Recovery of forest understories buried by tephra from Mount St. Helens*

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Abstract

To determine the effects of tephra (volcanic aerial ejecta) on forest understory plants, six sites were chosen along a tephra depth gradient (23 to 150 mm) northeast of Mount St. Helens, USA. All sites were in old forests beyond the limits of direct blast damage from the volcanic eruption. At each site, 150 one m^2 plots were permanently marked; all tephra was removed from 50 of these in 1980. Cover and density of plant species were recorded during 1980, 1981, and 1982.

Tephra 23 mm deep had almost no effect on cover and density of vascular plants, and reduced bryophyte cover for only two years. Tephra 45 mm deep destroyed almost all bryophytes. Although damaged by 45 mm tephra, deciduous herbs recovered by 1982, but some evergreen species did not. Tephra 75 mm deep reduced herb cover in 1982 to 32% and density to 26% of that in cleared plots. At two sites with an average tephra depth of 150 mm, almost all herbs were eliminated except in microsites where tephra was thin, but shrub abundance was greatly reduced only where snow had been present during tephra deposition. Almost all cover was contributed by plants established previous to the eruption; seedling cover never exceeded 0.2%. Refugia with thin tephra, resulting from erosion, were vital to the survival of many species, especially bryophytes.

Introduction

The importance of volcanism in the Cascade Mountain Range of Western North America was dramatically demonstrated in 1980 by Mount St. Helens after decades of quiescence. The massive eruption of 18 May 1980 destroyed forests over almost 500 km^2 and deposited tephra (volcanic aerial ejecta) over a much larger area (Lipman & Mullineaux, 1981; Rosenfeld, 1980). Mount St. Helens, the most active Cascade volcano, has erupted at intervals averaging a few hundred years (Crandell *et al.*, 1975; Crandell & Mullineaux, 1978; Heusser & Heusser, 1980; Mullineaux *et al.*, 1975).

Volcanoes change vegetation in two ways: (1) destruction of plants by blowdown, chemical damage, or burial by ejecta, and (2) long-term soil modification that influences species composition. Data on vegetation changes caused by volcanic eruptions are sparse and mostly anecdotal (Antos & Zobel, in press). Reports of plant damage from the Mount St. Helens eruption have concentrated on areas where trees were destroyed or absent (del Moral 1981, 1983; Means *et al.*, 1983); Mack (1981) studied the effects of relatively thin tephra far from the volcano.

After many volcanic eruptions, including the

* Nomenclature of vascular plants follows Hitchcock & Cronquist (1973); moss nomenclature follows Lawton (1971).

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1980 Mount St. Helens event, an extensive area is covered by tephra of insufficient depth to kill canopy trees (Waitt & Dzurisin, 1981). Although this area is not as impressive as the destroyed forest, it is often much larger. In this paper we examine cover and density changes in understory plants buried by tephra 23 to 150 mm deep for the first three years following the 1980 Mount St. Helens eruption.

Because its effect was primarily caused by burial, the disturbance investigated here differs from the other major disturbances (fire, windthrow) that affect these forests.

Methods

Our study area was in the region of maximum tephra depth northeast of Mount St. Helens. The terrain is mountainous, with long ridges about 1700 m elevation and valleys incised below 500 m elevation. The climate is wet maritime with heavy winter precipitation. Snowpacks accumulate at higher elevations and can be 5 m deep at our highest elevation sites. The landscape is forested with natural coniferous stands except for some ridge crests and recently cut areas. The lower elevation forests we studied are part of the *Tsuga heterophylla* zone; most sites occur in the higher elevation *Abies amabilis* zone (Franklin & Dyrness, 1973).

We chose six sites representing four tephra depths northeast of Mount St. Helens (Fig. 1, Table 1). The sites were selected to represent a gradient from relatively shallow tephra to the deepest available deposits outside the devastated area. All sites were located in old forest on relatively level terrain. *Abies amabilis* or *Tsuga heterophylla* dominated the tree canopy at all sites. Site A had a rich herb layer but few shrubs and was considerably lower in elevation than the other forests. All other sites had well developed shrub layers dominated by deciduous Ericaceae. Site B had a herb layer dominated by *Xerophyllum tenax*, a caespitose, evergreen monocot. Sites C, D, and F had well developed deciduous herb layers; site E had few herbs. At all sites the herb layer was composed exclusively of perennials.

