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Plant Survival, Growth Form and Regeneration Following the 18 May 1980 Eruption of Mount St. Helens, Washington

Abstract

The composition of plant communities changes after cataclysms such as volcanic eruptions. These community changes might be more accurately forecast if the floristic composition of communities is known prior to an eruption because recovery of plants depends upon the mechanisms by which they normally respond to disturbances. To identify some of these mechanisms and their consequences for plant community recovery, we followed the recovery of plant communities after the 18 May 1980 lateral blast of Mount St. Helens and examined both species that survived and those that regenerated. Plants with subterranean dormant buds (geophytes) and those that could regenerate from fragments survived the eruption best. As a result, the proportion of geophyte species and relative plant cover of geophytes was significantly higher than that of other growth form types. Initial recruitment onto the hummocky-surfaced debris slide (i.e., mounded-surface) was strongly biased toward geophytes and annuals, possibly due to extreme environmental conditions on this new substrate. In contrast, other habitats (blowdown, mud flow and scorched, dead forest) created by the eruption have higher vegetation cover and are dominated by plants that survived the eruption. Because plants have evolved in response to frequent disturbances such as fires, snowslides and floods, they are preadapted to similar, but less frequent, disturbances that are associated with volcanic eruptions.

Introduction

After large-scale ecosystem disturbance accurate assessments of plant regeneration are necessary for determining resource availability for terrestrial and aquatic fauna, estimating the quantity of sediment to be expected downstream, and assessing the magnitude of competition that commercial plantations may encounter. The effects of volcanic disturbances on plant communities and the importance of growth forms in plant reestablishment have been described (Smathers and Mueller-Dombois 1974, Man'ko 1974, Griggs 1933, Franklin *et al.* 1985, Antos and Zobel 1985a,b). The pre-eruptive influence of climate and recurrent disturbances such as fires, floods, and snowslides have been recently considered as selective agents of adaptations that increase the probability of surviving eruptions (Adams and Dale 1987, Antos and Zobel 1985a,b). A variety of plant responses to burial have been described by Antos and Zobel (1987) including the formation of adventitious roots, upward growth of rhizomes, and movement of perennating buds.

Influences of climate, time, and substrate have been formulated in a predictive model for long-term biomass accumulation on lava substrates by Eggler (1971). Halpern and Harmon (1983), based on initial observations of revegetation of the Lower and Upper Muddy River mud flow at Mount St. Helens, predicted successional patterns to be variable following this volcanic disturbance because there is a variety of surface substrates for colonization, means of reproduction and distances to seed source. Differential plant survival within and between disturbance types has not been statistically tested after past debris avalanches and associated lateral venting of stratolayer volcanoes such as those that occurred at Bandai-san, Japan, in 1888 (Sekiya and Kikuchi 1889), and at the Russian volcanoes Bezymianny in 1956 and 1964 (Tokarev 1981). Griggs (1933) working four years after the 1912 eruption of Mount Katmai, Alaska, noted both the importance and difficulty in differentiating between hold-over plants and new colonizers following volcanic eruptions.

The eruptions of Mount St. Helens, Washington (Lipman and Mullineaux 1981, Swanson *et al.* 1983, Weaver *et al.* 1983, and Waitt *et al.* 1983), provide opportunities to develop methods for predicting the mechanisms and magnitude of

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vegetation recovery following cataclysmic eruptions. Since quantifying differences in plant growth forms would allow us to substantiate or refute past observations for vegetation following other volcanic eruptions and provide a means for assessing future successional trends, we decided to use the Mount St. Helens blast zone to test for differential survival as a function of growth form. By looking in the time period immediately following the lateral blast, we were easily able to separate hold-over plants from new colonizers. We believe that the methods and results presented in this paper provide a simple way of using pre-eruptive plant composition and associated types of plant regeneration for forecasting potential plant recovery in the aftermath of a large-scale natural disaster.

