivors produced seeds, spores, and offspring, which served as source populations for adjacent areas where those species did not survive. The in situ reproduction of nearly all the flora and fauna of the southern Washington Cascade Range from thousands of epicenters of survival was paramount. This process greatly reduced the potentially lengthy process of dispersal from distant sources and strongly influenced the rate and spatial pattern of succession.

Survivors developed important ecological linkages among organisms and facilitated the establishment and spread of other species. Within days of the eruption, for example, surviving gophers mixed underlying mineral soil with tephra. These gopher-modified soils contained fungal spores and buried seeds and were suitable sites for seedling establishment and plant growth (Andersen and MacMahon 1985b; Allen et al., Chapter 15, this volume). Surviving plants and dead wood provided food resources and habitat for colonizing plants and animals.

Large conifer snags provided the nesting and foraging sites necessary for several birds to colonize the blast area (Crisafulli and Hawkins 1998). Small mammals transported seeds from surviving patches of vegetation to barren areas where they later germinated. Shading from surviving plants ameliorated hot surface conditions and created safe sites for wind-dispersed seeds. In this way, surviving plants and other structures were nuclei of establishment that promoted the colonization and spread of plants, which in turn attracted animals. Through time, these areas of surviving plants developed into large patches of vegetation supporting complex communities.

Surviving animals also became important consumers in posteruption communities (i.e., predators herbivores, scavengers, and decomposers), in some cases impeding colonization by other species. Survivors did not always persist in the new landscape because of desiccation, heat, lack of nutrients, and other causes of mortality (see Figure 20.1).

20.3.2 Dispersal

With the elimination or reduction in species and the creation of open terrain, dispersal became a very important initial process of succession within the most severely disturbed areas at Mount St. Helens. The pattern and rate of dispersal was influenced by the distance to source populations, local wind patterns, landscape permeability, and species and propagule mobility. Distance and landscape permeability were filters restricting the number of species capable of reaching a location within the disturbed landscape (see Figure 20.1). The distance to source populations was determined by the size and shape of the disturbance zones for the most severely disturbed, legacy-free areas, such as the pyroclastic-flow and debris-avalanche zones. Wind flows along the river valley may best explain the high number of wind-dispersed seeds in the center of the debris-avalanche deposit (Dale 1989). In zones with high survival, such as parts of the blast area, local sources of colonists of most species were often nearby in the numerous scattered epicenters of survival. These in situ sources of propagules greatly accelerated the pace of succession by reducing the importance of species vagility, dispersal distance, and landscape permeability. In areas lacking survivors or in areas where a species was extirpated during the eruption, highly mobile species such as birds, ballooning spiders, windblown seeds, and large mammals were the first to arrive. Within 10 years after the eruption, most of the plant species with long-distance dispersal capabilities and that were present elsewhere in the southern Washington Cascade Range had reached most disturbed areas. During the second decade, many animal populations became widely distributed, and animals disseminated plant species that have limited dispersal capacity, such as species with berries and fleshy fruits.

For less-mobile organisms, distance appeared to be a barrier to colonization. For example, tailed frogs (*Ascaphus truei*) survived in many watersheds within the blowdown zone, but by 2003 they had yet to colonize streams in the pyroclastic-flow or debris-avalanche zones despite the presence of suitable habitat (Crisafulli et al., Chapter 13, this volume). Many individual organisms and propagules of diverse taxonomic groups exhibited surprising ability to traverse substantial distances (e.g., several kilometers), sometimes over harsh terrain, to colonize more-favorable habitats (Dahm et al., Chapter 18, this volume; Crisafulli et al., Chapter 13, this volume; Crisafulli et al., Chapter 14, this volume). Many of these movements appeared to be random dispersal events, suggesting that chance was an important aspect of dispersal (del Moral et al., Chapter 7, this volume). Overall, a remarkably diverse assemblage of fungal, plant, and animal species or their propagules had successfully dispersed through each disturbance zone within the first quarter century after the eruption.

20.3.3 Secondary Disturbance and Succession of Geophysical Processes

Secondary disturbance by erosion, scour, and deposition processes, such as lateral channel migration and small landslides, is a direct result of the primary disturbance processes and influenced succession in many areas. The type and magnitude of these processes varied in time across the volcanic landscape, creating a geophysical succession of prominent processes. Because the new deposits were easily eroded and the terrain was steep, remobilization of tephra was common during the first few years after the eruption. Small gullies that developed in fall and winter cut down to preeruption soil, facilitating plant survival and growth by releasing perennial rootstocks, exposing soil, and trapping windblown seeds. However, other physical processes, such as shifting river channels and landslides, retarded succession by scouring or burying plants and animals, thereby resetting succession in substantial parts of the landscape. Landslides and sediment that traveled down lake-inlet streams created shoal habitat, alluvial fans, and deltas in many lakes, which promoted establishment of emergent wetland plant communities. Many streams on the Pumice Plain and debris-avalanche deposit were subjected to chronic secondary disturbance from 1980 and continued through the following decades, which set back development of riparian vegetation and associated animal communities. With the exceptions of continued river-channel instability in the debris-avalanche deposits and precipitation-triggered landslides during 1996 and 1997, secondary geophysical disturbances lessened dramatically after the early 1980s.

