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Ecological Responses to the 1980 Eruption of Mount St. Helens

With 115 Illustrations

With a Foreword by Jerry F. Franklin

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Plant Succession on the Mount St. Helens Debris-Avalanche Deposit

Virginia H. Dale, Daniel R. Campbell, Wendy M. Adams, Charles M. Crisafulli, Virginia I. Dains, Peter M. Frenzen, and Robert F. Holland

5.1 Introduction

Debris avalanches occasionally occur with the partial collapse of a volcano, and their ecological impacts have been studied worldwide. Examples include Mt. Taranaki in New Zealand (Clarkson 1990), Ksudach in Russia (Grishin et al. 1996), the Ontake volcano in Japan (Nakashizuka et al. 1993), and Mount Katmai in the state of Alaska in the United States (Griggs 1918a,b, 1919). Analyses have shown that as many as 18 previously undetected debris avalanches have flowed from the Hawaiian island volcanoes (Moore and Clague 1992). Following the debris avalanche at Mount Katmai in Alaska, Griggs (1918c) found that the deposit depth influenced plant survival. As a volcano collapses, glaciers, rocks, soil, vegetation, and other material are moved with great force down the mountain. Debris avalanches are typically cool and can bury surfaces with as much as 200 m of material. They tend to follow the original topography, have abrupt edges, and produce steep, undulating topography that can persist for many millennia.

The largest debris avalanche in recorded history occurred at Mount St. Helens on May 18, 1980. The debris avalanche flowed in three general locations north and west of the volcano. A portion slammed into and traveled through Spirit Lake, another portion overtopped a 300-m-high ridge about 7 km north of the volcano's summit and traveled down South Coldwater Creek, and the third and largest lobe traveled down the North Fork Toutle River valley (Voight et al. 1981). In this chapter, we focus solely on the portion of the debris avalanche that was confined to the North Fork Toutle River valley. That debris avalanche traveled 25 km, removing and burying nearly all components of the forest in its path. The debris-avalanche material was variable in temperature and included blocks of glacier ice and hot chunks of rock that originated from the volcano's cryptodome, the body of magma injected into the volcano leading up to the May 18, 1980, eruption. Near the mountain, the path of the deposit bisected areas of the blowdown zone; and toward its terminus, the deposit cut through forested areas that were largely unaffected by the 1980 volcanic events. The new deposit created environments in the valley floor that were largely free of living organisms, viable seeds, or organic matter as well as areas near the valley walls with clumps of organic material, soil, and surviving plants. The debris-avalanche deposit provided an opportunity to examine factors important under conditions closer to primary succession than the blowdown, tephra-fall, or mudflow zones created by the 1980 eruption of Mount St. Helens. Vegetation establishment has been affected by the nearly complete loss of plant life and seeds on the deposit, nature of the deposit, local climate conditions, herbivores, and surviving plant life and seeds in adjacent areas.

This chapter presents an overview of factors affecting plant establishment on the Mount St. Helens debris-avalanche deposit during the initial 20 years after the 1980 eruption. The chapter summarizes the initial physical and biological conditions on the debris-avalanche-deposit surface. Next, it describes a set of permanent plots, large-animal exclosures, and other measures used to document patterns, rates, and mechanisms of community development. It details the observations made and experiments performed to evaluate the role of these factors in determining patterns of plant establishment. The chapter concludes with a discussion of changes during the 25 years since the last eruption and implications for the future.

5.1.1 Formation of the Debris-Avalanche Deposit

The debris-avalanche deposit was created when the north side of Mount St. Helens collapsed during the May 18, 1980 eruption (Voight et al. 1981). Weakened by a bulging magma intrusion and jarred by earthquakes, 2.5 km^3 of material plunged down the side of Mount St. Helens and spread over a 60-km^2 area. The timing of the release and respective physical makeup of individual slide blocks greatly influenced the physical structure of the deposit (Glicken 1998). The magnitude 5.1 earthquake involved with initiation of the eruption triggered the release of the first slide block. Failure of the second slide block exposed the cryptodome, releasing a lateral blast that exploded outward through slide block two. The third slide block resulted from a series of failures caused by fragmentation from the exploding cryptodome (Glicken 1998). The successive timing of the debris avalanche and blast, coupled with the varying composition of individual blocks, produced a hummocky deposit composed of discrete blocks in a mixture of blast-homogenized material.

During the afternoon of May 18, 1980, earthquake-induced liquefaction of the debris deposit produced a massive mudflow that moved down the North Fork Toutle River to the Cowlitz River (Fairchild 1985). Just as a slurry of sand and water in a bucket separates when shaken, the many earthquakes on May 18 caused liquid to rise to the deposit surface, which eventually formed a mudflow that moved over the newly emplaced debris material. This mudflow eroded and deposited material on the debris-avalanche-deposit surface; erosion exceeded deposition by about 4 million m^3 (Fairchild 1985).

5.1.2 Initial Physical and Chemical Conditions

Deposits average 45 m deep and have a maximum thickness of 195 m (Voight et al. 1981). The landslide was hot and moist, both containing ice blocks and having an estimated emplacement temperature of 100°C in some locations (Voight et al. 1981). Probe measures of temperature varied from 68° to 98°C between 10 to 12 days after the May 18 eruption, depending on distance from the mountain (Banks and Hoblitt 1981).

The debris-avalanche deposit has heterogeneous topography. In areas where the mudflow moved across the debris deposit, the terrain is flat. These flatlands generally retain the thin (less than 1- to 2-cm) layer of air-fall tephra that was emitted by the volcano during subsequent eruptions. In other areas, mounds composed of lithic blocks derived from the interior of Mount St. Helens (Voight et al. 1981; Fairchild 1985; Glicken 1998) rise up to 50 m above the deposit surface. The extremely irregular topography consists of large mounds and pits typically measuring tens of meters in diameter. Pits resulted, in part, from subsidence caused by the melting of large blocks of glacial ice that were transported by the debris avalanche. Many new ponds, lakes, and wetlands were created on the surface as depressions filled with water.

Initial physical and chemical characteristics of the substrates were adequate, but not optimal, for plant establishment and growth (Adams et al. 1987). The debris-avalanche deposit consisted of poorly sorted material dominated by sand (63% by weight of the less than 2-mm fraction), but larger rocks constituted a variable component (36.4% $\pm$ 28.9% by weight). The sandy texture limited moisture retention. Nitrogen levels and conductivity were low (703 ppm NH_3 and 0.84 $\pm$ 0.71 mmho cm^{-1}, respectively). The low carbon-to-nitrogen ratio (1:0.23) reflected low levels of organic matter (0.31% weight loss on ignition). The soils were acidic (pH was 4.8 $\pm$ 0.5). Low moisture availability and high temperatures caused by solar radiation on the exposed surfaces were especially stressful during plant establishment. Growth conditions were also poor because of low fertility and moisture-holding capacity (saturation was 5.3% $\pm$ 0.9% per 15 atm). Jenny pot tests (Jenny et al. 1950), performed with the use of lettuce as a bioassay, showed a poor response to all nutrient additions to the debris-avalanche material but a positive response to the addition of a combination of nitrogen and phosphorus to mudflow material (Adams and Dale 1987). This lack of growth in the debris-avalanche substrate may have resulted either from soil-chemistry limitations or from structural limitations of the debris material.

Both erosion and deposition of material have occurred since the debris-avalanche deposit formed. Fluvial-erosion processes have been active on the debris-avalanche deposit primarily in developing new channels and in expanding and extending existing channels (Lehre et al. 1983; Swanson and Major, this volume Chapter 3). Channel and gully walls are typically steep, with a slope of 30° to 70°, a depth of 3 to 50 m, and a channel width of 3 to 120 m. Lehre et al. (1983) estimated that 42×10^6 m^3 of debris material (about 2% of the total volume of the avalanche deposit) eroded between June 1980 and May 1981. Deposition of material included up to 1 m of fragmental debris in the areas inundated during a small mudflow that occurred on the debris-avalanche deposit on March 19, 1982 (Waitt et al. 1983). Erosion remains a major factor, with annual suspended sediment yield from the debris-avalanche deposit being 100 times (10^4 Mg km^{-2}) above typical background levels ($\sim 10^2$ Mg km^{-2}) 20 years after the 1980 eruption (Major et al. 2000).

5.2 Methods of Monitoring Plant Establishment

During the first 20 years after the 1980 eruption, various sampling schemes have been used to characterize the establishment of the vegetation and the factors that influence observed patterns. First, extensive field reconnaissances were done to determine if any survival had occurred, and then a system of permanent plots was put in place to monitor emerging vegetation. A series of experimental treatments was subsequently established to assess the role of various factors on plant establishment. Our work focused on the central portion of the debris-avalanche deposit and not the marginal facies, where surviving plants were pushed to the edge of the river valley by the debris avalanche.