Methods

Sampling within Disturbance Habitats

The post-eruptive habitats selected to examine differences among growth forms were: 1) blowdown; 2) standing scorched (seared), dead forest; 3) mud flow; and 4) debris avalanche (Figure 1). Ocular estimates of percent cover by species (obtained by dividing the plots into quarters and summing to give a total estimate for each plot), the number of species above the ash, phenological stages (seedling, emerging, immature plant, flowering, setting seed or dead) represented by each species, ash depth and distance from the crater were recorded for 25 m^2 circular plots from late June to August of 1980 in blowdown and scorched, dead forests, and mud flow habitats. Because plant cover was markedly lower on the debris slide relative to the other three habitats considered in this research, we predicted that plant establishment onto the debris would be related for the most part to survival of seedlings. This would allow a contrast of growth forms in a habitat recolonized by seeds with habitats in which a greater proportion of the flora survived. Therefore, we considered annual and seasonal variability in growth forms on the debris slide by sampling over a three year period (15, 83 and 103 250 m^2 permanent circular plots during August of 1980, 1981, and 1982, respectively) and for three time intervals during the summer of 1982 (June, July and August). In addition to the information collected for the plots in the other three habitats, for the debris slide plots we recorded the number of stems/species at the soil surface.

Growth Form Classification and Spectra

Plants were classified by the location of dormant meristematic tissue relative to the ground surface (Raunkiaer 1934, Mueller-Dombois and Ellenberg 1974). Growth form spectra were constructed for species classified as annuals (A), plants with buds below ground (G or geophytes), plants with buds at the ground surface (H or hemicryptophytes), plants with buds 2.5 to 50 cm above the surface (C or chamaephytes), tall shrubs (S), deciduous trees (D) and evergreen trees (E). The percent of species for pre-1980 data (256 spp.) was constructed using the data of St. John (1976). The growth form spectra of percent species for the four disturbance habitats were determined using species lists constructed on forays through the habitats and from established plots. The percent cover of growth form types averaged for the total area was determined by summing the average cover of each growth form within a given habitat and then dividing this sum by the total number of habitats. The cumulative mean number of individuals per plot was calculated by dividing the total number of individuals of each growth form by the number of plots and summing the growth forms for each sampling period.

Analysis of Types of Plant Regeneration

Three types of regeneration were considered in our field work: 1) regeneration from newly deposited seeds (recruitment or establishment of new genets); 2) regeneration from *in situ* surviving plants; and, 3) regeneration from plant fragments transported by the energy forces associated with the eruption (e.g., the blast, avalanche and mud flows). The presence of seeds was documented with seed traps (0.25 m^2) (Adams and Adams 1982, Adams and Dale 1987). Seedlings were distinguished from emergent residual plants by the presence of cotyledons and the absence of subterranean tissue from previous years' growth. Plants were unearthed to determine if regeneration was occurring from fragments or from *in situ* rootstocks sprouting in mineral soil. To ascertain the potential of subalpine lupine (*Lupinus latifolius*) to regenerate vegetatively, a single lupine rootstock was placed

