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December 2017

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This article was originally published at:
https://doi.org/10.1002/ecs2.2045

Citation for this paper:

Zobel, D. B. & Antos, J. A. (2017). Community reorganization in forest understories buried by volcanic tephra. *Ecosphere*, 8(12), article e02045. DOI: 10.1002/ecs2.2045 esa ECOSPHERE

Community reorganization in forest understories buried by volcanic tephra

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Citation: Zobel, D. B., and J. A. Antos. 2017. Community reorganization in forest understories buried by volcanic tephra. Ecosphere 8(12):e02045. 10.1002/ecs2.2045

Abstract. Disturbance is a key factor contributing to community organization. Deposition of tephra (aerially transported volcanic ejecta) is a widespread disturbance of global relevance, but its effects on ecosystems have received limited attention. We studied forest understory community change for 30 yr following tephra deposition from the 1980 eruptions of Mount St. Helens (Washington State). Four old-growth, subalpine conifer stands had a wide range of initial damage and patterns of community re-development. We measured understory diversity, structure, and species composition and calculated relationships of plant cover with environment and cover of other plants. Overall, those communities that were altered greatly by tephra tended to converge with time on their pre-eruption characteristics; however, substantial divergence occurred in some situations. For example, moss cover failed to reach pre-eruption levels in all stands, whereas importance and diversity of woody plants sometimes greatly exceeded pre-eruption values. Plant–environment relationships that were significant before the eruption disappeared and did not re-develop. Smaller plants were more affected by environment than larger ones. Relationships before the eruption and also 30 yr after the eruption were primarily with other plant species, whereas relationships just after the eruption were with tephra depth and factors that modified its impact. Understory plant importance was usually lower beneath a tree canopy than in gaps, but there was little sign of interference from understory growth forms. Post-eruption soil disturbance usually increased understory plant importance, while woody debris sometimes decreased herb and tree seedling cover. Tephra deposition, which did not immediately kill canopy trees, differed from the disturbances usually studied (e.g., fire, windthrow, bark beetles). Even so, these lessons from our study should be widely applicable: Similar species may respond differently; minor, early environmental differences may induce major, long-term community change; successional trajectories may diverge from the pre-disturbance community; and secondary disturbances may modify successional trajectories.

Key words: community development; conifer forest; disturbance; Mount St. Helens; plant–environment relationships; secondary disturbance; succession; understory plants; volcanic tephra.

Received 8 October 2017; accepted 12 October 2017. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Disturbance changes plant communities by killing some plants, injuring others, and creating conditions in which new species have a competitive advantage over resident plants. Following the disturbance, during succession, communities change as survivors grow and reproduce, new species invade, and the environment again is altered. Post-disturbance vegetation may eventually develop properties similar to pre-disturbance vegetation, converging on the original community. In other cases, the developing community may continue to differ significantly from vegetation occupying that location before the disturbance, diverging from the original community. The potential exists for the system to move to an alternate state, which might be stable (Beisner et al. 2003, Schröder et al. 2005). Such a transition could be considered a regime shift, with major implications for ecosystem function and biodiversity (Folke et al. 2004). When most individuals are destroyed by disturbance, the assembly of a new community can be strongly affected by various contingencies and priority effects from initially established species (Chase 2003, Kardol et al. 2013, Fukami 2015, Sarneel et al. 2016).

Determining the extent to which systems converge on an initial or earlier ecosystem state and whether an alternate state may have developed is critical to understanding disturbance effects on vegetation and assessing the success of restoration treatments (Suding et al. 2004, Suding and Hobbs 2009, Matthews and Spyreas 2010, Kirkman et al. 2013). In order to assess the presence and degree of community divergence during succession, one needs details about the pre-disturbance community and a long timescale; changes of vegetation are often slow and may not be linear. Most studies of succession lack one or both requirements; only a few (Halpern 1988, 1989, Halpern and Lutz 2013) have both pre-disturbance composition data and a long duration.

Most studies of succession describe changes in species composition. But community diversity, structure, function, relationships among organisms, and relationships of organisms with environment also help to define a community (Whittaker 1975). Likewise, other ecosystem and community properties have been used to assess succession (Kahmen and Poschlod 2004, Fukami et al. 2005, Romme et al. 2016). Here, we present a chronology of vegetation change that can be related to pre-disturbance conditions, has a long duration, and includes aspects of composition, structure, inter-plant relationships, and plant relationships to environment, including ongoing small-scale disturbances. Descriptions of relationships among plant types and of plants with environment allow the development of data-based hypotheses about which environmental properties control species composition and which changes in environment cause succession. We assess the degree of divergence from pre-disturbance communities and consider whether survivors of a highly disturbed vegetation constitute a community.

Our study system is the understory vegetation of old-growth subalpine conifer forests that received volcanic tephra (aerially transported volcanic ejecta) from the 1980 eruptions of Mount St. Helens, Washington. We studied four communities that had different degrees and types of disturbance associated with that tephra deposit, with a wide range of impacts; one understory showed limited damage; another was nearly obliterated (Antos and Zobel 1985*a*, 2005, Zobel and Antos 1997, 2007, 2009, *in press*). Here, we report for the first time changes in the overall species composition, the influence of the environment at the time of disturbance, and the influence of small, continuing disturbances over a 30-yr period.

Tephra deposition occurs frequently in many parts of the world (Ayris and Delmelle 2012), including the Pacific Northwest of the United States (Mullineaux 1986), and often has major effects on vegetation (Griggs 1918, Eggler 1948, Franklin and Dyrness 1973, Efford et al. 2014, Eddudóttir et al. 2017). Understanding plant response to tephra is important to society, as future volcanic activity is inevitable.

We endeavor to answer these questions: (1) What patterns of succession were shown by different community properties (diversity, community structure, species composition, environmental relationships) and types of plants? (2) To what extent did the re-developing vegetation diverge from pre-eruption conditions? (3) Based on plant–environment relationships, what appear to be the likely mechanisms of community change?

METHODS

Study sites and data acquisition

We report temporal patterns of vegetation change in the understory beneath intact old-growth subalpine conifer forest canopies during the first three decades after plant burial beneath volcanic tephra from the 18 May 1980 eruption of Mount St. Helens, Washington. Our study area is in the heavily forested *Abies amabilis* vegetation zone of Franklin and Dyrness (1973). The study area was affected only by tephra (aerially transported volcanic ejecta, primarily pumice with texture of volcanic ash and lapilli; Zobel and Antos 1991*a*), not the more extreme events that destroyed trees closer to the volcano (Dale et al. 2005).

We studied four communities that differed in original composition, environment, and degree of disturbance (Table 1; Antos and Zobel 1985*a*, Zobel and Antos 1997). Two sites received deep tephra (~15 cm, denoted by "D" in the site code), and two, shallow (4.5 cm, "S"). Two sites were herb-rich ("R") and two were herb-poor ("P"). Sites with more herb species had later snow melt, more concave topography, and higher concentrations of Ca, Mg, and total N in the pre-eruption soil than sites with few herb species (Zobel and Antos 1991*a*). Most tephra fell atop snow pack at the herb-rich sites (Fig. 1a, c), but not at the herb-poor sites. This combination of circumstances produced four distinctive post-eruption situations (Antos and Zobel 1985*a*, Zobel and Antos 1997; Table 1):

Table 1. Site characteristics at the time of the eruption.

Property	Site code			
	SP	SR	DP	DR
Location				
Distance to crater (km)	58	58	22	22
Elevation (m)	1245	1290	1160	1240
Pre-eruption vegetation properties and their reduction by the disturbance†				
Moss cover (%)	28.3	19.8	8.4	27.9
Moss cover reduction (%)	99	99	97	99
Herb diversity (species/m^2)	1.56	3.60	0.98	2.90
Herb cover (%)	23.2	20.4	4.8	22.3
Herb cover reduction (%)	41	0	99	99
Herb density (individuals/m^2)	7.7	33.5	13.2	78.2
Herb shoot size (%)	3.01	0.61	0.37	0.29
Shrub diversity (species/m^2)	1.54	2.12	1.53	1.22
Shrub cover (%)	21.5	37.2	31.3	13.4
Shrub cover reduction (%)	21	66	30	99
Shrub density (individuals/m^2)	3.8	6.1	4.4	3.7
Shrub shoot size (%)	5.72	6.14	7.06	3.59
Tree seedling diversity (species/m^2)	1.00	1.42	0.83	1.06
Tree seedling cover (%)	7.3	7.9	6.1	12.2
Tree seedling cover reduction (%)	0	45	36	83
Environmental factors‡				
Canopy gap-C	0.03	0.12	0.04	0.33
Abies amabilis canopy-C	0.76	0.61	0.81	0.56
Chamaecyparis nootkatensis canopy-C	0.04	0.55	0.05	0
Pseudotsuga menziesii canopy-C	0.04	0	0.10	0
Tsuga heterophylla canopy-C	0.53	0.16	0.56	0.01
Tsuga mertensiana canopy-C	0.04	0.03	0.03	0.18
Light intensity (percentage of open)-Q	14.0	16.3	9.2	23.4
Slope (degrees)-Q	1.9	3.6	3.3	1.6
Cover by snow pack, 1980 (%)-Q	27.5	92.0	11.0	89.3
Cover by large wood, 1980 (%)-Q	10.7	3.7	5.4	4.3
Tephra depth (mm)-Q	42.9	46.1	134.3§	139.1
Minimal tephra depth (mm)-Q	26.5	25.8	–§	104.2

Note: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich.

