

Plant Succession on the Mount St. Helens Debris-Avalanche Deposit and the Role of Non-native Species

Virginia H. Dale and Elsie M. Denton

8.1 Introduction

The debris-avalanche deposit is one of the most disturbed areas created by the 1980 eruption of Mount St. Helens (MSH), with little survival of a few plant fragments and primary succession mostly being initiated by the seeds dispersed onto the newly emplaced material. Vegetation establishment on the debris-avalanche deposit was affected by the nearly complete loss of organic matter, the nature of the deposit, local climate conditions, surviving plant life in adjacent areas, and patterns of plant colonization and growth. There was great concern about the potential for erosion of the newly emplaced volcanic material; US\$2 million was spent to aerially distribute seeds of eight species (only one of which was native) over a large part of the disturbed area (Dale et al. 2005c). Seeding of the western but not the eastern portion of the deposit set up conditions for examining effects of such human interventions on plant establishment and succession. This chapter analyzes vegetation changes on the debris-avalanche deposit during the first 30 years post eruption, considers the role of non-native species, and discusses potential future vegetation patterns on the deposit. In particular, we compare measures of plant cover and species richness in permanent plots that were seeded in 1980 with plots that were not seeded to determine the 30-year effects of the seeding of mostly non-native plants on patterns on vegetation establishment.

8.1.1 Creation of the Debris-Avalanche Deposit

The 18 May 1980 eruption of MSH was immediately preceded by the largest debris avalanche in recorded history (Fig. 8.1). A debris avalanche occurs when an unstable slope collapses and soil, rocks, and other debris are transported downslope. Debris avalanches typically move rapidly and are common on steep volcanoes. The MSH debris avalanche was triggered by a magnitude 5.1 earthquake and followed by a laterally directed pyroclastic density current, commonly referred to as a lateral blast (hereafter, the blast PDC). About 2.8 billion m³ of material rushed down the north side of MSH and spread over a 60-km² area. Later that day, earthquake-induced liquefaction of the debris deposit spawned a massive lahar that flowed down the North Fork Toutle and Toutle Rivers to the Cowlitz River (Fairchild 1985). The lahar both eroded and deposited material on the surface of the debris-avalanche deposit, with erosion exceeding deposition by about 4 million m³ (Fairchild 1985).

Some of the debris-avalanche material was deposited in the Spirit Lake basin and the South Fork Coldwater Creek watershed, but the largest portion moved quickly down 25 km of the North Toutle River valley (Voight et al. 1981), which is the focus of this chapter. As the debris avalanche traveled, it passed through areas where the forest had already been leveled by the blast PDC. The debris-avalanche material varied in temperature, for it included blocks of glacial ice and hot rocks from the magma that had risen up into the volcano prior to the eruption. Near its end, the deposit moved through forested areas that were not otherwise affected by the eruption, toppling and burying the forest in its path.

The new environment created by the debris-avalanche deposit was mostly barren of any living organisms, viable seeds, or organic matter. Emplacements near the valley walls retained some clumps of organic material, soil, and surviving plants. Hence, the debris-avalanche deposit provided an opportunity to examine primary succession.

V.H. Dale (✉)
Department of Ecology & Evolutionary Biology, The University
of Tennessee, Knoxville, TN 37996, USA
e-mail: vdale@utk.edu

E.M. Denton
U.S. Department of Agriculture, Agricultural Research Service,
Eastern Oregon Agricultural Research Center,
10726 OR-205-A, Burns, OR 97720, USA

© Springer Science+Business Media LLC 2018
C.M. Crisafulli, V.H. Dale (eds.), *Ecological Responses at Mount St. Helens: Revisited 35 years after the 1980 Eruption*,
https://doi.org/10.1007/978-1-4939-7451-1_8

about the potential for erosion of the newly emplaced volcanic material; US\$2 million was spent to aerially distribute seeds of eight species (only one of which was native) over a large part of the disturbed area (Dale et al. 2005c). Seeding of the western but not the eastern portion of the deposit sets up conditions for examining effects of such human interventions on plant establishment and succession. This chapter analyzes vegetation changes on the debris-avalanche deposit during the first 30 years post eruption, considers the role of non-native species, and discusses potential future vegetation patterns on the deposit. In particular, we compare measures of plant cover and species richness in permanent plots that were seeded in 1980 with plots that were not seeded to determine the 30-year effects of the seeding of mostly non-native plants on patterns on vegetation establishment.

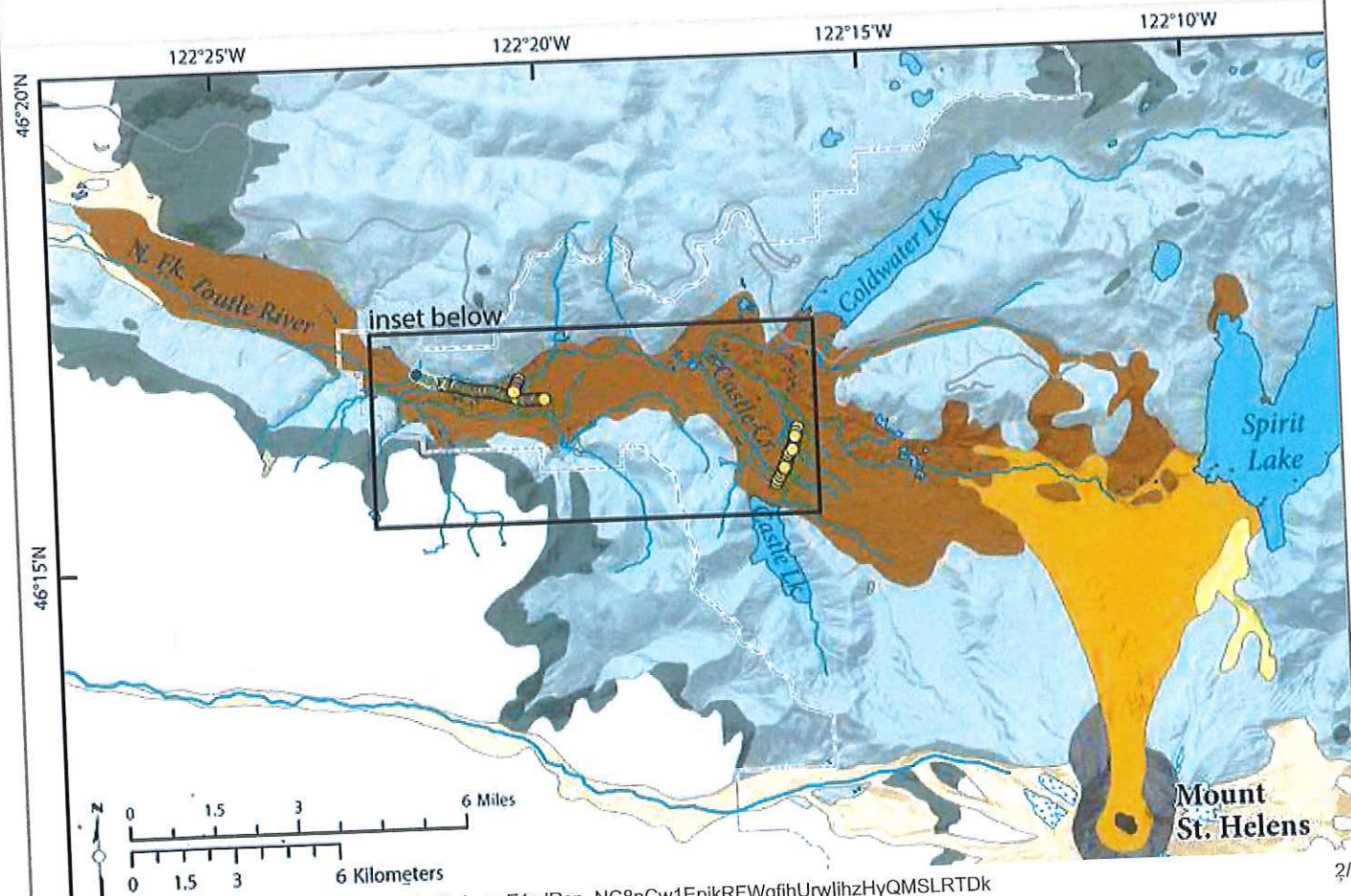
8.1.1. Creation of the Debris-Avalanche Deposit