5.2.1 Initial Field Surveys for Vegetation

Field reconnaissance of the debris-avalanche deposit for vegetation was conducted numerous times during the summer of 1980. Several surviving plants were dug up to determine their mode of survival. About 1 m^3 of avalanche material was collected from several areas, hand sifted, spread into flats, and watered to determine if viable seeds were present.

5.2.2 System of Permanent Plots

A system of permanent plots for documenting vegetation development was established on the central portion of the

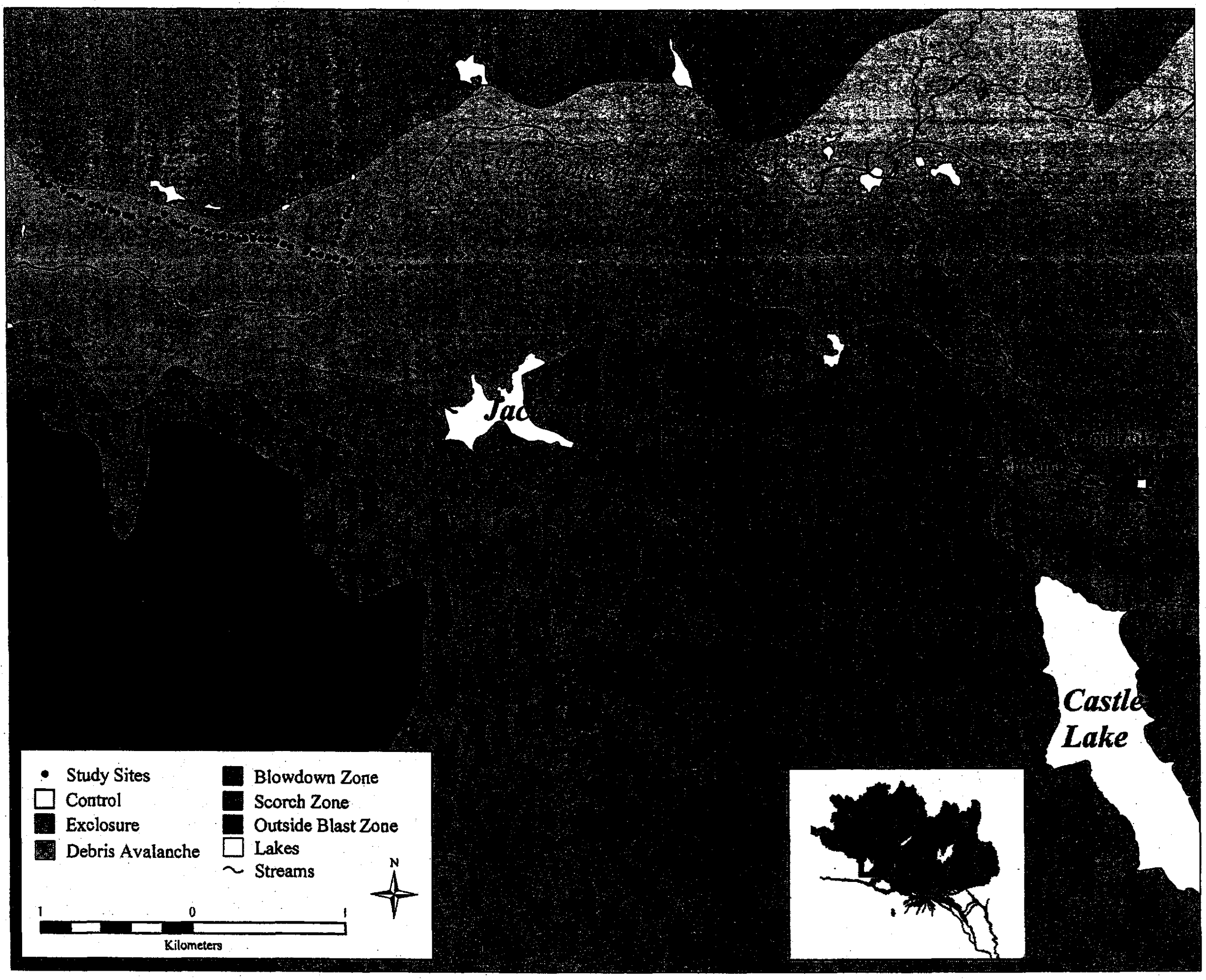


FIGURE 5.1. Location of study sites on the debris-avalanche deposit and of blowdown and scorched zones that held vegetation that was a source of seeds for the deposit.

debris-avalanche deposit during 1981 and 1982 and measured in 1981, 1982, 1983, 1984, 1989, 1994, and 2000. These circular plots are 250 m^2 and placed at 50-m intervals along transects between Castle and Coldwater lakes and down the length of the deposit (Figure 5.1). The initial 103 plots were placed to represent the variety of geological conditions on the debris-avalanche deposit and distances from surviving vegetation in the adjacent landscapes. However, during the ensuing two decades, many of these plots were lost to erosion and mudflows, and many could not be replaced because the steep terrain was impassable. By 1994, 98 plots remained; and by 2000, an additional 17 plots had been lost because of massive erosion and another 18 plots could not be reached because the bridge providing access to them was no longer passable. Thus, the 2000 estimate of plant cover is based on 63 plots.

In each sample year, the plots were monitored for the presence and cover of vascular plant species and for tree density (when individual trees could be distinguished). Plant density was recorded in 1981, 1982, and 1983. Plant cover was estimated by the line-intercept method (Mueller-Dombois and Ellenberg 2002) and then adjusted according to visual estimates because Bråkenhielm and Qinghong (1995) demonstrated that visual estimates provide the most accurate, sensitive, and precise measure of vegetation cover. Height and diameter of the largest tree and tree sexual maturity were recorded. In addition, topographic conditions of each plot were described in the field. Subsequently, each plot was assigned to one of six topographic categories: level, steeply sloped, deep channel cuts into level terrace, irregular mounds, high mound, and streambed.

Traps designed to catch wind-dispersed seeds were placed in the center of 31 plots between Castle and Coldwater lakes and 72 plots running the length of the deposit. These traps were monitored in 1981, 1982, 1983, and 1994. The traps were constructed of 0.25-m by 0.25-m squares of cloth made sticky and placed vertically, with their bases 0.25 m above the surface, for about 10 days. Seeds were counted and identified by comparing them to a reference collection of seeds collected from plants in the vicinity.

To characterize surviving and invading plants, the species were grouped according to the Raunkiaer (1934) life-form classification. This system of grouping plants had previously been related to climate gradients (Cain 1950), and we hypothesized that disturbance type could also influence life-form distribution of surviving and reestablishing vegetation. In this system of classification, perennial plants were classified by the location of perennating tissue in relation to the ground surface (Kershaw and Looney 1985). Raunkiaer's life form at the highest level of classification consists of chamaephytes (plants with buds that are 0.1 to 0.5 m above ground), cryptophytes (plants with belowground dormant tissue), hemicryptophytes (plants with buds at the ground surface), phanerophytes (trees or shrubs with buds greater than 0.5 m above ground), and therophytes (annuals).

To test for the effects of microtopography on seed resting site and seedling establishment, 60 experimental sets of mounds, depressions, and control sites were established at about 50-m intervals on the transect running east to west across the deposit (Dale 1989). Each test site consisted of two 25-cm^3 depressions, two mounds (made from the material removed from the depressions), and two controls sites per plot. One of each of the mounds and depressions was hand smoothed, and the other was left with rough surface microtopography. The treatments were conducted in June 1982 and monitored for seeds and seedlings in August and September of 1982 and in September 1983 by observing the surface of each treatment with a magnifying lens.

Because abnormally high precipitation during some of the 20-year observation period was likely to cause large-scale erosion, we refer to the annual precipitation from the nearest long-term weather station. Data have been collected since 1929 at Longview, Washington, which is about 60 km west of Mount St. Helens. Those data sets are available from the U.S. Historical Climatology Network (Easterling et al. 1996) and the Carbon Dioxide Information Analysis Center at Oak Ridge National Laboratory. The Longview station experiences less precipitation than the higher-elevation station at Spirit Lake reported in Figure 2.5d of this volume. The Longview precipitation record continued to be collected after the 1980 eruption.

5.2.3 Elk Exclosures

North American elk (*Cervus elaphus*) rapidly colonized the debris-avalanche deposit and attained large populations within the decade after the eruption. These large herbivores can have profound positive and negative influences on early plant succession (Hanley and Taber 1980; Hanley 1984; Hobbs 1996; Case and Kauffman 1997; Singer et al. 1998; Campbell 2001). The effects of elk on vegetation were quantified by constructing a 70.75- by 70.75-m exclosure on the vegetated area of the debris-avalanche deposit in 1992 (see Figure 5.1). An adjacent, companion site on the debris-avalanche deposit was identified to serve as an unfenced control. Within each site, one hundred twenty-five 1-m^2 microplots and fifteen 15-m line intercepts were randomly placed at least 5 m distant from the exclosure fence line to avoid edge effects. Thus, the effective sample area was 60 m by 60 m. Plant species were recorded, and cover was visually estimated in the microplots and measured to the nearest centimeter along the line transects in August of 1992 and 1999. Cover of plants not emerging from within microplots, but extending over microplot perimeters, was included in the estimates of cover. Species were divided into five growth forms: (1) grasses; (2) rushes and sedges; (3) forbs, ferns, and fern allies; (4) shrubs and woody vines; and (5) trees. Nonnative plants ($n = 22$) and modal forest species [e.g., species typical of local coniferous forests, *sensu* Curtis (1959); $n = 11$] were identified for analyses.