Table 1. Study site characteristics.

Site	Tephra depth (mm)	Elevation (m)	Dates of tephra removal (1980)
A	23	550	2, 6 August
B	45	1245	7, 8 August
C	45	1290	9, 10 August
D	75	880	23, 24 August
E	150	1160	17, 18 July
F	150	1240	11, 12 September

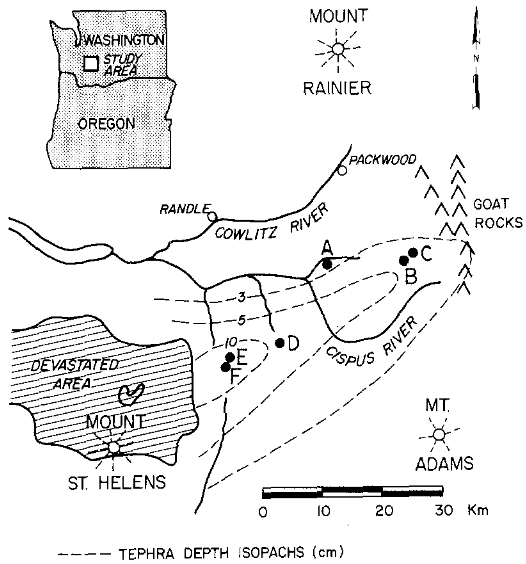

Fig. 1. Study site locations.

The deepest tephra (at sites E and F) was composed predominately of gravel-sized pumice (to about 1 cm diameter) with a fine textured crust and basal layer, each about 1 cm thick. At site D the pumice was finer textured; the crust and basal layers were thin. The deposit at sites B and C was coarse sand with finer textured crust and basal layers. Site A had a silty deposit.

At each site we permanently marked 150 one m^2 plots along paired transects. The transects were located to sample a relatively homogeneous stand covering 1 ha or less. We left 100 plots undisturbed, 'natural plots'. On adjacent, paired transects we removed all tephra from the remaining 50 plots during summer 1980, 'cleared plots'. We removed the tephra with a variety of implements, including a vacuum cleaner, in an attempt to minimize plant damage. Erosion refilled some cleared plots during winter 1980–81, which we recleaned in spring 1981. There was little additional erosion.

During the summers of 1980, 1981 and 1982, we recorded stem density and estimated canopy cover for all vascular plant species in all plots. We recorded values separately for plants established previous to the eruption and newly established seedlings. All cover and density values reported in this paper are for plants which were present prior to 1980; data for seedlings established following tephra deposition will be reported elsewhere. For mosses we estimated cover by species, or collectively for those we could not distinguish in the field. For leafy liverworts we estimated only total cover. We determined 'density' of shrubs and non-stoloniferous herbs as the number of stems at the tephra surface. For stoloniferous herbs we considered all visibly connected stems as a single individual. For small trees we estimated cover of foliage that was below about 1.5 m in height.

For each plot at every reading we estimated the percent cover of litter, wood, and type of tephra surface (smooth, cracked, eroded). We recorded microsite characteristics such as slope, aspect and canopy type for each plot.

We sampled the plots each year after growth was mostly complete but before leaf senescence. In these forests the growing season is short and all species are in full leaf simultaneously, allowing us to estimate maximum cover accurately for all species on the same date. At site D, snowshoe hares (*Lepus americanus*) each year trimmed some herbs before sampling. The stems or petioles usually remained so we could make accurate counts and adjust the cover estimates to compensate for the loss (usually less than 10% of a species' cover). Tephra removal during summer 1980 inevitably damaged the annual shoots of some herbs. Consequently, the 1980 cleared plot readings were poor estimates of herb abundance and we will not use them. The 1981 and 1982 cleared plot values are our best estimates of plant abundance before the eruption. Because most of the herbs at our sites are long-lived perennials with well developed rhizomes, stolons, or corms, we feel that damage to aerial shoots in 1980 probably did not destroy many plants. In addition we would not expect major changes in the herb layer from year to year because the forests sampled are very old and have not been affected by fire for at least 200 years. Thus, we feel that the cleared plots give a reasonable approximation of normal understory cover and density at the sites.