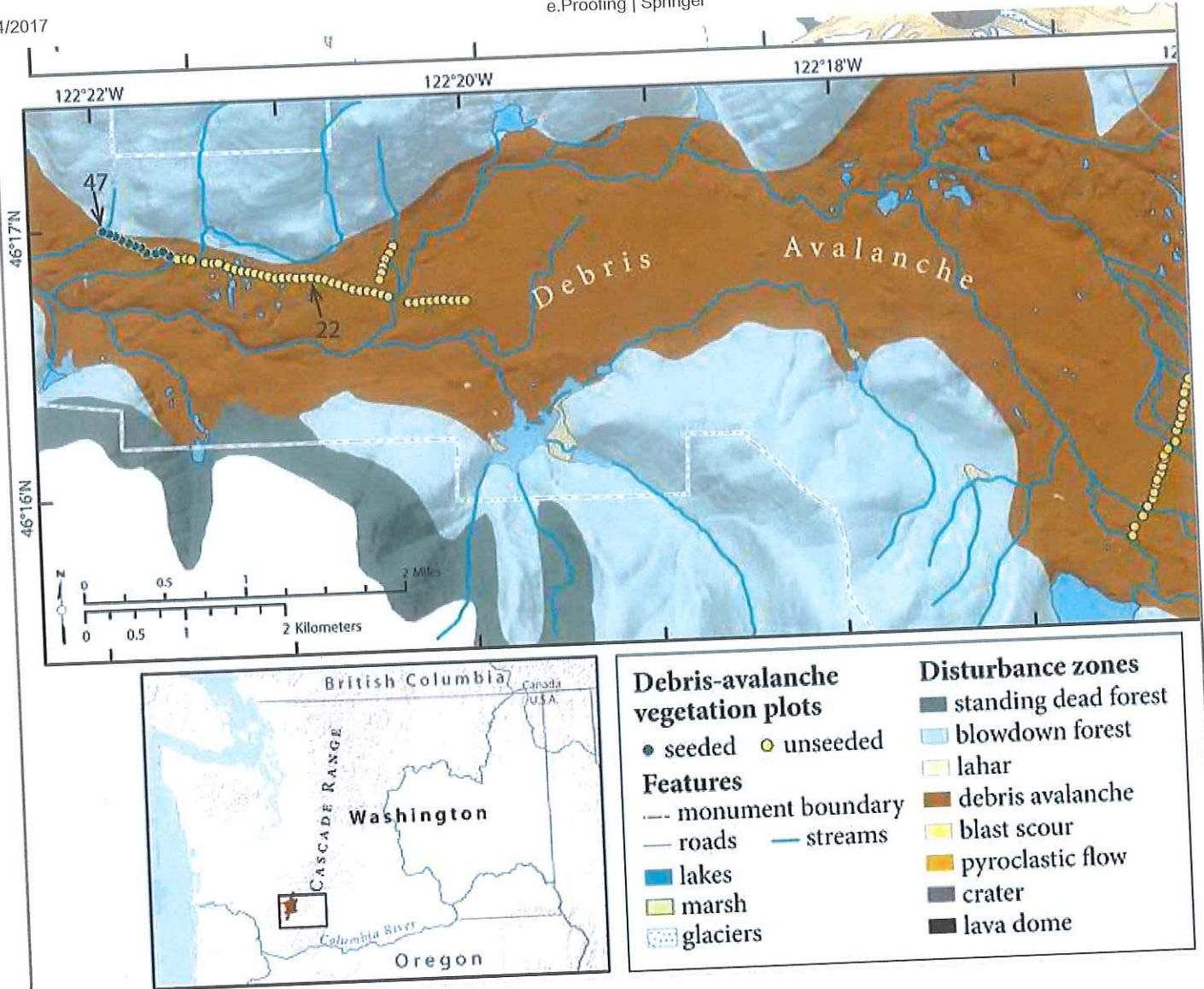
The 18 May 1980 eruption of MSH was immediately preceded by the largest debris avalanche in recorded history (Fig. 8.1). A debris avalanche occurs when an unstable slope collapses and soil, rocks, and other debris are transported downslope. Debris avalanches typically move rapidly and are common on steep volcanoes. The MSH debris avalanche was triggered by a magnitude 5.1 earthquake and followed by a laterally directed pyroclastic density current, commonly referred to as a lateral blast (hereafter, the blast PDC). About 2.8 billion m^3 of material rushed down the north side of MSH and spread over a 60- km^2 area. Later that day, earthquake-induced liquefaction of the debris deposit spawned a massive lahar that flowed down the North Fork Toutle and Toutle Rivers to the Cowlitz River (Fairchild 1985). The lahar both eroded and deposited material on the surface of the debris-avalanche deposit, with erosion exceeding deposition by about 4 million m^3 (Fairchild 1985).

Fig. 8.1

Mount St. Helens' area showing location of study plots on the debris-avalanche deposit, the boundary of the MSH National Volcanic Monument, and nearby areas affected by the eruption (Cartography by Kathryn Ronnenberg, USDA Forest Service, Pacific Northwest Research Station)

AQ2





Some of the debris-avalanche material was deposited in the Spirit Lake basin and the South Fork Coldwater Creek watershed, but the largest portion moved quickly down 25 km of the North Toutle River valley (Voight et al. 1981), which is the focus of this chapter. As the debris avalanche traveled, it passed through areas where the forest had already been leveled by the blast PDC. The debris-avalanche material varied in temperature, as it included blocks of glacial ice and hot rocks from the magma that had risen up into the volcano prior to the eruption. Near its end, the deposit moved through forested areas that were not otherwise affected by the eruption, toppling and burying the forest in its path.

The new environment created by the debris-avalanche deposit was mostly barren of any living organisms, viable seeds, or organic matter. Emplacements near the valley walls retained some clumps of organic material, soil, and surviving plants. Hence, the debris-avalanche deposit provided an opportunity to examine primary succession. Both the pyroclastic-flow zone and the debris-avalanche deposit were more barren of biological remnants than the blowdown, tephrafall, or lahar zones created by the Mount St. Helens eruption (Swanson and Major 2005). Disturbance characteristics affect plant survival, and prevailing climate and flora in the local species pool affect plant reestablishment (Dale et al. 2005b; Swanson and Crisafulli, this volume).

8.1.2. Initial Physical and Chemical Conditions of the MSH Debris-Avalanche Deposit

The MSH debris avalanche resulted in a massive deposit composed of discrete blocks from the prior mountain in a mixture of blast-homogenized material (Glicken 1998). The heterogeneous topography of the deposit averages 45 m thick, with a maximum of 195 m (Voight et al. 1981). The terrain is relatively level where the lahar inundated the distal end of the deposit. In other locations, large mounds rise up to 50 m above the deposit surface. These hummocks are derived from lithic blocks that originated in the former interior of the volcano (Voight et al. 1981; Fairchild 1985; Glicken 1998). Many depressions formed when the deposit settled or as a result of the subsequent melting of embedded blocks of ice, creating new ponds and wetlands as these basins filled with water.

The landslide was hot, with an emplacement temperature of 100 °C in some locations (Voight et al. 1981). 10 to 12 days after the eruption, temperature varied from 68 to 98 °C measured at 1.0–1.5 m depth, with cooler temperatures occurring at a greater distance from the volcano (Banks and Hoblitt 1981).

Once it cooled, conditions on the deposit were adequate but not ideal for plant establishment and growth (Adams et al. 1986). The deposit material was poorly sorted and dominated by sand (63% by weight of the <2-mm fraction). Rocks, including all material >2 mm, constituted a variable component ($36.4 \pm 28.9\%$ by weight) (Adams and Dale 1987). The sandy texture of the deposit limited moisture retention, potentially causing stressful conditions for seedling establishment and plant growth. Nitrogen levels and electrical conductivity were initially low (703 ppm NH_3 and $0.84 \pm 0.71 \text{ mmho cm}^{-1}$, respectively). The substrate had low levels of organic matter (0.31% weight loss on ignition), a low carbon-to-nitrogen ratio (4.3:1), and was acidic, with an initial pH of 4.8 ± 0.5 . For comparison, C:N ratio of forest soils in the Pacific Northwest typically ranges from 21:1 to 31:1 (Sun et al. 2004) and is acidic. The debris-avalanche deposit substrates had low moisture-holding capacity—saturation was $5.3 \pm 0.9\%$ per 15 atmosphere moisture (atm), where 15 atm is the water content at the wilting point and represents the point at which plant roots cannot draw any more water from the void space. Adams and Dale (1987) used lettuce (*Lactuca sativa*) to bioassay the debris-avalanche material. Seedlings were planted and well watered under greenhouse conditions; they survived but grew little even in response to added nutrients. The limited plant growth may have been due either to soil chemistry (e.g., excessive salt) or to structural properties of the debris material (e.g., texture).

Both massive erosion and deposition have occurred on the debris-avalanche deposit since the 1980 eruption. Fluvial erosion created new channels that have grown wider and deeper over time, with channels and gullies that have steep walls (30–70°), variable incision depths (3–50 m), and widths of 3–120 m (Lehre et al. 1983; Waite et al. 1983; Major et al. 2000). Twenty years after the eruption, erosion remained a major factor, with annual suspended sediment yield from the debris-avalanche deposit 100 times (10^4 Mg km^{-2}) typical background levels as compared to similar undisturbed rivers in the region ($\sim 10^2 \text{ Mg km}^{-2}$) (Major et al. 2000). Increased peak flows occurred in the autumn and winter for the first 10 years after the eruption (Major and Mark 2006).

8.1.3. Plant Propagule Survival on the Debris-Avalanche Deposit

The debris avalanche and the blast PDC removed the coniferous forests and riparian vegetation that existed in the North Fork Toutle River valley floor prior to the eruption (Adams and Adams 1982; Fairchild 1985). Adams and Dale (1987) found no seeds in assayed debris-avalanche material samples, and no seedlings germinated from test flats of deposit material. During June 1980, a search for plants was conducted across the deposit, which was found to be largely barren. No seedlings and only a few vegetatively propagating plants were found. Individual plants of 20 species survived by growing from roots or stems that had been transported in the debris-avalanche deposit and came to rest near the surface (Adams et al. 1986; Dale 1986). Most of these scattered plants were fireweed (*Chamerion angustifolium* ssp. *angustifolium*), Canada thistle (*Cirsium arvense*), and broadleaf lupine (*Lupinus latifolius*). No woody plants survived on the central portion of the debris-avalanche deposit.

Initially, there was abundant vegetation and organic debris at the terminus of the deposit, as the avalanche had scoured and transported many plants down the valley (Glicken 1998) (Fig. 8.2). However, this pile of living and

dead vegetation did not influence plant reestablishment, because the Army Corps of Engineers removed it during construction of a sediment-retention structure downstream of our study sites.

Fig. 8.2

As seen in summer 1980, the material at the terminus of the debris-avalanche deposit that was subsequently removed



8.1.4. Patterns of Vegetation Establishment on the Debris-Avalanche Deposit

The colonists with the greatest contribution to plant cover were early-successional, wind-dispersed species that survived on the adjacent blowdown-zone hillslopes and nearby clear-cuts outside the blast-PDC area (Fig. 8.1, Dale 1986). In the first 5 years after the eruption, average plant cover on the deposit was less than 1% (Dale 1986) but averaged greater than 65% by 20 years post eruption (Dale et al. 2005a). The pattern of vegetation establishment was spatially variable as related to heterogeneity of the deposit. Wetlands were areas of high plant species richness and cover, and locations near streams were susceptible to erosion, which prevented long-term plant establishment. Red alder, *Alnus rubra*—a fast-growing, early-maturing, and nitrogen-fixing tree—is established quickly, had the second highest cover of any plant species by 20 years post eruption, and is predicted to be important for the next several decades (Dale et al. 2005a).

Most seeds dispersed to the deposit were transported by wind (Dale 1989). Of those seeds caught by seed traps set at 50-m intervals along the two transects on the deposit in 1981, 1982, 1983, and 1994 (1, 2, 3, and 14 years after the eruption), the number of seeds was greatest in the second year (1982), possibly because that was an unusually wet summer (Dale et al. 2005a). However, 1983 was even wetter than 1982, but fewer seeds were trapped. Heavy lupine seeds appeared in the traps for the first time in 1994. These seeds could not have been transported by the wind and likely came from plants near the traps on the deposit, evidence of the growing importance of in situ reproduction (Dale et al. 2005a).