5.3 Results and Discussion

5.3.1 Vegetation Survival on the Debris-Avalanche Deposit

The coniferous forests and riparian vegetation that existed in the Toutle River valley floor before the eruption of Mount St. Helens were eliminated by the debris avalanche (Adams and Adams 1982; Fairchild 1985). No seedlings germinated from test flats of debris-avalanche-deposit material that were placed in a greenhouse and watered, and no seeds were found in any of the hand-sifted, debris-avalanche material samples (Adams and Dale 1987). Although these samples were very small relative to the size of the debris-avalanche deposit, it appeared that no viable seeds survived the landslide. Even if they had, their density would have been exceedingly low. In June 1980, the area was largely barren, and extensive searches revealed no seedlings and only a few vegetatively propagating plants (fewer than 1 km^{-2}). These surviving plants developed from rootstocks or stems that were transported in soil blocks which floated down valley in the debris-avalanche deposit and came to rest near the surface (Adams et al. 1987). Individual plants of at least 20 species survived on the debris deposit by this mechanism. The most common species were fireweed (*Chamerion angustifolium*), Canada thistle (*Cirsium arvense*), and broadleaf lupine (*Lupinus latifolius*). Lupine regeneration from root fragments was demonstrated by the regrowth of whole plants from root fragments that had been transported by the avalanche and subsequently placed in pots and watered (Dale 1986). No woody plants were found to have survived on the central portion of the debris-avalanche deposit.

Another feature of the debris-avalanche deposit was the abundance of vegetation and organic debris at the terminus of the deposit (Glicken 1998). During the movement of the avalanche, the vegetation in the Toutle River valley was scoured by the leading edge of the flow and pushed down the valley to the flow's terminus, much as a glacier pushes soil and organic material in its path. However, the Army Corps of Engineers removed this heap of vegetation during construction of a debris-retention dam, so it did not influence plant reestablishment.

5.3.2 Changes in Cover and Species Richness

Plant establishment and spread on the debris-avalanche deposit were slow during the first years after the eruption. Three years after the eruption, the average cover of the plots was less than 1%, although a few plots had as much as 30% cover. Between 1983 and 2000, plant cover dramatically increased to an average value of about 66% (Figure 5.2).

By year 14, the debris-avalanche-deposit plots averaged 38% cover, a value that was about double the cover estimated for the debris-avalanche deposit by Lawrence and Ripple (2000) for the same time period from remote-sensing imagery and classification and from regression-tree analysis. This difference between the estimate from ground-based plot measurements and that from the remotely sensed data indicates a need for considering the spatial arrangement of the study plots (as influenced by the river change that washed away many plots). Study plots remained only on the upland areas that appeared to support higher plant cover as suggested by our reconnaissance of the debris-avalanche deposit on foot and from low-flying helicopters. Vegetation cover was much reduced on the extensive riparian areas, partially because the meandering river removes many plants.

The average number of species per plot increased up to 1994 and then declined in 2000 (Figure 5.3a). The total number of plant species in the plots on the deposit also increased to 1994 and declined in 2000 (Figure 5.3b). Figure 5.3 shows only the data from those plots that survived throughout the two-decade sampling period to avoid the possibility that the decline in mean and total richness in 2000 related to the 37 plots that were not resampled. Those plots supported species typically found in moist woods [e.g., foamflower (*Tiarella trifoliata*) and youth-on-age (*Tolmiea menziesii*)] and in wetlands [e.g., horsetails (*Equisetum hyemale* and *E. palustre*)]. The loss of the 37 plots was caused by a large flood that was induced by heavy rains in 1996 and 1997 (see Figure 2.5d); that flood and the accompanying mudflow eliminated 17 of the plots and made another 18 inaccessible. Hence, ongoing disturbances need to be considered as an influence on species richness.

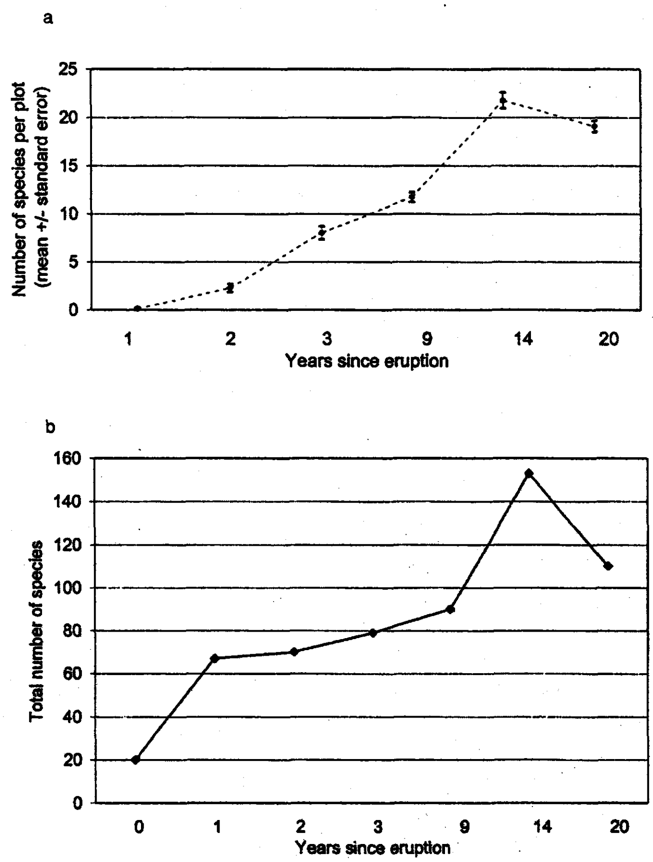


FIGURE 5.3. Changes over time in (a) the number of plant species per 250-m^2 plot on the debris-avalanche deposit for the plots that survived until 2000 and thus were sampled for all years and (b) the total number of plant species in all plots.

A shift in the life-form spectrum occurred during vegetation development on the deposit (Figure 5.4). All the plant species surviving on the debris-avalanche deposit were cryptophytes, species with dormant buds located below the surface. During the second year following the eruption, annual species invaded the debris-avalanche deposit, and in subsequent years they gradually became less abundant. All life forms were represented by 1981, although cryptophytes remained the most common life form 20 years posteruption. In 2000, hemicryptophytes, plants with buds at the ground surface, were the most different from their preeruption composition [as inferred from the species list for the slopes of Mount St. Helens complied by St. John (1976)], indicating the area was still in a reestablishment phase. There will undoubtedly be shifts in the life-form composition before the spectrum attains a composition similar to that before the eruption, as has occurred at other locations undergoing succession [e.g., Csecserits and Redei (2001) and Prach and Pysek (1999)]. Based on the preeruption life-form spectrum, it is anticipated that species with their buds below the ground will become less dominant and tall shrubs and vines

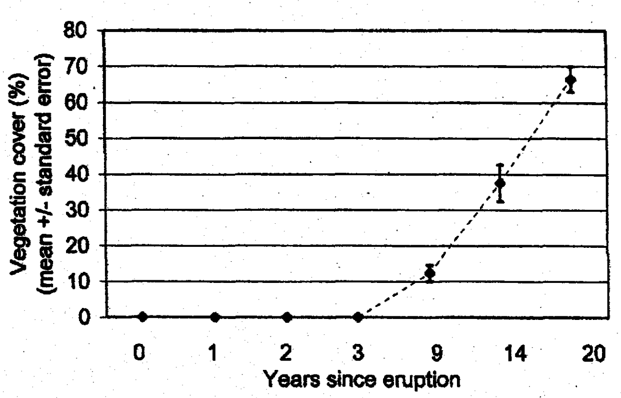


FIGURE 5.2. Changes over time in mean plant cover percent (with bars indicating the mean plus and minus the standard error) for the plots between Castle and Coldwater lakes and plots running the length of the debris-avalanche deposit.