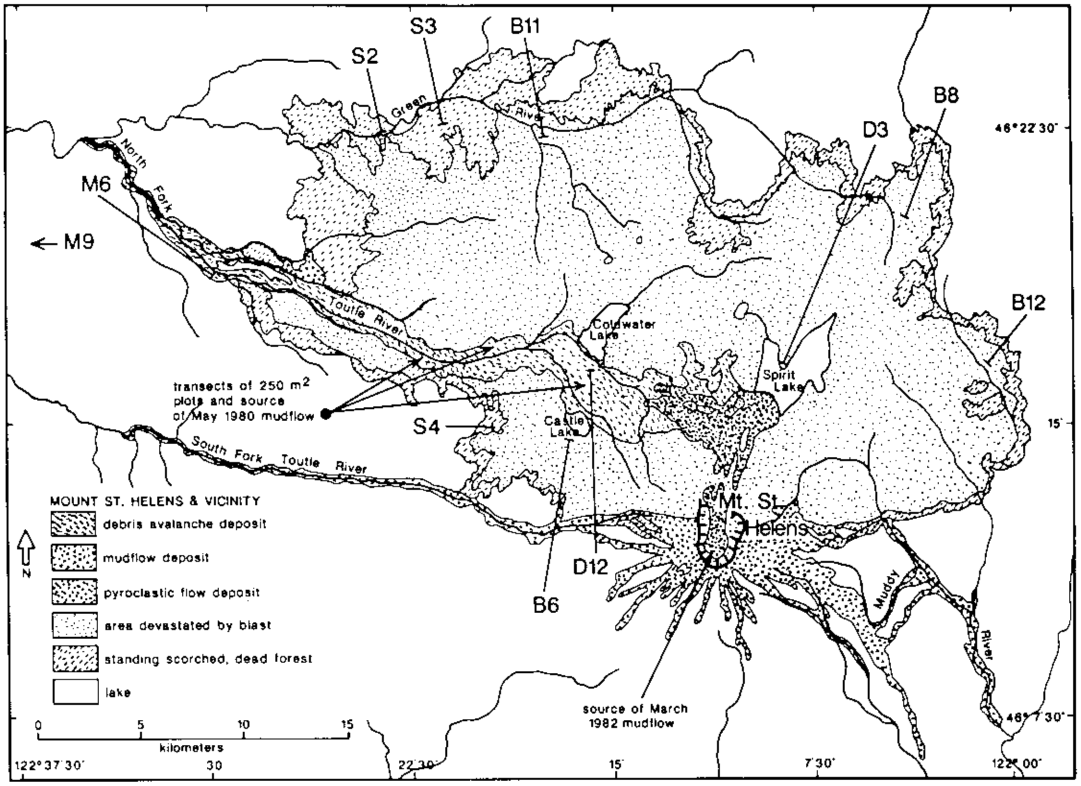

Figure 1. Map of study area relative to the confluence of the Cowlitz and Toutle Rivers and the Mount St. Helens crater. The location of 25 m^2 circular plots and transects in 4 disturbance habitats are shown. The bold letters indicate the disturbance type and the associated numbers denote the number of plots at each location. Disturbance types are blowdown (B), standing scorched, dead forests (S), mud flows (M) and debris slide (D). The set of plots designated M9 represents 9 plots located west of the map approximately 1 km east of the confluence of the Cowlitz and Toutle Rivers. The 250 m^2 permanent circular plots on the debris slide used in 1980 ran south to north from Castle Lake to Coldwater Lake and 3 plots were located on portion of the debris slide that splashed across Spirit Lake and was deposited just north of Spirit Lake. In 1981 and 1982 the plots ran from 5 km east of the terminus of the debris slide to Castle and Coldwater Lakes. Plots are spaced at 50 m intervals along line transects in all habitats.

in six clay pots filled with debris substrate and the rootstocks were watered daily at the University of Washington greenhouse. Methods used to determine substrate physical and chemical properties, and moisture stress troughs used in documenting regeneration from transported fragments are described in Adams and Dale (1987).

Statistical Analyses

To test the significance of distance relative to ash depth in residual plant recovery, a multiple regression was run utilizing number of species as the dependent variable versus ash depth and distance as the independent variables. To determine the significance of differences in abundance of growth form types, a two-way ANOVA with unequal frequencies was performed on the log transform (Y + 0.0005) of percent cover with growth form and disturbance type as factors. For the debris slide data collected in permanent 250 m^2 circular plots during August of 1980, 1981, and 1982, a two-way ANOVA with unequal frequencies was performed on the log transform of number of individuals with growth form and year as factors. Significant differences between growth form types were determined by computation of Scheffe's pair-wise contrast tests (Winer 1971).

Results

Similarities and Contrasts in Growth Form Spectra of the Four Habitats

Disturbance types had different growth form spectra (Figure 2) and different types of plant regeneration. Annuals were poorly represented in the pre-eruption flora and were absent from all four habitats in the summer subsequent to the eruption of Mount St. Helens (Figure 2A). All six other growth form types were represented by residual or surviving species. The relative proportion of geophytes was higher for the total area than existed in the pre-1980 flora, whereas hemicryptophytes and chamaephytes are notably less. No major changes in the relative proportions of species of tall shrubs, deciduous or evergreen trees were noted when the spectrum for the pre-1980 flora is compared with the cumulative percent of species for the total.

Growth form spectra of cumulative percent of species were similar for blowdown and scorched, dead forests, but these two spectra differed from those that occurred on lahars (mud flows and the debris slide) (Figure 2A). Since species compositions were identical for blowdown and dead, scorched forests (100 spp.), these spectra are presented as a single spectrum in Figure 2A. In the blowdown and scorched, dead forests, above-ground plant tissue was removed by the lateral blast. Here most plants regenerated *in situ*. Over 70 percent of these species and 89 percent of the relative cover consisted of plants with perennating buds below the ground. The mud flow (22 spp.) and debris slide (20 spp.) habitats differed from the blowdown and scorched, dead forests by the occurrence of relatively fewer geophytes. The mud flow differed from the debris slide spectra by having a higher proportion of species that have buds projecting above the mud's surface (shrubs >50 cm, deciduous and evergreen trees) and fewer species with buds below the surface.