20.3.4 Site Amelioration

Site amelioration occurs when the conditions on a site improve, typically with respect to soil, microclimate, and other physical conditions, and enable a species to establish, grow, and reproduce. The harsh physical conditions of recently disturbed sites greatly influence the process and pace of succession. During the dry, hot summers, the fresh geological material deposited over much of the area disturbed by Mount St. Helens was more like a desert than the lush Pacific Northwest forest. Site amelioration was of great importance during the first few years after the eruption when the new deposits blanketed the ground, and survivors, where present, were in their initial stages of response. The fresh substrates had low nutrient status, little moisture-retention capability, and limited shade in the blast area and pyroclastic-flow and debris-avalanche zones, which hindered establishment and growth. Thus, materials deposited during the 1980 eruption were far from optimal for plant growth and required weathering and nutrient input from windblown material, precipitation, and (where present) plants and animals for biotic development to proceed. The volcanic events also produced high concentrations of sediment, especially fine material, in the benthic layer and water column of lakes and streams. These conditions impeded establishment and growth of immigrating fungi, plants, and animals. Amelioration was most important where biological legacies were few or absent.

A variety of physical processes, such as erosion that created favorable microsites, ameliorated site conditions and promoted establishment and growth. Physical weathering by freeze-thaw and wet-dry cycles fragmented surface tephra particles. The resulting production of fine-textured, inorganic material, combined with accumulation of organic matter, hastened the development of soil and increased water-holding capability and nutrient content. Continued flow through stream systems over the years has removed a great deal of fine sediment from the channels and exposed cobble streambeds characteristic of Cascade Range streams. Suspended sediment settled to the bottom of lakes, resulting in increased light transparency, which was necessary for photosynthesis.

Animals also played a role in site amelioration. Northern pocket gophers created vast tunnel systems, which were used by amphibians and other animals to escape from the hot, dry surface conditions during the summer (Crisafulli et al., Chapter 14, this volume). Wind-dispersed insects landed in surprisingly large numbers and mass on nutrient-poor pyroclastic-flow deposits, where they died and their bodies contributed nitrogen and other nutrients and trace elements important for plant growth (Edwards and Sugg, Chapter 9, this volume).

As time elapsed, substrates were modified, species colonized, and conditions generally improved so that site amelioration presumably became less critical in many locations. Further amelioration will undoubtedly be required for species requiring the development of duff or other characteristics to establish.

20.3.5 Establishment

Establishment of individuals and populations involves several steps; organisms must either survive in or disperse to the disturbed area and then find suitable conditions under which they can colonize, grow to maturity, and reproduce. Critical factors limiting establishment included the ability of seeds and spores to germinate and grow in the fresh volcanic substrates and, in the case of animals, the presence of appropriate habitat and food resources. Substrate quality influenced which species were able to establish because seed germination and plant growth were initially less than optimum on the new volcanic material. Microtopography created slope, moisture, and shading conditions that were important to plant establishment and growth. Vertebrates with high vagility established in lockstep with the development of suitable habitat, with little apparent lag time between their establishment and the presence of suitable habitat. Thus, habitat structure was a reliable predictor of vertebrate establishment.

Specific characteristics of species either promoted or limited those species establishment. For example, neoteny, the attainment of sexual maturity while maintaining larval characteristics, enabled three species of salamanders to establish populations in some disturbance zones. For these species, suitable habitat was available for the aquatic neotenic forms, but the forest habitat required by terrestrial life-history stages was absent. Thus, the portion of the population that metamorphosed into terrestrial adults often perished.

Failure of some organisms to establish may reflect inadequate habitat or dispersal limitations or both. Many of the species that have not colonized may have been limited by their habitat requirements rather than by dispersal limitation, such as species associated with forest canopy. The diversity of habitats that had developed on the landscape by 2005 suggests that even many late-seral-forest understory species and woodland salamanders could exist in certain microsites (i.e., seeps, upper reaches of streams, and ravines) in the highly disturbed zones and that it is dispersal distance that has precluded their establishment. For example, many of the plant species that reached the Pumice Plain lacked the requirements for establishment, and those that could readily establish did not arrive because of low dispersal capability (del Moral et al., Chapter 7, this volume).

A tremendous number of organisms and propagules dispersed into disturbed areas and established; however, several hundred known and perhaps many more unknown species arrived but failed to establish (Edwards and Sugg, Chapter 9, this volume). As succession proceeds and appropriate habitat develops, it is anticipated that many of these species will become established. The simultaneous establishment of both early- and late-successional species has important long-term consequences for succession. In particular, several late-successional conifer tree species established on the debris-avalanche and pyroclastic-flow deposits in the early 1980s.

Many of the establishment events that occurred at Mount St. Helens have gone against conventional wisdom and suggest that we lack a clear understanding of the conditions under which many species may establish. Chance also plays a large role in the establishment of many species, particularly as it relates to the dispersal of propagules and organisms by animals and to the settling of wind-dispersed seeds onto favorable safe sites.

20.3.6 Mechanisms of Succession and Biotic Interactions

Interactions among species are very important components of succession because they influence the rate and pattern of colonization, the accumulation of biomass and plant cover, population dynamics, and trophic interactions. Biotic interactions in the Mount St. Helens landscape have been incredibly diverse, and all of these phenomena are integral to succession. Connell and Slatyer (1977) proposed three broad models of mechanisms of succession: facilitation, tolerance, and inhibition. Each of these has been observed at Mount St. Helens, often at the same place and time, demonstrating that multiple mechanisms of succession are likely to occur simultaneously, and any one model should not be expected to have universal explanatory power. Facilitation was the most conspicuous mechanism of succession at Mount St. Helens and involved virtually all taxonomic groups. Facilitation is exemplified by patches of lupines on the Pumice Plain that trapped seeds and detritus and helped contribute nitrogen to the soil, thereby facilitating establishment of additional plant and animal species (del Moral et al., Chapter 7, this volume; Halvorson et al., Chapter 17, this volume). Although Connell and Slatyer's (1977) facilitation model was specific to plant–plant interaction, we note that microbes and animals also facilitated the establishment of other species. For example, microbes in Spirit Lake swiftly altered nutrient and oxygen concentrations and ushered in suites of new bacteria (Dahm et al., Chapter 18, this volume). Beavers (*Castor canadensis*) created impoundments on all major streams in the blowdown zone, thereby establishing habitat that supported colonization by several pond-breeding amphibians (Crisafulli et al., Chapter 13 this volume).