Because cover and density data were not normally distributed, non-parametric statistical tests were used in comparisons among years and between natural and cleared plots (Sokal & Rohlf, 1981). To test for the significance of differences between cleared and natural tephra plots in a given year we used the Mann-Whitney *U*-test. For the paired comparisons of plots between years we used the Wilcoxon's signed ranks test. All statistical analyses were performed with SPSS statistical programs (Nie *et al.*, 1975).

Results

Tephra Morphology, Erosion, and Litter Accumulation

The tephra deposit in the forest was not uniform. Variation in both total depth and relative thickness of its layers developed as the material sifted through the tree crowns. On the ground, slumping occurred from steep substrates such as windthrow mounds and logs. At sites C and F, tephra fell on snow and thus developed a rough, cracked surface as a result of non-uniform melting of the underlying snowpack (Antos & Zobel, 1982). At the other sites, the tephra had a smooth crust.

During the winter of 1980–81, extensive erosion occurred and the area covered by thin tephra increased approximately two to four times at sites B, C, E, and F. At site D both the crust and basal layer were relatively thin, facilitating infiltration and decreasing erosion. Rains smoothed the crust at sites C and F, obliterating most surface cracks. Both the pumice layer and old soil were very permeable at all sites, but the tephra crust and basal layer had such low permeability to water that puddles remained in low spots for up to two days following rains. Water retained by either of these layers drained rapidly upon puncturing of the layer. This low permeability contributed to the formation of erosion channels. Very little change occurred in the tephra deposit during the winter of 1981–82, reflecting stabilization by the accumulation of organic matter and that the tephra on the most vulnerable microsites had already eroded. Litter cover of the tephra increased from 3–23% in 1980 to 42–85% in 1982 with most change from 1980 to 1981. Most litter was conifer needles, although cover of twigs and cones reached between 4% and 7% by 1982.

Plant survival

In all three years, virtually all the cover at every site was from plants which survived the eruption. By 1982, seedlings were common but their cover reached a maximum of only 0.2% and was generally below 0.1%.

Cover of small trees was lower than on cleared plots at sites C, E, and F (Table 2). Trees and shrubs taller than the tephra was deep were buried only where they were under snow, as we have explained elsewhere (Antos & Zobel, 1982). Effects of snowpack explain much of the reduction in tree cover at sites C and F, whereas cover loss at site E was mostly due to burial of small trees by the deep deposit. Tree density was reduced more than cover because numerous very small individuals were buried. Some partially buried trees died after 1980.

Shrubs averaged 1–1.5 m tall at most sites and thus few individuals were totally buried except where snow had been present. Leaves were dirty all during summer 1980 because of secondary deposition of tephra retained in the canopy. *Vaccinium* leaves dropped early, by mid-August, 1980. From 1980 to 1981, shrub cover increased at most sites (Table 2). Sprouting of buried ericaceous shrubs was poor the first summer, but many new shoots

Table 2. Percent cover of major plant growth-forms by site, year and treatment (N = natural tephra plots, C = cleared plots). The significance of differences between numbers is indicated by * = $p < 0.01$.