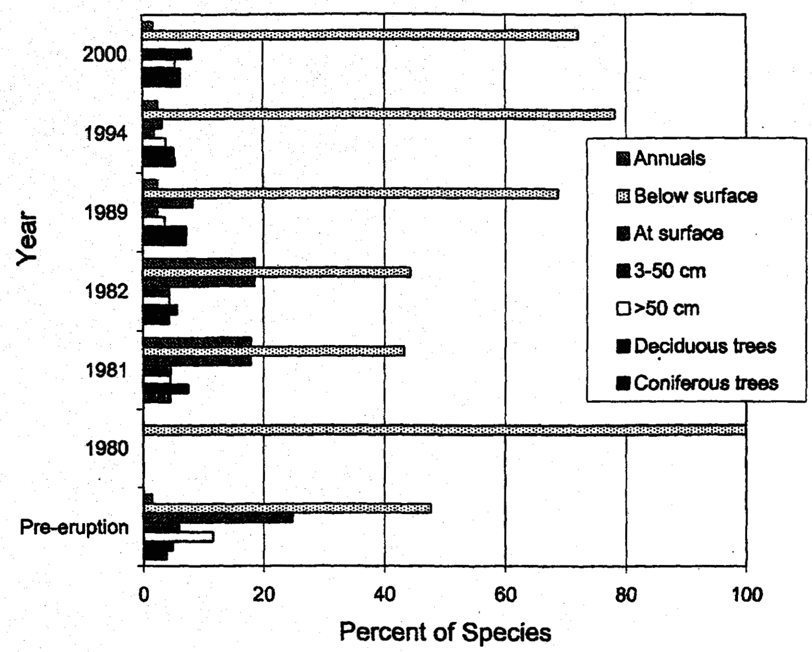


FIGURE 5.4. Changes in the life-form distribution over time by percent of species and mean number of plants based on the 250-m^2 plots between Castle and Coldwater lakes and plots running the length of the debris-avalanche deposit. The preeruption data are derived from the list in St. John (1976) for the entire mountain.

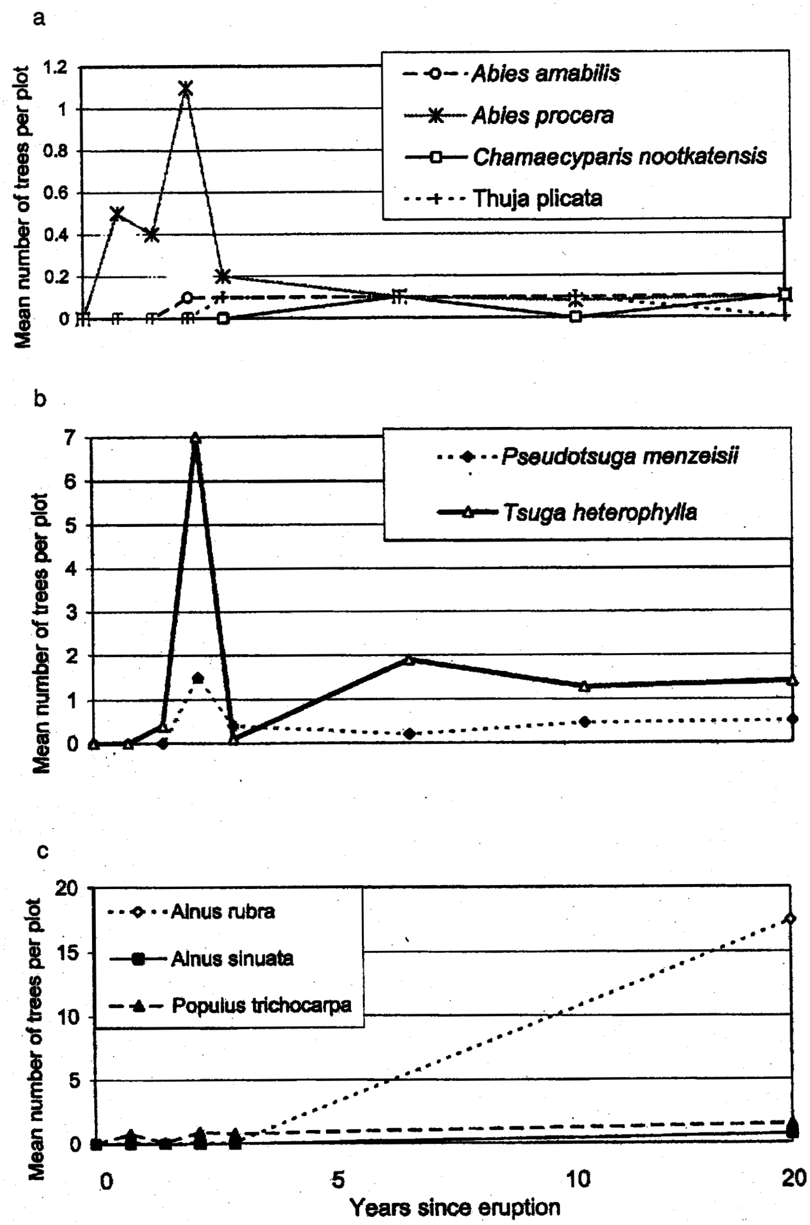
(species with their buds at the surface) will become more important.

The status of trees on the debris-avalanche deposit is of particular interest because a forest is expected to occupy the area eventually. No woody plants were found to have survived on the debris-avalanche deposit, and none was present in 1980 (Figure 5.5). Both deciduous and coniferous seedlings occurred on the debris-avalanche deposit by August 1981 (Dale 1986). A decrease in deciduous trees from 1981 to 1982 may have resulted from their elimination by the March 1982 mudflow because deciduous trees were more common than conifers close to the river channel and streambeds where the mudflow passed. The density of western hemlock (*Tsuga heterophylla*) seedlings increased greatly from 1982 to 1983 but declined in 1984 (Figure 5.5). Numerous noble fir (*Abies procera*) seedlings also died. Average tree-seedling density declined to 6 per 250-m^2 plot by 1984 from more than 16 per plot in 1983 (Dale 1986). The decrease in tree density in 1984 may have been related to the poor moisture-holding capacity of the soils and the fact that 1984 was such a dry year (see Figure 2.5d), or it may have been related to reduced seed rain coupled with the lack of suitable germination conditions. In 1984 there was a greater decrease of conifers than deciduous trees. Conifer seedlings are generally thought to be more tolerant of drought conditions than are deciduous trees; however, deciduous saplings were more tolerant of drought stress in (1) moisture-stress experiments that tested five conifers and red alder (*Alnus rubra*) growing on the debris-avalanche material (Adams et al. 1986b) and (2) field trials on the debris-avalanche deposit that used five conifers and four deciduous species (Russell 1986). Furthermore, deciduous trees tend to be rooted in seeps and along channel margins, where they experience drought impact to a lesser degree but are more susceptible to elimination by large floods and mudflows. By 20 years after the 1980 eruption, red alder was the tree species with the highest stem density on the debris-avalanche deposit.

Alnus became the most important tree genus on the debris-avalanche deposit. Up to 3 years after the eruption, red alder was rare on the debris-avalanche deposit, occupying only 15% of the plots (Table 5.1). By 9 years after the eruption, red alder occupied 37% of the plots, and those alder were vigorous and tall (up to 5 m). Predictions that red alder would become dominant (Dale 1986) have come to fruition. By 20 years posteruption, red alder contributed more to vegetation cover than did any other species (Table 5.1) and had the highest tree density; 26% of the 1066 red alder located in the plots were mature and producing seeds. The only other tree or shrub species found to be producing seeds on the avalanche deposit by 20 years posteruption were slide alder (*A. viridis* ssp. *sinuata*, of which 35% of the 46 shrubs in plots were mature in 2000) and black cottonwood (*Populus triochocarpa*, of which 2% of the 95 trees in the plots were mature in 2000). The tallest red alder in the plots was 10 m tall and had a diameter at breast height (dbh) of 21.1 cm by 20 years after the eruption. The largest trees on the debris-avalanche deposit were black cottonwoods (the largest in the plots having a height of 15 m and a dbh of 38 cm). However, black cottonwood was only 8% as common as red alder.

Even though alder often grows in more moist conditions, it likely became very abundant on the debris-avalanche deposit for four reasons. (1) Alder seeds germinated successfully on the debris material (23% germination rate; Adams and Dale 1987), and seedlings grew very quickly [e.g., 5 months after germination, the seedling-to-seed dry weight ratio was 3.6,

FIGURE 5.5. Number of trees per 250-m^2 plot over time on the debris-avalanche deposit for conifers with (a) lowest density and (b) highest density sampled in 1980, 1981, 1982, 1983, 1989, 1994, and 2000, and (c) for most dense deciduous trees sampled in 1980, 1981, 1982, 1983, and 2000 (except for *Salix* spp., because distinguishing individual willow plants was not possible).



more than three times higher than that for six conifers tested (Adams and Dale 1987)]. In field trials, planted alder saplings had a high survival rate (greater than 80%) and greater height development after 4 years than did eight other species (Russell 1986). In laboratory moisture-stress experiments with debris-avalanche soil, alder had the greatest height increment after 5 years for both very wet and very dry conditions compared with five conifer species (Adams et al. 1986b). (2) Alders fix nitrogen by means of association with symbiotic bacteria and, therefore, are better able to survive and grow in the nitrogen-poor environment. (3) Alders were less sensitive to browsing than other species (Russell 1986). Red alder was only rarely browsed, and slide alder was grazed but readily sprouts. (4) Alders produce abundant seed crops from plants as young as 3 years old (Schopmeyer 1974). Mature alders were an abundant seed source on the Toutle River mudflow directly downstream of the avalanche deposit (Russell 1986). By 1985, they were producing seed on the debris-avalanche deposit.

