Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche

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Received June 17, 1988


Seed dispersal and plant establishment were monitored for 4 years on the debris avalanche created by the 1980 eruption of Mount St. Helens. The number of plants on the deposit increased over time to a high of almost 2 plants/m² by 1983. The number of species per 250-m² plot has increased to a mean of 10.3 in 1983 with 76 species being present over the entire deposit. Four years after the eruption only 30% of the species present before the eruption had reestablished themselves, and average plant cover was less than 1%. The debris avalanche has been invaded primarily via wind-dispersed seed of early successional species that survived or have become established in adjacent disturbed areas. Most of the early successional species on the avalanche have plumed seeds that are adapted not only for long distance dispersal, but also for being trapped in wet areas or by spider webs. Fluctuations in the density of seeds dispersed to the deposit were related to variation in precipitation. Neither seed abundance nor plant density correlated with absolute distance to a seed source or soil texture conditions. Colonization patterns are more influenced by the available biota and prevailing climate conditions than by substrate alterations resulting from the eruption.


La dissémination des graines et l’établissement des plantes ont été suivis pendant 4 ans sur l’avalanche de débris créée par l’éruption de 1980 du Mont Ste-Hélène. Le nombre de plantes sur le dépôt a augmenté avec le temps pour atteindre 2 plantes/m² en 1983. Le nombre d’espèces par parcelle de 250 m² a augmenté pour atteindre une moyenne de 10,3 en 1983 avec la présence de 76 espèces partout sur le dépôt. Quatre ans après l’éruption, seulement 30% des espèces présentes avant l’éruption s’étaient rétablies et le couvert végétal moyen était moins que 1%. L’avalanche de débris a été envahie principalement par des graines dispersées par le vent, d’espèces pionnières qui avaient survécu ou qui étaient établies dans les régions perturbées voisines. La plupart des espèces pionnières sur l’avalanche ont des graines aigretées adaptées non seulement pour la dispersion à longue distance, mais aussi pour être attrapées dans des régions humides ou par des toiles d’araignée. Les fluctuations dans la densité des graines dispersées vers le dépôt étaient en relation avec les variations de précipitation. L’abondance des graines, de même que la densité végétale étaient en corrélation ni avec la distance absolue vers une source de graine ni avec les conditions de la texture du sol. Les patrons de colonisation sont plus influencés par le biote disponible et les conditions climatiques courantes que par les altérations du substrat dues à l’éruption.

Introduction

Plant recovery following devastation of an area is from seeds that are transported into the denuded area. The fate of seeds depends on the characteristics of seeds that are transported, conditions under which seeds come to rest, and the relationship between temporary and final seed resting sites. Successful plant establishment depends on species physiology, competition, and local physical and microclimate conditions. Together, differential seed availability and differential seedling performance are the critical factors determining species composition during early succession (Pickett et al. 1987a, 1987b). Differentiating between the influence of seed availability and seedling performance is difficult.

The debris avalanche resulting from the 1980 eruption of Mount St. Helens offers a unique opportunity to examine patterns of plant colonization. Sixty square kilometres on the North Fork of the Toutle River were cleared of vegetation by the massive landslide during the eruption that created the debris avalanche. Because it is now within the Mount St. Helens National Monument, the debris avalanche will be protected from major human intervention.

Previous studies of dispersal have concentrated on either short distances, usually proximal to the parent plant (Issac 1930; Cremer 1969; Poole and Cairns 1940; Harper 1977), or very long distance transport of seeds (e.g., Carquist 1966). This study examines dispersal of an intermediate distance from 0.1 to greater than 1.1 km from the parent plant. Intermediate-distance dispersal is important not only for recovery from large scale or devastating disturbances, but also has implications for patterns of plant migration.

To obtain information on the most critical factors affecting plant establishment, a variety of observations and experiments were done on the Mount St. Helens debris avalanche. The objective was to monitor early stages of succession and to characterize the major biological and physical properties affecting colonization. Permanent plots were established to monitor plant colonization in relation to time, soil texture, and distance from a seed source. The seed deposition was monitored within each plot for 4 years, and the seed characteristics of major species were examined. Experimental microtopographic conditions were established in which rates of seed deposition and seedling establishment were monitored.