Site	Year	Small trees			Shrubs			Deciduous herbs			Evergreen herbs			Bryophytes		
		N		C	N		C	N		C	N		C	N		C
A	1980	2.81		–	10.71		–	9.80		–	3.66		–	6.83		–
		*						*						*		
	1981	3.21		1.87	11.68		8.78	16.69		12.20	4.48		7.69	35.26		42.23
		*		*	*		*	*		*	*		*	*		*
	1982	3.87		2.29	17.00		13.94	25.43		19.85	6.52		12.05	45.92		48.69
B	1980	10.55		–	13.19		–	0.01		–	11.63		–	0.08		–
					*						*			*		
	1981	12.05		7.25	16.90		21.50	0.18		0.01	13.46		23.15	0.37	*	28.29
					*		*				*			*		*
	1982	11.44		7.15	21.40		24.65	0.35		0.04	16.11		24.11	0.50	*	31.42
C	1980	4.31		–	5.76		–	9.83		–	0.99		–	0.03		–
					*			*			*			*		
	1981	4.35	*	7.97	12.75	*	37.19	20.76		17.33	1.80	*	3.11	0.22	*	19.81
					*		*	*		*	*		*	*		*
	1982	4.84	*	7.43	19.84	*	47.86	28.40		28.89	3.74	*	5.32	0.53	*	22.45
D	1980	5.03		–	21.98		–	6.90		–	0.42		–	0.54		–
					*									*		
	1981	5.51		6.57	40.04		39.86	7.44	*	31.00	0.71	*	2.64	2.07	*	22.38
				*									*	*		
	1982	8.58		9.35	41.77		42.00	8.92	*	27.46	0.87		3.49	2.60	*	21.06
E	1980	4.24		–	14.92		–	0.03		–	0.03		–	0.06		–
					*									*		
	1981	3.96	*	6.09	22.33		31.26	0.74	*	1.40	0.04	*	3.44	0.54	*	8.35
							*			*				*		
	1982	4.36	*	6.16	23.06		35.68	1.03	*	2.44	0.06	*	4.22	0.74	*	8.96
F	1980	1.82		–	0.01		–	0.12		–	0.00		–	0.05		–
														*		
	1981	2.00	*	12.16	0.22	*	13.37	1.39	*	16.23	0.17	*	6.09	0.47	*	27.89
							*			*				*		*
	1982	2.00	*	12.17	0.35	*	16.97	2.20	*	23.86	0.50	*	9.08	0.75	*	30.52

Table 3. Density (number/m²) of major plant growth-forms by site, year and treatment (N = natural tephra plots, C = cleared plots). The significance of differences between numbers is indicated by * = $p<0.01$.

Site	Year	Small trees			Shrubs			Deciduous herbs			Evergreen herbs		
		N		C	N		C	N		C	N		C
A	1980	1.08		–	2.37		–	19.78		–	0.43		–
					*			*					
	1981	1.02		1.90	2.63		2.28	27.44		25.03	0.54		1.03
					*			*					
	1982	1.04		1.80	3.34		2.58	30.11		26.77	0.63		1.07
B	1980	1.27		–	3.10		–	0.02		–	4.62		–
		*			*								
	1981	1.08	*	4.02	4.08		3.76	0.22		0.02	4.68		7.68
		*			*		*				*		
	1982	0.82	*	3.76	5.09		4.40	0.25		0.28	5.68		8.56
C	1980	0.27		–	1.99		–	12.48		–	2.93		–
					*			*			*		
	1981	0.23	*	5.50	3.65	*	6.06	25.01		24.74	4.31	*	8.76
					*		*	*		*	*		*
	1982	0.27	*	5.70	5.49	*	7.54	35.53		39.48	6.64	*	11.32
D	1980	0.88		–	2.84		–	13.13		–	0.93		–
								*					
	1981	0.82		0.82	3.05		2.76	8.45	*	43.84	1.04	*	4.70
								*					
	1982	0.92		0.82	3.53		3.00	11.77	*	44.68	1.57		6.62
E	1980	0.41		–	3.57		–	0.15		–	0.11		–
	1981	0.58	*	3.57	3.40		4.43	1.99	*	6.30	0.17	*	6.94
				*			*						
	1982	0.22	*	2.81	3.54		5.04	2.27	*	7.28	0.17	*	7.13
F	1980	0.05		–	0.01		–	0.37		–	0.00		–
	1981	0.05	*	10.08	0.09	*	3.73	3.73	*	68.59	0.39	*	9.63
							*			*			*
	1982	0.04	*	10.08	0.15	*	4.80	5.99	*	95.51	0.95	*	19.24

emerged from the tephra in 1981 and 1982. In 1982 shrub cover was markedly lower than in cleared plots only at sites C and F (Table 2). Shrub density responded similarly to cover (Table 3), although differences between natural and cleared plots were smaller.