The barplots of each separate habitat represent the cumulative sum of the means of each growth form type (Figure 2B). Total mean percent cover was low in all four habitats ($\leq 25\%$), but nevertheless higher than we had expected. Plants with buds below the surface represented the highest percent cover/plot, followed by deciduous and then evergreen trees. A two-way ANOVA utilizing percent cover with growth form and disturbance type as factors, showed that the growth form-disturbance type interaction was significant ($p<0.001, F_{15,48} = 8.02$). Computation of pair-wise contrast tests indicated that the main differences were associated with the relative importance of conifers and deciduous trees on the mud flow and geophytes in other disturbance types. In 1980, percent cover for hemicryptophytes and trees was low; nevertheless, cover was 16 times higher for plants with buds at the surface and twice as high for trees in the scorched, dead forests than in the blowdown.

Mechanisms of Regeneration

In 1980 survival of seedlings was found to be virtually nonexistent in all four habitats (Adams and Adams 1982). In 1980 regeneration in the blowdown and scorched, dead forests was almost entirely from *in situ* plant parts sprouting from mineral soil. No regeneration from transported plant fragments was found in these two habitats. The number of species regenerating seemed to be related to erosion in that the greatest number of species were found on moderately steep slopes

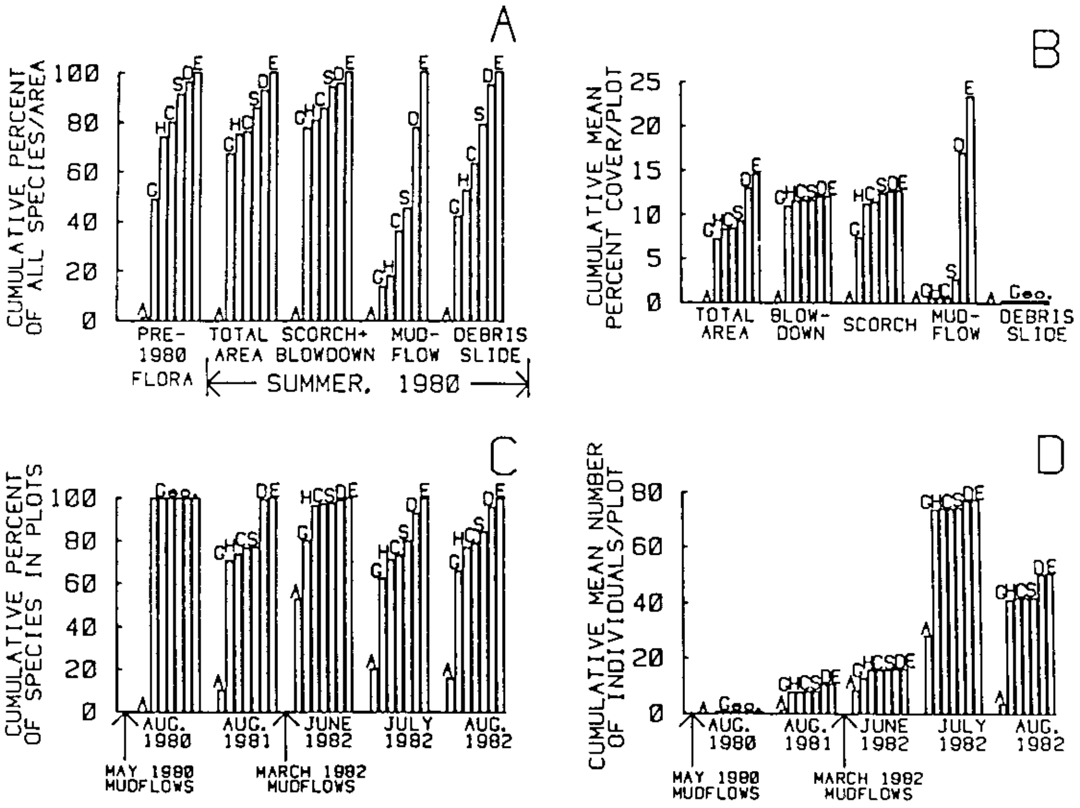

Figure 2. Growth form spectra are reported for species classified as annuals (A), plants with buds below ground (G), plants with buds at the ground surface (H), plants with buds 2.5 to 50 cm above the surface (C), tall shrubs (S), deciduous trees (D) and evergreen trees (E). (A) The percent of species for pre-1980 data (256 spp.) (St. John 1976) and for 4 disturbance habitats sampled from June to July, 1980. (B) The percent cover of growth form types averaged for the total area (sum of average cover of each habitat divided by the total number of habitats) and for the 4 disturbance types for 25m^2 circular plots sampled during July and August of 1980. (C and D) Growth form spectra for 250m^2 plots located on the debris slide. (C) Cumulative percent of species in debris avalanche plots. (D) Cumulative mean number of individuals per plot calculated by dividing the total number of individuals of each growth form by the number of plots and summing the growth forms for each year. On 19 March 1982 an explosive eruption generated a lahar that covered a large portion of the debris slide as far as 8 km from the crater (Waitt *et al.* 1983). This secondary disturbance is noted on Fig. 2C-D.