The most common conifer 20 years posteruption was western hemlock, but its high fluctuation in numbers over the two decades after the 1980 eruption suggested that future variation is likely (see Figure 5.5). The tallest conifer in the plots by the year 2000 was a 2.5-m Douglas-fir (*Pseudotsuga menziesii*), and the tallest western hemlock was 1.0 m in height. In 2004, a few Douglas-fir produced cones on the debris-avalanche deposit. The local production of seed on the deposit, rather than relying on long-distant transport, will likely

[redacted]

Species	1983 (3 years since eruption; 97 plots)		1989 (9 years since eruption; 97 plots)		1994 (14 years since eruption; 97 plots)		2000 (20 years since eruption; 63 plots)	
Early-successional herbs with wind-dispersed seeds								
Pearly everlasting (*Anaphalis margaritacea*)	0.00701	(70)	0.28443	(74)	0.82619	(91)	0.0166	(98)
Canada thistle (*Cirsium arvense*)	0.00268	(27)	0.01196	(18)	0.07402	(23)	0.00144	(22)
Fireweed (*Chamerion angustifolium*)	0.00649	(65)	0.00536	(54)	0.04794	(69)	0.00299	(46)
Smooth willowherb (*Epilobium glaberrimum*)	0.00588	(59)	0.00372	(38)	0.30289	(51)	0.00289	(44)
Autumn willowherb (*Epilobium brachycarpum*)	0.0034	(34)	0.06423	(27)	0.08691	(47)	0.00175	(27)
Cat's ear (*Hypochaeris radicata*)	0.00598	(60)	0.34598	(69)	2.99505	(90)	0.28299	(100)
Wood groundsel (*Senecio sylvaticus*)	0.00588	(59)	0.01165	(14)	0.00103	(10)	0.05247	(16)
Sowthistle (*Sonchus arvensis*)	0.00082	(8)	0.00423	(42)	0.00082	(8)	0.00021	(3)
Grasses and upland sedges								
Thin bentgrass (*Agrostis diegoensis*)	0.00258	(45)	0.22113	(65)	0.00062	(6)	0.56041	(67)
Spike bentgrass (*Agrostis exarata*)	0.00052	(14)	0.41515	(38)	0.01577	(56)	0.00247	(38)
Rough bentgrass (*Agrostis scabra*)	0.00052	(5)	0.00165	(16)	0.21268	(72)	0.01206	(29)
Silver hairgrass (*Aira carophyllea*)	0.0001	(1)	0.03134	(6)	1.69402	(51)	0.07598	(65)
Slender hairgrass (*Deschampsia elongata*)	0.00041	(9)	0.00082	(11)	0.06515	(35)	0.05206	(11)
Rat-tail fescue (*Festuca myuros*)	0.00021	(2)	0.00021	(2)	0.98186	(33)	0.09464	(38)
Velvet-grass (*Holcus lanatus*)	0.00041	(11)	0.05381	(27)	5.22041	(68)	4.3633	(95)
Merten's sedge (*Carex mertensii*)	0.0001	(1)	0.00031	(3)	0.05402	(28)	0.00103	(16)
Showy sedge (*Carex spectabilis*)	0.00165	(16)	0.07474	(28)	0.2801	(21)	0.0132	(46)
Wetland species								
Water horsetail (*Equisetum fluviatile*)	0.00103	(10)	0.23784	(10)	0.66	(11)	0.02072	(5)
Sharp-fruit rush (*Juncus acuminatus*)	0.60398	(1)	1.12315	(5)	4.27459	(22)	0.93549	(3)
Toad rush (*Juncus bufonius*)	0.00062	(6)	0.08392	(16)	0.09351	(9)	0.0001	(2)
Common rush (*Juncus effusus*)	0.00052	(5)	0.21784	(15)	0.04216	(12)	0.01052	(5)
Swordleaf rush (*Juncus ensifolius*)	0.00072	(7)	0.02247	(20)	0.03247	(18)	0.0001	(2)
Field rush (*Juncus tenuis*)	0.0001	(1)	0.20701	(11)	0.45495	(21)	0.00052	(8)
Cattail (*Typha latifolia*)	0.00052	(5)	0.05227	(19)	0.05268	(13)	0.0001	(2)
Nitrogen-fixing legumes (introduced)								
Birdsfoot-trefoil (*Lotus purshiana*)	0.00041	(4)	5.24866	(29)	4.77526	(43)	0.7133	(54)
Creeping clover (*Trifolium repens*)	0	(0)	0.02134	(9)	1.28959	(20)	0.17987	(19)

TABLE 5.1. (*Continued*)

Species	1983 (3 years since eruption; 97 plots)		1989 (9 years since eruption; 97 plots)		1994 (14 years since eruption; 97 plots)		2000 (20 years since eruption; 63 plots)	
Nitrogen-fixing legumes (native)								
Broadleaf lupine (*Lupinus latifolius*)	0.00103	(10)	0.66186	(30)	0.98196	(46)	1.34175	(43)
Prairie lupine (*Lupinus lepidus*)	0.00031	(3)	1.28021	(26)	0.80784	(48)	1.55876	(54)
Trees								
Red alder (*Alnus rubra*)	0.00082	(15)	0.51835	(39)	12.52814	(68)	19.0933	(84)
Black cottonwood (*Populus trichocarpa*)	0.00309	(36)	0.12763	(47)	0.13	(67)	0.36381	(48)
Douglas-fir (*Pseudotsuga menziesii*)	0.00536	(56)	0.00134	(36)	0.0033	(33)	0.02278	(35)
Sitka willow (*Salix sitchensis*)	0.00289	(33)	0.11495	(26)	0.31237	(38)	1.99351	(87)
Western hemlock (*Tsuga heterophylla*)	0.00753	(82)	0.02464	(65)	0.02619	(48)	0.01289	(41)

change establishment dynamics, with Douglas-fir becoming much more abundant during the next few years. Within the coming decade, other conifers will likely mature and produce seed on the debris-avalanche deposit as well. For example, western hemlock can produce seeds on trees as young as 20 years. Subsequently, the density of conifers will rise, and as this next cohort of trees matures, vegetation cover will shift to being largely conifers. Until that time, deciduous trees will dominate vegetation cover on the debris-avalanche deposit. Indeed, red alder may preempt the debris-avalanche deposit for a few decades, thus limiting the development of coniferous forests. In the longer run, however, the presence of alder may benefit longer-lived, slower-establishing conifers by enriching nutrient conditions on the debris-avalanche deposit.

5.3.3 Factors Affecting Plant Establishment

Because residual plants were so rare, vegetation development of the debris-avalanche deposit depended on the ability of plants to colonize the deposit. Factors influencing plant establishment by seedlings were (1) distance from seed sources, (2) species-specific dispersal capabilities, (3) germination and growth characteristics of colonizing species, and (4) substrate conditions.

5.3.3.1 Seed Dispersal

Most of the seeds transported onto the debris-avalanche deposit were dispersed by wind (Dale 1989). Differences were observed among years 1, 2, and 14 posteruption in the number of seeds transported onto the debris-avalanche deposit, with the greatest number of the seeds occurring in the second year (1982) (Figure 5.6). This observation contradicts expectations that the number of seeds would increase over early-successional time. One explanation proposed for the increase in seeds trapped in August 1982 compared to August 1981 is that the source plants could have produced more seeds during the unusually wet summer of 1982 (see Figure 2.5d); however, 1983 was even wetter but had many fewer seeds than in August 1982. By 1994, the traps for the first time contained heavy lupine seeds, which probably came from the explosive release of seeds from the dried pods of nearby plants. The presence of lupine seeds in the traps was indicative of the importance of reproduction on the avalanche deposit itself.