† Cover and density are estimates of pre-eruption values (1981 data from plots cleared of tephra in 1980). Cover reduction = % (1981 cover in natural tephra plots compared to pre-eruption estimates). Diversity is expressed as species density (number of species/m^2). Shoot size (%) = cover/density.

‡ All environmental variables except tephra depth and minimal tephra depth were assumed to be the same before and after the eruption. C = categorical factor—the mean is the proportion of plots with the factor present; Q = quantitative factor—the mean is the mean value of the factor. Environmental factors differ among sites ($P \leq 0.007$), as do growth form covers ($P \leq 0.019$), based on a Kruskal–Wallis test.

§ Tephra depth was not measured at each plot at site DP; the depth value is the mean depth (10 measurements) in 1987. No minimum depth estimate is available.

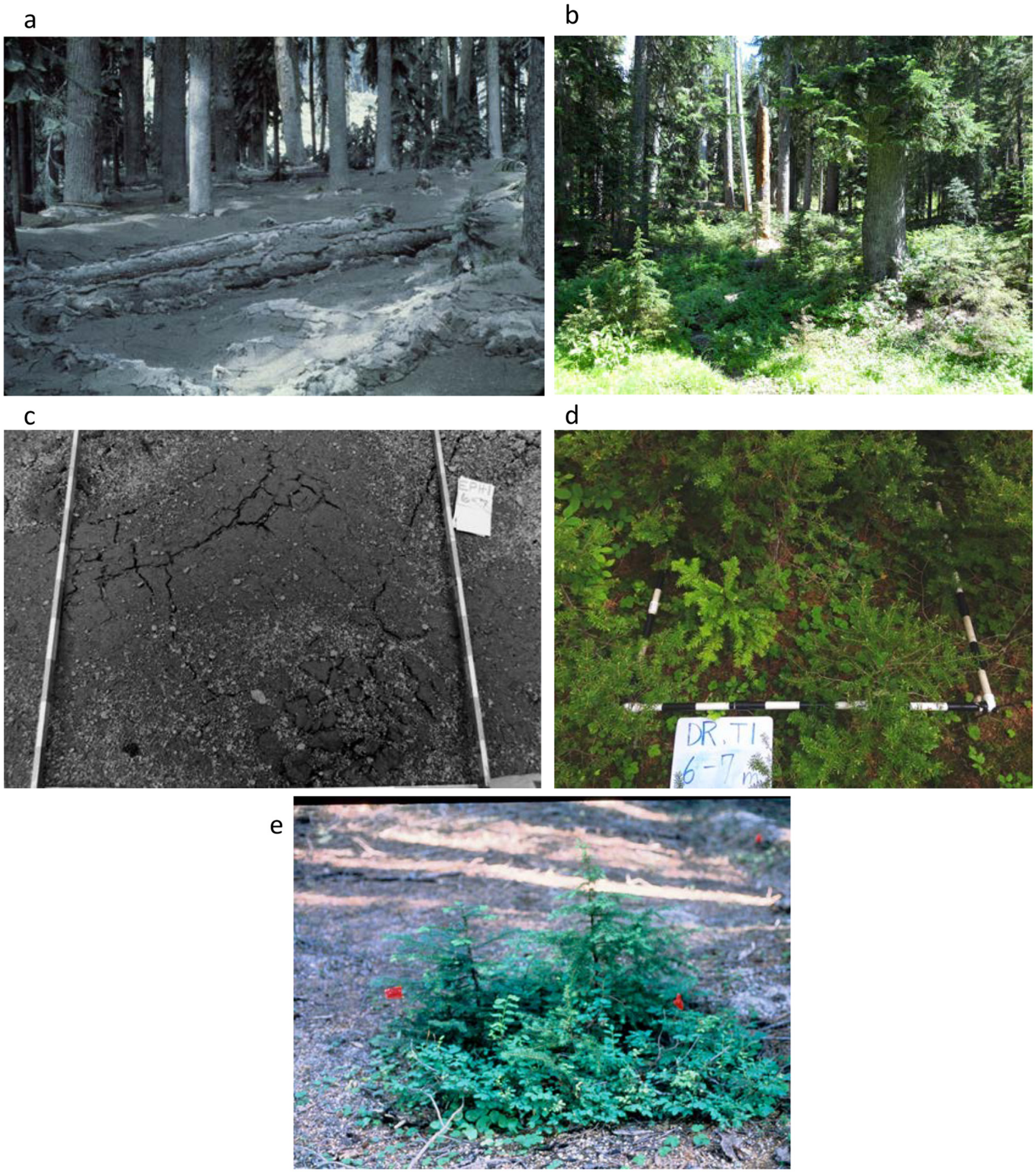

Fig. 1. View of the most heavily impacted study site (site DR) and representative 1-m^2 plots soon after tephra deposition and at or after the end of the study. (a) 1980, general photograph, showing effects of 12- to 15-cm tephra that prevented most herb regrowth; most of the tephra fell on snow, also destroying smaller woody plants. Photograph by Don Zobel. (b) 2010, general photograph, showing major colonization by tree seedlings as well as shrubs and herbs, in a location different than photograph (a). Photograph by Matt Blakely-Smith. (c) 1980, plot on undisturbed tephra. Cracked tephra crust indicated that the tephra fell on snow. Black-and-white photograph by Joe Antos. (d) 2016, the same plot as in c, showing vegetation recovery. In 2010, at the end of this study, percent cover was as follows: bryophytes 50, herbs 7, shrubs 15, and tree seedlings 26. Photograph by Dylan Fischer. (e) 1983, plot from which tephra was removed in 1980 and from which pre-eruption vegetation was estimated in 1981. Photograph by Don Zobel.

1. Almost complete destruction of all four understory layers (tree seedling, shrub, herb, and bryophyte, hereafter, "moss"; site DR, Fig. 1).
2. Almost complete loss of moss and herbs, with survival of most small woody plants (site DP).
3. Loss of moss and much of the shrub and tree seedling layers (site SR).
4. Loss of moss and some herbs (site SP).

We estimated the nature and relationships of pre-eruption vegetation at each site using post-eruption (1981) sampling of 50 1-m^2 plots from which tephra was removed 2–4 months after the eruption (Antos and Zobel 1985*a*; Fig. 1e). Tephra was carefully removed using small excavating implements, brushes, and a small vacuum cleaner. Almost all tephra was removed, although minor amounts remained where removal would have damaged plants. We followed post-eruption vegetation change by sampling 100 permanent 1-m^2 plots with natural tephra at each site (Fig. 1c, d) in 1980–1983, 1989 or 1990, 2000, 2005, and 2010; we also sampled deep-tephra sites in 1984 and 1987. Plots were spaced at 3-m intervals along six to ten transects per site; cleared-plot transects were interspersed among those with undisturbed tephra. Because of substantial natural variation, tree seedlings were more abundant in natural than cleared plots at site SP; thus, we considered there to be no change in tree seedling cover during the eruption in this site with shallow tephra and little snow pack. Taxonomic nomenclature follows Hitchcock and Cronquist (1973); some names have changed, but we wish to keep nomenclature consistent with our earlier reports.

We grouped plants into four growth forms (moss, herbs, shrubs, and tree seedlings). We measured shoot canopy cover and density for all vascular species (as discussed by Zobel and Antos 1997), and cover for moss. For herbs and shrubs, we calculated shoot size (cover/density), except for a few situations where density was not measured due to limited sampling time. Due to problems separating pre- and post-eruption tree seedlings as time progressed, we provided analyses only for pre-eruption tree seedlings for 1981 in cleared and natural plots and for all branched tree seedlings in natural plots in 2010. Diversity was expressed as the number of species per plot (species density) for herbs, shrubs, and tree seedlings.

This paper presents data from all plots at all sites. Previously, we excluded a few deep-tephra plots in which erosion occurred during the first winter after the eruption, thus removing the influence of tephra erosion from our analysis (Antos and Zobel 1985*a*, 2005, Zobel and Antos 1997). We did this to focus specifically on the influence of the tephra deposit. In this paper, we consider the effects of secondary disturbances, including early erosion. Our data here are more representative of actual stand-level conditions, but less so of the precise effects of tephra, than our earlier reports.

We sampled environment primarily in 1980, determining for each 1-m^2 plot:

1. mean and minimal tephra depth (except at site DP, for which we have a mean site value for 1987; Zobel and Antos 1991*a*);
2. percent cover of large exposed wood in the plot;
3. percent cover of snow pack at the time of the eruption, based on the observation that where tephra fell on snow, the tephra crust cracked (Antos and Zobel 1982). We assumed that the distribution of snow among plots in 1980 was indicative of relative snow-melt timing in other years;
4. micro-topography: slope of the surface for evenly sloping plots and categories of micro-topographic type (including convex, concave, and types based on slope steepness) for all plots;
5. tree canopy: Each plot was scored for presence of each canopy tree species above the plot. Plots with no tree foliage above them were considered to be in a canopy gap; and
6. light intensity as percentage of that in the open on the same clear summer day, measured at the ground surface in 1982 using ozalid paper (Friend 1961, Bardon et al. 1995).