Inhibition, where one species has a negative effect on another, was conspicuous in the Mount St. Helens landscape in the cases of herbivory on lupines by larvae of several lepidopteran species and where woody vegetation shaded the ground, resulting in the decline of sun-requiring herbs. Tolerance was evident on the Pumice Plain and debris-avalanche deposit, where late-successional tree species colonized alongside early-successional herbs. Numerous boom-and-bust cycles occurred as colonizing species encountered favorable conditions upon arrival at Mount St. Helens and their populations flourished, essentially unregulated. However, these burgeoning populations were eventually found by herbivores, predators, or parasites, which in turn grew rapidly and decimated their resource base, only to have their own populations eventually collapse.

Interactions such as predation, herbivory, parasitism, and mutualism that permeate complex, species-rich ecosystems were particularly notable in the sparse ecological systems characteristic of the early stages of response to the disturbances at Mount St. Helens. As communities grew in complexity, virtually all forms of species interactions could be found in the area.

20.3.7 Species Accrual and Community Structure

The 1980 eruption greatly reduced or eliminated vegetative cover and structure and the species richness and abundances of virtually all taxonomic groups. However, over the subsequent years, a remarkable reassembly process unfolded as survivors grew and spread and were joined by migrants that colonized and filled in much of the landscape and interacted with one another and their environment. Over time, all disturbance zones experienced increases in the number of species, percent vegetation cover, complexity of vegetation structure, abundance of animals, and community complexity. For example, plant-species richness was very low (commonly no species was present) in the most severely disturbed terrestrial sites following the eruption. In 13 years, however, at least 150 species of vascular plants had colonized these areas (Titus et al. 1998b) [as compared to the almost 300 species that St. John (1976) reported from the slopes of the mountain before the eruption]. Terrestrial animals also underwent rapid colonization, and by 2000, even the most heavily disturbed zone supported nearly all small mammals indigenous to the southern Washington Cascade Mountain Range (Crisafulli et al., Chapter 14, this volume). Colonization by aquatic taxa was also rapid; for example, 135 species of phytoplankton established in Spirit Lake between 1983 and 1986 (Dahm et al., Chapter 18, this volume). During the first quarter century since the eruption, a steady accrual of species has occurred, with few examples of species replacements (Parmenter et al., Chapter 10, this volume; Dahm et al., Chapter 18, this volume). During the accrual process, species from all taxonomic groups of the regional pool, spanning all trophic levels had colonized the Mount St. Helens landscape. Many of these species flourished in the posteruption conditions.

Vegetation cover (percent of land area covered by live plant material) increased dramatically in all disturbance zones from 1980 to 2005. The rate of cover increase was greatest in areas with high survival, which corresponded with lowest disturbance intensity. In areas undergoing primary succession (the debris-avalanche and pyroclastic-flow zones), cover went from zero in 1980 to as high as 70% by 2000, but typically ranged from 10% to 40%. Cover increases were commonly related to the growth form of the species present. Many plants spread by vegetative growth from stolons or rhizomes. In the case of prostrate plants, the rooting of stems made them dominant players in many of the disturbance zones. Cover increased dramatically in the ponds created by the eruption, and by 2000 the percent cover of emergent and submergent species frequently exceeded 80%.

Herbivory and secondary disturbances have strongly shaped percent cover of many plant communities. Herbivory by several lepidopteran larvae reduced the abundance and cover of their target species on the Pumice Plain (Bishop, Chapter 11, this volume). Elk herbivory on the debris-avalanche deposit resulted in an increase in plant cover and richness as compared to ungrazed areas (Dale et al., Chapter 5, this volume).

Cover of nonnative species experienced an especially high increase with elk grazing, yet understory species typical of the Pacific Northwest forests declined in cover. Secondary geophysical disturbances also dramatically affected cover and in some cases eliminated the plant cover in large areas.

After the eruption, vegetation structure (physiognomy) became increasingly complex within each disturbance zone; this had important consequences for succession. As composition or dominance of plant species changed and plants grew, vegetation structure increased, which created habitat for a host of new species. This change was particularly true of riparian zones that developed a continuous growth of willow during the second posteruption decade and was followed by the colonization of numerous animals. Differences in physiognomy across the disturbance zones were related to the dominant life forms, stem density, and growth rates.

20.3.8 Human Influences on Succession

Human actions following the 1980 eruption modified the composition and structure of both aquatic and terrestrial systems in ways that both accelerated and retarded succession (Dale et al., Chapter 19, this volume) (see Figure 20.1). These human activities were undertaken to reduce hazardous conditions; to salvage economic value; and to enhance restoration, tourism, and recreation. Some management actions, such as broadcast seeding of nonnative plant species in an effort to control erosion, had minimal success over much of the treated area. In other locations, it had deleterious effects on the native flora (Dale et al., Chapter 5, this volume). In many cases, multiple objectives involving tradeoffs with protection of ecological values were at stake. For example, extensive salvage of blown-down timber eliminated snags for their wood value, for reduction of future fire hazard, and for the safety of loggers removing valuable toppled trees. But this activity also removed habitat for cavity-nesting birds. By 2005, the forest that was planted after salvage logging had grown into dense plantations with animal assemblages that differed substantially from areas undergoing natural succession. For example, field inventories of the avifauna revealed much higher species abundance and more numerous foraging guilds in the naturally regenerating blast area than in dense, young plantation forests that had been salvage logged and planted with tree seedlings. Some lakes were stocked with fish, which altered the lake ecosystems (Bisson et al., Chapter 12, this volume). Some of these management actions also required ongoing human intervention, such as management of the sediment-retention structure on the Toutle River and the associated transportation of fish moving upstream.