Study area

Pre-eruption conditions
Mount St. Helens is an active volcano in southwest Washington. Before 1980 the 2950-m mountain was surrounded by a patchwork of forested and clear-cut land in varying stages of reforestation. The forests were typical of the Abies amabilis zone (Franklin and Dymess 1973), being composed primarily of Abies amabilis Doug. ex Forbes, A. procera Rehd., Pseudotsuga menziesii (Mirb.) Franco, and Tsuga heterophylla (Raf.) Sarg (Lawrence 1938). Clear-cut land had been replanted with Pseudotsuga seedlings and had a lush cover dominated by herbs (e.g., Epilobium angustifolium L. and Anaphalis...
margaritacea (L.) B. & H.) and shrubs (e.g., Acer circinatum ref, Rubus ursinus Cham. & Schlecht.). The riparian vegetation along the Toutle River comprised primarily deciduous trees (Alnus rubra Bong., Populus trichocarpa T. & G., Salix scouleriana Barratt, and S. stenensis Sanson).

**Conditions created by the 1980 eruption**

The 1980 eruption of Mount St. Helens created a variety of disturbances: a 0.25-km² pyroclastic flow north into Spirit Lake, a 550-km² area of blown-down trees bordered by 96 km² of scorched trees, a 60 km² debris avalanche, and massive mudflows down the major streams draining the area (Lipman and Mullineaux 1981) (Fig. 1). Most of the area was covered by layers of tephra (airborne material from the volcano that was primarily sand-sized particles). Each of the disturbances caused by the eruption resulted in a different pattern of surviving plants (Adams and Adams 1982; Adams et al. 1987).

The debris avalanche was formed by the massive landslide of the north flank of the mountain. The material from the crater averages 45 m in depth, 2 km in breadth, and extends 25 km from the crater along the North Fork of the Toutle River (Voight et al. 1981). It comprises a diverse array of surface configurations. Expanses of flat sandy areas merge into boulder fields or areas with large mounds. Erosion has greatly altered parts of the debris surface (Lehre et al. 1983). A March 1982 mudflow inundated parts of the debris avalanche.

Few seeds or plants (<0.001/m²) survived the landslide that created the debris avalanche in 1980 (Adams and Adams 1982), but rare individuals of at least 20 species survived on the debris deposit with Epilobium angustifolium, Cirsium arvense, and Lupinus latifolius Agardh being the most common species (Dale 1986). The plants apparently grew from plant fragments that had been transported by the debris slide (Dale 1986). The most common surviving trees were Salix spp. (which also readily regenerate from pieces of roots or stems) that were found primarily in the western portion of the avalanche and farthest from the crater.

Primary seed sources for the debris deposit are three areas nearby that were less disturbed by the eruption. On the blowndown and scorched slopes above the deposit, these herbaceous perennials which have light, plumed seeds survived on sites that had been clear-cut prior to the eruption (Franklin et al. 1985). On the mudflows along the Toutle River, tree survival was high enough that plant cover averaged 25% in the summer of 1980, and rapid colonization of Alnus rubra and other riparian vegetation has occurred (Adams et al. 1987). On the undisturbed slopes above the South Fork of the Toutle River, the forest vegetation was not significantly impacted by the eruption.

Soil characteristics of the debris avalanche greatly influence the ability of a plant to grow. The debris avalanche has an adequate balance between moisture retention and aeration properties (Adams and Dale 1987); pH values averaged 4.7, percent organic matter is low but adequate for plant growth, particle size analyses for soil
fractions less than 2 mm demonstrate that all samples from the debris deposit are sand or silty sand, and the greater than 2-mm fractions comprise about 65% of the samples.