8.1.5. Non-native Species Introduced by Natural Dispersal and by Seeding

Most of the arriving windblown seeds originated from areas adjacent to the debris-avalanche deposit that were less disturbed by the eruption. Those areas were dominated by private industrial forests, many of which had been recently cut, and those clear-cuts supported an abundance of early-successional species having light, plumed seeds. In 1981, 87% of seeds trapped were native fireweed, but seeds of the three other captured species were not native: Canada thistle, field sow thistle (*Sonchus arvensis*), and woodland ragwort (*Senecio sylvaticus*) (Dale 1989). Fireweed continued to be the most common seed trapped 2, 3, and 14 years post eruption, likely because

of the abundance of that species on clear-cuts near the deposit and the high vagility of the seeds (Dale et al. 2005a).

In forests of the Pacific Northwest, non-native species are uncommon (Ares et al. 2009). However, 57 non-native species are considered a problem in forested ecosystems of the region (Gray et al. 2011), and over time, seeds of most of these species have dispersed onto the debris-avalanche deposit and are established. Following the 1980 eruption, there was extreme apprehension about the potential effects of massive erosion of the debris-avalanche deposit and other disturbed areas, and the United States government made funds available to address these concerns. The United States Soil Conservation Service (SCS) planned to aeri ally seed non-native species over most of the area disturbed during the eruption in order to stabilize the recently emplaced volcanic substrates and to promote plant recovery (Dale et al. 2005c). Because many scientists objected to this management activity, which was considered a threat to research opportunities in this natural laboratory (Dale et al. 2005c), the proposed area to be seeded was reduced from 1640 to 320 km² in the vicinity of Mount St. Helens (Stroh and Oyler 1981). The selected species included those available from existing seed collections and were characterized by rapid germination, tolerance to a variety of environmental conditions, suitability as food or cover for wildlife, and ability to fix nitrogen via association with bacteria (Stroh and Oyler 1981). The type of volcanic disturbance and elevation determined species mixes used in specific locations across the landscape.

In the autumn of 1980, the SCS distributed seed by helicopter over about 24 km² on the westernmost portion of the debris-avalanche deposit and on the lahar deposit that extends downstream to the west (Figs. 8.1 and 8.3). The first author was present on the debris-avalanche deposit during the seed application and documented where the seeds fell relative to established permanent plots. The SCS used a mixture of herbaceous plants on the debris deposit that included legumes (*Trifolium repens*, *Lotus corniculatus*, and *Melilotus officinalis*) and grasses (*Lolium perenne*, *Dactylis glomerata*, *Schedonorus arundinaceus*, *Agrostis capillaris*, and *Festuca rubra*) (Stroh and Oyler 1981). Of these species, only red fescue (*F. rubra*) is native. By September 1981, plant cover of the seeded area on the lower debris avalanche created a stark contrast with unseeded areas (Fig. 8.4) (Dale 1991). Nevertheless, large-scale erosion still occurred (Major et al. 2000).

Fig. 8.3

Seeds being distributed by helicopter onto the debris-avalanche deposit in 1980



Fig. 8.4

The initial flush of vegetation, as seen in September 1981, that grew from the non-native seeds distributed onto the debris-avalanche deposit. The abrupt line between the *yellow* vegetation and the *gray*, barren deposit marks the distinct edge of the seeded area



Because the westernmost, downstream part of the debris-avalanche deposit was seeded in 1980 and the eastern part was not, the area offered an opportunity to compare successional processes occurring with and without introduction of non-native seeds. 11 of 62 permanent plots remaining in 2010 fell in the 1980 seeded area. By 1989, the seeded plots differed from those that had not received seed mix; these plots had greater cover and plant species richness but less native plant richness and greater mortality of conifer trees than the unseeded areas (Dale 1991). By 2000, 20 years post eruption, the seeded plots continued to have greater cover; overall plant richness, including non-native species, was also higher (Dale and Adams 2003). Presumably, the plant communities across our entire study area will eventually converge toward a mature coniferous forest typical of the Pacific Northwest (Franklin and Dyrness 1973), if they are not reset once more by a future eruption.

This chapter examines 30 years of vegetation data from the debris-avalanche deposit to determine if the effects of non-native seeding were still present in 2010 and whether there is evidence that these effects might be fading with time. The analysis builds upon the knowledge described above and data described below.

8.2. Methods

8.2.1. Methods of Monitoring Plant Establishment

To monitor vegetation establishment, a network of permanent plots was established in 1981 and 1982. The vegetation in these permanent plots was measured during nine summers over a 30-year period: 1981–1983, 1989, 1994, 2000, 2004, and 2010. The 250-m² circular plots were placed at 50-m intervals along transects between Castle and Coldwater Lakes and down the western extent of the deposit (Fig. 8.1). The plots were located on the central portion of the debris-avalanche deposit, not along the marginal facies where the debris avalanche shoved surviving plants to the edge of the valley. The initial 101 plots represented the variety of geologic and topographic conditions on the debris-avalanche deposit and distances from surviving vegetation in the adjacent landscapes. However, during the first two decades after the eruption, 39 of the unseeded plots were lost to erosion and lahars or could not be located in 1 or more years. None of the seeded plots were lost.

AQ3

Ground cover and species composition are useful for monitoring the ecological integrity of ecosystems (LaPaix et al. 2009). In each sample year, presence and ground cover (vegetation up to 1 m in height) of vascular plant

species, along with tree density when individual trees could be distinguished, were measured in each plot. A team that included the same botanists over the 30 years of sampling visually estimated plant cover for each species. Bråkenhielm and Qinghong (1995) found that visual estimates provide the most accurate, sensitive, and precise measure of vegetation cover. In 1982, topographic conditions of each plot were described in the field. When a tree canopy began to establish, canopy cover was recorded for all plots using a concave spherical densitometer (Peck et al. 2003).

Because abnormally high or low precipitation during parts of the 30-year observation period was likely to affect plant growth and establishment as well as erosion, annual precipitation from the nearest long-term weather station was recorded. Data have been collected since 1929 at Longview, Washington, which is about 60 km west of MSH. These data are available from the US Historical Climatology Network (Easterling et al. 1996) and the Carbon Dioxide Information Analysis Center at Oak Ridge National Laboratory. The Longview station receives less precipitation than the higher-elevation station at Spirit Lake, but the Longview precipitation record has been collected continuously before and since the eruption, whereas the Spirit Lake station was established in 1986 and thus has no pre-eruption records.

8.2.2. Methods of Data Analysis

8.2.2.1. Ground Cover and Richness

We examined changes in ground cover using repeated measures analysis of variance (ANOVA) on all plots, with seeding and years since eruption used as factors. To normalize variance, cover values were square-root transformed. Years 2 and 3 (1982 and 1983) still had such low cover that it was necessary to examine them separately from years 9 to 30. Final p-values were adjusted using a Bonferroni correction for two multiple-comparison tests (Dunn 1961). Since sampling years were not equally spaced, we used a spatial power covariance structure (Jennrich and Schluchter 1986). We tested the effects of seeding on ground plant richness using repeated measures ANOVA as well, but transformations and splitting the test over multiple years were not necessary as variance was more normally distributed. We still used a spatial power covariance structure to account for uneven distribution of sampling years.

We analyzed differences in species composition of ground vegetation using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with a Bray-Curtis difference matrix (Bray and Curtis 1957); seeding was included as a factor. Because the communities were not at equilibrium and multiple years elapsed between most sampling periods, including repeated measures ANOVA in the PERMANOVA analysis were unnecessary, it was unlikely that strong similarities would exist between sampling periods; therefore, we conducted PERMANOVA tests separately for each of the 7 years. Final p-values were adjusted with a Bonferroni correction for seven multiple testings. As cover was very low in the early years and many plots had zero cover, we included a dummy variable with a cover value of 0.01 (the lowest possible non-zero cover value) for all plots in all years to avoid the problem of zero sums. To minimize the effect of extreme low and high cover values on the data, we applied a fourth-root transformation before analysis. Additionally, we reduced noise in the data set by removing species with a less than 5% occurrence over all years, as recommended by McCune and Grace (2002). This reduced the total number of species included in the analysis from 204 to 65 and made the data fit the assumptions for the test much better. Additionally, we ran the PERMANOVA with all 204 species to verify that using the reduced data set did not change conclusions.

To further assess the contributions of individual species to the community differences between the seeded and unseeded plots, we looked at similarity percentages using the Bray-Curtis difference matrix from the analysis of species composition (i.e., percent cover) for the ground vegetation. We applied the same dummy variable (0.01), data reduction, and transformations described above and used to examine differences in ground cover and species composition. We separately examined each year for differences in ground vegetation species composition between seeded and unseeded plots, but as conclusions were not drawn across years, we did not apply a correction for multiple testing.

8.2.2.2. Trees

We examined total stem density of all tree species using repeated measures ANOVA with plot as a subject and years since eruption as the repeated factor and seeding as the treatment. Data were log-10 transformed (accounting for zeros) before analysis to improve normality of variance. To account for uneven spacing of sampling across years, we used a spatial power covariance structure.

Using PERMANOVA with a Bray-Curtis difference matrix and seeding as a factor, we also analyzed difference in stem density of tree species. Again, we ran each year as a separate test and applied a Bonferroni correction for seven multiple testings to final p-values. To account for years where no stems of any species were found within a plot, we included a dummy variable with a count of 1 (the lowest possible non-zero count value) in all plots, across all years. Before analysis, we used a log-10 transformation that accounts for the presence of zeros on the count data (McCune and Grace 2002) to reduce the influence of extreme values. Since only 14 species of trees were found in these plots across all years, we retained all tree species in the analysis.

With seeding and years since eruption as factors, we used repeated measures ANOVA on plots to examine total tree canopy cover. Variance and distribution were both normally distributed. No correction to final p-values was used, but we maintained the spatial power covariance structure for consistency with other tests even though only 2 years were included in this analysis (2004 and 2010).