with gullies that penetrated through the ash to the surface of the pre-eruptive mineral soil. Multiple regression of data from blowdown and scorched, dead forests shows number of species (N)/25 m^2 plot surviving and emerging above the ash in July 1980 to be related to depth of ash (D in cm), and not to distance from the mountain ($N = 5.75 - 0.22D$, $p = 0.002$, $r^2 = 0.40$, $n = 50$ plots); [addition of distance increases r^2 by 0.005 and the coefficient is not significantly different from 0 ($p = 0.620$)]. Regeneration from *in situ* geophytes and hemicryptophytes was rare on both the mud flow and debris slide. Regeneration from transported fragments occurred throughout the North Fork Toutle mud flow sites. On the debris slide vegetative regeneration was mostly in tributary backfills and the outer margins of lateral terraces (Voight *et al.* 1981) associated with rootwads, clumps of mineral soil and distal clumps of forest fragments deposited at the western terminus of the slide.

On the North Fork Toutle mud flow and debris slide more than 20 species regenerated from fragments and from plants transported on root wads, stumps and soil torn from the valley walls. Regeneration occurs from tubers [western starflower (*Trientalis latifolia*)]; corms [trillium-leaved wood-sorrel (*Oxalis trilliifolia*)]; rhizomes [beargrass (*Xerophyllum tenax*)]; and taproots [pearly everlasting (*Gnaphalium microcephalum*)]. In 1980, on the debris slide, fireweed (*Epilobium angustifolium*), Canadian thistle (*Cirsium arvense*) and lady fern (*Athyrium filix-femina*) sprouted from axillary buds of transported rhizomes. In mud flow material of the North Fork Toutle valley located four km west of the debris slide terminus up to five fragments were found sprouting within a 25 m^2 plot in 1980 [Mertens' sedge (*Carex mertensii*), dagger-leaf rush (*Juncus ensifolius*) and horsetails (*Equisetum* spp.) from rhizomes]. Broken branches of black cottonwood (*Populus trichocarpa*) and willows (*Salix* spp.) developed leaves and stems from preformed primordia embedded in bark on stem sections on both the mud flow and debris slide. Nine fragments [soft rush (*Juncus effusus*), *C. mertensii* and bentgrass (*Agrostis diegoensis*)] sprouted from mud flow substrate spread over an area of 13 m^2 as part of a moisture stress trough experiment conducted within the University of Washington research greenhouse (Adams and Adams 1982, Adams *et al.* 1986). *Lupinus latifolius* became established on the debris slide and set seed in 1981. All six rootstock sections of this lupine placed in debris substrate sprouted shoots and roots within two weeks.

Yearly and Seasonal Trends on the Debris Slide

Only geophytes were found in the debris slide plots in 1980 and geophytes remained predominant in August samples during the three year study period. With the exception of small shrubs, all growth forms showed relative increases in importance to the total spectra subsequent to 1980. Yearly changes in cumulative percent of species in 250 m^2 circular plots on the debris slide were pronounced (Figure 2C). In particular, the proportion of annuals and deciduous trees increased.