**Methods**

**Permanent plots**

Permanent plots were established along two transects on the debris avalanche: one running north-south between Castle and Coldwater lakes and the other running east-west (Fig. 1). Since the avalanche was only accessible by helicopter until 1982, there were logistic difficulties in establishing permanent plots. The area north of Castle Lake was first surveyed in July 1980. In August 1981, 31 250-m² circular plots were placed at regular 50-m intervals on a transect between Castle and Coldwater lakes; the center and four radii were marked and numbered, and any plants seen were marked with a stake. In June 1982 when the area was finally accessible by road, an additional 72 plots were established on a transect running east to west on the debris avalanche. All plants in each plot were identified and counted at regular intervals (September 1981; June, July, August, September, and October 1982; and September 1983). The frequent measurements in 1982 were taken to identify temporal variability during one growing season. In particular, one objective was to identify the time of the greatest seed deposition to ensure yearly collections of seeds were timed correctly. In June 1985 percent cover was estimated for each plot, and each tree taller than 5 cm was measured.

The soil texture of each 250-m² plot was assessed in August 1982 to relate the diversity in surface structure with plant establishment. Field estimates were made of the percent surface area comprising boulders, cobbles and gravel, sand, silt, and clay. The general topography of each plot was mapped.

**Seed data**

Sticky seed traps were placed in the center of each circular plot to monitor wind-dispersed propagules. The 0.25-m² traps were made of cheesecloth spread with grease, stapled to a wooden frame 0.25 m off the ground, and placed vertically facing the prevailing winds out of the southwest. Trials had demonstrated that heavy seeds (corn kernels) were trapped and retained on the sticky traps. In 1980 four traps were placed near Castle Lake (the site on the debris avalanche closest to abundant surviving downwind vegetation in the blow-down area). In August 1981, traps were placed in the 31 vegetation plots between Castle and Coldwater lakes. In 1982, 72 additional traps were added on the transect running east-west on the debris slide. The sticky cheesecloth was left in place 10–25 days and then removed. Seeds were counted and identified using a magnifying lens by comparing unknown seeds to seeds collected from intact plants in the blow-down area. In 1980 and 1981, all seeds were enumerated. In 1982 and 1983, due to the large number of seeds, the traps were subsampled by identifying all seeds in two randomly distributed 100-cm² portions of each side of each trap to estimate the total number of seeds per trap. The achene and plume diameters of seeds of the most common species, Epilobium angustifolium and Senecio sylvaticus L., were measured from seeds collected in the vicinity of Mount St. Helens as well as from seeds on pressed specimens of plants collected from southwest Washington and stored at the University of Washington Herbarium.

In 1982 horizontal seed traps framed by 0.3 x 0.6 m wooden strips and underlain with wire mesh were placed on the ground in an attempt to catch some of the heavy seeds that may be missed by the sticky seed traps. These traps did not catch any seeds, either because of the paucity of heavy seeds or because of the ineffectiveness of this type of trap (Johnson and West 1988). However, heavy seeds were trapped on the ground in the microtopography experiments described below.

**Microtopography experiments**

A "mound–depression" experiment was designed to assess the role of microtopography on seed settlement and germination. The treatments consisted of two controls, a rough mound, a smooth mound, a rough depression, and a smooth depression. Depressions were created by digging a hole 20 cm deep, and the material removed was formed into a mound. One of each pair of mounds and depressions was hand smoothed and the other left rough. The controls were not manipulated other than marking the corners with galvanized nails. All treatments were 0.25-m² squares oriented randomly and placed at a 1.5-m distance from each other. One set of the six treatments was set up in a homogeneous spot close to 60 of the plots running east to west across the avalanche. The experiment was set up in June 1982 and measured in August and September 1982, and September 1983. Measurement consisted of enumerating and identifying all seeds and seedlings in each of the treatments for all plots. No material was removed. To test for the effects of microtopography on seed settling and seedling establishment, analysis of variance was performed on the number of seeds and seedlings considering differences due to treatment, date of measurement, and plots.

**Results**

**Plant establishment and seed dispersal**

In 1980, the only recolonization observed on the debris deposit was six seedlings of Epilobium angustifolium which were located in one of 12 250-m² plots examined. Also in 1980, Epilobium was the most common genus of seed being dispersed, comprising 87% of the seed trapped in sites adjacent to the blow-down area where large numbers of plants survived.