The tephra strongly affected herbs and bryophytes. Tephra depth was the major factor controlling damage and recovery for both groups, but bryophytes were more easily destroyed (Fig. 2).

The herbaceous species at our sites represent a wide range of growth forms. We classified species as deciduous, those having exclusively (or nearly so) current year leaves, and evergreen, those having a large proportion of second year or older leaves.

Herb cover at sites A and C came primarily from deciduous species and was similar in natural tephra and cleared plots in 1981 and 1982 (Fig. 2, Table 2). Cover on natural tephra approximately doubled from 1980 to 1981, and increased further in 1982. However, cover on cleared plots also increased from 1981 to 1982. The difference in evergreen herb cover between natural and cleared plots at sites B and C resulted from burial of long-lived leaves, which are replaced slowly.

Most herbs at site D are deciduous. Cover was one-quarter of the cleared plot value in 1981 and one-third in 1982 (Fig. 2, Table 2). In contrast, density decreased in 1981, then increased in 1982 (Table 3). Many herbaceous shoots were unable to penetrate the 75 mm deposit even though the crust almost disappeared by 1981.

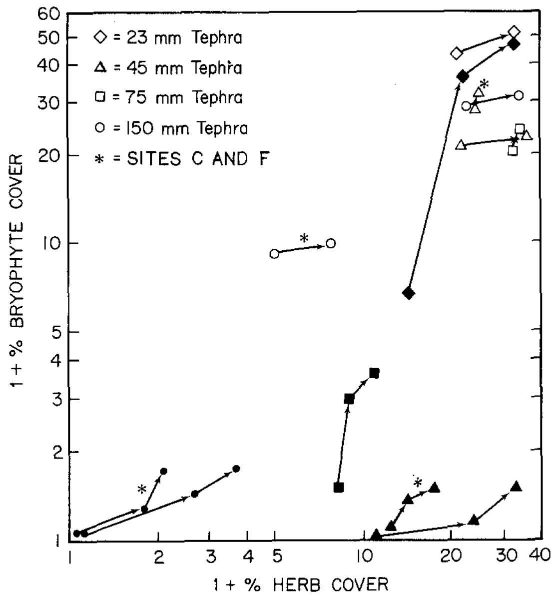

Fig. 2. Herb and bryophyte cover changes at the six sites. (Note the logarithmic scale). Closed symbols represent natural plots; open symbols cleared plots. Arrows connect data points from different years for the same set of plots.

Tephra 150 mm deep killed almost all pre-existing herbaceous plants (Tables 2, 3); they survived primarily where erosion thinned the deposit. At both sites E and F most of the herb cover was in a few eroded plots. At site F almost all the herbs outside cleared plots occurred in five heavily eroded plots. When these plots are removed from the average, deciduous herb cover on natural plots was only 0.15% in 1981 and 0.08% in 1982.

At site A moss cover increased over five-fold from 1980 to 1981 (Fig. 2, Table 2). Tephra barely covered the large mosses abundant at site A, and they grew through what covering there was. Bryophyte cover on the natural tephra in 1982 was 94% of that in cleared plots. Few, if any, mosses at our sites grew through tephra greater than 40 mm deep. Where the tephra depth exceeded 30 to 40 mm, mosses survived only in eroded areas, especially on logs; there was little relationship between moss cover and further increase in tephra depth. In 75 mm tephra, moss cover exceeded that with 45 mm tephra (Table 2), largely because of the abundance of logs and resulting slumping to tephra at site D. We observed very little moss establishment on the tephra surface.

Species responses

Although many species showed the same relationships to tephra depth as already described for the general growth form to which they belong, there are some interesting exceptions.

Of all the vascular plants at our sites, *Gaultheria humifusa* was most easily damaged by tephra. It is a prostrate, evergreen subshrub with relatively slow growth; 45 mm of tephra completely buried most plants. There has been no recovery; buried plants produced small erect shoots but these almost never reached the surface.