Although total plant cover remained less than one percent on the debris slide through 1982, there were three orders of magnitude increase in the number of individuals/250 m^2 plot from 1980 to 1982 (Figure 2D). The two-way ANOVA with unequal frequencies performed on number of individuals with growth form and year as factors was significant ($p < 0.001$, $F_{20,203} = 13.21$). The interaction of growth form with year was insignificant. Contrast tests indicate the main difference is due to the increase of plants with buds underground, and to a lesser degree to the change in annuals, and to an even smaller increment of increase from deciduous trees.

In 1982 the total number of plants on the debris slide increased from June to July and then decreased from July to August (Figure 2D). Deciduous trees in 1982 showed an increase throughout the sampling period but represented < 10 percent of the total number of individuals. Annuals and geophytes show the largest increases from June to July of 1982, whereas annuals decrease and geophytes remain unchanged from July to August. As expected, over 99 percent of the increase in numbers of individuals on the debris slide was from seed dispersal and seedling survival during 1981-82 as was easily determined by the presence of cotyledons and lack of tissue from previous years' growth.

Discussion and Conclusions

General Features of the Growth Form Spectra

The structure of flora surrounding Mount St. Helens both before and after 1980 is distinguished from other vegetation at temperate latitudes of the northern hemisphere as described by Whittaker (1960), and differs from nearby volcanoes such as Mount Rainier, Washington, by a high proportion of geophytes relative to hemicryptophytes and chamaephytes. After the eruption, survival and recruitment of growth form types varied significantly between habitats considered. The type and magnitude of vascular plant recovery in the first growing season following the eruption of Mount St. Helens appeared to depend upon the relationship between the nature of the disturbance which an area experiences, aspect, time of snowmelt and ongoing disturbances such as erosion.

Preadaptation to Fires and Snow

Periodic fires and climate (in particular heavy precipitation, much of it in the form of snow) may explain, in part, the high proportion of geophytes in the floristic composition of communities surrounding volcanoes of the Cascade Mountains. Similarly, the relatively frequent eruptions of Mount St. Helens (Mullineaux and Crandell 1981) may have a selective effect on vegetation structure that results in a higher proportion of plants with dormant primary meristematic tissue underground being found near Mount St. Helens. The chances for survival were found to be higher for plants buried by snow at the time of the eruption within the blast zone (Means *et al.* 1982, Adams and Adams 1982), but the reverse was found to be true in forests outside the blast zone where Antos and Zobel (1982) found reduced cover at sites with tephra on top of snow for shrubs, tree seedlings and erect evergreen herbs. Antos and Zobel, in commenting on the scarcity of *X. tenax* in habitats surrounding Mount St. Helens relative to its occurrence in similar habitats in other parts of the Cascades, note that timing of volcanic eruptions in relation to snow packs may greatly influence initial damage or survival of vegetation.

Montane forests and subalpine meadows of Washington do have recurrent fires and snowslides which remove above-ground plant biomass in a manner similar to that of the 18 May lateral blast of Mount St. Helens. Plants that regenerated in blowdown and scorched, dead forest habitats also regenerate after fires (Miller and Miller 1976, Agee and Scott 1983, Hitchcock and Cronquist 1981) and snowslides (Cushman 1981, Adams and Dale 1987). In the blowdown and scorched dead forests, most surviving plants regenerated from *in situ* buds of rhizomes, tubers, bulbs and corms. Antos and Zobel (1985a,b) found simliar results when investigating understory species covered by tephra from Mount St. Helens. In addition, these researchers noted that long-term survival was dependent upon reestablishment through the production of adventitious roots within the tephra, as well as surviving the burial. Species with the ability to regenerate from meristematic tissue located several cm below the surface have the greatest survival rate during fires (Flinn and Wein 1977, McLean 1969). Also, in blowdown and seared forest habitats some tall shrubs [*e.g.*, thimbleberry (*Rubus parviflorus*), salmonberry (*R. spectabilis*), and elderberry (*Sambucus racemosa*)] which had their above ground parts destroyed by the blast responded via adventitious buds forming epicormic shoots as they do following fires and snowslides. In this sense these species act as facultative geophytes.