8.2.2.3. Native Versus Non-native Species

Using repeated measures ANOVA, we analyzed changes in cover of non-native and native species separately. Plot was the repeated term, and we analyzed all 7 years together, with years since eruption and seeding as factors. To improve normality of variance, we used a log-10 transform accounting for zeros, along with a spatial power covariance structure to account for the lack of uniform time periods between samplings.

To perform repeated measures ANOVA, we used SAS 9.3 (SAS Institute, Cary NC). For PERMANOVA analysis, we used the Adonis package in R 3.1.1 (R Core Team 2014) and double checked using Primer 6 (PRIMER-E Ltd., Ivybridge United Kingdom). We conducted similarity percentage analyses with Primer 6.

8.3. Results

Seeded plots did not differ from unseeded plots in topographic conditions or soil particle-size distributions (Table 8.1). The 11 seeded plots contained examples of five of the six topographic categories, with only the rarest type not represented, and plots with a single high mound.

Table 8.1

Mean and standard error of particle-size distribution for the >2-mm fraction of seeded and unseeded plots in August 1982

	% boulders	% cobbles	% gravel, sand, silt, clay
Not seeded			
Mean	5.8	19.4	75
S.E.	0.6	1.6	2
Seeded			
Mean	7	18.8	71.6
S.E.	2.1	3.4	5.4

% boulders % cobbles % gravel, sand, silt, clay

The sampling and analysis methods are described in Adams and Dale (1987)

8.3.1. Ground Cover and Richness

Ground cover increased in all plots over time (Fig. 8.5). Seeding had a significant effect ($p < 0.02$) on cover (Table 8.2), as was evident from photographs (Fig. 8.6). Total cover was higher in the seeded plots than the unseeded plots in all years except year 2 ($p = 0.17$). There was a significant interaction between seeding and years since eruption in later years ($p = 0.0028$), but this result seems to be driven exclusively by year 14, when the cover in the seeded plots spiked sharply and cover in unseeded plots did not (Fig. 8.5). The year-14 spike in cover was largely a result of an increase in non-native species in seeded plots (Fig. 8.7b). The spike observed in native-species cover in the seeded plots in year 9 (Fig. 8.7a) suggests that this year may also have had a steeper increase in total cover in the seeded plots than the unseeded, but, because years 2 and 3 and 9–30 were analyzed separately, this hypothesis could not be tested directly.

Fig. 8.5

Change in total cover over time in seeded (*solid line*) and unseeded plots (*dashed line*). *Inset* shows total cover in all plots over time on the debris-avalanche deposit. *Bars* are standard error

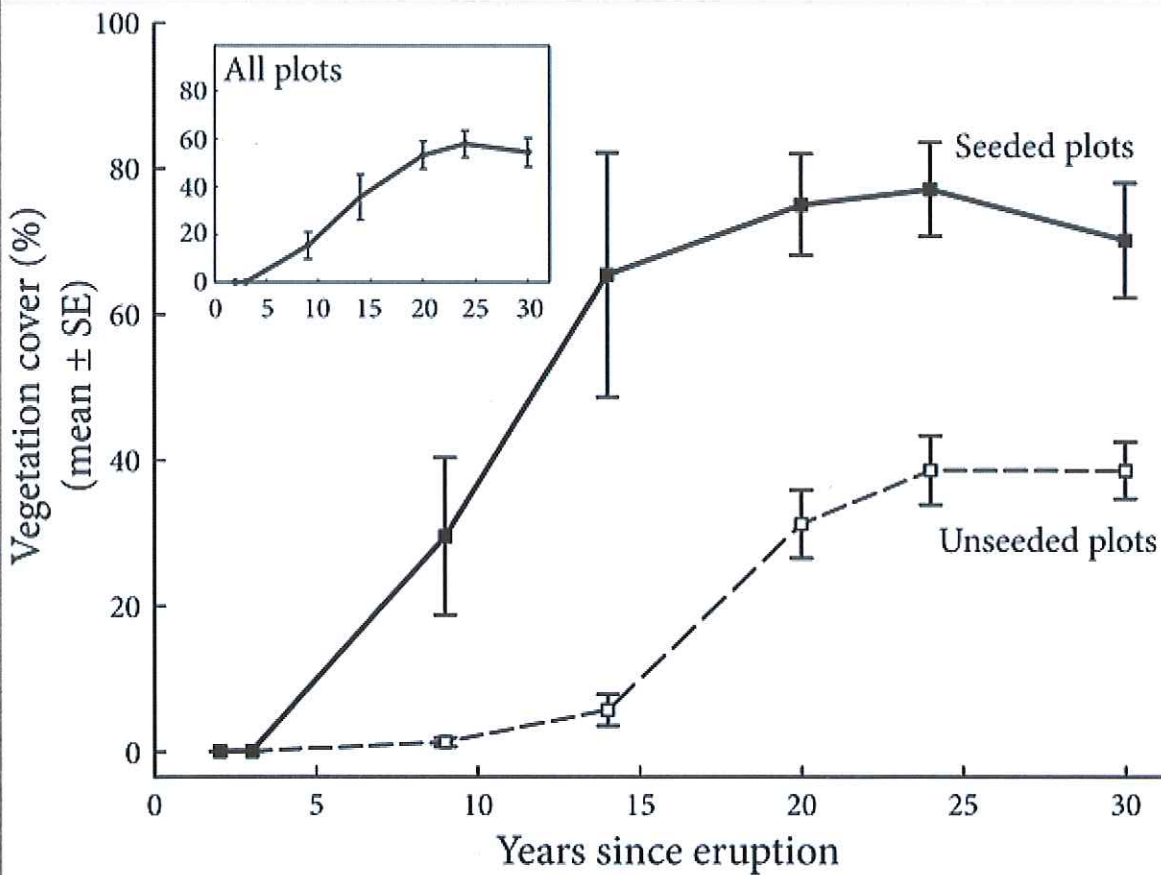


Table 8.2

Repeated measures analysis on total cover of all species

	<i>F</i> value	<i>p</i> -value
Years 2–3		
Seeded	7.11	0.02*
Yse	69.68	<0.0002**
Yse*seeded	1.85	0.36
Years 9–30		
Seeded	31.64	<0.0002**
Yse	21.31	<0.0002**
Yse*seeded	4.59	0.0028**

Plot was the subject and years since eruption (yse) and seeded were factors. Years 2 and 3 and 9 through 30 were analyzed separately owing to variance issues

A Bonferroni correction for two multiple testings was used on final *p*-values (* denotes significance at the 0.05 level and ** at the 0.01 level)

Fig. 8.6

Time series of photographs for plots 22 and 47. Plot 47 was seeded in 1980, whereas plot 22 was not seeded



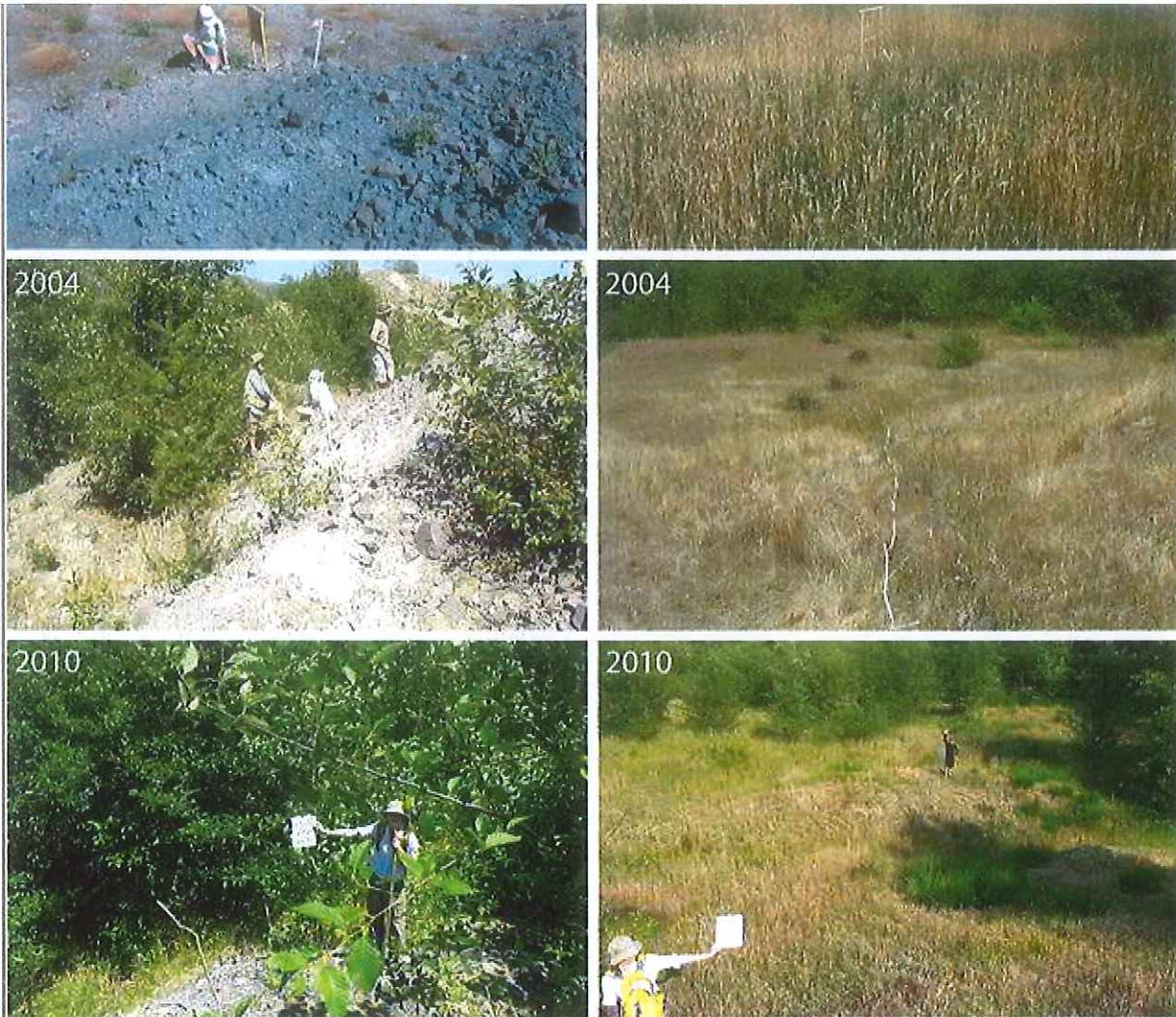
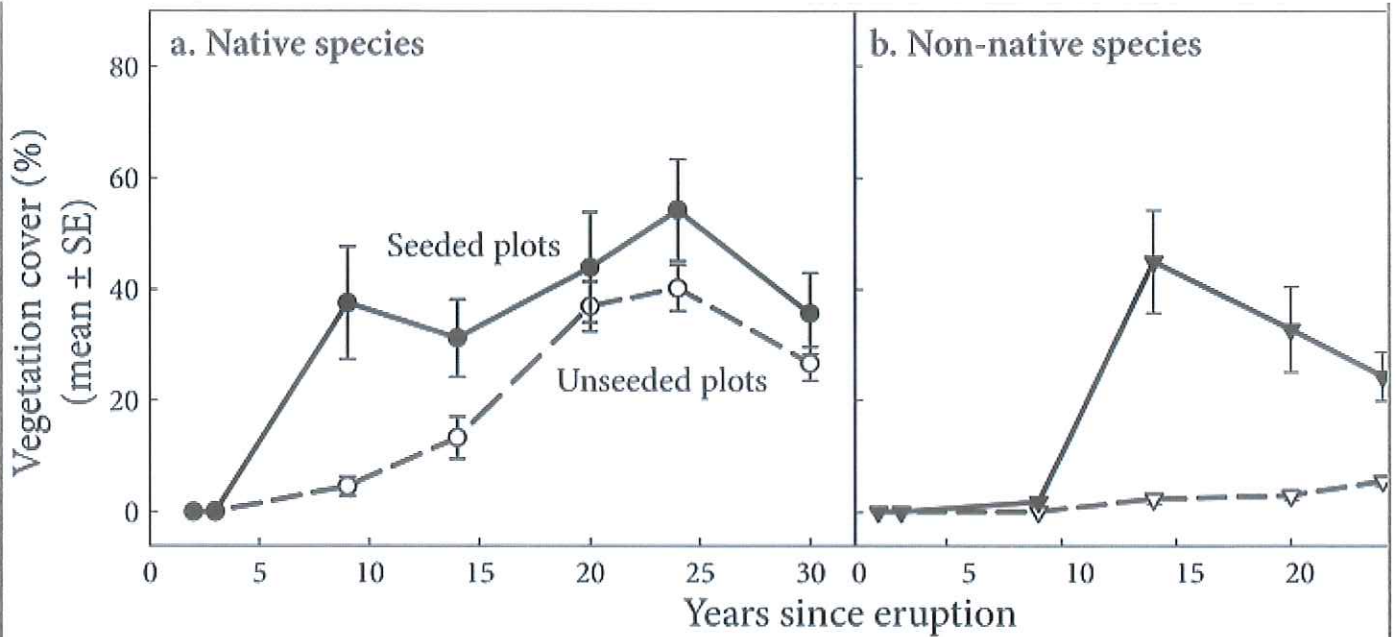