We also recorded the percent of each plot affected by three types of post-1980 disturbances during each sampling year: soil disturbance (erosion by slumping or by water, elk activity, animal burrowing, and tree fall producing pit-and-mound micro-topography); woody debris deposited on the plot surface (tree stems, large branches, and bark and rotting wood from snags and downed logs)—stems suspended above the soil surface were not counted; and branches with intact foliage deposited on the plot surface.

Defining community properties and relationships

We analyzed data for all four understory growth forms and for eight widespread taxa (the mosses *Rhytidiopsis robusta* and *Dicranum* spp., the herb *Rubus lasiococcus*, the shrubs *Vaccinium membranaceum* and *Vaccinium ovalifolium*, and the tree seedlings *A. amabilis, Tsuga heterophylla,* and *Tsuga mertensiana*). We also used four herbs at site DR to illustrate species differences within a growth form (*Erythronium montanum, R. lasiococcus, Tiarella unifoliata*, and *Valeriana sitchensis*).

To track the re-development of each understory growth form and each widespread taxon at each site, and to judge how widely post-disturbance vegetation diverged from the pre-eruption communities, we considered the following community attributes and relationships: diversity, importance (cover, density), shoot size (cover/density), plant species composition, relationships of plant cover with environmental factors at the time of the eruption, relationships of cover with cover of other growth forms at each sampling date, and relationships of cover with post-eruption disturbance.

We analyzed cover, density, and plant size for vascular plants and cover for the moss layer. We calculated diversity (species density) for herbs, shrubs, and tree seedlings. We analyzed each of the growth forms and widespread taxa separately. We used the Mann–Whitney *U* test to determine significance of differences between values of diversity, cover, density, and shoot size on natural tephra (in 1990, 2000, and 2010) and values representing pre-eruption vegetation, that is, values in 1981 in plots from which tephra was removed in 1980.

To evaluate temporal changes in overall species composition, we used non-metric multidimensional scaling (NMS) ordinations with PC-ORD version 6, using cover data and the Sorensen distance measure (McCune and Mefford 2011). All sampling dates were included for natural tephra, which allowed examination of successional changes on the tephra as indicated by the temporal trajectories of the species composition in ordination space. The 1981 data from plots cleared in 1980 were used to indicate the pre-disturbance composition; how trajectories of change moved toward this reference point can be considered an indication of the convergence in composition upon the original community. We used various subsets of the species to evaluate how different growth forms changed through time. For considering patterns of change within and among sites, we constructed ordinations for individual sites and for all sites combined. Interpretations were similar among ordinations; here, we present ordinations using all sites for (1) all species, (2) herbaceous plants only, and (3) shrubs only.

We identified relationships among cover of different growth forms and taxa, and relationships of cover with environment, at three times: in pre-eruption vegetation (based on 1981 sampling of 1980 cleared plots) with environmental properties that did not change during the eruption; first year post-eruption (1981 sampling of natural tephra plots), adding tephra properties to environmental factors present before the eruption; and 30 yr post-eruption (2010 sampling in natural tephra plots).

For relationships with cover that, from 1981 to 2010, changed sign or that gained or lost significance, we conducted analyses for all intervening sampling years, to determine when the change occurred. Relationships that lacked significance during pre-eruption, 1981, and also 2010 were excluded, as they were not obviously connected with the eruption, did not persist, and were thus of less interest than the relationships we used. We lacked appropriate data for tree seedlings for intervening years.

We used several environmental properties, both quantitative and categorical (Table 1). Each data point referred to a single 1-m^2 plot during a specific sampling year. For all periods, we used the categorical factors micro-topographic type and canopy type, and the quantitative factors light intensity, micro-topography quantified as slope, cover of large woody debris, and percentage of plot covered by snow during tephra deposition. After the eruption, we added mean and minimal tephra depth. We interpreted some environmental factors differently than others. For example, the location of early- and late-melting snow in 1980 probably represented a pattern that was consistent among years, and we included snow as a factor in the analysis for the whole time span of the study, including pre-eruption communities. Likewise, we assumed that presence of canopy species, micro-topography, and cover of large wood in 1980 did not change substantially during the eruption.

We also correlated cover of a given growth form and major species with that of other growth forms, correlating cover, for example, of moss with that of herbs, shrubs, and tree seedlings for natural plots within each site for a sampling year. We used combinations in which one growth form could reasonably be expected to compete with the other. Moss and herbs may reciprocally affect each other. Tree seedlings, which start smaller than some mosses, could be affected by moss, herb, and shrub cover. Shrubs, with few seedlings, are unlikely to be influenced by herbs and mosses. A significant negative relationship between a pair of growth forms could indicate competition or other interference. A positive relationship could indicate some "nurse-plant" effect or simply that both types grow well in similar environments.

In addition, we related cover to measures of post-eruption disturbance. The level of disturbance for a sampling year was quantified as the sum of the percent of plot affected by that disturbance since the eruption, except for twigs with needles, which were assumed to lose their influence after two years.

Significance of relationships of plant cover to environmental factors and to cover of other growth forms was judged with two analyses; we consider only relationships that were significant ($P < 0.05$) in both of the following analyses: (1) a single-factor analysis relating cover of a plant type to a factor; knowing this one-to-one relationship allowed us to develop causal hypotheses involving specific factors. For quantitative factors (Table 1), we used Spearman rank correlation between each plant type and the factor. For categorical factors, a Kruskal–Wallis test was used to determine significance of differences among categories within each factor. (2) A multi-variable analysis. Many factors are intercorrelated, and this analysis eliminated those factors that lost their significance when other significant factors were present in the analysis. We used a general linear model for variables that could be transformed to normality; for other variables, we used logistic regression on presence/absence data.

Using $P < 0.05$, and requiring simultaneous significance of both analyses, provided an overall $P < 0.0025$, which helped to compensate for the large number of individual analyses involved (approximately 306 per site for relationships with environment, 96 per site with growth form cover, and 90 per site with post-eruption disturbance).

For relationships significant in either 1981 or 2010, analyses were done for intervening years, to determine when relationships present in 1981 disappeared or when those absent in 1981 first became significant. The time to lose significance was quantified as the last year when the relationship was significant. Where the significance was intermittent, a single non-significant year was not considered. After two sequential sampling years with non-significance, the relationship was considered absent.

We used multi-variate analyses of cover at the end of 30 yr to suggest which variables might be most useful for developing hypotheses about mechanisms responsible for changes we observed after the eruption. Each analysis related cover in 2010 to three types of independent variables (environment, post-eruption disturbance, or influence of other growth forms), using only those factors that were judged significant using the two criteria described above. We did separate analyses for each growth form and taxon at each site.

We present all post-eruption results using the time since the eruption, rather than the calendar year, for example, 1981 = year 1 and 2010 = year 30. Statistical analyses were carried out using Statgraphics Plus for Windows, version 5.1 (Manugistics 2005), except for the Mann–Whitney *U* test, for which we used Statistix 9 (Analytical Software 2008).

RESULTS

Temporal course of diversity

The temporal course of diversity, quantified as species density (number of species/m^2), differed with growth form and degree of disturbance (Fig. 2, Table 2). Reductions of diversity occurred during the eruption for all growth forms at all sites, but for several situations diversity returned to pre-eruption levels by year 3. In other situations such as site DR, return toward pre-disturbance diversity was slow, taking 20 yr or more, and herb diversity at site DP remained below pre-eruption levels. Herb diversity at site SR (Fig. 2a) and tree seedling diversity in deep tephra (Table 2) eventually exceeded pre-eruption levels.

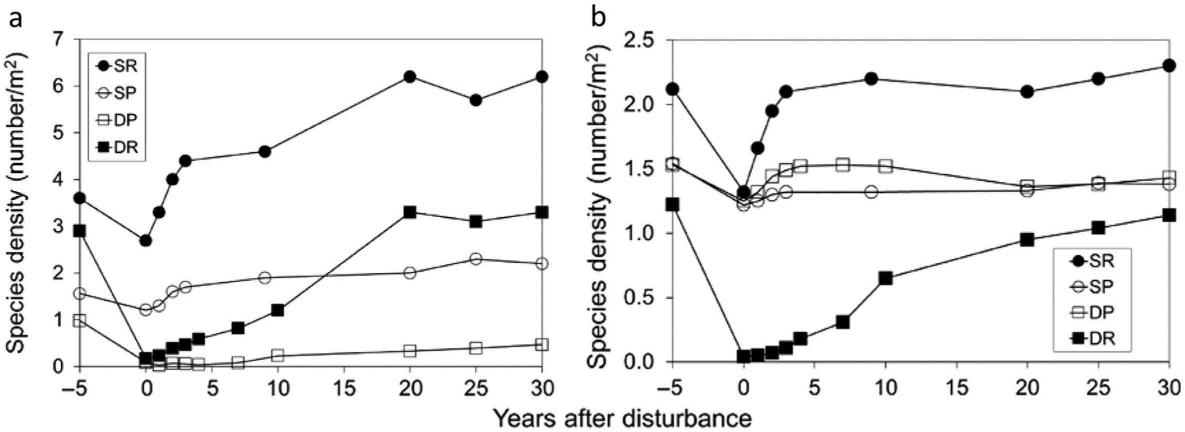

Fig. 2. Changes in species diversity (species density = species/m^2) with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) Herbs. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.66, site SR 0.21, site DP <0.001, and site DR <0.001; (2) year 20: site SP 0.26, site SR 0.001, site DP <0.001, and site DR 0.58; and (3) year 30: site SP 0.053, site SR 0.002, site DP 0.004, and site DR 0.35. For values after the eruption, a simple regression was positive and significant for all sites. (b) Shrubs. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.99, site SR 0.59, site DP 0.99, and site DR <0.001; (2) year 20: site SP 0.98, site SR 0.70, site DP 0.52, and site DR 0.014; and (3) year 30: site SP 0.86, site SR 0.18, site DP 0.82, and site DR 0.74. For values after the eruption, a simple regression was positive and significant for sites SP and DR, while a regression of 1/*x* vs. 1/*y* was positive and significant for site SR.