Over the four growing seasons since the eruption, the number of plants in the permanent plots increased (Fig. 2A). From September 1982 to September 1983 there was an increase from 66 to 494 per 250-m² plot, and even then the average cover of the plots was still less than 1% by June 1985, although some plots had as much as 30% plant cover. There was no significant increase in the number of plants per plot.
The number of species per plot and on the entire deposit increased monotonically over the four growing seasons since the eruption (Fig. 2B). There was no significant establishment of species during the winter of 1981—1982, but a significant increase in number of plant species occurred during the summer of 1982. By September 1983, 76 species or 30% of the 256 species in the vicinity before the eruption (St. John 1976) had recolonized the debris deposit. St John’s (1976) species list includes species from a larger area than the debris avalanche, but it is not clear which species to exclude from the list for the comparison. For example, *Lupinus lepidus* Dougl., *var lobbii* (Gray) Hitch. is normally thought of as a subalpine species but was present on the debris avalanche at elevations of about 580 m.

There were large fluctuations in the seed deposition over the four growing seasons (Figs. 2C, 3). The number of seeds trapped during September 1982 as compared with that of other collection times during 1982 confirms that September is the time of most abundant seed production in vicinity of Mount St. Helens. When the different years are compared, more seeds were dispersed onto the debris avalanche during September of 1982.

Neither the plant density nor the number of seeds present on the debris avalanche depended on the nearest distance to the seed source of the surviving vegetation (Fig. 3). Although there is a general decrease in the number of seeds with distance up to distances greater than 1.1 km, the abundance of seeds could not be predicted by the distance from surviving vegetation. Many seeds were trapped at sites intermediate in distance from the surviving vegetation. In 1983 there was an increase in the proportion of seeds transported greater than 1.1 km. The similarity in physical characteristics of the trapped seeds indicates the importance of wind as the prime mechanism of seed transport. Most seeds trapped throughout the 4-year period were small, light, and plumed. For example, in August 1981 *Epilobium angustifolium*, *Salix* spp., *Carex* spp., and *Cirsium arvense* accounted for 92% of the seeds in the sticky traps (Table 1).

Some plants with heavy, winged seeds have been recruited onto the debris surface even though all of the seeds collected on the sticky seed traps and most from the depression mounds experiments were plumed. Conifer seedlings were found at a density of 3/ha in September 1981 and 4.5/ha in the summer of 1982 even though many seedlings were washed away by mudslides during the winter of 1981—1982. These rare trees may be important to the recovery process due to their longevity (up to 1000 years for *Pseudotsuga menzeisii*) and future contribution as a potential seed source. On a survey of the area in August 1988, a few *Pinus contorta* seedlings were found on the debris avalanche west of Castle Lake where the seeds could have been transported from the surviving vegetation on the slopes above the South Fork of the Toutle River.

Surface soil texture characteristics did not have a significant influence on either the number of seeds or plants established (Fig. 4). Both seeds and plants occurred over a wide range of textural conditions ranging from areas that were predominately boulders to substrates composed of gravel, sand, silt, and clay. Although local topographic conditions might have been expected to affect wind patterns and thus seed occurrence, it is likely that more than one factor was responsible for the presence of plants under different textural conditions. For example, many of the sites that had a preponderance of gravel, sand, and clay were also in seepage areas that remained wet during the summers.