20.4 The Mount St. Helens Landscape of 2005

The Mount St. Helens landscape shortly after the eruption in 1980 appeared stark, simple, and seemingly sterile (see Figure 1.1b). However, within a few months, it became clear that life persisted in much of the landscape. During the next two decades, the biology of lakes, streams, and terrestrial systems responded dramatically (Figure 20.2). In the areas nearly devoid of biological legacies (the debris-avalanche and pyroclastic-flow zones), much of the land was covered with herbaceous vegetation by 2005. That vegetation included lupines and numerous other herbs and grasses, with scattered shrubs and low densities of conifer and deciduous tree saplings (Figure 20.2a,b). Animal communities in these habitats tended to be depauperate and to include species characteristic of open terrain. Dense thickets of willow (*Salix* spp.) and alder (*Alnus* spp.) grew at most seeps and along streams with stable flow regimes. These deciduous woody plant communities provided habitat for several diverse animal assemblages, most notably mammals, birds, and invertebrates. The large number of animals that established in these structurally complex habitats greatly increased the overall diversity of the pyroclastic-flow and debris-avalanche zones. Streams with flashy flow regimes and unstable bed and bank material remained quite dynamic environments, which impeded establishment of riparian and aquatic communities. Accordingly, these streams had a low diversity of aquatic insect species. Lakes stabilized physically and biologically and quickly attained characteristics similar to undisturbed lakes in the southern Washington Cascade Range. The newly formed ponds on the debris-avalanche deposit included a broad array of wetland types, ranging in hydrologic regime from ephemeral to perennial. By 2005, these highly productive ponds supported complex, species-rich plant communities and were used extensively by a diverse assemblage of aquatic and semiaquatic animals.

In the blast area, where natural succession was substantially influenced by living and dead biological legacies, vegetation patterns were quite heterogeneous by 2005 (see Figure 20.2c). Herbaceous vegetation and large shrubs provided extensive cover, shrub-dominated riparian and lakeshore vegetation was well developed, and numerous individual and patches of conifer trees were present. These patches of conifers were legacies that were shielded as small saplings under snowpack at the time of the eruption and have since grown several meters tall and developed the characteristics of a young natural forest. Many of the large standing, dead trees and downed logs were decomposing and fragmenting. In the scorch zone in 2005, the variety of community types was based largely on the extensive biological legacies that remained after the eruption. In areas where snow was present during the eruption, vigorous stands of conifers and understory species were growing among the boles of standing dead trees. In areas where snow was not present during the eruption, shrubs and early successional herbs were dominant. Areas of standing, dead forest had high bird-species diversity. In sharp contrast to naturally regenerating portions of the blowdown and scorch zones, areas that were salvaged logged and planted with conifer seedlings in the first few years after the eruption became dense plantations with trees commonly exceeding 10 m in height. Animal assemblages in parts of the blast area were very diverse, and for vertebrates included the majority of species indigenous to the southern Washington