Temporal course of cover

The pattern of change in cover differed among growth forms, among species within growth forms, and among sites (Figs. 3–5, Table 3). Moss cover was strongly reduced and remained below pre-eruption levels at all sites, with the rate of increase slowing after year 20 at three sites (Fig. 3). Recovery by *Rhytidiopsis robusta* exceeded that of *Dicranum* spp. except at site DR (Fig. 3b, c).

Table 2. Diversity (species/m^2) of understory tree seedlings at three times.

Site	Pre-eruption†	Year 1‡	Year 30§
SP	1.00	0.75	0.78
SR	1.42	0.29	1.01
DP	0.83	0.32	1.48
DR	1.06	0.18	1.81

Note: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich.

† Pre-eruption tree seedlings before the eruption, based on cleared plots in year 1.

‡ Pre-eruption tree seedlings in natural tephra plots in year 1.

§ All branched tree seedlings in natural tephra plots in year 30.

Herb cover was strongly reduced in deep tephra and has remained far below pre-eruption levels (Fig. 4a). In shallow tephra, however, initial reductions were smaller and herb cover increased quickly, exceeding pre-eruption levels after year 2 at site SR and being near pre-eruption levels since year 10 at site SP. Individual herb species differed in response among sites. *Rubus lasiococcus* (Fig. 4b) returned to pre-eruption levels by year 20 at all sites except DP. Differences also occurred among herb species at a given site. At site DR (Fig. 4c), *Tiarella unifoliata*, *R. lasiococcus*, and *Valeriana sitchensis* cover reached pre-eruption levels by year 20; the pre-eruption dominant *Erythronium montanum* did not increase after the eruption.

Shrub cover was most strongly reduced where there was extensive snow pack (Fig. 5a). It rapidly increased with time at three sites, exceeding pre-eruption levels at sites SR and DP. Although shrub cover increased at site DR, it

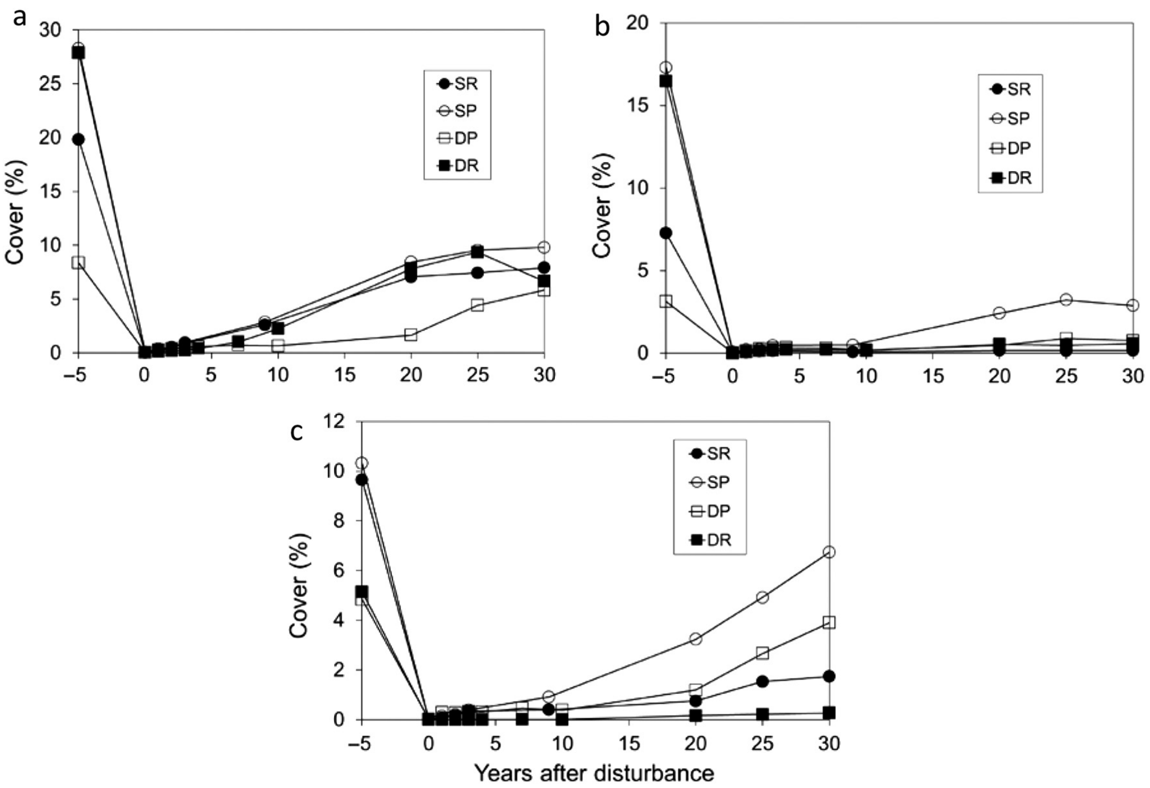

Fig. 3. Changes in moss cover with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) All mosses (and other bryophytes). *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: all sites <0.001; (2) year 20: all sites <0.001; and (3) year 30: site SP <0.001, site SR <0.001, site DP 0.029, and site DR <0.001. For values after the eruption, a simple regression was positive and significant ($P < 0.0002$) for all sites. (b) *Dicranum* spp. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: all sites <0.001; (2) year 20: all sites <0.001; and (3) year 30: site SP <0.001, site SR <0.001, site DP 0.007, and site DR <0.001. For values after the eruption, a simple regression was positive and significant ($P < 0.04$) for all sites. (c) *Rhytidiopsis robusta. P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: all sites <0.001; (2) year 20: all sites <0.001; and (3) year 30: site SP 0.002, site SR <0.001, site DP 0.001, and site DR <0.001. For values after the eruption, a simple regression was positive and significant ($P < 0.0002$) for all sites. Values through year 20 are also reported in Antos and Zobel (2005).

remained far below the pre-eruption level. There was no significant change at site SP. The two dominant shrubs, *Vaccinium membranaceum* and *Vaccinium ovalifolium*, each regained pre-eruption cover at all sites (Fig. 5b, c). *Vaccinium membranaceum* surpassed pre-eruption levels at site SR, while *Vac. ovalifolium* exceeded them at sites SR and DP.

Tree seedling cover was reduced at three sites, most strongly in deep tephra with much snow (Table 3). It increased beyond pre-eruption levels in deep tephra, especially at site DR where a dense seedling layer developed over much of the site. *Abies amabilis* dominated tree seedling populations throughout, but its relative importance declined with time in most cases.