Production of new foliage by plants with buds at the surface, small shrubs, and coniferous trees was restricted to areas protected by snow, north and northwest facing slopes, or to the scorched, dead forests in the case of hemicryptophytes and chamaephytes. Plants of the Pacific Northwest which possess buds 2.5 to 50 cm above ground level often have sclerophyllous evergreen leaves. The total loss of buds and leaves explains the scarcity of small shrubs in the devastation zone during the first growing season following the spring eruption. Both the proportion of chamaephyte species and their relative percent cover had decreased following the 18 May eruption. Many chamaephyte species [*e.g.*, Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*) and twin flower (*Linnaea borealis*)] are residual components of burned areas in the Pacific Northwest and regenerate vegetatively within a year after a fire (Miller and Miller 1976). These species would be expected to be more abundant after the eruption. Adventitious buds can form on roots (especially injured roots), but this is least likely to happen during the spring (Hartmann and

Kester 1975). Dispersal of small shrubs back into the devastation zone should be relatively rapid in the Pacific Northwest because birds and mammals are major seed vectors for species possessing this growth form type (Best 1981).

Non-vascular plants that respond to fires were also the taxa that responded to the eruption of Mount St. Helens. For example, the most common moss found during our ongoing studies has been *Funaria hygrometrica,* a circumboreal species often found after forest fires and in campfire pits (Lawton 1971). Similarly, Discomycetes sporocarps (*e.g., Peziza violacea* and *Pyronema* spp.) were found throughout the devastation zone in 1980. These thermophilic fungi are often found after fires and in pasteurized soil used in greenhouses (Dennis 1978).

Preadaptation to Floods

At Mount St. Helens, some disturbances were similar to seasonal floods caused by heavy rains and snowmelt. On lower portions of the Toutle and Muddy Rivers, and Pine and Swift Creeks a slurry of mud, water and organic material washed down from the mountain sweeping away much of the vegetation. Marks on standing trees show the water levels were as much as 15 m above normal stream level as far as 33 km from the crater of Mount St. Helens. The largest flows occurred on the North Fork Toutle River where conifers and broad leaf deciduous trees were left standing but buried by meters of mud. Often standing trees had a ring of bark removed by the force of the flow leaving the cambial layer exposed.

Plant responses after mud flows are similar to methods of regeneration that these same species utilize following floods. Observations from the mud flows of Kautz Creek, Mount Rainier, Washington (Frehner 1957) and Mount Lassen, California (Beardsley and Cannon 1930) indicate that many trees died up to three years after being partially buried probably due to insufficient oxygen supply to their roots or from cambial damage. On the Kautz mud flow buried trees set seed the following spring and fall, and tree establishment was most abundant where snags provided protection against extreme temperatures and drought stress.

The difference in the growth form spectrum of mean percent cover for the mud flow habitat has broad implications for predicting the potential for vegetation recovery in this habitat type. *Populus trichocarpa* and *Salix* spp. partially covered by mud flows actually produced seed in 1980 after the eruption. Other species, including conifers, seeded in 1981. The short-term survival of trees on mud flows provided a seed source, and snags are more favorable habitat for germination and growth. As such, their short-term survival has a significant impact on future vegetation trends. Our results are slightly different than those of Halpern and Harmon (1983) who reported results for data collected in 1981 for the Muddy River mud flow which is closer to Mount St. Helens than our mud flow plots on the North Fork Toutle, and apparently had much fewer surviving tree snags in 1981 than we found in 1980. Our work is similar to that of Halpern and Harmon in that we too found regeneration from fragments to be present, and we found microsites within habitats to be diverse and to explain much of the diversity of the flora. Fragment regeneration appears to be more important on the North Fork Toutle mud flow than on the the Muddy River mud flow.

Potential for Fragment Regeneration as a Function of Habitat

Fragments were dispersed by the energy associated with lahars. Vegetative regeneration from transported fragments, such as that which might occur following a flood, occurs in mud flow and debris substrate. Regeneration from fragments has not been documented for volcanic eruptions. We found that mud flow and debris slide materials possess properties that enhance their potential as rooting media (Hartmann and Kester 1975, Adams and Dale 1987), such as: 1) neutral pH (6.7 ± 0.2, standard deviation); 2) low conductivity (less than two mmhos/cm); 3) sufficient aeration due to a predominance of sand; 4) moisture retention provided by silt and clay; 5) a small, but significant quantity of nitrogen; and, 6) emplacement temperature of deposits hot enough to kill root pathogens [*e.g.,* nematodes *Heterodera*) and water molds (*Rhizophotinia* and *Phythium*)], but not too hot to destroy beneficial bacteria (maximum temperature for debris and mud flow was 92°C) (Banks and Hoblitt 1981).