Fig. 8.7

Native (a) and non-native (b) species cover in seeded (*solid lines*) and unseeded (*dashed line*) plots over time. *Error bars* are standard error



Cover of both native and non-native species was higher in the seeded plots than the unseeded plots ($p < 0.0001$), but not significantly so in all years, as there was a year-by-treatment interaction ($p < 0.0001$) (Table 8.3). The pattern in native cover increase over time seems to be fairly consistent in seeded versus unseeded plots; the two treatments differed only in 2 years (9 and 14) ($p < 0.0001$) (Fig. 8.7a). However, non-native cover differed between seeded and unseeded plots in years 9 through 24 ($p < 0.004$). In the seeded plots, non-native cover spiked in year 14, and then remained fairly consistent, whereas in the unseeded plots, total cover slowly but consistently crept upward over time (Fig. 8.7b). The proportion of cover from non-native species was highest in the first year of sampling in unseeded plots and in year 14 in the seeded plots (Fig. 8.8). The proportion of total cover from non-native species varied over time. The contribution of non-native species to overall cover was greatest in the unseeded plots in year 14 and in the seeded plots in year 30 (Fig. 8.8 inset).

Table 8.3

Results of repeated measures on species richness and native and non-native cover per plot in the debris-avalanche deposit over seven sampling periods from year 2 to year 30 after the eruption. Plot was the subject and years since eruption (yse) and seeded were factors

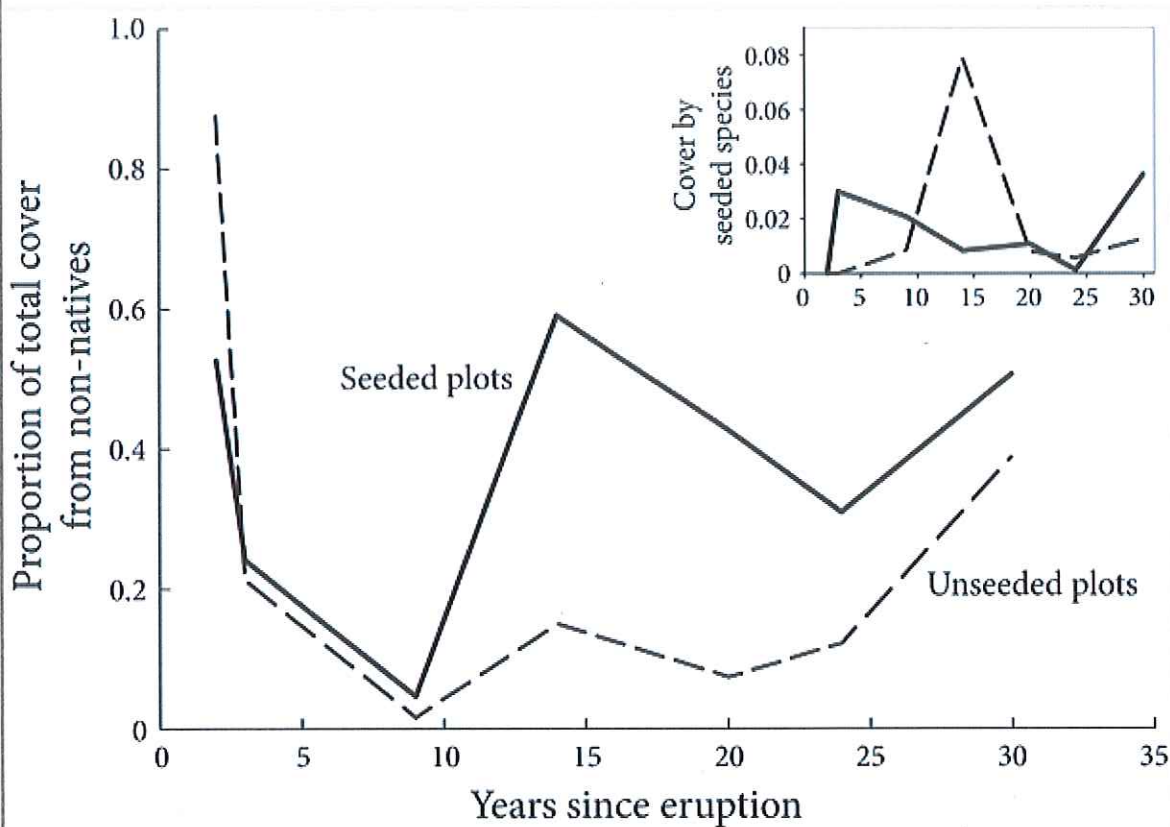
	<i>F</i> value	<i>p</i> -value
Native cover		
Seeded	16.44	0.0001***
Yse	93.03	<0.0001***
Yse*seeded	10.45	<0.0001***
Non-native cover		
Seeded	39.64	<0.0001***
Yse	61.29	<0.0001***
Yse*seeded	7.33	<0.0001***

	<i>F</i> value	<i>p</i> -value
Richness		
Seeded	22.34	<0.0001***
Yse	103.36	<0.0001***
Yse*seeded	3.39	0.0029**

** denotes significance at the 0.01 level and *** at the 0.0001 level

Fig. 8.8

Proportion of total cover from non-native species through time for plots that were seeded (*solid line*) and unseeded (*dashed line*). *Inset* is proportion of total cover from seeded species through time in both seeded and unseeded plots



Like cover, species richness increased over time in all plots (Fig. 8.9). Species richness was higher in seeded plots compared with unseeded plots but only significantly so in years 3, 9, 24, and 30 after the eruption ($p < 0.01$). Richness on the debris-avalanche deposit as a whole has increased in every year and has followed a nearly linear trend since year 3 (Fig. 8.10). Non-native species have made up a fairly consistent proportion of all species found on the debris-avalanche deposit in all years—between 20% and 30% of total richness (Fig. 8.10, inset).

Fig. 8.9

Change in number of species per plot over time in seeded (solid line) and unseeded (dashed line) plots. Bars are standard error. *Inset* is richness per plot over time for all plots