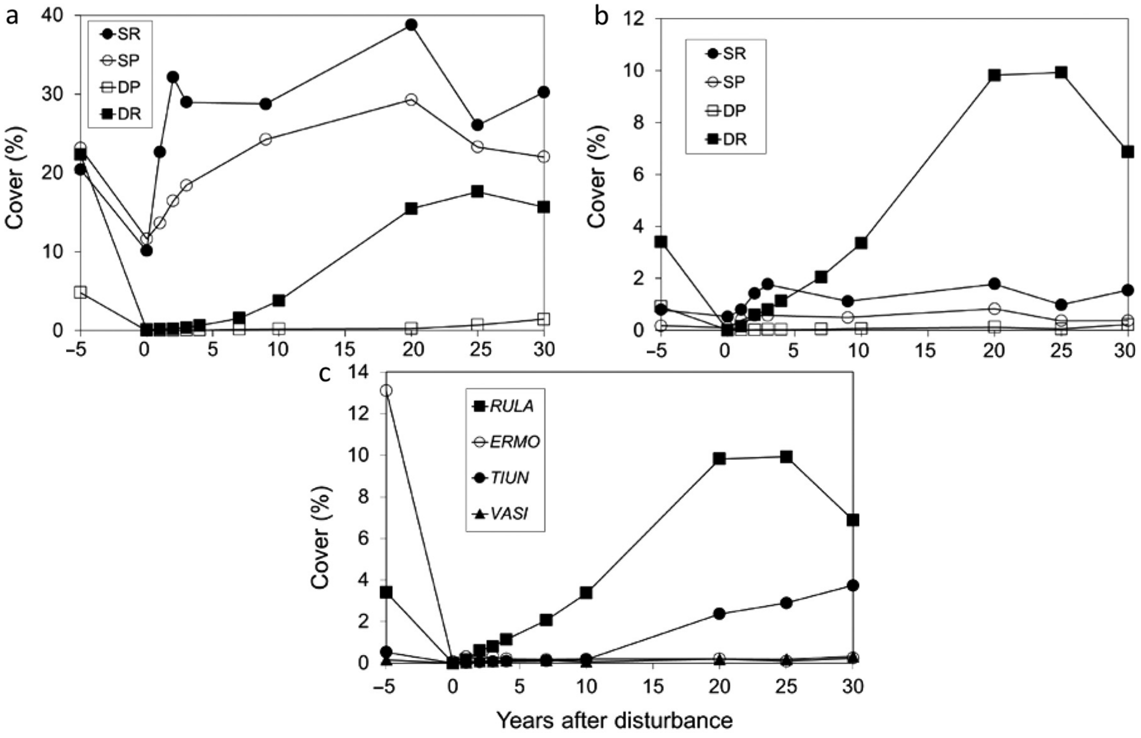

Fig. 4. Changes in herb cover with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) All herb species at all sites. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.90, site SR 0.35, site DP <0.0001, and site DR <0.0001; (2) year 20: site SP 0.31, site SR 0.010, site DP <0.001, and site DR 0.014; (3) year 30: site SP 0.82, site SR 0.037, site DP 0.002, and site DR 0.005. For values after the eruption, a simple regression was positive and highly significant ($P < 0.001$) for sites DP and DR, just significant for site SP ($P = 0.042$), and non-significant for site SR. (b) *Rubus lasiococcus* at all sites. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.32, site SR 0.39, site DP <0.001, and site DR <0.001; (2) year 20: site SP 0.21, site SR 0.33, site DP 0.001, and site DR 0.72; and (3) year 30: site SP 0.72, site SR 0.99, site DP 0.001, and site DR 0.70. For values after the eruption, a simple regression was positive and significant ($P < 0.002$) for sites DP and DR; for sites SP and SR, a double-reciprocal plot was significant ($P < 0.006$) with positive sign. (c) Four herbs at site DR. *RULA* = *R. lasiococcus*; *ERMO* = *Erythronium montanum*; *TIUN* = *Tiarella unifoliata*; *VASI* = *Valeriana sitchensis*. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: *E. montanum* <0.001, *R. lasiococcus* <0.001, *Ti. unifoliata* 0.015, and *Val. sitchensis* 0.064; (2) year 20: *E. montanum* <0.001, *R. lasiococcus* 0.72, *Ti. unifoliata* 0.13, and *Val. sitchensis* 0.31; and (3) year 30: *E. montanum* <0.001, *R. lasiococcus* 0.70, *Ti. unifoliata* 0.24, and *Val. sitchensis* 0.35. For *R. lasiococcus, Ti. unifoliata,* and *Val. sitchensis* values after the eruption, a simple regression was positive and significant ($P < 0.001$), but for *E. montanum*, no regression was significant. Values through year 20 are also reported in Antos and Zobel (2005).

Temporal course of density

Before the eruption, herb and shrub density were highest at the herb-rich sites, especially site DR (Fig. 6). Density of both herbs and shrubs was initially reduced by the tephra deposit, but recovered rapidly in shallow tephra, reaching pre-eruption levels before year 3. By year 30, herb and shrub density exceeded pre-eruption levels at both shallow-tephra sites. In contrast, at deep-tephra sites, shrub density reached but did

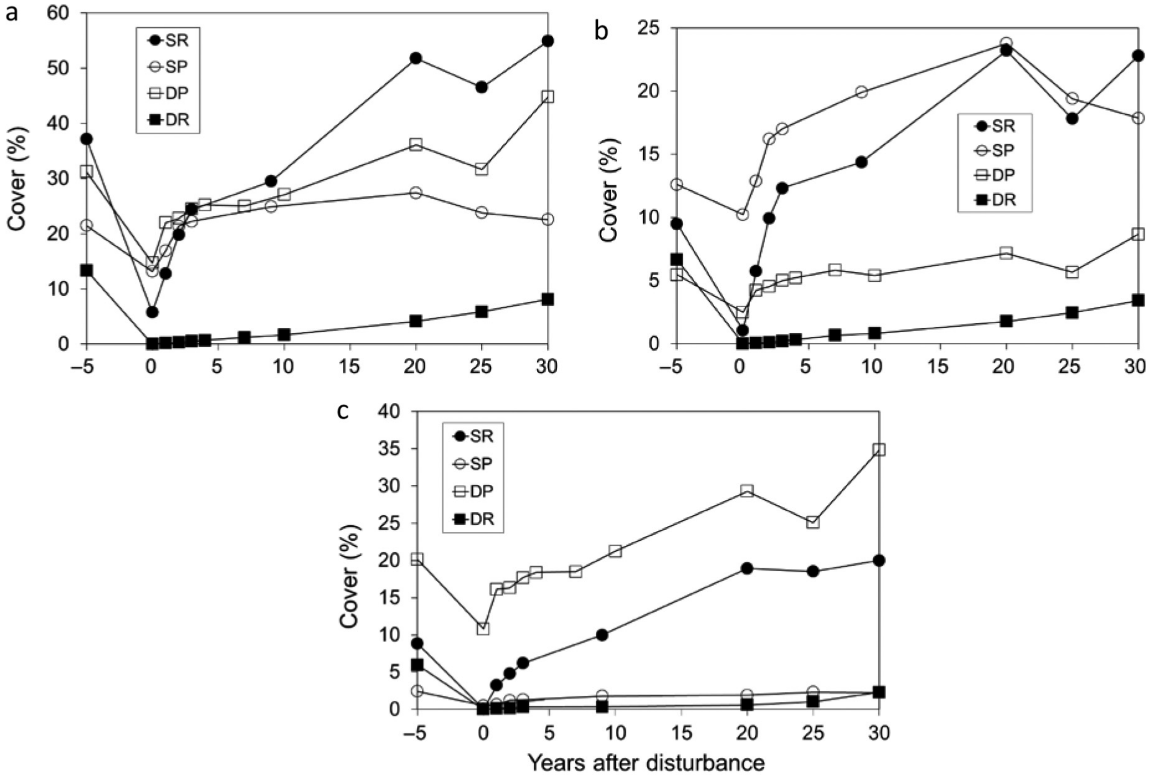

Fig. 5. Changes in shrub cover with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) All shrubs. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.44, site SR 0.10, site DP 0.41, and site DR <0.001; (2) year 20: site SP 0.78, site SR 0.010, site DP 0.35, and site DR <0.001; and (3) year 30: site SP 0.68, site SR 0.001, site DP 0.031, and site DR 0.038. For values after the eruption, a simple regression was positive and significant ($P < 0.0004$) for three sites, but not significant at site SP. (b) *Vaccinium membranaceum*. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.065, site SR 0.005, site DP 0.90, and site DR <0.001; (2) year 20: site SP 0.002, site SR <0.001, site DP 0.93, and site DR <0.001; and (3) year 30: site SP 0.12, site SR <0.001, site DP 0.93, and site DR 0.11. For site SP after the eruption, a double-reciprocal regression was positive and significant ($P = 0.0001$); for other sites, a simple regression was significant ($P < 0.005$) and positive. (c) *Vaccinium ovalifolium*. *P*-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.30, site SR 0.25, site DP 0.91, and site DR <0.001; (2) year 20: site SP 0.41, site SR 0.029, site DP 0.13, and site DR 0.24; and (3) year 30: site SP 0.94, site SR 0.004, site DP 0.015, and site DR 0.76. For values after the eruption, a simple regression was positive and significant ($P < 0.002$) for all sites. Values through year 20 are also reported in Antos and Zobel (2005).

not exceed pre-eruption levels, while herb density remained below them.

Temporal course of shoot size

Herb shoot size (cover/density) before the eruption was greater in sites that received shallow tephra, especially site SP where the robust, grass-like *Xerophyllum tenax* dominated (Fig. 7a). In contrast, shrubs were largest at site DP and smallest at site DR (Fig. 7b). After the eruption, patterns of shoot size differed among sites and growth forms. Herb shoot size eventually declined below pre-eruption values in shallow tephra, while it did not differ in deep tephra

Table 3. Cover (%) of understory tree seedlings at three times and the percentage of total cover accounted for by the major species at each site.

	Pre-eruption†		Year 1‡		Year 30§			
Site	Total	Percentage of *Abies amabilis*	Total	Percentage of *A. amabilis*	Total	Percentage of *A. amabilis*	Percentage of *Tsuga heterophylla*	Percentage of *Tsuga mertensiana*
SP	7.25	84	12.29	62	9.45	50	23	<1
SR	7.91	79	4.35	59	6.85	67	29	1
DP	6.09	99	3.92	97	10.98	68	31	1
DR	12.16	74	2.11	95	44.16	71	1	25

Notes: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich. Pre-eruption and year 1 data for total cover are also reported in Zobel and Antos (1997).

† Pre-eruption tree seedlings before the eruption, based on cleared plots in year 1.

‡ Pre-eruption tree seedlings in natural plots in year 1.

§ All branched tree seedlings in natural tephra plots in year 30.

(Fig. 7a). At sites with extensive snow in 1980, shrub shoot size after 30 yr did not differ from pre-eruption values, while shrubs were smaller than where snow had been sparse.

Comparison of temporal changes in growth form attributes

The overall pattern of change in attributes with time differed among growth forms, attributes, and sites (Figs. 2–7; Appendix S1: Table S1). The number of sites with diversity, cover, and density equal to or greater than the pre-eruption value increased with time, earliest and most for shallow tephra. The total number of values less than before the eruption for diversity, cover, and density declined from 21 in year 1 to 8 in year 30, whereas values that were equal or greater increased from only 3 in year 1 to 16 in year 30. In contrast, shoot size changed sporadically.