The three major seed source areas were the slopes adjacent to the river valley in the blowdown zone, the downstream river banks and floodplain (which were inundated by the May 18, 1980 mudflow), and intact forests south and west of the volcano. The slopes above the North Fork Toutle River valley and the downstream areas had different patterns of plant

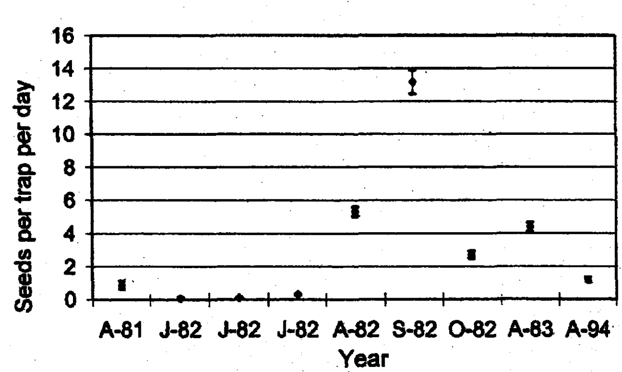


FIGURE 5.6. Changes over time in the number of seeds collected per 0.25-m by 0.25-m trap per day based on the 31 plots between Castle and Coldwater lakes and the 72 plots running the length of the avalanche deposit. Seeds were sampled for the entire growing season in 1982 [June (J), July (J), August (A), September (S), and October (O)] and in August of 1981, 1983, and 1994.

survival and vegetation development than did the valley where the avalanche deposit settled (Adams and Adams 1982; Adams et al. 1987). The slopes above the valley were a patchwork of forested and clear-cut land before to the eruption. Many early-successional annuals and perennials on the blowdown areas adjacent to the debris-avalanche deposit survived the eruption. Rapid revegetation of these tracts was partially caused by many sites having been previously logged; perennial herbs were already established on these cutover areas and quickly emerged from belowground buds (Adams et al. 1987; Stevens et al. 1987). Furthermore, the fine-grained composition of the west-side blast deposits contributed to rapid runoff and formation of gullies, which influenced survival and resprouting of plants on hill slopes (Lehre et al. 1983). These surviving plants provided abundant seed to the debris-avalanche deposit.

The second source of seeds was from areas downstream that had been inundated by the 1980 mudflow. That mudflow extended down the Toutle River valley and covered or washed away most of the herbaceous species. The main survivors in the direct path of the mudflow were trees that had branches above the surface of the flow (Adams et al. 1987). In contrast, herbaceous plants survived in marginal areas with minimal mudflow inundation. By 10 years after the eruption, the mudflow deposits were largely vegetated by red alder, willows, and other riparian vegetation. Thus, the abundance of alder and other deciduous trees and shrubs on the debris-avalanche deposit may have come from seeds that were dispersed up the river valley.

A third seed source for the debris-avalanche deposit was intact forests on the south-facing hill slopes above the South Fork Toutle River that were minimally affected by the eruption. It was likely that seeds of some tree species found on the debris deposit, such as the rare lodgepole pine (*Pinus contorta*), were dispersed from these distant, intact forests.

Both distance and wind patterns from a seed source affected the number of seeds arriving at this disturbed site. In 1982 and 1983, the number of seeds trapped on the avalanche deposit declined over a distance of less than 1.1 km from the edge but increased for the greater distances sampled (1.1 to 1.29 km from edge) (Dale 1989). Thus, more seeds were collected at the greatest distance from the vigorously establishing vegetation in the blast zone. The initial decline with distance probably relates to the ability of seeds to be transported by the wind from the adjacent blowdown zone. The increase in seed abundance for plots in the middle of the debris-avalanche deposit for 1983 (1.1 to 1.29 km from the edge) may be from seeds that were transported up the middle of the debris-avalanche deposit from plants which had colonized the mudflow deposit lower on the Toutle River. Although this is a longer distance than that from the adjacent blowdown areas, wind currents flow up the valley much of the time. Alternatively, the seed-dispersal pattern may result from seeds traveling over the blowdown-zone ridge lines and not descending precipitously over the valley wall. Instead, they may remain aloft and gradually descend to the center of the deposit. In either case, the observed pattern of wind-dispersed seed suggests that the general notion of declining numbers of seeds with increasing distance from parent plants should be modified to emphasize the variability at the tail end of the distribution.

The number of plants revegetating the debris-avalanche deposit decreased with distance from the edge of surviving vegetation and was related to seed abundance (Dale 1989). More plants were found on the debris-avalanche deposit in 1983 than in the previous year [an average of 494 plants per plot in 1983 compared to 66 plants per plot in 1982 (Dale 1989)]. This difference was likely caused by the high precipitation in 1983 (see Figure 2.5d). Time since the eruption and the abundance of seeds dispersed onto the avalanche deposit during the previous season also contributed to that increase.

As animals have become more abundant on the debris-avalanche deposit, they have likely begun to contribute to seed dispersal. Although initially quite rare, small mammals, birds, and elk were common by 20 years after the eruption. The mature forests that are expected to become established on the debris-avalanche deposit will likely support relatively few understory plants that depend on wind for seed dispersal, and the dominant trees will use both wind and animals to transport seeds.

5.3.3.2 Species Characteristics

The most dominant herbaceous species on the deposit can be classified into four groups: early-successional herbs, grasses and upland sedges, wetland species, and nitrogen-fixing legumes (see Table 5.1). The most common early colonists were early-successional species that produce many light, wind-dispersed seeds, grow rapidly, and mature early. The low cover of these species in the years just after the May 18 eruption belies their importance because total plant cover of the debris-avalanche deposit was also sparse. For example, pearly everlasting (*Anaphalis margaritacea*) increased in cover from 1981 to 1994 but thereafter declined (Table 5.1). The presence of these individuals probably facilitated establishment of other species by providing shade and organic material and by trapping seeds. Most of these early-successional plants established from seeds that were blown onto the debris deposit.

Grasses on the debris-avalanche deposit produce abundant light seeds and are able to survive droughts. Grass seeds are transported both by wind and by animals via their feces. During the 20 years since the eruption, of the 17 grasses found on the debris-avalanche deposit, 7 significantly increased in cover (Dale and Adams 2003; see Table 5.1). None of these were the grass species that were seeded onto the western debris-avalanche deposit in the summer of 1980 by the Soil Conservation Service to reduce erosion because those grasses failed to establish (Stroh and Oyler 1981). Velvet-grass (*Holcus lanatus*), a nonnative species, became one of the more abundant species on the debris deposit by 1994 and has since declined slightly in cover.

Wetland species quickly established in the numerous groundwater seeps and ponds that formed shortly after emplacement of the deposit. In the first years after the eruption, we would sink into the mud up to our knees as we sampled some of these plots, but by 10 years after the eruption, the ground was not saturated with water. Subsequently, most species have decreased in abundance (e.g., the horsetails, *Equisetum* spp.). Areas that were initially very wet, along with the riparian areas, now support some of the highest vegetation cover. Although wetlands (seeps, riparian zones, and ponds) were typically heavily vegetated, they were probably not important source areas for propagules for upland sites because many species growing in the wetlands are unable to establish on more xeric uplands. However, the presence of these species may have facilitated the establishment and growth of other plants. Species restricted to the wetlands include sedges (*Carex deweyanna* and *C. disperma*), three species of horsetail (*Equisetum fluviatile*, *E. hyemale*, and *E. palustre*), soft rush (*Juncus effusus*), and cattail (*Typha latifolia*).

Herbs associated with nitrogen-fixing bacteria have increased in cover during the period of record, probably because of their ability to grow in nitrogen-poor substrates. Broadleaf lupine increased in abundance on the debris-avalanche deposit. A few broadleaf lupine survived the eruption, and the species has expanded through seed production. The large seeds are primarily dispersed by gravity and water, so seedlings tend to occur near the parent plant. A few prairie lupine (*Lupinus lepidus*) also survived the eruption. By 1989, they provided more cover than broadleaf lupine did; and by 1994, they were more widely distributed across the debris-avalanche deposit (particularly close to the volcano). White clover (*Trifolium repens*), a common nonnative legume, also became widespread on the debris-avalanche deposit. Bird's-foot-trefoil (*Lotus unifoliolatus* var. *unifoliolatus*), a nonnative annual legume that was seeded to reduce erosion, is another nitrogen-fixing plant that has established high cover. More than 20 years after the 1980 eruption, this species dominated only those plots on the western part of the avalanche deposit. This dominance of the westernmost plots allowed us to document the role of nonnative species on plant reestablishment.

5.3.3.3 Effects of Nonnative Species Seeded onto the Debris-Avalanche Deposit

Nonnative species were introduced to the area through aerial seeding in hopes of reducing erosion. Because only the western portion of the avalanche deposit was seeded, the deposit offers the opportunity to compare successional processes with and without such introduced species. Long-term revegetation trends and effects of nonnative species on succession are important to understand because vegetation-recovery practices often rely on nonnative species for enhancing vegetation development of denuded sites along roadsides, strip mines, or other human-generated clearings.

Fifteen years after the eruption, plots invaded by nonnative species had greater vegetation cover and more native-plant richness than did plots that were not invaded (Dale and Adams 2003). These results suggest that nonnatives fostered the recruitment of native species, likely by trapping and nursing seeds. However, significantly greater mortality of conifers occurred in the plots dominated by introduced species shortly after the invasion of those species (Dale 1991), but no difference in conifer mortality occurred in the subsequent 5 years. The initial conifer mortality was likely caused by the rapid population increase of voles (*Microtus* spp.), which thrived with the abundance of seeds produced by the introduced grasses and herbs (Franklin et al. 1988). Under winter snows and with little other food, the voles apparently ate the living tissue around the conifer sapling stems and killed many of them (Franklin et al. 1988). The plots dominated by introduced species had fewer conifer trees 20 years after the eruption. Thus, the short-term pulse of conifer mortality after the invasion of introduced species may have long-term effects on the development of the forest vegetation. This pulse of conifer mortality demonstrates the importance of herbivory in early-successional situations, a theme that is revisited later in this chapter.