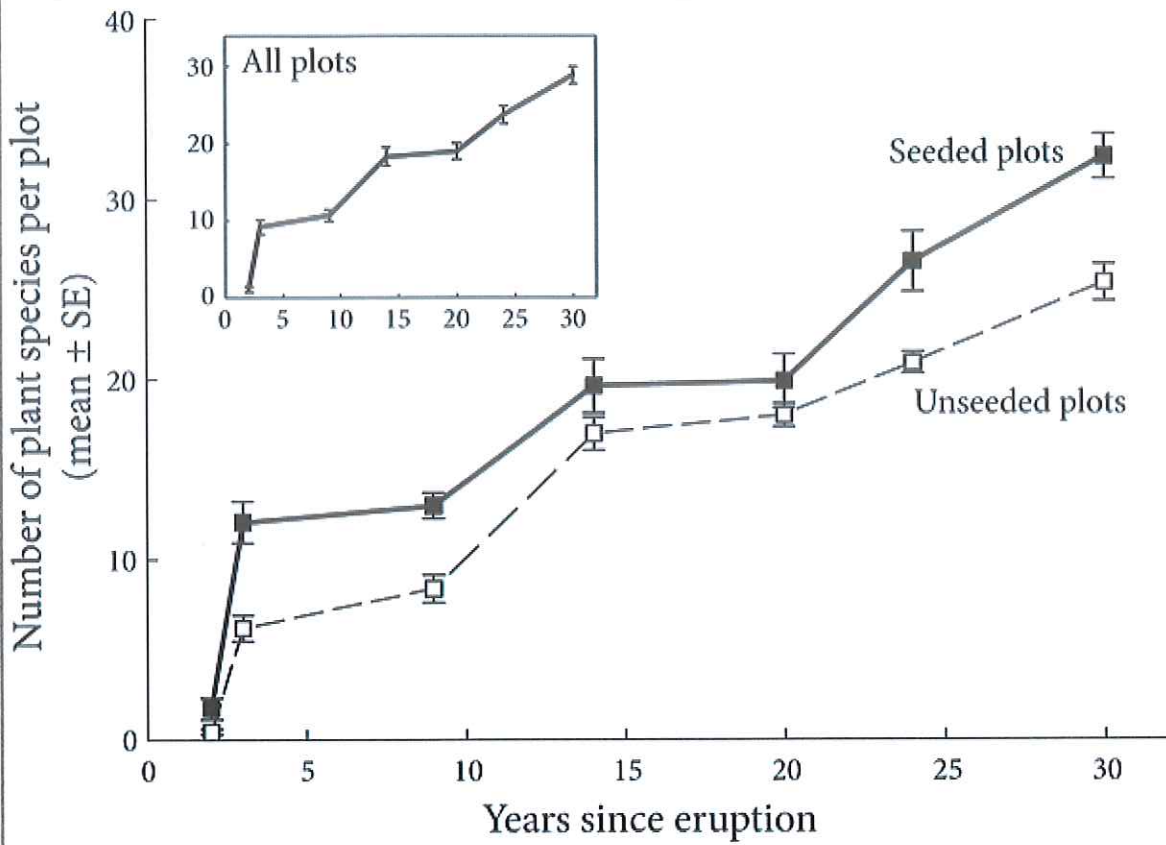
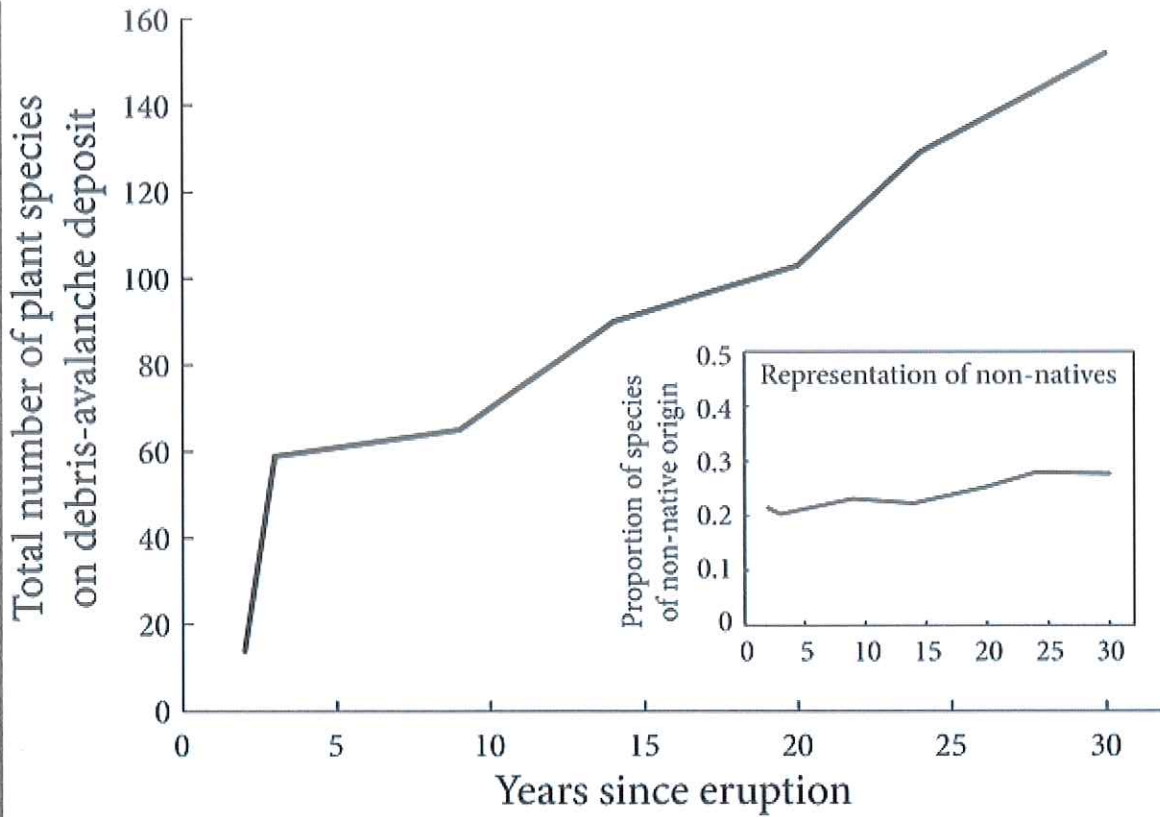


Fig. 8.10

Richness of all species on the debris-avalanche deposit over time. *Inset*: proportion of richness made up of non-native species



8.3.2. Species Composition

There was a significant difference in species composition comparing the seeded versus unseeded plots in all years ($p < 0.035$) (Table 8.4). Based on R^2 values, seeding explained the highest percent of difference in community composition in years 2 (15%), 9 (10%), 14 (14%), and 20 (10%), but the influence of seeding on plant community in later years was reduced, explaining only 7% of the difference between treatments in years 24 and 30. Seeding explained the lowest percent difference in ground-cover plant communities in year 3 ($R^2 = 6\%$).

Table 8.4

PERMANOVA analysis of species composition and seeded versus unseeded plots

Year since eruption	df	Pseudo-F	R^2	Adj. p-value
2	1	10.4	0.15	0.007**
3	1	3.56	0.06	0.035*
9	1	6.38	0.10	0.007**
14	1	9.95	0.14	0.007**
20	1	6.37	0.10	0.007**
24	1	4.87	0.07	0.007**
30	1	4.47	0.07	0.014*

Test for each year was run separately, and a Bonferroni correction for seven tests was applied to final p-values. Species composition values were fourth-root transformed, and a reduced data set including only species with >5% cover in all years was used (total species = 65)

Year since eruption

df

Psuedo-F

R

Adj. p-value

* denotes significance at the 0.05 level and ** at the 0.01 level

In the similarity percentage analysis (Table 8.5), a total of 28 species, 19 native and 9 non-natives, were responsible for at least 50% of the divergence between seeded and unseeded plots over all sampled years. Among species contributing to differences, geophytes (perennial plants that resprout by means of underground bulbs, tubers, or corms) were the most abundant plant life form (14 total species), though annuals (5 species) were also important. Deciduous trees first appeared among the most abundant species in year 9 post eruption and increased in contribution from then onward. Only one species of hemicryptophyte (perennial plants with overwintering buds at soil level), *Hypochaeris radicata*, occurred frequently and was a large contributor in 5 of the 7 years it was present. For the first 14 years of the study, those species contributing to dissimilarity always occurred in higher abundance in the seeded plots. However, starting in year 20, some such species occurred in higher abundance in the unseeded plots (forbs *Lupinus lepidus*, *L. latifolius*, and *H. radicata* and deciduous shrubs *Salix sitchensis* and *Alnus viridis*). In year 30, *Alnus rubra* occurred in higher frequencies in the unseeded plots, even though it had occurred in higher abundance in the seeded plots in years 14–24 (Table 8.5). Among those species found in greater abundance only in the unseeded plots, all but *H. radicata* were native, but the sample size is small, so this is more likely to be random variation than a significant pattern. Also, a number of new forest understory species (e.g., *Claytonia sibirica* var. *sibirica*, *Rubus leucodermis*, and *Prunella vulgaris*) first explained community divergence in the plots in year 30, so there seems to have been a community shift toward closed-forest conditions between year 24 and 30. Overall, contribution of any one species to divergence declined over the course of the study.

Table 8.5

The results of the similarity percentage analysis on the species composition data from all years

Species	Contribution (%)	Origin	Life form
Year 2: average dissimilarity = 94.63			
<i>Senecio sylvaticus</i>	44.7	Non-native	A
<i>Anaphalis margaritacea</i>	13.1	Native	G
Year 3: average dissimilarity = 57.55			
<i>Epilobium brachycarpum</i>	8.1	Native	G
<i>Chamerion angustifolium</i> ssp. <i>angustifolium</i>	7.9	Native	G
<i>Senecio sylvaticus</i>	7.5	Non-native	A
<i>Epilobium glaberrimum</i>	7.4	Native	G
<i>Hypochaeris radicata</i>	7.3	Non-native	H
<i>Anaphalis margaritacea</i>	6.3	Native	G
<i>Abies procera</i>	6.0	Native	PE
Year 9: average dissimilarity = 76.49			
<i>Lotus unifoliolatus</i> var. <i>unifoliolatus</i>	24.1	Native	A
<i>Agrostis exarata</i>	7.2	Native	G

Species	Contribution (%)	Origin	Life form
<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>	5.7	Native	PD
<i>Agrostis pallens</i>	5.7	Native	G
<i>Anaphalis margaritacea</i>	5.3	Native	G
<i>Holcus lanatus</i>	4.7	Non-native	G
Year 14: average dissimilarity = 73.27			
<i>Lotus unifoliolatus</i> var. <i>unifoliolatus</i>	9.9	Native	A
<i>Holcus lanatus</i>	8.2	Non-native	G
<i>Aira caryophyllea</i>	7.9	Non-native	A
<i>Hypochaeris radicata</i>	7.8	Non-native	H
<i>Alnus rubra</i>	6.1	Native	PD
<i>Vulpia myuros</i>	5.2	Non-native	A
<i>Epilobium glaberrimum</i>	3.8	Native	G
<i>Salix scouleriana</i>	3.3	Native	PD
Year 20: average dissimilarity = 61.44			
<i>Holcus lanatus</i>	11.0	Non-native	G
<i>Alnus rubra</i>	10.4	Native	PD
<i>Lotus unifoliolatus</i> var. <i>unifoliolatus</i>	6.3	Native	A
<i>Trifolium repens</i>	5.0	Non-native	G
<i>Agrostis pallens</i>	4.3	Native	G
<i>Salix sitchensis</i>	4.0	Native	PD
<i>Lupinus lepidus</i>	4.0	Native	G
<i>Hypochaeris radicata</i>	3.7	Non-native	H
<i>Lupinus latifolius</i>	3.5	Native	G
Year 24: average dissimilarity = 59.73			
<i>Alnus rubra</i>	8.5	Native	PD
<i>Holcus lanatus</i>	7.2	Non-native	G
<i>Hypochaeris radicata</i>	5.0	Non-native	H
<i>Vulpia myuros</i>	4.3	Non-native	A
<i>Lupinus latifolius</i>	3.5	Native	G
<i>Alnus viridis</i> ssp. <i>sinuata</i>	3.4	Native	PD