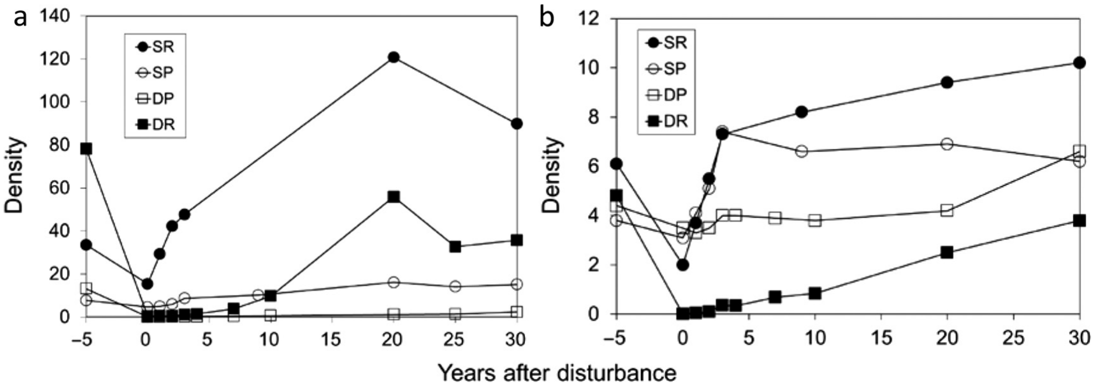

Fig. 6. Changes in shoot density (individuals/m^2) with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations: S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) Herbs. P-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.37, site SR data not available, site DP <0.001, and site DR <0.001; (2) year 20: site SP 0.012, site SR <0.001, site DP <0.001, and site DR 0.007; and (3) year 30: site SP 0.004, site SR <0.001, site DP 0.002, and site DR 0.001. For values after the eruption, a simple regression was positive and significant ($P < 0.03$) for all sites. (b) Shrubs. P-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.002, site SR 0.010, site DP 0.25, and site DR <0.001; (2) year 20: site SP 0.001, site SR 0.001, site DP 0.64, and site DR 0.004; and (3) year 30: site SP 0.001, site SR <0.001, site DP 0.43, and site DR 0.29. For values after the eruption, a simple regression was positive and significant ($P < 0.02$) for all sites except SP. Some early data are reported in Zobel and Antos (1997).

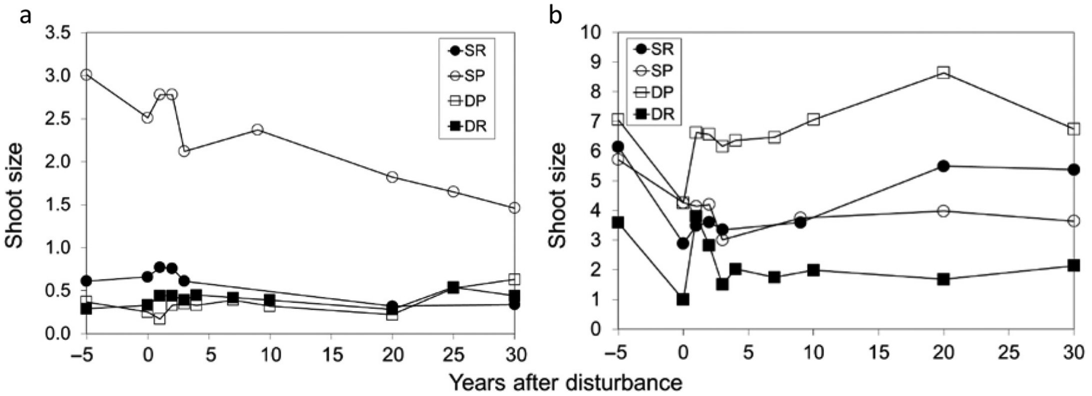

Fig. 7. Changes in shoot size (%, where 1% = 100 cm^2; cover/density) with time. Values plotted at year −5 are pre-eruption estimates (based on cleared plots in 1981); values plotted at year 0 were measured in 1980 on natural tephra. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow. (a) Herbs. P-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.30, site SR not available, site DP 0.027, and site DR 0.17; (2) year 20: site SP 0.13, site SR 0.015, site DP 0.012, and site DR 0.70; and (3) year 30: site SP 0.002, site SR 0.029, site DP 0.070, and site DR 0.63. For values after the eruption, a simple regression was negative and significant ($P < 0.05$) for sites SP and SR, and positive and significant for site DP. (b) Shrubs. P-values for the differences between natural plot values in a specific year and pre-eruption values are as follows: (1) year 9 or 10: site SP 0.011, site SR <0.001, site DP 0.54, and site DR 0.013; (2) year 20: site SP <0.001, site SR 0.92, site DP 0.044, and site DR 0.002; and (3) year 30: site SP <0.001, site SR 0.62, site DP 0.033, and site DR 0.080. For values after the eruption, a simple regression was positive and significant only for site SR.

Temporal course of species composition

Species composition of the understory, represented as the coordinates in ordination space, was drastically altered at all sites by the tephra (Fig. 8a). In addition, the composition based on all species in the understory has changed greatly since the eruption, moving toward that prior to the disturbance (represented by year 1 cleared-plot values), with trajectories that are roughly parallel among sites (Fig. 8a). The composition was altered most at site DR, where deep tephra that fell on snow decimated all growth forms (Figs. 3–5, Table 3). The two sites with the least snow had the smallest alteration in composition, but still underwent substantial change, followed by pronounced movement toward their pre-disturbance composition (Fig. 8a).

Compositional changes differed notably among growth forms (Fig. 8b, c). Herbs were minimally altered in composition by shallow tephra, but deep tephra produced major changes in herb composition (Fig. 8b). In contrast, shrubs showed only limited effects of tephra depth but were drastically altered by high coverage of snow (Fig. 8c). All sites, though, were fairly close to their pre-disturbance shrub composition in year 30.

Relationships of plant cover to environment

Environment at the time of the eruption differed substantially among (Table 1) and within sites. Analysis of relationships between cover of growth forms or major species and plot-specific environmental factors at three times produced 121 cases that were significant in both a single-factor analysis and a multi-variable analysis (Table 4; Appendix S2: Tables S1–S3). Each case represented one plant type with a single factor at a single site at one time. Of the 121 significant relationships, 23 were in cleared plots in 1981, representing the pre-eruption situation (year 0; Appendix S2: Table S1). All of these 23 relationships disappeared following tephra deposition (Appendix S2: Table S2), and none of them reappeared in year 30 (Appendix S2: Table S3). Of the 46 new cases on natural tephra in year 1, nine remained significant with the same sign in year 30, and one changed sign. In addition to these 10

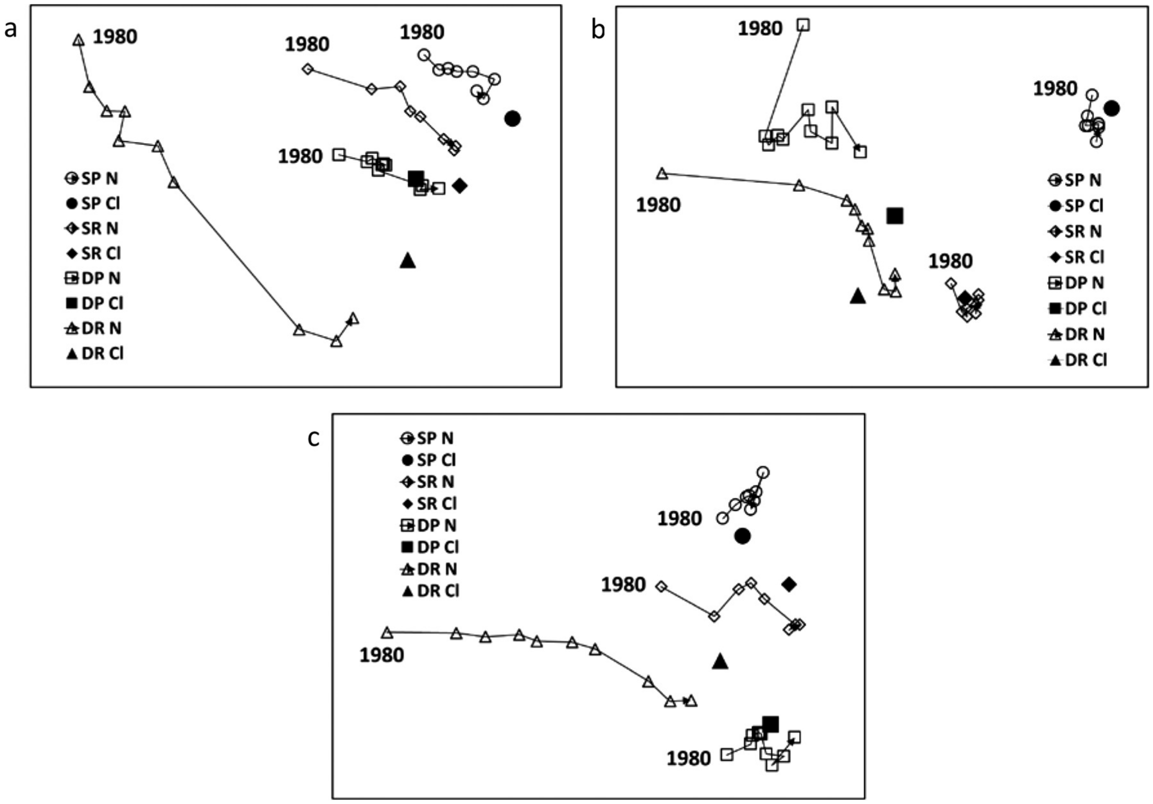

Fig. 8. Temporal changes in species composition as indicated by non-metric multidimensional scaling ordinations based on cover data. Letters represent site designations (Table 1): S = shallow tephra; D = deep tephra; P = herb-poor with little snow pack during the eruption; R = herb-rich with much snow during the eruption. Cleared-plot data for year 1 are used to indicate pre-disturbance composition (labeled Cl after the site code). Points for the sampling times on tephra are connected by lines with arrows to indicate temporal changes (N after the site code); years of sampling are presented in *Methods*. The first point is indicated by "1980" next to the point. (a) All species (86 species). (b) Herbs (66 species). (c) Shrubs (11 species). For all ordinations, the two-dimensional solutions presented were optimal.

cases carried over from year 1, there were 52 newly significant relationships, for a total of 62 significant in year 30.