Many seedlings were found in plots with abundant soil moisture. In the summer of 1981, the main channel of the North Fork of the Toutle River had not defined itself, and quicksand occurred where ground water was close to the surface. These areas have gradually dried out over the ensuing four growing seasons, but the plants that established in these wet areas persisted even after these areas dried out. *Epilobium*
of timing, plot location, and substrate conditions for seed and microtopography experiments

**angusfolium**, Salix spp., and Equisetum sp. were particularly abundant in the wet areas.

**Microtopography experiments**

The mound—depression experiment showed the importance of timing, plot location, and substrate conditions for seed and seedling establishment (Table 2). Significant interactions were also evident between all three factors. The rough depressions had the greatest number of seeds. Fewest seeds were found in mounds. With abundant moisture, plants in the blown-down area produced many seeds that were transported to the debris deposit. The number of seeds invading the debris avalanche does not follow a linear relationship to distance from surviving vegetation as is often found in island biogeography studies (e.g., Diamond 1974). Instead, seed dispersal is largely influenced by prevailing winds from either the adjacent blown-down and scorch areas or the Toutle River valley. Many of the species surviving in those areas have seed characteristics appropriate for wind dispersal to the adjacent debris deposit.

Most of the seeds dispersed to the deposit had plumes and were transported by the wind. Seed dispersal distance increases as the ratio of plume to achene diameter increases due to a reduction in the resistance coefficient and an increase in terminal velocity Burrows (1973). A comparison of the aerodynamic properties of the four most abundant species in the seed traps in 1981 (Table 1) shows that Epilobium angustifolium has the ability to be dispersed farthest in constant winds and has contributed most to the seed deposition.

Plumed seeds are also adapted for selecting sites with adequate moisture because humidity reduces plume diameter (Burrows 1973). In open habitats ungerminated seeds can be picked up from their initial settling sites by turbulent winds and eventually trapped in rills, mounds, depressions, or seeps (Ridley 1930). I observed that seeds would land on the smooth surfaces of the deposit, be picked up by the wind, and blown just above the ground level, but would abruptly drop out of the wind currents when above a wet area. Sheldon and Burrows (1973) have shown that increases in relative humidity cause closure of the plume which reduces the resistance coefficient so that the seed cannot be held aloft. Thus, soil moisture influences not only successful germination and establishment, but also the probability of seeds dropping out of the wind.

Patterns of vegetation recovery following other types of disturbances in the Pacific Northwest are different from those on the debris avalanche largely because of the influence of surviving plants. For example, vegetation cover exceeds 60% as
quickly as 5 years after logging or burning of old-growth Douglas-fir forests, largely due to the regrowth of residual plants (Dymess 1973). In contrast, plant cover on the avalanche averaged less than 1% 5 years after the eruption. As another example, plant recovery on the Kautz Creek mudflow at Mount Rainier was influenced by the short-term survival of large trees (Frehner 1957; Frenzen et al. 1988) because seedlings grew in the shade of the trees. The few plants that survived on the debris deposit made little contribution to biomass, cover, or the seed deposition even 5 years after the eruption.

The avalanche deposit is not expected to have vegetation such as that at Goat Marsh on the south side of Mount St. Helens (Franklin and Wiberg 1979) where 400-year-old pyroclastic deposits are now dominated by small *Pinus contorta* with an understory of *Arctostaphylos* spp. Thus far, no *P. contorta* seed and few seedlings have been seen on the deposit, although the seeds are small and winged, a seed source is only a few kilometres away, and greenhouse studies demonstrate that they can grow on the debris substrate (Adams and Dale 1987). The rarity of *P. contorta* may be because the prime seed source for the deposit is from downstream vegetation rather than from ridges where *P. contorta* are located.

The mound—depression experiment shows that microtopography influences on plant establishment can be overridden by biotic factors. Spider webs effectively trap plumed seeds on the mounds and probably alter microclimate conditions so the sites are more favorable for seedling establishment. The mound—depression experiment suggests that web building by spiders on mounds is a major factor contributing to successful seedling establishment. Also, mounds built by pocket gophers (*Thomomys talpoides*) may indirectly influence seedling establishment. Gopher mounds were observed on the debris avalanche in June 1985 (personal observation). Mounds created by gopher activity may provide a surface area for spiders to build their webs and thus increase the rate of seedling establishment. Andersen and MacMahon (1985) surmise that the mounds created by pocket gophers on the tephra deposits of Mount St. Helens have higher seedling establishment rates than surrounding areas because the burrowing of the gophers mixes the underlying mineral soil with tephra. My results suggest that the gopher mounds may be sites for the establishment of spider webs on the debris avalanche and elsewhere. Gophers cannot reach the mineral soil on the debris avalanche because it averages 45 m deep.