Species	Contribution (%)	Origin	Life form
<i>Salix sitchensis</i>	3.2	Native	PD
<i>Lotus unifoliolatus</i> var. <i>unifoliolatus</i>	3.1	Native	A
<i>Lupinus lepidus</i>	3.0	Native	G
<i>Epilobium glaberrimum</i>	2.7	Native	G
<i>Anaphalis margaritacea</i>	2.5	Native	G
<i>Cytisus scoparius</i>	2.5	Non-native	S
<i>Digitalis purpurea</i>	2.5	Non-native	G
Year 30: average dissimilarity = 60.89			
<i>Epilobium glaberrimum</i>	7.1	Native	G
<i>Holcus lanatus</i>	6.7	Non-native	G
<i>Claytonia sibirica</i> var. <i>sibirica</i>	6.5	Native	A
<i>Hypochaeris radicata</i>	4.9	Non-native	H
<i>Rubus leucodermis</i>	4.9	Native	H
<i>Festuca rubra</i>	3.7	Native	G
<i>Cytisus scoparius</i>	3.4	Non-native	S
<i>Prunella vulgaris</i>	3.4	Native	G
<i>Rumex acetosella</i>	3.1	Non-native	G
<i>Trifolium repens</i>	3.0	Non-native	G
<i>Lupinus latifolius</i>	2.8	Native	G
<i>Alnus rubra</i>	2.8	Native	PD

Species explained up to 50% of the observed difference were included. Other information not included in the test but relevant to the reported species was included as well

Species in **boldface** occurred at higher abundances in unseeded plots

Origin, non-native or native; and life form: *G* geophytes, plants with buds below ground, *H* hemicryptophytes, plants with buds 0–50 cm above soil surface, *A* annual, *PE* phanerophyte, evergreen tree, *PD* phanerophyte, deciduous tree, *S* shrub

AQ4

8.3.3. Tree-Count Analysis and Canopy Cover

Total stem density of tree species increased through time in all years except year 14, but stem counts were not different in seeded versus unseeded plots ($p = 0.69$) (Fig. 8.11). *Alnus rubra* made up the largest fraction of stems counted in most years: year 2 (21%), 3 (1%), 9 (78%), 14 (59%), 20 (91%), 24 (89%), and 30 (92%). Additionally, no difference was found in tree species composition between the seeded and unseeded plots in any

year ($p > 0.12$) (Table 8.6). Overstory canopy cover was examined only in years 24 and 30. Values did not differ between the seeded and unseeded plots ($p = 0.53$), and mean canopy density was 27%.

Fig. 8.11

Stem density counts of trees in seeded (*solid line*) and unseeded (*dashed line*) plots. *Error bars* are standard error

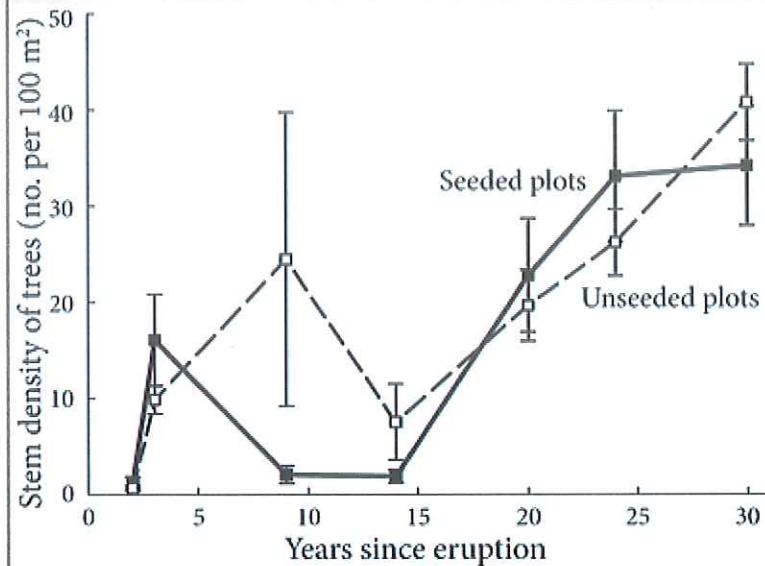


Table 8.6

PERMANOVA analysis of tree-stem counts in seeded vs unseeded plots

Year since eruption	df	Pseudo-F	R ²	Adj. p-value
2	1	0.46	0.01	1
3	1	0.82	0.01	1
9	1	2.03	0.03	0.91
14	1	3.49	0.06	0.12
20	1	2.51	0.04	0.34
24	1	2.96	0.05	0.2
30	1	1.72	0.03	1

Test for each year was run separately, and a Bonferroni correction for seven tests was applied to final p-values. Tree-count values were log-10 transformed before analysis to account for zeros. Data were not reduced to species with <5% occurrence as only 14 tree species were found

8.4. Discussion and Conclusions

Thirty years after the eruption of MSH, the debris-avalanche deposit has undergone extensive vegetation development. This study sought to determine whether initial differences seen in the trajectory of vegetation

establishment have persisted, comparing areas that were seeded with a largely non-native plant mix in 1980 with areas that were left to undergo natural primary succession, or if these differences are likely to continue into the future.

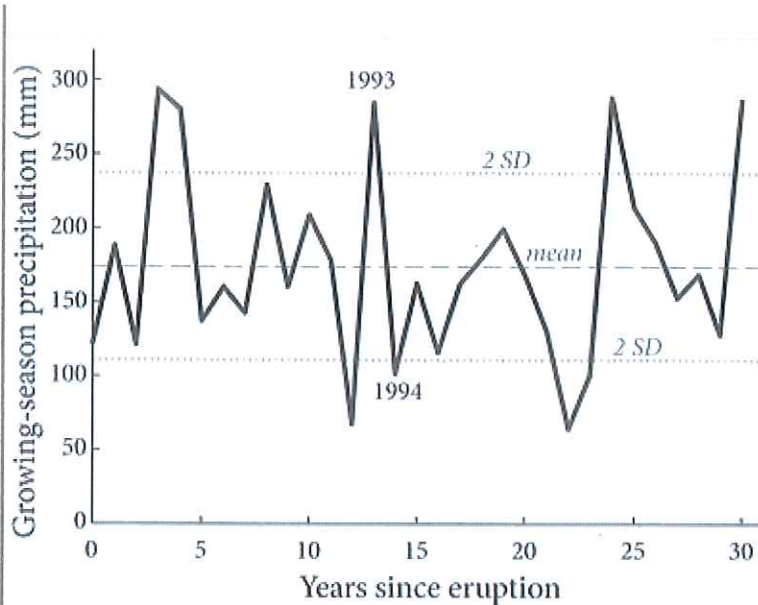
Total species richness on the debris-avalanche deposit increased in the 30 years since the eruption and continues to increase, as is expected for primary succession in the northwestern United States (Lichter 1998). However, cover of herbaceous vegetation plateaued at around 50% after year 20 (Fig. 8.5, inset). In future years, ground cover may even decrease as the overstory canopy closes (Halpern and Lutz 2013), altering the light regime and leading to a reduction in abundance of shade-intolerant species. The dominance of early-seral species has declined with time. Year 30 appears to have been a transition year, with species that are found in forest understories (*Claytonia sibirica* var. *sibirica*, *Rubus leucodermis*, and *Prunella vulgaris*) becoming drivers of community divergence for the first time.

Ecological effects of several volcanic debris-avalanche deposits have been studied at a number of other volcanoes—Mt. Taranaki in New Zealand (Clarkson 1990), Ksudach in Russia (Grishin et al. 1998), the Ontake volcano in Japan (Nakashizuka et al. 1993), and Mount Katmai in the state of Alaska in the United States (Griggs 1918a, b, c, 1919). However, plant recovery has not been followed at any of those sites over the decades subsequent to the initial deposit. The very few non-native species in the flora of Katmai make up only 2% of total richness a century after its eruption (<https://www.nps.gov/katm/learn/nature/parkspecieslists.htm>). In contrast, on the MSH debris-avalanche deposit 30 years post eruption, non-natives make up 27% of total species richness (Fig. 8.10) and 50% of total cover (Fig. 8.8).

The aerial distribution of largely non-native seeds on a subset of plots at MSH in 1980 has had a pronounced and enduring effect on subsequent vegetation communities. The trajectory of both cover and species richness in the seeded and unseeded plots appears similar; however, total values differ. Cover and richness were higher in seeded plots throughout the entire period of this study (Fig. 8.5). Interestingly, this pattern does not seem to be driven only by higher abundance of species from the original seeding mix, as both native and non-native species had higher cover in the seeded plots (Fig. 8.7). Furthermore, seeded species never contributed more than 5% to the total cover in the seeded plots (Fig. 8.8, inset). The community analysis supports the assumption that the seeded species may not be the direct cause of the observed differences between the seeded and unseeded plots. Only two species from the original mix, *Trifolium repens* and *Festuca rubra*, are among the top contributors to community divergence (in years 20 and 30), even though ground-cover vegetation communities differed between treatments in all years. However, the presence of those seeded species may have facilitated the establishment of other non-native species, for example, by providing vegetative cover and shade. If the seeded species are not driving the community differences, it is unclear what else might be causing community divergence. Certainly there is a strong difference in the cover of non-native species in the seeded plots after 1994, but why non-native species should have increased there and not in the unseeded plots is unclear (Fig. 8.7b). At first glance, it seems tempting to conclude that the anomalous increase in cover is a response to climatic conditions, as the summer of 1993 was considerably wetter than average (Fig. 8.12), which can result in an increased production legacy (Sala et al. 2012). However, it is puzzling that only non-native plant cover in seeded plots would respond in this fashion, since weather events should affect all plots similarly. Certainly, MSH has a higher percentage of non-native species than the Pacific Northwest in general. Of the 107 species of non-native plants reported to occur in Cowlitz County, Washington (Washington Native Plant Society 2006), 40 have been found on the debris-avalanche deposit since the eruption, and 16 species of non-native plants have apparently arrived from outside the county. As compared to native species, non-native species have been arriving at a nearly constant rate and have made up 20–30% of the richness on the debris-avalanche deposit in the 30 years since the eruption, a high proportion for the Pacific Northwest. Non-native species represent about 12% of overall species richness in forests across the region, though non-natives often make up a large amount of total cover (Stapanian et al. 1998) as is also the case at MSH, particularly in the seeded plots (Fig. 8.7).