The location and nature of relationships changed with time (Table 4). Herb-rich sites had more pre-eruption relationships, whereas herb-poor sites had more relationships in year 1. New relationships appeared at all sites between years 1 and 30 (Appendix S2: Table S3). Canopy factors (canopy gap, presence of individual canopy species) became less important immediately after the eruption, then increased in year 30 (Table 4). Tephra depth and factors that affect the damage caused by tephra (snow, micro-topography) became important after the eruption. Moss was involved in many relationships throughout the time period, whereas involvement of tree seedlings increased with time. After a balance of negative and positive relationships in year 0, negative relationships dominated in year 1, and positive, in year 30. The time course for factor type and sign for growth forms other than tree seedlings are presented in Appendix S2: Table S4.

Of the 23 relationships significant in pre-eruption forests (Appendix S2: Table S1), only three were present at more than one site. Most significant relationships involved tree canopy conditions. This pattern changed drastically following the eruption (Appendix S2: Tables S2–S4). Besides the disappearance of all 23 pre-eruption relationships, the factors involved in significant relationships changed markedly. In general, the

Table 4. Location and properties of relationships of cover of growth forms and major species to environmental factors before the eruption (year 0, based on year 1 sampling of plots cleared in 1980), year 1, and year 30.

Characteristic	Level	Year 0	Year 1	Year 30
Location	Site SP	1	12	17
	Site SR	8	6	12
	Site DP	4	17	15
	Site DR	10	11	18
Type of factor	Canopy	16	9	27
	Tephra	*	9	5
	Snow	1	6	10
	Micro-topography	0	9	9
	Wood	4	7	7
	Light intensity	2	6	4
Growth form	Moss	9	17	19
	Herb	7	7	9
	Shrub	6	13	12
	Tree seedling	1	9	22
Sign of relationship	−	12	25	26
	+	11	15	34
	†	0	6	2

Notes: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich. Data were summarized from Appendix S2: Tables S1–S3.

† Significance of micro-topographic type, which does not have a sign.

* denotes not relevant

significant correlations changed from those expressing understory–canopy interactions to those reflecting the intensity of disturbance and factors that interacted with tephra to modify damage to plants. Influence of tephra depth and of individual tree species in the canopy was usually negative except for *Chamaecyparis nootkatensis*. The influence of canopy gaps and large woody debris was primarily positive. With time after the eruption, the relationships with light, snow, and large wood became more positive, while the frequency of relationships with tephra depth declined.

Factors significant in year 1 differed in their duration of significance (Appendix S2: Table S2). The last year of significance differed among growth forms ($P = 0.015$), being much earlier for moss (mean = year 4) than for other growth forms (means, years 16–22), but did not differ among sites or environmental factors. Differences did occur among the five widespread species ($P = 0.018$), with *Dicranum* spp. (a moss) having a much later mean year of significance (year 16) compared to the other species (means = years 3–5). Factors significant in year 30 but not year 1 generally became significant in year 20 or later (Appendix S2: Table S3). There were no significant differences in year of appearance for a factor among sites, environmental factors, growth forms, or species. Relationships significant in year 30 (Appendix S2: Table S3) differed markedly from those in year 1 (Appendix S2: Tables S2, S4). At no site did negative relationships dominate in year 30.

Relationships between cover of different plant types

Thirty relationships between cover of different plant types were significant (Table 5; Appendix S3: Tables S1–S3), 11 present in pre-eruption vegetation, eight first present in year 1, and 11 first after year 1. Site SR had few relationships in years 0 and 30, but several in year 1; other sites showed the opposite pattern. Smaller growth forms showed more relationships. Only three of the 30 relationships were negative; all three appeared in year 1 and disappeared before year 3.

Three of the 11 relationships present before the eruption persisted through the disturbance, remaining significant in year 1 (Appendix S3: Table S1); two of these disappeared by year 4, but re-appeared before year 30. Also unlike relationships in Appendix S2, five of the eight that were lost during the eruption became significant again by year 30 (Appendix S3: Table S1). Most relationships that first appeared in year 1 were of

Table 5. Location and properties of relationships between pairs of plant growth forms that were significant in years 0, 1, and 30.

Characteristic	Level	Year 0	Year 1	Year 30
Location	Site SP	3	1	3
	Site SR	1	5	0
	Site DP	4	1	2
	Site DR	3	1	6
Growth form†	Moss	8	6	7
	Herb	6	7	5
	Shrub	2	0	3
	Tree seedling	6	3	7
Sign	−	0	3	0
	+	11	5	11

Notes: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich. Data were summarized from Appendix S3: Tables S1–S3.

† Each relationship involved two growth forms.

short duration (Appendix S3: Table S2), but two remained significant in year 30. Most of the relationships present in year 30 that developed after year 1 required two or three decades to become significant (Appendix S3: Table S3).

Relationships of plant cover to post-eruption disturbance

In year 1, plant cover was often related significantly to the degree of soil disturbance (Table 6), reflecting major erosion of tephra from several plots at each deep-tephra site during the first winter after the eruption. Cover of all growth forms increased after early erosion; the only case of decline with soil disturbance was for herbs at site SP, where uprooting of trees damaged herbs when roots broke the tephra surface. The influence of soil disturbance often was long-lasting: Of 13 cases, five remained significant for the whole 30-yr period and two others for 25 yr. In addition, shrub cover at site DR was increased by soil disturbance from year 2 to year 30. Accumulation of woody debris and branches with needles eventually reduced plant cover in two cases each.

Vegetation–environment relationships in year 30

Multi-variable analyses were used (Table 7) to relate year 30 cover to independent variables of all three types (1980 environment, cover of other growth forms, and post-eruption disturbance) that had been identified as significant in previous analyses (Table 6; Appendices S2, S3). Most analyses were highly significant but explained only 3–29% of variability, after adjusting for degrees of freedom. Exceptions were for *R. lasiococcus* and *Tsuga mertensiana*, with 40–47% of variation explained (Table 7). All 1980 environmental factors except tephra depth; all understory growth forms; and all post-eruption disturbance types except woody debris were significant in at least one case. Significant independent variables differed among sites and between growth form totals and individual taxa. Correlations with cover of other understory growth forms were all positive.

Table 6. Sign of the relationships of plant cover to three types of secondary disturbance in years 1 and 30, with the last year of significance for those losing significance between years 1 and 30, and the year of first significance for relationships first significant after year 1.

Growth form	Taxon	Site	Disturbance†	Year 1	Latest year‡	Year 30	First year§
Moss	All	SP	Soil	+	10	0¶	Na¶,#
		SR	Soil	+	3	0	Na
		DP	Soil	+	Na	+	Na
		DR	Soil	+	25	0	Na
	Dicranum spp.	SP	Soil	+	Na	+	Na
		DP	Soil	+	4	0	Na
		DR	Soil	+	10	0	Na
	Rhytidiopsis robusta	DP	Soil	+	25	0	Na
Herb	All	SP	Soil	–	Na	–	Na
		SP	Wood	0	Na	–	20
		DP	Soil	+	10	0	Na
		DR	Soil	+	Na	+	Na
		DR	Branches	0	Na	–	30
	Rubus lasiococcus	DP	Soil	+	Na	+	Na
Shrub	All	DR	Soil	0	Na	+	2
	Vaccinium membranaceum	DR	Soil	+	4	0	Na
Tree seedling	All	SP	Branches	0	Na	–	30
	All	DR	Wood	0	Na	–	25

Note: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich.

† Soil = all soil disturbances; Wood = all accumulation of woody and bark debris; and Branches = the short-term effect of branches with dense clumps of attached needles.

‡ Latest year refers to time after the eruption that a relationship significant in year 1 was last significant.

§ First year refers to the year that a relationship not significant in year 1 but significant in year 30 first became significant.

¶ 0 = relationship was not significant in that year.

Na = the factor did not gain or lose significance during the appropriate period.