Succession is a complex expression of species characteristics in relation to prevailing ecosystem properties and deficiencies (McIntosh 1979). In addition to dispersal ability, species that have successfully invaded the avalanche have the ability to proliferate in size or number under existing conditions, (ii) alter physical conditions, or (iii) both. Species can be assigned to one of the three categories listed above although the groupings are not discrete.

An example of the first category is *Senecio sylvaticus*, the most numerous plant on the debris deposit, yet a plant that has little total biomass because of its small size. *Senecio sylvaticus* will probably not contribute to the successional process after a few years as demonstrated by experiments following clear-cutting in the western Cascade (West and Chilcote 1968; Dymess 1973).

*Lupinus latifolius* is in the second category because it alters...
the local soil moisture conditions by shading, and alters soil nutrient status by nitrogen fixation. It produces a few, heavy seeds that are transported primarily by water within a few metres of the parent plant. Thus *Lupinus* is locally important, but it contributes to the successional development at only a few sites.

*A. rubra* exemplifies the third category because it both alters environmental conditions and is large and becoming abundant on the deposit. No *A. rubra* seeds were trapped and few seedlings colonized the plots (one plant in the 103 plots in 1981 and five in 1982). However, 21 *A. rubra* taller than 0.5 m (the tallest being 4.2 m) were found outside the plot in the debris avalanche in June 1985, and by 1988 the alder were taller than 6 m and producing seed. Alder are likely to become very abundant on the debris deposit for seven reasons. (i) Alders germinate and grow rapidly on the debris soil (Adams and Dale 1987). (ii) Alder saplings have the greatest height increment growing in debris soil for both very wet and very dry conditions as compared with eight other tree species (Adams et al. 1986; Russell 1986). (iii) Alder saplings have a high survival rate (>80%) (Russell 1986). (iv) Alder produces many seeds from plants as young as 3 years old (Fowell 1965). (v) Alder are abundant on the Toutle River mudflow directly downstream of the avalanche (Russell 1986). (vi) Elk and insect damage only slightly reduces tree growth whereas conifers are severely affected (Russell 1986). (vii) Alder stimulates soil moisture and nutrient properties by its size and ability to fix nitrogen (Trappe et al. 1968). It is this third category of species that has the most significant and long-term impact on succession because it contributes to both present and long-term conditions.

An understanding of the importance of native species to long-term succession is important for environmental managers who need to alter or speed up successional pathways. For instance, federal agencies spent more than one million dollars on a reseeding effort using exotic grasses and herbs to reduce erosion after the eruption. Many of the seeded species did not grow well on the new substrates, and there is no evidence that erosion was reduced. If species that grow well, can reproduce, and are integral to the seral process had been seeded, the effects might have been different. Ecological studies need to produce accurate understandings of interactions between organisms and their environment but also need to demonstrate how these principles contribute to management of the environment. This study shows how colonization is influenced by substrate conditions, distance to a seed source, and species characteristics and suggests that native species such as *A. rubra* that grow well, reproduce early, and change soil conditions should be considered for revegetation management.

**Acknowledgements**

Logistic support was provided by J. F. Franklin, the USDA Forest Service, and the Washington State Department of Natural Resources. A. B. Adams, D. Donohue, H. Haeemmerle, L. C. Hensley, R. Holland, E. Smith, and J. Wallace assisted with some of the field work. J. Dudley and P. Dudley did the geomorphic analysis. E. P. Smith assisted in the experimental design. The manuscript was reviewed by J. F. Franklin, M. Huston, D. Johnson, W. M. Post, and R. Turhington. The research was funded by the National Science Foundation, EARTHWATCH and The Center for Field Research of Belmont, Massachusetts. This is publication No. 3179, Environmental Sciences Division of the Oak Ridge National Laboratory operated by Martin Marietta Energy Systems, Inc., for the U.S. Department of Energy under contract No. DE-AC05-84OR21400.


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