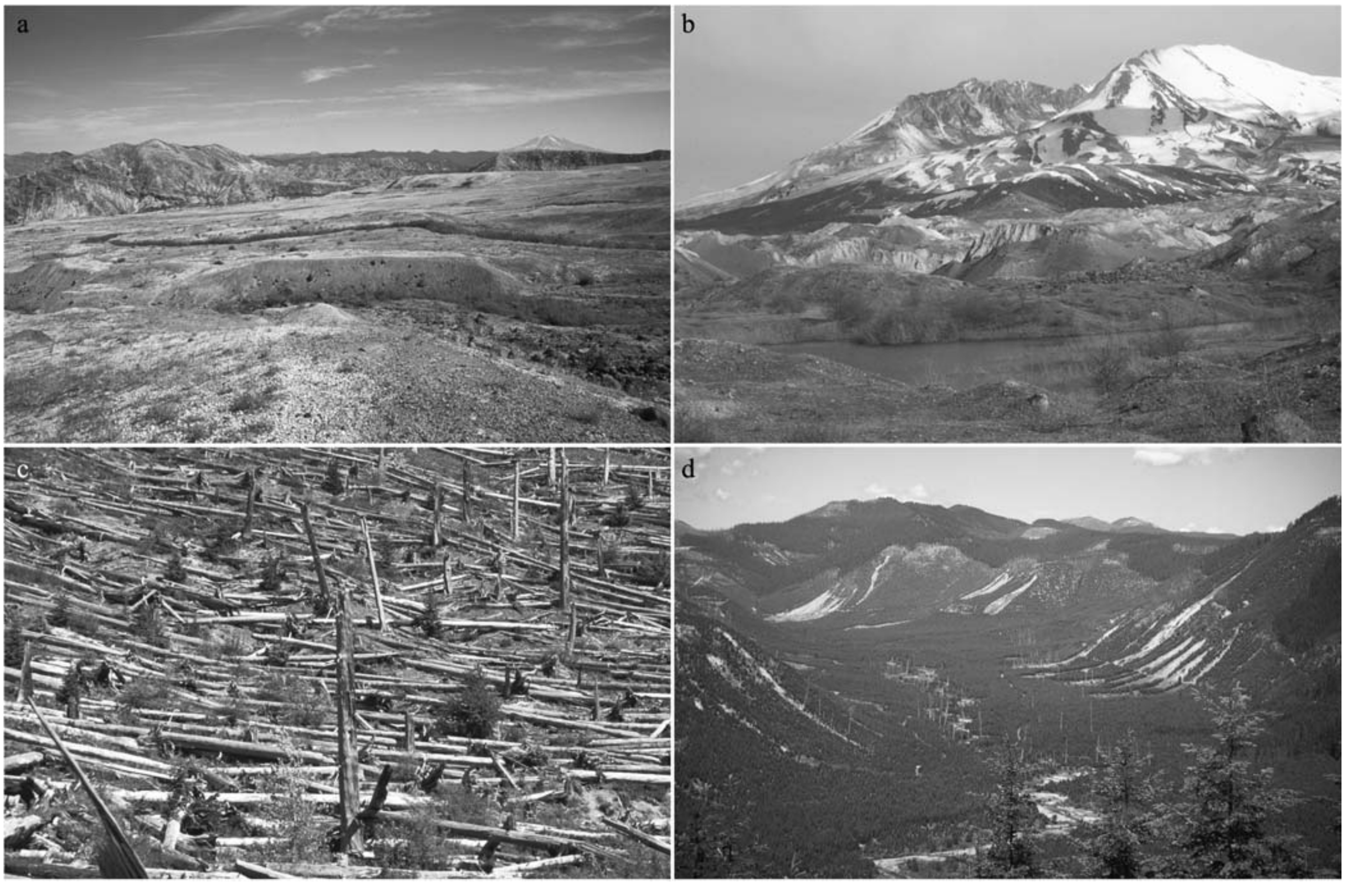

FIGURE 20.2. Photographs of several disturbance zones at Mount St. Helens: (a) pyroclastic-flow zone with invader hotspot (2002); (b) debris-avalanche deposit (2003); (c) blowdown forest in upper Green River (2004); (d) Clearwater Valley showing plantations punctuated with landslides.

Cascade Range. In contrast, the plantation forests had fewer vertebrate species, but those present tended to be at high densities, reflecting the simpler and extensive habitat structure and composition.

By 2005, most streams in the blast area had flushed away the fine volcanic sediment, exposing coarse substrates typical of the region, and their riparian zones were lined with shrubs that provided shade and stabilized daily temperature. Their biota was composed of a suite of vertebrates and invertebrates typical of the region. Blast-area lakes had regained physical and biological conditions similar to undisturbed lakes, despite the lack of coniferous forest along their shores and in-flowing streams (Dahm et al., Chapter 18, this volume).

Vegetation characteristics of the tephra-fall zone in 2005 were substantially different between sites that had been clear-cut before the eruption and those which had been forested. Vegetation and animals in preeruption clear-cuts were typical of clear-cuts of the same age that were not disturbed by the eruption and supported a very dense growth of grasses, herbs, and shrubs. In contrast, tephra-fall forest sites have been slow to regenerate an understory component, which remains sparse and depauperate. Understory legacy species, primarily conifer saplings and ericaceous shrubs, dominate most stands, with numerous understory herbs associated with logs and tree buttresses.

Mudflow-impacted streams and riparian areas were located mainly at lower elevation and bordered by forested systems. In many cases, they have tributary streams little affected by the eruption. These and other factors have led to speedy ecological responses and recovery approximating preeruption conditions, except for the North Fork Toutle River, which continues to carry exceptionally high sediment loads from the debris-avalanche deposit. In most areas of mudflow impact, the river position has stabilized, and dense stands of alder and willow have developed on the floodplain, although gravel bars within the floodway are turned over annually. Fish populations have established through natural colonization and stocking, but the upstream movement of anadromous species is blocked by the sediment-retention structure on the North Fork of the Toutle River and requires human intervention.

The diverse patterns of terrestrial vegetation can be viewed in a simplified framework of being composed of sites of slow or rapid development situated within a matrix of intermediate conditions (see Figure 20.2a,b,c). Sites with substantial legacies of preeruption plants developed relatively rapidly, forming *survivor hotspots* for organisms that lived through the eruption. Survivor hotspots occurred where the smothering effects of the new deposits were ameliorated by erosion, snowpack, bioturbation, or other processes and where deposits were thin enough that organisms could penetrate them from either above or below. In contrast, areas with thick deposits that were dominated by primary succession had some sites with physical conditions favorable to ecological establishment where high densities of immigrant species and biomass accumulated. These *invader hotspots*, sites with concentrations of invading plants (Figure 20.2a,b), were located on substrates with adequate physical stability, nutrients, and water, such as the stable flows of groundwater seeps and spring-fed streams. Sites with very slow establishment of plant and animal communities, termed *coldspots*, occurred on areas of severe nutrient and water limitation, very poor microclimate conditions, and persistent or pulsed secondary disturbance (see Figure 20.2d). These hotspots and coldspots occur in a matrix of intermediate site conditions, where the pace of biotic development was determined mainly by the initial disturbance processes, by local factors, and by subsequent in situ soil development.