With 75 mm of tephra, responses of deciduous herbs varied. In 1981, cover of *Gymnocarpium dryopteris* dropped to less than half the 1980 value; then it returned to near the 1980 value in 1982. In contrast, the cleared plot values changed little between 1981 and 1982. *Clintonia uniflora*, similar in growth form to *Gymnocarpium*, increased in cover and density in 1981. After this initial rapid recovery, probably resulting from upward rhizome growth, change was slow.

Erythronium montanum was the most abundant deciduous herb at site F. In contrast to other species, it decreased in cover and density from 1981 to 1982. This decrease probably resulted from its failure to shift the location of perennating buds upward into the tephra.

Species diversity

Few species have been eliminated completely from any stands. Erosion was very important in this respect because it removed tephra from low, wet spots which contained many of the less common species. Logs and slopes of mounds were also important refugia, especially for bryophytes that occur preferentially on wood. Only at site F was there much reduction in total number of species: there were 26 herbaceous and five shrub species in cleared plots compared to 19 herbs and two shrubs in natural tephra plots in 1982. Even so, it is interesting that individuals representing many species were occasionally able to penetrate 150 mm of tephra.

A second measure of diversity is number of species per m^2 plot (species density). Shrub species density varied little among years or between cleared and natural plots at four sites. At site C there was

Table 4. Average number of herbaceous species per m² plot. N = natural tephra plots. C = cleared plots.

Site	Plot type	1980	1981	1982
A	N	3.05	3.75	4.27
	C	–	3.46	4.08
B	N	1.21	1.33	1.59
	C	–	1.72	1.88
C	N	2.75	3.28	3.95
	C	–	3.58	4.16
D	N	2.37	3.02	3.17
	C	–	4.11	4.44
E	N	0.09	0.18	0.23
	C	–	0.97	0.97
F	N	0.30	0.57	0.76
	C	–	2.89	3.14

an increase with time as buried shrubs sprouted. In 1982, at site F, there were only 0.1 shrub species per natural plot versus 1.4 per cleared plot.

Herbaceous species density was about the same in natural tephra and cleared plots at the 23 and 45 mm sites, but it increased with time (Table 4). With 75 mm tephra, diversity per plot was reduced 25%. In sites with 150 mm tephra, many species have been eliminated over large patches; herbaceous species density was reduced to about 25% of the cleared plot value (Table 4). In both 150 mm sites, areas up to 20 m across were devoid of herbaceous plants.

Discussion

Cleared plots

We would like to have had pre-eruption data to use as a basis for determining damage to plants caused by the tephra deposit, and also for evaluating subsequent changes in species cover and density. Such data did not exist. Consequently, we cleared plots to get some indication of pre-eruption plant composition. These plots have greatly aided the interpretation of plant changes in the tephra, but they do not serve as a strict control. Damage by both tephra and tephra removal in 1980 suppressed cover and density values for a year or more for at least some species. Conversely, large buried rhizome systems may have concentrated their aerial shoot production in the cleared plots. Thus, plant abundance in cleared plots was probably lower, but could have been higher for some species, than if the 1980 eruption had never happened. Judging from our experience with the sites and these types of forests in general, we believe that herb abundance was depressed in the cleared plots and probably was approaching pre-eruption levels by 1982.

Instead of using cleared plots we could have, in theory, directly compared matched sites with different tephra depths. This proved unfeasible. Natural vegetation is highly variable and matching sites, even under the best circumstances, is difficult; after tephra deposition it was impossible. Our sites differ and very few species occur in abundance at all four tephra depths. Nonetheless, the sites are sufficiently similar to allow a reasonable interpretation of how the common growth forms present in the conifer forests around Mount St. Helens respond to tephra deposits of different depth.

Responses of established plants

During the three post-disturbance growing seasons we examined, almost all cover at all sites came from plants present before tephra deposition. This generalization covers all growth forms, including bryophytes.

Tephra 23 mm deep resulted in only minor cover changes even in the moss layer. Most plants, including many bryophytes were able to grow through this depth of deposit.