Plant fragments were also dispersed by the force of the blast itself. The capacity for the blast to disperse fragments is demonstrated by eyewitness accounts of the eruption. For example, climbers at 2400 m on Mount Adams reported that plant fragments up to a meter in length and conifer cones landed around them shortly after 15:32 U.T. on 18 May 1980 (a minimum of one fragment/10m^2) (Jack Christiansen, pers. comm.). Fragments were found dispersed throughout the blowdown and seared forests, yet no fragments were found regenerating here. In this case, fragment regeneration might have been prevented by: 1) high temperatures that destroy meristematic tissue and beneficial symbionts; (blowdown and scorch emplacement temperatures ranged from 100 to 350°C) (Banks and Hoblitt 1981, Winner and Casadevall 1983); 2) coarser particle sizes that reduce moisture retentivity; and, 3) an almost impermeable cement-like layer with low porosity created when water combines with the fine-grained surface tephra layer that covers most of the potential regeneration sites in the blowdown and seared forests.

Vegetation Trends on the Debris Slide

The debris slide underwent a significant change in growth form spectra from 1980 to 1982 and showed seasonal variation in 1982. Although the proportion of annuals increases in temperate zones of the northern hemisphere following disturbances (Whittaker 1975), 60 percent for the July 1982 debris slide data is high. The reason for the abundance of annuals is believed to be due to the hot, dry conditions that exist on the surface of the debris slide. Other habitats in the northwest (e.g., serpentine outcrops and arid regions east of the Cascade Mountains) that support high proportions of annuals also have high temperature and low available water supplies. Alpine lupine (*Lupinus lepidus* var. *lobbii*), yellow monkey-flower (*Mimulus guttatus*) and miner's lettuce (*Montia sibirica*) which are often perennial, acted similar to many arid region species on the debris slide in that some individuals flowered and set seed the first year and then died, thus becoming annual. Temporary streams and pools common on the debris slide provide ephemeral resources similar to desert habitats. Annuals are able to exploit these temporary resources and then spend the more stressful periods as dormant seeds.

Overall, vegetation trends in our plots were not set back by the 19 March 1982 mud flow (Figure 2C-D). Nevertheless, this disturbance did vary in the magnitude of its impact on the debris slide, depositing more than 1 m of mud and pyroclastic material in some spots to lightly mantling other areas (Waitt *et al.* 1983). If localized disturbances such as this have high rates of occurrences on the debris slide, annuals such as wood groundsel (*Senecio sylvaticus*) and annual hairgrass (*Deschampsia danthonioides*) and geophytes adapted to chronic disturbances may remain dominant here. With more moderate disturbance rates, deciduous trees may become established and survive by producing adventitious roots, regenerating from fragments, and dispersing copious amounts of seeds.

The distance of seed sources from disturbance sites is critical to future vegetation trends, and is already a major factor in the Mount St. Helens area. For example, red alder (*Alnus rubra*) (a major component of flood plains of western Washington) did not survive in the blast zone. *Alnus rubra* performs well when started from seed on both mud and debris substrate (Adams *et al.* 1986), and this deciduous tree already has become dominant on lower reaches of the 1980 and 1982 mud flow deposits in the North Fork Toutle floodplain where seed sources are nearby. This same species is rare on the debris slide where seeds are less common. The rate at which *A. rubra* establishes may influence long-term successional trends. For instance, if the disturbances occur at even lower frequencies, then a mixed coniferous forest may have a chance to become established provided that *A. rubra* saplings do not become rapidly established and shade out conifer seedlings.

In our studies at Mount St. Helens we have been able to establish that plant growth form is important not only to initial recruitment onto newly deposited substrates of this stratolayer volcano, but in addition, is a significant factor in the composition and quantity of residual, surviving plant populations. Geophytes are not only the predominant survivors, but in addition, they are important in initial seedling recruitment from the blowdown above the Toutle River onto the debris slide.

Groups of species possess common adaptations (e.g., the position of dormant meristematic tissue) that influence survival. Initial prognosis of the Mount St. Helens impact areas underestimated the regenerative potential of the vegetation and overestimated the success of aerial seeding with non-native grasses (Brown 1981, Carlson *et al.* 1982). If mechanisms of survival are understood and the composition of the preexisting flora is known, then more accurate predictions of species response and magnitude of vegetation recovery may be possible.

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