Biotic landscape patterns at Mount St. Helens have changed with time, and in some cases earlier patterns have been overprinted by more recent ones. Some small, initial survivor hotspots have coalesced, creating much large patches. Invader hotspots began developing within the first few years after the eruption, but typically were represented by a few, small individuals that took 6 to 10 years to develop into compositionally and structurally distinct communities covering many square meters or even hectares. Hotspots became most conspicuous along stream courses, which by the 1990s were lined with verdant growth of deciduous shrubs and trees in sharp contrast with the matrix areas of the pyroclastic-flow and blowdown zones. In some cases, survivor hotspots served as stepping stones for immigrants that then colonized the matrix. In other cases, surviving species achieved negligible colonization of neighboring matrix areas, probably because of unsuitable habitat conditions (Fuller and del Moral 2003). Planted forests in the outer parts of the blast area developed homogeneous, closed-canopy forest cover, overprinting the earlier, more complex patterns of natural vegetation, which had been dominated by survivor hotspots. Some parts of the blast area switched from a gray landscape in the summer of 1980 to scattered survivor hotspots of green within the gray matrix, followed by development of the continuous green canopy of plantation forest punctuated by gray, deforested patches created by secondary disturbance (e.g., small landslides and channel shifting) (see Figure 20.2d).

Lake, stream, and terrestrial systems were strikingly different in their rates of ecological response following the 1980 eruption (Figure 20.3). These contrasting rates were regulated by

- The degree to which the various systems became nutrient enriched or nutrient limited,
- The pace of adjustment to those changes,
- Physical factors that promoted or inhibited biotic response, and
- The speed of species maturation and longevity.

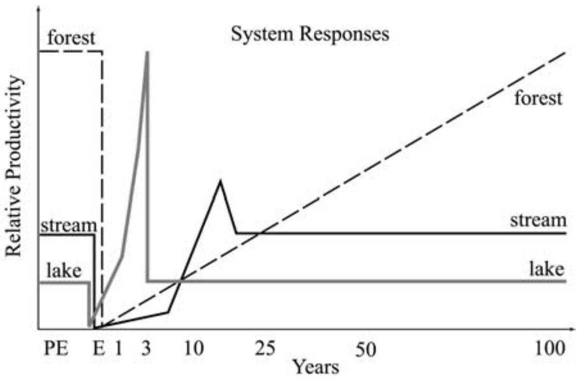

FIGURE 20.3. Conceptual response curves depicting temporal changes in productivity in terrestrial, lake, and stream systems after the 1980 eruption of Mount St. Helens. *PE*, preeruption values; *E*, values at time of eruption.

Systems that became nutrient enriched underwent a rapid rate of change relative to systems that became nutrient impoverished. The most disturbed lakes, for instance, were greatly enriched in nutrients by the eruption and underwent rapid biogeochemical cycling that returned water quality and other aspects of habitat to conditions approaching undisturbed lakes of the southern Washington Cascade Range within several years (Dahm et al., Chapter 18, this volume). Succession in streams was more strongly influenced by the rates of change of sediment levels, habitat structure, and condition of riparian vegetation (Hawkins and Sedell 1990). For example, in the blowdown zone, 10 to 15 years of physical habitat and vegetation development led to the establishment of faunal communities typical of forested streams in the region. In contrast, by 2005 streams in the pyroclastic-flow and debris-avalanche zones remained in the early stages of ecological response because of persistently high sediment levels and failure of riparian vegetation development. Succession of terrestrial plant and animal communities was slower than lakes or streams, and in all but the tephra fall zone, sites of natural forest development were in the early stages of development by 2005. It will likely be a century or more before these forests become mature conifer-dominated communities typical of the Pacific Northwest. This slow pace of response was driven in part by the slow pace of establishment, the slow growth and great longevity of individual trees, and the protracted development of structural heterogeneity of forest stands (Franklin et al. 2002).

20.5 Ecological Response at Mount St. Helens: Broader Contexts

This book has focused on ecological change in the Mount St. Helens landscape from 1980 to 2005, but it is important to view this period in the context of longer-term ecological and volcanic change in the vicinity of Mount St. Helens and of volcanic and other major disturbance in the Pacific Northwest and elsewhere.

20.5.1 Mount St. Helens Events from 1980 to 2005 in Relation to the Longer-Term, Local Disturbance History

Geological and ecological events associated with the 1980 eruption of Mount St. Helens had attributes both characteristic of and quite different from the disturbance regime of the landscape over the preceding millennia (see Table 2.1). Earlier disturbances by volcanic flows were more restricted to the lower flanks of the volcano, except in the cases of extensive mudflows down rivers draining the mountain. Tephra fall from the 1980 eruption was more limited in thickness and extent than several of the previous eruptions but was consistent with past patterns of principal deposition being northeast of the vent. The most distinctive features of the 1980 eruption were the debris avalanche and the lateral blast, which are rare events that had a relatively large areal extent. Legacies of earlier eruptive episodes in the forms of tephra deposits blanketing hill slopes and landforms, such as the blockage forming Spirit Lake, affected the ecological response to the 1980 eruption.

Nonvolcanic disturbance processes have also been integral components of the southern Washington Cascade landscape, and these processes interact with volcanic events and their aftermath. Wildfire has been a prominent process in this landscape, typically functioning as stand-replacement disturbance, leading to establishment of the extensive conifer forests so characteristic of the west slope of the Cascade Mountains (Agee 1993; Yamaguchi 1993). The frequency of wildfire 10 to 20 km northeast of the volcano was similar to the frequency of substantial tephra deposition, and both occur more frequently that the maximum lifetimes of individuals of dominant tree species (Yamaguchi 1993).