5.3.3.4 Substrate Conditions

Large variation in substrate conditions on the debris-avalanche deposit has produced a complex pattern of plant establishment. Differences between the upland areas and wetlands (e.g., riparian habitats, seeps, and streamside areas) are quite noticeable. Moist areas have greater species richness, higher plant density, and higher cover.

Groundwater seeps produced the greatest increase in plant cover. In these seeps, the surface of the deposit remains moist throughout the year but is not subjected to high flows that might disturb the plants. Twenty years after the 1980 eruption, vegetation in seeps was limited to comparatively few species, the most abundant being the common wetland horsetail, willow (*Salix scouleriana* and *S. sitchensis*), and willow-herb (*Epilobium ciliatum spp. watsonii*). Other species present include cattail, pearly everlasting, and fireweed.

The debris-avalanche surface is characterized by great variation in surface microtopography, which influences the distribution of seeds and seedling establishment. Pits tended to be moister than mounds, and plumed seeds were observed to fall into large depressions, probably because the plume diameter abruptly decreases with small increases in relative humidity (Burrows 1973). Experimental mounds and depressions on the deposit were tested for their ability to trap seeds and to support seedlings as an indication of the effect of microtopography on seed settlement and seedling establishment (Dale 1989). There were no significant differences between the seeds and seedlings in the depressions and on the mounds, and yet both had more seeds and seedlings than did level control sites. Mounds had a significantly greater density of seeds than the controls did because spider webs occurred on the mounds; these webs trapped

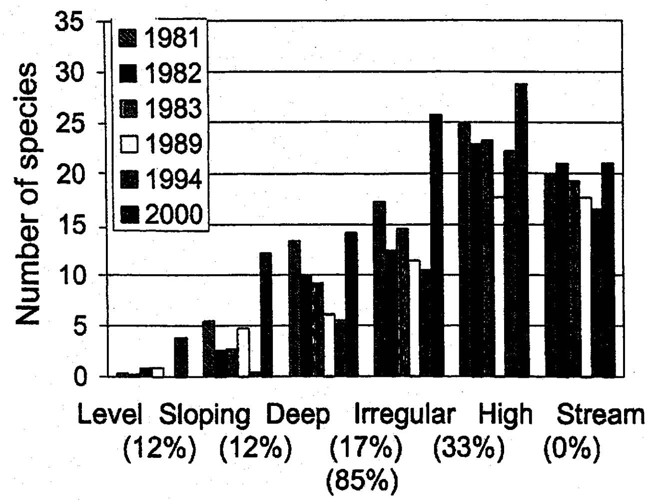


FIGURE 5.7. Number of species per 250-m^2 plot over time by topographic category: *Level*, *Sloping* (plots with a sloping side), *Deep* (plots with a deep channel between level terraces), *Irregular* (plots with irregular mounds), *High* (plots with a single, high mound), and *Stream* (plots containing a streambed).

windblown seeds, and moisture accumulated on the threads (Dale 1989). Thus, physical conditions were important in depressions in trapping seeds, and biological factors (the spider webs) were important on the mounds.

Time since the eruption was a major influence in development of species richness. Classifying the plots into topographic groups revealed patterns in revegetation over time (Figure 5.7). For example, in the year 2000, more species appeared in all topographic categories than in earlier years. The second growing season after the eruption (1981) supported a high number of species for all topographic groups except the level category. Yet, for all years except 2000, the level plots supported few species. The plots with streams running through them were disproportionately eliminated by the flood of 1997. The high mounds, however, consistently supported the greatest plant diversity because they were not affected by the mudflows.

5.3.3.5 Subsequent Physical Disturbances

The portion of the deposit that has consistently remained the most poorly vegetated is the area adjacent to the mainstream channels of the North Fork Toutle River. Deposits in these areas were subject to repeated disturbance as the channels meandered across and cut through the unconsolidated deposits. Most seedlings that became established in moist sediment along channel margins were swept away or buried by sediment the following winter.

Volcanic disturbance subsequent to the 1980 eruption has not had a major effect on plant reestablishment. Tephra fall has been minor. The largest single volcanic disturbance on the debris-avalanche deposit was an explosive eruption on March 19, 1982, that melted snow in the crater and produced a mudflow that deposited more than 1 m of sand and gravel in a few locations and lightly affected others (Waitt et al. 1983). The ground was cleared of plants in a few locations. Most vegetation reestablishment was not set back by this mudflow (Adams et al. 1987) because, just a few years after the flow, plants with underground buds that withstood the disturbance and annual species such as wood groundsel (*Senecio sylvaticus*) were more common on the areas covered by the mudflow than on areas not inundated. These disturbed areas evidently supported the survival of plants with underground buds and were good sites for colonists.

Heavy rain and snowmelt also produced floods and small mudflows down the North Fork Toutle River. Such disturbances caused erosion and several large-scale washouts of debris-avalanche material. More than 1.78 m of rain fell in 1996, the highest precipitation over the 71-year record (see Figure 2.5d), and that winter a large mudflow (Major et al. 2000) eliminated 17% of the study plots. In one case, a stretch of floodplain more than 200 m long was replaced by a channel with steep sides. Floods, mudflows, and streambank failures will continue to modify the debris-avalanche deposit.

5.3.3.6 Herbivory

Herbivores affected vegetation even in the first years after the eruption, when they were rare. For example, in the summer of 1982, the only bitter cherry trees (*Prunus emaginata*) observed were leafless and did not survive (apparently the leaves had been consumed by animals). Also, an outbreak of horned caterpillars (Sphingidae) eliminated a population of fireweed in the middle of the debris-avalanche deposit. The documented effect of herbivores on prairie lupine on the adjacent Pumice Plain (Fagan and Bishop 2000) may also be occurring on the debris-avalanche deposit. Experimental removal of insect herbivores from prairie lupine on the Pumice Plain increased the growth of lupine plants and the production of new plants (Fagan and Bishop 2000).

Elk also had an impact on vegetation. Deciduous trees (alder, willows, and black cottonwood) experimentally planted on the debris material near the North Fork Toutle River were more tolerant of elk browse than were the conifers (Russell 1986). Because of the seasonal (late winter and early spring) nature of their activity, elk preferentially browsed conifer species more than deciduous species because only coniferous trees were green at that time. Later in the season, the elk moved to higher elevations. In experimental plots, elk browse on deciduous trees caused minimal damage (except for trampling effects), whereas elk damage to conifers produced 82% mortality and reduced the height of surviving conifers by about one-half (Russell 1986).

The effects of elk herbivory were documented by an elk-exclosure study on the debris-avalanche deposit. Plant cover from 1992 to 1999 in both the elk exclosure and on an adjacent, unfenced, grazed control plot increased by almost

TABLE 5.2. Information from elk exclosures and controls on the [illegible] (12 years since eruption) and 1999 (19 years since eruption).

Type of data	1992 Control grazed	1992 Exclosure ungrazed	1999 Control grazed	1999 Exclosure ungrazed	Change from 1992 to 1999 Control grazed	Change from 1992 to 1999 Exclosure ungrazed
Species richness data						
Mean richness per plot	8.3 ± 0.3	10.3 ± 0.4	9.4 ± 0.3	7.7 ± 0.3	1.1	−2.6
Total richness	46	44	62	65	16	21
Shannon–Weiner diversity index	3.133	3.171	3.346	3.368	0.213	0.197
Sorensen's community similarity coefficient	0.89		0.8		−0.09	
Mean microplot cover						
All species	17.8 ± 2.3	29.8 ± 3.0	102.6 ± 4.6	116.7 ± 4.7	94.8	86.9
Exotic species	1.4 ± 0.2	1.3 ± 0.2	14.5 ± 1.9	4.3 ± 0.8	13.1	3
Modal forest species	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	1.4 ± 0.4	−0.1	1.2
Cover by growth forms						
Grasses	0.4 ± 0.1	0.4 ± 0.1	1.8 ± 0.2	0.2 ± 0.1	1.4	−0.2
Sedges and rushes	1.6 ± 0.4	3.0 ± 0.4	1.9 ± 0.4	0.9 ± 0.2	0.3	−2.1
Forbs, ferns, and allies	6.3 ± 1.2	6.4 ± 0.8	26.5 ± 2.4	22.7 ± 1.9	20.2	16.3
Shrubs and woody vines	9.0 ± 1.4	18.2 ± 2.3	25.5 ± 2.6	33.3 ± 3.6	16.5	15.1
Trees	0.5 ± 0.1	1.8 ± 0.9	47.5 ± 4.0	59.6 ± 4.1	47	57.8