Burial by 45 mm of tephra destroyed all bryophytes; abundance of most herbs dropped but increased rapidly between 1980 and 1982. Cover in natural plots was similar to that in cleared plots, and was probably approaching that present before the eruption, at least for deciduous species by 1982. Evergreen species were slower to respond, largely because of longer leaf turnover times. *Gaultheria humifusa* was a pronounced exception to this pattern of rapid recovery. This low, prostrate subshrub appears to have about as much ability to survive tephra burial as a large moss; it was destroyed except in a few microsites where erosion removed the tephra.

In contrast to 45 mm tephra, many herbs failed to grow through 75 mm tephra. In 1982 cover in tephra was only one third of that in cleared plots at site D. The loss of individuals was widespread among species. Herb cover was increasing, but only slowly. Hare grazing may be important in slowing the recovery and causing differences in species response.

Tephra 150 mm deep destroyed almost all individuals of all herbaceous species at our sites. The few individuals that did grow through 150 mm tephra are potentially important as a source for revegetation, even though their density is low.

Shrubs and trees were not greatly damaged even by 150 mm tephra except where snow was present (Antos & Zobel, 1982). Shrub recovery has been rapid at site C but not site F. Apparently shoots have difficulty emerging from the deeper tephra.

Refugia

We cannot overemphasize the importance of microsite refugia from the tephra disturbance. Logs were crucial to moss survival and also aided herb survival. Logs have many important structural and functional roles in old-growth coniferous forests (Franklin *et al.*, 1981; Franklin & Hemstrom, 1981); another role is producing plant refugia during tephra fall. As with some other functions, larger logs were more important.

Erosion greatly facilitated plant survival. Many herb species survived deep tephra only where erosion thinned the deposit. Some plants can survive at least a full year of burial and grow when exhumed; we are experimentally testing the results of two years burial.

Our sites were all located on relatively level ground in generally mountainous topography. Consequently, the erosion on them was minimal for the area. On some steep slopes, herbs were common due to erosion of the deposit.

Future changes

The unvegetated forest floor at the 150 mm tephra sites can be colonized by vegetative expansion of surviving plants or establishment of new genets. Many of the forest herbs spread by rhizomes or stolons and this process, along with emergence of new shoots from buried plant parts, accounts for the observed increases in cover during the first three years following the disturbance. Most of the shrubs also spread by rhizomes. Seedlings of trees and a few herbaceous species were common on the tephra by 1982, but we found few or no seedlings of most of the forest herbs at our sites. Only species which were already present in the forest were successfully establishing from seed, thus, ruderal species will not be a component of vegetation change following this disturbance. It will probably take many years for herb and bryophyte cover to reach pre-eruption levels at the deep tephra sites, and it is too early to evaluate the relative long-term importance of vegetative expansion versus genet establishment. Species composition may be altered indefinitely.

Comparisons with other disturbances

The tephra deposit differs from other disturbances common in Cascade Mountain forests; although the canopy remained, understory vegetation was greatly altered and a new substrate was added. In contrast, fire and windthrow often destroy the canopy and do not bury understory plants. After most other disturbances new species colonize the site, but not following tephra fall. Even where the herb and shrub layers were almost destroyed, revegetation is occurring entirely by species that were originally present on the site. The residual tree canopy is probably responsible for this lack of invading species, and is an important characteristic of the tephra disturbance.

The deposit of tephra was more similar to other phenomena that bury plants than to the disturbances common in the Cascade Mountains. Alluvial deposition on floodplains may be the disturbance most similar to tephra fall, in that understories are buried while the canopy is left intact. Tephra deposition is the only process likely to bury plants on our sites.

Mount St. Helens created a variety of disturbances (del Moral, 1981; Lipman & Mullineaux, 1981). The devastated area is covered with tephra or landslide debris of varying depth but the tree layer is gone; shrubs and small trees were also destroyed except where they were protected by snow (Means *et al.*, 1982). Thus shrubs survived in the devastated area when buried by snow, while snow in tephra fall areas outside the devastated area contributed to their demise (Antos & Zobel, 1982). This complete reversal of the role of snow is characteristic of the great difference between local areas and types of disturbance produced by a single event.

The tephra fall is a unique type of disturbance and data from other common disturbances have only limited applicability in predicting plant response.

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