20.5.2 Mount St. Helens 1980 Eruption in a Pacific Northwest Regional Context

Large-scale, infrequent disturbances have been important forces shaping ecological systems of the western Cascade Range for millennia. Extensive and severe disturbances, such as catastrophic stand-replacement wildfire and volcanism, create large areas where succession proceeds from early seral stages. These early stages of succession are very important in providing habitat for a wide array of the region's biota and may be integral to maintaining regional biodiversity. Distinctive, large areas of early-successional habitat and their associated large source pool of early seral species are becoming increasingly rare in the Pacific Northwest because of recent and current management direction. Fire suppression has reduced the number of large fires; and when they have occurred, managers have been quick to undertake salvage logging and planting of conifers, which removes legacy structures (e.g., snags and downed wood) and suppresses herb and shrub vegetation (which provides vital, diverse habitat and food resources for many species). Also, clear-cut logging and subsequent intensive silvicultural practices have created vast areas of conifer plantations in the Pacific Northwest landscape, greatly limiting the extent of the early seral (herb and shrub) successional stage. The net result of these activities is the reduction in area of early-successional herb- and shrub-dominated communities and a highly heterogeneous successional process in which plant communities develop at different rates and with different species compositions. The resulting habitat diversity is important to a wide suite of organisms (e.g., lepidopterans, birds, and amphibians). The 1980 eruption of Mount St. Helens and establishment of the National Volcanic Monument created conditions that allowed a natural succession to occur and will likely play a vital function for the larger Pacific Northwest region.

20.5.3 Mount St. Helens in Relation to Major Disturbances Elsewhere

Many other disturbance events, both large and small, have been studied around the globe. Among well-studied volcanic eruptions, the 1980 Mount St. Helens events stand out in terms of complexity, real-time observations, and diversity and intensity of detailed posteruption analyses by geologists and ecologists. However, the event was far from the grandest volcanic eruption in terms of magnitude of energy release, size of affected areas, or severity of ecological disturbance. Flood basalt flow and massive pyroclastic flows, for instance, have affected much larger areas (Harris 1988) with more profound and protracted ecological impacts. The 1980 Mount St. Helens events lack lava flows, which are common in many volcanic eruptions and geological settings.

Similarly, Mount St. Helens events of 1980 were dwarfed in extent and impact by some nonvolcanic events, such as bolide impacts on the earth that may have caused major, worldwide extinctions observed in the geological record. Yet, the 1980 eruption of Mount St. Helens has provided a useful example of volcanic-disturbance processes and associated ecological responses in the context of analysis of large, infrequent disturbances (Turner et al. 1997; Turner and Dale 1998). In comparisons with wildfire and windstorms, the Mount St. Helens eruption had notable distinctions, including widespread deposition of fresh rock debris. These tephra deposits have gradients of thickness over kilometers, localized sites of greater or lesser thickness affecting survival and colonization, and spatial superposition of processes and deposits, all of which complicate interpretation of disturbance effects.

20.6 Conclusions

Mount St. Helens after the 1980 eruption is a landscape of strong impressions. The initial disturbances were immense and highly varied in the types of processes involved and ecological systems influenced. The affected ecological systems exhibited remarkable resilience in many ways. Yet, a quarter century after the 1980 eruption, we have witnessed only the initial stages of the ecological responses. Most areas have undergone rapid, dramatic change in substrate condition, species diversity, and vegetative cover and physiognomy since the eruption. On the other hand, biological responses in some parts of the landscape have been quite slow, particularly where secondary disturbances have repeatedly reset biological development. Forests of this region undergo succession spanning a millennium or more, so we have viewed only a tiny fraction of the potential duration of successional sequences.

Prior analysis of succession and disturbance has been useful to varying degrees for interpreting events at Mount St. Helens to date. During more than a century of debate, many concepts of succession have been put forth, yet none of these appears to be comprehensive enough to adequately capture the dynamic and highly variable processes that occur during succession. The Mount St. Helens landscape provides examples of most, if not all, extant models of succession and illustrates that many mechanisms of succession can operate concurrently in one location. Hence, the Mount St. Helens experience provides a clear example of how complex succession may be and demonstrates that most models are far too simplistic to account for all the variation that occurs as systems respond to disturbance. Some of this complexity appears to be related to random processes, chance, and contingencies that unfold during the initial disturbance and subsequently as succession proceeds. These properties of succession are difficult to incorporate into mechanistic models and have likely limited the extent to which succession can be predicted precisely. Disturbance ecology, another scientific point of view relevant to interpreting the Mount St. Helens story, took shape as a discipline after the 1980 eruption, so the studies at Mount St. Helens have contributed to the development of the field. However, both succession concepts and the field of disturbance ecology have struggled to find generality (McIntosh 1999; White and Jentsch 2001), and neither field has sufficient scope to give a comprehensive framework for interpreting events at Mount St. Helens. Therefore, we summarize the story of Mount St. Helens in terms of 11 lessons that have been affirmed or have expanded thinking concerning ecological response to major physical disturbance.