600% in the grazed plot and by nearly 400% in the ungrazed plot (Table 5.2). Plant species diversity (as measured by the Shannon–Weiner index) was similar in both years in the two plots. Species richness (the number of species per microplot) differed between sites and years. Mean species richness increased from 8.3 to 9.4 in the grazed plot but decreased from 10.3 to 7.7 in the ungrazed plot (Table 5.2). From 1992 to 1999, cover of nonnative species increased 935% in the grazed plot and 231% in the ungrazed plot. In contrast, mean microplot cover of modal forest species, such as sword fern (*Polystichum munitum*), increased by 1.2% in the ungrazed plot and decreased by 0.1% in the grazed plot. As expected, cover of grazing-tolerant graminoids increased in the grazed plot by 1.4% but declined by 0.2% in the ungrazed plot (Table 5.2). Again, as expected, shrub cover was greater in the ungrazed plot in 1999 (Table 5.2). However, the response of shrubs to ungulate herbivory differed from other ungulate-exclusion studies in that cover increased at a greater rate in the grazed site than in the ungrazed site (Case and Kauffman 1997; Table 5.2b). The rapid response in the grazed plot was indicative of vigorous compensatory growth of sitka willows, the dominate shrub species. The proliferation of nonnative species in the grazed site can be explained by elk herbivory and trampling. Moreover, the establishment and growth of modal forest species typical of local coniferous forests may have been facilitated by the greater amount of shade and litter provided by red alder and sitka willow in the ungrazed plot [in 1999, mean litter cover was 63.7% (SE = 3.4) for the ungrazed plot and 33.0% (SE = 3.5) for the grazed plot]. Although elk herbivory has influenced the composition of herbaceous species, the increase of woody cover in both sites suggests that elk herbivory was not intense enough to impede the development of a red alder/willow-dominated community on the debris-avalanche deposit. Herbivory was just one of many factors affecting the dynamic landscape as vegetation became established and plant–animal relationships developed.

5.3.3.7 Succession

In the first two decades after the 1980 eruption, plant species richness and vegetation cover increased. The characteristics of species that established on the deposit spanned a wide range, from short-lived, early-successional species (e.g., pearly everlasting) to long-lived, late-successional species (e.g., western hemlock). The simultaneous presence of both early and late seral species a few years after the May 18 eruption showed that establishment of late-successional species need not be facilitated by early-successional species [see discussion in Connell and Slatyer (1977)]. Thus, relay floristics (the replacement of one species by another over time), as strictly interpreted, has not occurred on the deposit. Instead, early-successional species were most abundant in the initial years of vegetation development. The late-successional species were present, but not common, in the early years. Some, such as western hemlock, have declined in density.

The extent to which early-successional species facilitated the development of the late-successional species by modifying the environment was variable. Most species played a role in facilitation only by their physical presence in trapping seed and providing shade and organic material, which increased soil moisture retention. However, red alder and lupines were exceptions. As these plants became established, they influenced ecological development by ameliorating the environment. By fixing nitrogen, alder and lupine can improve the soil fertility (Trappe et al. 1968). Moreover, the rapidly growing alder trees created shade and added organic material to the ground surface, thus facilitating seedling establishment of shade-tolerant species and inhibiting establishment of shade-intolerant species. Alder has also been an important factor in recolonization on other volcanic substrates in the Pacific Northwest (Frehner 1957; Frenzen et al. 1988).

Species with the highest cover on the debris-avalanche deposit in the first years after the 1980 eruption are characterized as ruderal because they can survive in areas with a high frequency of disturbances (Grime 1977). They are the early-successional species of Table 5.1. Ruderal species are of small stature, grow rapidly, produce abundant, widely dispersed seeds, and are typically annuals. Their dominance runs counter to Grime's (1979) proposition that plants have not yet evolved to survive in both high-disturbance and high-stress habitats. He defines stress as external constraints that limit plant production. However, the plants on the debris-avalanche deposit are abundant in high-disturbance areas (e.g., after fires or clear-cuts) and yet they occur on the highly stressed debris-avalanche deposit, where both water and nutrient deficiencies limit plant productivity.

The plasticity of ruderal species may be the primary feature allowing them to establish and reproduce in stressful habitats. Plasticity refers to the ability of an organism to adjust its morphology or life-history characteristics to accommodate prevailing environmental conditions. For example, mature wood groundsel is generally about 50 cm tall, yet it was 5 to 20 cm tall on the debris-avalanche deposit. As another example, in 1982 and 1983, several individual plants of the normally perennial prairie lupine, yellow monkey-flower (*Mimulus guttatus*), and miner's lettuce (*Montia siberica*) completed their life cycles in one season on the deposit. By putting all their energy into seeds at the end of the season and then dying, these typically perennial species altered their normal life cycle. As a result, the species were able to survive in the stressful habitat. Thus, plasticity of plants may allow them to reproduce in both highly disturbed *and* highly stressed habitats.

Tree growth and maturity are likely to be important forces of succession in both the short and long term. The conifers have such low densities and are so small that they are not likely to contribute to successional dynamics for some decades. Although these species can mature in 10 or 20 years, only a few Douglas-fir trees on the debris-avalanche deposit were producing seeds after 24 years. However, with red alder contributing the most to plant cover 20 years after the eruption, a forest is gradually being established in some locations. Where the canopy becomes closed, the understory is shaded, which reduces surface temperature and enhances soil moisture retention. Hence, in future years, the difference between sites dominated by closed forests and those open to the sun will likely become more pronounced.

5.4 Prospects for the Future

The long-term potential vegetation for the debris-avalanche deposit is a coniferous forest dominated by Douglas-fir, Pacific silver fir (*Abies amabilis*), and western hemlock on upland areas and by deciduous trees on riparian areas (see the discussion of preeruption vegetation in Chapter 2, this volume). We predict that, within the next decade, vegetative cover will exceed 75% on sites where red alder becomes dominant. Thus, plant cover is expected to increase and spread except on the sides of eroding hummocks and active floodplains, where the patchy nature of the vegetation will likely continue. Revegetation has been slow on most areas on the debris-avalanche deposit because (1) removal of the previous ecological system was so complete, (2) the seed sources are distant, (3) conditions on the debris-avalanche deposit are stressful, (4) disturbances continue to occur, and (5) herbivory has influenced the successional trajectory. Although vegetation cover was greater on areas with abundant nonnative species, those sites have also experienced higher conifer mortality and thus may be slower to develop into a coniferous forest.

Even though some of the anticipated climax species are already present on the deposit, we expect that the area will go through the typical stages of succession characterized by increases in plant cover, decreases in soil bulk density, and increases in litter (Odum 1969). The expected pattern of succession is similar to that observed after glacial retreat (Adams and Dale 1987), with early-successional species being dominant for the first 15 years, deciduous trees becoming dominant for years 15 to 80, and coniferous forest producing a transition in years 80 to 115 [e.g., Crocker and Major (1955)]. However, the timing of succession on the debris-avalanche deposit will likely be longer than in glacial succession because the source vegetation is distant (Adams and Dale 1987).

Future disturbances will influence pathways and rates of succession. Potential disturbances include drought stress; geomorphic processes, such as erosion and deposition; volcanic activity; mudflows associated with heavy rainfall; herbivory; fire; and plant breakage caused by snow, ice, or wind. These disturbances will not occur uniformly across the deposit but will be influenced by topography, distance from a stream, and status of the vegetation. Succession on the debris-avalanche deposit will likely be set back or redirected for those sites that experience such disturbances. The result will be a mosaic of successional states on the debris-avalanche deposit.

5.5 Summary

During the first 20 years after the 1980 eruption, plant colonization and the subsequent development of plant communities on the debris-avalanche deposit were influenced by the low numbers of survivors, proximity to source propagules, substrate moisture, nutrient conditions, and herbivory. We found:

1. The few surviving plants were herbaceous species that have their dormant buds below the surface. No seed survival was detected.
2. Invading plants were much more important to vegetation development than were the very few survivors.
3. The early colonists with the greatest contribution to plant cover were early-successional, wind-dispersed species that survived on the adjacent blowdown-zone hill slopes.
4. Average plant cover on the debris-avalanche deposit was less than 1% 5 years after the eruption but averaged greater than 65% by 20 years after the May 18, 1980 eruption.
5. The number of species increased linearly over time up to 14 years after the 1980 eruption and declined slightly thereafter.
6. The rate of vegetation development has been spatially variable and related to habitat heterogeneity. Wetlands are particularly important as areas of high plant diversity. Areas near streams are susceptible to mudflows and flooding events.
7. Trees established successfully on the debris-avalanche deposit, demonstrating long-distance dispersal. Red alder, a fast-growing, early-maturing, and nitrogen-fixing tree, will be particularly important in the vegetation-development process during the next several decades.
8. Herbivory has influenced successional patterns. Elk herbivory increased plant cover and caused the proliferation of nonnative species.

Eventual vegetation will be a conifer-dominated forest with alder, willow, and cottonwood abundant in riparian zones. In the next decade, vegetative cover is expected to reach more than 75% in sites where red alder is or becomes dominant, and patchy vegetation is expected to remain on steep slopes and floodplains. Ongoing disturbances will continue to shape this dynamic landscape.

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