Fig. 8.12

Precipitation during the growing season (1 May to 31 August) from the weather station at Longview, Washington



Seeding by the SCS in 1980 was based on the assumption that there would be no effect other than short-term increases in plant cover, which would result in reduced erosion. At the time, little research had been done to suggest otherwise. Because erosion from the seeded and unseeded plots was not measured, it is difficult to say whether seeding achieved its desired goal. None of the original 11 seeded plots were lost to erosion, but a number of the original 90 unseeded plots were. However, there were many more unseeded plots, and some were in the path of stream channels that eroded over time. Certainly erosion from the entire debris-avalanche deposit remained high, two orders of magnitude above background levels in the Pacific Northwest (Major et al. 2000) 20 years post eruption. Seeding after other types of disturbance has not been found to consistently reduce erosion. Post-wildfire seedings in rangelands had little effect on erosion during the first year after fire, and when they did it was only in years of high establishment (Pyke et al. 2013). Whether or not seeding achieved the stated goal of reduced erosion, the differences in cover, species richness, and community composition on the seeded versus unseeded plots continue to persist after three decades.

At least one previous study in Washington state examining plant communities and comparing erosion after seeding treatments found differences that persisted for decades, though successful soil stabilization occurred only if the seeding treatments were combined with straw and clay (Cline and Uresk 1979), which was not done at MSH. Furthermore, the Cline and Uresk (1979) study seeded a well-known invasive, cheatgrass (*Bromus tectorum*). Although seeding with an invasive species might be expected to produce effects that last for decades, the record from MSH demonstrates that even seeding treatments of more benign species may produce long-lasting community effects.

The difference between the seeded and unseeded areas seems unlikely to continue indefinitely. It is expected that the plant community on the debris-avalanche deposit will eventually develop into a forest typical of the Pacific Northwest (Franklin and Dyrness 1973). Results from the present study may provide evidence that this transition is already happening. Thirty years post eruption, herbaceous communities continue to differ between seeded and unseeded plots, but seeding explains a smaller percentage of the difference seen than in previous years, only 7% 30 years post eruption as compared with a maximum of 15% in year 14. Further, trees, which will presumably become the future overstory, do not differ between seeded and unseeded plots in either stem density, species composition, or canopy cover in any year in which these metrics were sampled (Table 8.6). This finding is fascinating, in part, because earlier in succession conifer tree seedling mortality was found to be higher in the seeded plots (Dale 1991), yet that result does not seem to have had a lasting effect on the developing tree community. It should be noted that the present tree community is largely red alder (92% of all tree stems counted in year 30), not species associated with the conifer forest that is expected to eventually dominate the area.

Resource managers dealing with the pressure to establish vegetation and reduce erosion in disturbed areas are often “hamstrung by resource shortages” and consider the use of non-native seed species (Kuebbing and Simberloff 2015). Proactive management should focus on realistic short-term and long-term costs and benefits of management options. After a large disturbance, funds are often available to “fix” the problem rather than to realistically deal with the new ecosystem properties (Dale et al. 1998). Furthermore, the rarity of benefits provided by non-native species (Kuebbing and Nuñez 2015) means that those species with potential for positive effects should be identified upfront. Kuebbing and Nuñez (2015) note that positive interactions are less frequent with grasses and herbs and more common with nitrogen-fixing species and tree species. Even though nitrogen fixers were included in the mix of seeds distributed in the aftermath of the eruption of MSH, no native tree species were considered. In 1980, the first author suggested to the SCS that the native red alder (*Alnus rubra*) be considered in the mix of species seeded at MSH, as it is both a tree and a nitrogen fixer, but the SCS lamented that no seeds were available. This study revealed that red alder was a major contributor to community divergence between years 14 and 30 at MSH and the most abundant tree in most years, a finding that is in line with earlier results from this system (Dale et al. 2005a).

Few studies using permanent plots over several decades exist that evaluate the effects of management choices on forest succession (Dale et al. 2005d; Kirby et al. 2014), and those that do mostly examine succession after logging or fire (see Halpern and Spies 1995). Thus, this study of vegetation succession at MSH over the last 30 years is a unique contribution. Although these results are of interest to the study of plant succession, they also have implications for resource management and response in the face of large disturbances. In spite of the US\$2 million spent on seeding, major erosion still occurred (Major et al. 2000), and effects of the seeding on vegetation cover and plant richness are still apparent after three decades. Even so, our findings suggest that the first forest to develop will show no difference between seeded and unseeded areas.

Acknowledgments

Logistic support was provided by the USDA Forest Service, the Washington State Department of Natural Resources, and Weyerhaeuser Company. Over the 30 years of the study, the fieldwork was conducted with the assistance of A.B. Adams, Wendy Adams, Charlie Crisafulli, Ginny Dains, D. Donohue, Margaret Evans, Howard Haemmaerle, Brad Hensley, Charlie Hensley, Asa Holland, Robert Holland, Keith Kline, Jasmine Kuliashi, Ian Kulaishi, Bridgette Nyberg, Eric Smith, Mandy Tu, and John Wallace. Over the years of this study, the research was partially funded by the National Science Foundation, the National Geographic Society, Earthwatch, and The Center for Field Research of Belmont, Massachusetts. The University of Washington Herbarium was used to verify plant species identifications. Statisticians from Colorado State University helped with the analysis: Phil Turk advised on PERMANOVA and James R. zumBrunnen advised on the repeated measures analysis. Comments of Charlie Crisafulli and two anonymous reviewers on an earlier draft were helpful. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US Department of Energy under contract DE-AC05-00OR22725.

References

- Adams, V.D., and A.B. Adams. 1982. Initial recovery of the vegetation on Mount St. Helens. In *Mount St. Helens: One year later*, ed. S.A.C. Keller, 105–113. Cheney: Eastern Washington University Press.
- Adams, A.B., and V.H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain Range of Washington, U.S.A. In *Mount St. Helens 1980: Botanical consequences of the explosive eruption*, ed. D.E. Bilderback, 70–147. Los Angeles: University of California Press.
- Adams, A.B., J.R. Wallace, J.T. Jones, and W.K. McElroy. 1986. Plant ecosystem resilience following the 1980 eruptions of Mount St. Helens, Washington. In *Mount St. Helens: Five years later*, ed. S.A.C. Keller, 182–207. Cheney: Eastern Washington University Press.

- Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Ares, A., S.D. Berryman, and K.J. Puettmann. 2009. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. *Applied Vegetation Science* 12: 472–487.
- Banks, N.G., and R.P. Hoblitt. 1981. Summary of temperature studies of 1980 deposits. In *The 1980 eruptions of Mount St. Helens, Washington*, Professional Paper 1250, ed. P.W. Lipman and D.R. Mullineaux, 295–314. Washington, DC: U.S. Geological Survey.
- Bråkenhielm, S., and L. Qinghong. 1995. Comparison of field methods in vegetation monitoring. *Water, Air, and Soil Pollution* 79: 75–87.
- Bray, J.R., and J.T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Clarkson, B.D. 1990. A review of vegetation development following recent (<450 years) volcanic disturbance in North Island, New Zealand. *New Zealand Journal of Ecology* 14: 59–71.
- Cline, J.F., and V.A. Uresk. 1979. Revegetation of disturbed grounds in the semi-arid climate of southcentral Washington. *Health Physics* 36: 289–294.
- Dale, V.H. 1986. Plant recovery on the debris avalanche at Mount St. Helens. In *Mount St. Helens: Five years later*, ed. S.A.C. Keller, 208–214. Cheney: Eastern Washington University Press.
- . 1989. Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Canadian Journal of Botany* 67: 1434–1441.
- . 1991. The debris avalanche at Mount St. Helens: Vegetation establishment in the ten years since the eruption. *National Geographic Research and Exploration* 7: 328–341.
- Dale, V.H., and W. Adams. 2003. Plant establishment fifteen years after the debris avalanche at Mount St. Helens, Washington. *Science of the Total Environment* 313: 101–113.
- Dale, V.H., A. Lugo, J. MacMahon, and S. Pickett. 1998. Ecosystem management in the context of large, infrequent disturbances. *Ecosystems* 1: 546–557.
- Dale, V.H., D.R. Campbell, W.M. Adams, C.M. Crisafulli, V. Dains, P.M. Frenzen, and R. Holland. 2005a. Plant succession on the Mount St. Helens debris-avalanche deposit. In *Ecological responses to the 1980 eruption of Mount St. Helens*, ed. V.H. Dale, F.J. Swanson, and C.M. Crisafulli, 59–74. New York: Springer.
- Dale, V.H., J. Delgado-Acevedo, and J. MacMahon. 2005b. Effects of modern volcanic eruptions on vegetation. In *Volcanoes and the environment*, ed. J. Marti and G.G.J. Ernst, 227–249. Cambridge: Cambridge University Press.
- Dale, V.H., F.J. Swanson, and C.M. Crisafulli. 2005c. Ecological perspectives on environmental management following the 1980 eruption of Mount St. Helens. In *Ecological responses to the 1980 eruption of Mount St. Helens*, ed. V.H. Dale, F.J. Swanson, and C.M. Crisafulli, 277–286. New York: Springer.
- . 2005d. Disturbance, survival, and succession: Context for understanding ecological responses to the 1980 eruption of Mount St. Helens. In *Ecological responses to the 1980 eruption of Mount St. Helens*, ed. V.H. Dale, F.J. Swanson, and C.M. Crisafulli, 3–12. New York: Springer.