1. **Mechanisms of disturbance** varied substantially among the types of disturbance processes that operated at Mount St. Helens in 1980. Consideration of the specific mechanisms of disturbance rather than disturbance types provides greater ability to interpret and predict ecological responses to disturbance. Pursuing an understanding of effects of specific mechanisms and their intensity on organisms is an ongoing theme of disturbance ecology.
2. **Gradients of disturbance intensity** occurred systematically across the different disturbance processes involved in the 1980 eruption of Mount St. Helens. Variation in impact force and depth of new deposits, for example, created gradients of disturbance severity reflecting the varying physical forces that occur with distance from the disturbance source. This pattern contributes to both coarse- and fine-scale spatial heterogeneity of disturbance effects across the impacted landscape, making it difficult to disentangle effects of disturbance gradients from effects of dispersal from distant seed sources.
3. **Biotic and abiotic legacies** were exceedingly abundant in much of the disturbed landscape at Mount St. Helens, and they played many vital roles governing the patterns and rates of succession. Areas with surviving organisms and dead biotic structures were among the most complex habitats in the posteruption landscape and promoted establishment of many additional species. Chemical legacies strongly influenced the response of aquatic systems, and legacy soils were important for supporting biological legacies and colonizers. The single most important characteristic influencing the pace and pattern of succession following disturbance may indeed be the type, amount, and distribution of biotic and abiotic legacies.
4. **Rapid ecological response** was perhaps the most striking impression of the posteruption landscape at Mount St. Helens. Several factors contributed to the fast pace at which biota spread, colonized, and grew throughout the disturbed area. The most important contributing factors were the presence of numerous, widely distributed survivors; important dead biological legacies; a diverse source population in the surrounding landscape; unconsolidated volcanic deposits in which plants could establish roots and animals could burrow; and a moist, maritime climate. During the initial decades following the eruption, species from all taxonomic groups of the regional pool of species, represented by all trophic levels, had colonized the Mount St. Helens landscape.
5. **Variability of system response trajectories** was profound among lakes, streams, and forests. This difference appeared to be driven primarily by nutrient levels and physical conditions. Lakes became nutrient enriched and responded rapidly and dramatically, attaining uncharacteristically high levels of primary productivity within days of the eruption. In contrast, terrestrial systems had greatly reduced productivity because vegetation was stripped away and the ground was covered with nutrient-poor volcanic deposits. By 2005, lakes had returned to preeruption productivity levels, whereas productivity of terrestrial systems had increased but remained far below that of a mature forest. This observation illustrates the complexity in evaluating the time required for a landscape to recover following disturbance and has important implications for management of areas following both natural disturbances and those caused by humans.
6. **Spatial heterogeneity** is a common hallmark of large, disturbed landscapes because of the complexities of both the primary disturbance processes themselves and the responses to them. One important consequence of this

heterogeneity is that biological legacies, which serve as sources of propagules for recolonization, may be widely dispersed across the affected landscape. This pattern may greatly accelerate ecological response at the landscape scale and influence alternative successional pathways.

7. **Secondary disturbances** and **succession of geophysical processes** are important consequences of some large, intense disturbances and are integral components of ecological responses to the primary disturbance events. It is important to recognize these phenomena as succession proceeds and to distinguish effects of biological and physical factors in environmental change.
8. **Successional processes** were multifaceted. Numerous processes of succession occurred in the area disturbed by the 1980 eruption, including facilitation, tolerance, inhibition, and relay succession. In many cases, these processes occurred concomitantly at one location and illustrate the complexity of succession. This observation underscores the limits of any one existing mechanistic model to explain succession and our inability to predict when and where certain processes will occur. In addition, nearly all forms of biotic interactions, such as herbivory, predation, and mutualism, were established among organisms shortly after the eruption and played an important role in succession.
9. **Human activities** influenced patterns and rates of ecological response. Even though a large area was designated for natural processes to proceed, many human concerns led to diverse and persistent ecological changes. The overriding concern for human life and welfare, for example, caused parts of the area to be manipulated to reduce downstream sediment movement. There are likely to be long-lasting effects of these interventions, such as the designed program to truck anadromous fish upstream and the continuing, unintended spread of nonnative plant species. Modification of fish and game species, such as stocking and harvest, affects these populations and the ecosystems in which they play critical roles, as does the salvage of downed trees to avoid economic loss.
10. **Chance and contingency** were important factors in ecological responses to the eruption. Chance was paramount in how the timing of the eruption influenced survival at multiple scales. Furthermore, the great size and complexity of the disturbed areas created many opportunities for surprising developments, such as side-by-side occurrence of early- and late-seral species. The importance of chance contributes to the difficulty of developing a general theory for predicting ecological responses to such events. Contingencies were important in determining how sequences of events, such as the order of species colonization, can affect succession. Contingencies are particularly important in succession because it is often the concomitant occurrence of several low-probability circumstances that greatly influences survival and colonization.
11. **Large, disturbed areas experiencing slow succession** may become integral components of regional biodiversity, especially in areas where fire suppression and intensive culture of forests aim to maximize the dominance of conifer forest canopy. Early-seral patches provide complex habitat and diversity of herb and shrub species that are hosts to very diverse communities and food webs involving birds, invertebrates, and other taxa.

Change will be the primary theme in the dynamic Mount St. Helens landscape during the coming decades. The extent and pace of this change will be influenced by the highly variable and complex processes of ecological succession and influenced by landscape position, topography, climate, and further biotic, human, and geophysical forces. We anticipate that the landscape will continue to develop toward a complex mosaic of vegetation patch types, both among and within the various disturbance zones, but that woody species, particularly shrubs, will become increasingly abundant, eventually cloaking most of the landscape. A variety of scattered coniferous and deciduous trees will likely emerge from the shrubs, giving the landscape an open parkland-forest appearance. Eventually, shade-tolerant conifers will become more abundant, and the landscape will appear more uniformly forested but still will express substantial variation because of physical and biological legacies of the 1980 eruption and subsequent successional processes. During this succession, streams and lakes will become more heavily shaded and receive increasing inputs from the terrestrial system. Given the eruptive history of Mount St. Helens, a major volcanic disturbance is likely to occur within the life span of long-lived species in the landscape, such as Douglas-fir (Yamaguchi 1993). Yet, we expect that many biotic, landform, and soil legacies of the 1980 eruption will be evident several centuries in the future.