Table 7. The significance of factors affecting cover of growth forms and major species in year 30.†

Growth form	Taxon	Site	Factor	Correlation‡	*P*-value§	Variation explained (%)¶
Moss	All	SR	*Abies amabilis* canopy	−0.30	0.008	12
			Herb cover	+0.51	0.012	
			Wood (year 1)	+0.25	0.048	
		DP	Soil disturbance	+0.55	0.006	9
			Tree seedling cover	+0.39	0.010	
		DR	*Tsuga mertensiana* canopy	−0.22	0.015	12
	Rhytidiopsis robusta	SP	Snow	+0.56	0.002	20
			Pseudotsuga menziesii canopy	−0.30	0.003	
			Herb cover	+0.32	0.007	
			A. amabilis canopy	+0.25	0.023	
		DP	Tree seedling cover	+0.42	0.0002	17
			P. menziesii canopy	−0.27	0.004	
			Wood (year 1)	+0.33	0.048	
Herb	All	SR	Shrub cover	+0.26	0.049	3
		DP	Moss cover	+0.28	0.012	27
		DR	*Ts. mertensiana* canopy	−0.29	0.004	29
			Branches with needles (year 30)	−0.23	0.005	
			Moss cover	+0.54	0.033	
			Shrub cover	+0.25	0.036	
			Soil disturbance	+0.39	0.047	
	Rubus lasiococcus	SP	Moss cover	+0.33	0.001	47
			Tree seedling cover	+0.25	0.003	
Shrub	All	DR	Soil disturbance	+0.28	0.007	6
			Tree seedling cover	+0.30	0.013	
	Vaccinium membranaceum	DR	Tree seedling cover	+0.25	0.004	3
Tree seedlings	All	SP	Moss cover	+0.24	0.001	12
			Branches with needles (year 30)	−0.23	0.008	
	A. amabilis	DP	Moss cover	+0.35	0.003	18
			Slope type	*	0.006	
			A. amabilis canopy	+0.22	0.008	
			Tsuga heterophylla canopy	−0.39	<0.0001	
	Ts. mertensiana	DR	Shrub cover	+0.40	0.034	40
			Light intensity	+0.39	<0.0001	
			Snow	+0.21	0.012	
			Canopy gap	+0.41	0.007	

Note: S = shallow tephra; D = deep; P = herb-poor; R = herb-rich.

† Variables include 1980 environment, secondary disturbance, and cover of other growth forms; only factors significant in earlier analyses at years 1 and 30 were considered (Appendices S2, S3). Only sites and species with significant relationships are listed. Variables that could be transformed to normality were analyzed using a general linear model, others using logistic regression on presence/absence data.

‡ Correlation = the Spearman rank correlation coefficient.

§ *P*-value is for the significance of the factor in the multi-variate analysis.

¶ Variation explained is determined as the adjusted R^2 value or as the percentage of deviance explained by the model for logistic regression.

* This factor has multiple levels and calculatiing a correlation is not possible

Thirty years after tephra deposition, moss cover was higher in microsites with more large woody debris, later snow melt, more herb and tree seedling cover, and more soil disturbance; moss cover was lower beneath *Ts. mertensiana* and *Pseudotsuga menziesii* canopy (Table 7). Herb cover increased with greater moss, shrub, and tree seedling cover, and with soil disturbance, but was reduced by leafy branch litter and *Ts. mertensiana* canopy. Shrub cover was greater where tree seedling cover was higher and after soil disturbance. Tree seedling cover increased with higher light intensity, greater snow cover, greater shrub cover, and *A. amabilis* canopy but was reduced by leafy branch debris and *Tsuga heterophylla* canopy (Table 7).

DISCUSSION

Mechanisms of community change

Succession is a long-term process in many systems; discussing its causal mechanisms based on short-term observation or experiment is tenuous. Although there are limits to drawing conclusions about mechanisms of succession from observations alone, possible causal factors can be identified from correlations observed in long-term field studies. Confirming causal relationships would require extensive, long-term experiments that realistically represent the tephra disturbance, which would be difficult, perhaps impossible. Here, we suggest mechanisms that appear to be responsible for changes in post-eruption understory communities.

Importance of a growth form or species can be modified by the presence of other plants. The presence or type of tree canopy was related to all understory growth forms and most widespread species. An effect of competition or other interference caused by presence of a canopy species would result in a negative sign for the relationship, which was common for most tree canopy species. In contrast, significant correlations with a canopy gap were primarily positive. The importance of canopy factors changed with time; for example, relationships of cover with canopy gaps were significant before the eruption but not in year 1, and then returned in small numbers in later years. The canopy can have major effects on understory plants, which may be related to foliar density, canopy height, and litter structure and chemistry (Sydes and Grime 1981, Barbier et al. 2008). Roots beneath the conifer canopy also affect understory in our region (McCune 1986, Riegel et al. 1992, Lindh et al. 2003) and in most forest types worldwide (Coomes and Grubb 2000). *Pseudotsuga menziesii* and *Tsuga mertensiana*, with all negative relationships, are primarily large individuals with sloughing bark and relatively large, persistent cones. The species with the most positive relationships, *Chamaecyparis nootkatensis*, has less acidic litter, sheds foliage in small bits that decompose quickly, and has much of its cover from near-prostrate sapling-sized individuals. Our results thus reinforce the conclusion that canopy species often differ substantially in their effects on understory vegetation (Augusto et al. 2003, Barbier et al. 2008, Chamagne et al. 2016). In contrast to the tree canopy, analysis of relationships among understory strata produced little sign of interference: Only three of 30 significant relationships among growth forms and widespread species were negative and those three disappeared after year 2. This positive relationship may indicate a nurse-plant (facilitation) effect or simply that most plants grow well in similar microenvironments (Wood and del Moral 1987, Steinbauer et al. 2016).

Different mechanisms may lead to different responses to tephra among growth forms and species. Mechanisms of survival differed. Herbs and shrubs often grew out of tephra after being buried for years; mosses also survived multi-year burial, but emerged only where erosion removed tephra (Zobel and Antos 1992). Most tree seedlings, in contrast, survived burial of all foliage for less than a year. Woody plant survival decreased where tephra fell on plants with their limbs prostrate beneath snow (Antos and Zobel 1982). Movement of belowground organs toward the tephra surface was common for most herb species, although the mechanisms and timing differed (Antos and Zobel 1984, 1985*b*, *c*). Rooting into tephra was common for shrubs other than *Vaccinium* spp. and for most tree seedlings (Zobel and Antos 1982), but highly variable for herbs. By year 20, most tree seedling cover in shallow tephra was still from survivors, whereas post-eruption seedlings dominated in deep tephra. New individuals developed from different sources. Mosses expanded mainly from new colonies. Some herb populations in year 30 were still composed mainly of survivors, while others contained mainly new ramets from vegetative spread or new genets from seedlings.

Shrub density changed in response to a variety of mechanisms. Shrub density was reduced when tephra covered individuals shorter than tephra was deep or that were prostrate beneath snow pack. Shrub density subsequently increased when erosion of tephra exposed live branches, when buried shoots broke through the tephra surface, or when new shoots from buried branches or rhizomes grew through the surface. Seedling establishment was of limited importance because few post-eruption shrub seedlings survived and those grew very slowly. New shoots that emerged from pre-existing belowground structures or buried stems accounted for most of the density increase.

Emergence of new shrub individuals continued years after the eruption, sometimes from buried stems with no previously emergent shoots (Zobel and Antos 1992).

A prime example of differences among species in mechanisms determining cover involved the four herbs studied at site DR (Fig. 4c), which differed widely in structure, response to burial, reproductive mechanisms, and resilience to the eruption, as discussed by Zobel and Antos (2007, 2009, 2016, *in press*): *Rubus lasiococcus* spread rapidly via stolons, unlike the other three, but produced few flowers. *Tiarella unifoliata* had no survivors, the most flowering, a moderate number of seedlings per flowering shoot, effective dispersal, and many new plants derived from seed. In contrast, *Erythronium montanum* and *Valeriana sitchensis* established few individuals after the eruption. *Valeriana sitchensis* had limited flowering and few seedlings, but effective dispersal. The pre-eruption dominant, *E. montanum*, flowered moderately but had poor seed dispersal and seedling survival; in addition, survivors, having failed to move the perennating organ from the buried soil into tephra, lost cover with time.

Environmental factors had pronounced and various effects on plant cover. The relationship of snow to plant cover was significant for all growth forms, being positive before the eruption, mostly negative in year 1, and then positive again in year 30. We interpret the negative effect in year 1 to represent a reduction in woody plant cover by the tephra-on-snow interaction (Antos and Zobel 1982), whereas positive effects seem likely to be associated with growing season water input from late-melting snow, which especially benefits mosses and tiny *Tsuga* seedlings in this region with limited summer rainfall. Moss also benefitted where tephra was sloughed from the elevated, uneven surface of large woody debris as indicated by the consistently positive effect of wood in year 1 on moss. In contrast, four of five relationships of wood for herb and shrub cover were negative, probably because the large woody debris usurped surface area. Soil disturbance was the primary form of post-eruption disturbance with positive relationships to moss and (in deep tephra) herb cover, especially just after the eruption, which reflected the concentration of survivors where tephra was eroded. Tephra erosion was also strongly related to plant survival in areas of more intense disturbance where canopy trees were destroyed at Mount St. Helens (Halpern et al. 1990). The only negative relationship with soil disturbance was associated with tip-up mounds where root systems of fallen trees broke up the soil surface.

Community patterns and definitions

Several patterns of change in diversity and abundance of growth forms or taxa occurred (Figs. 2–6). In some growth forms at some sites, damage was minor and little change has occurred. Most species present at 30 yr, and during earlier years, were there before the eruption. Can these examples be called succession? We think so, because all sites had at least two growth forms with substantial damage (Table 1); there have been some vascular species added; and one group of bryophytes, not recorded in the original forest, became important and then virtually disappeared again (Antos and Zobel 2005). All sites showed major changes in trajectory in all-species ordinations (Fig. 8a), and plant–environment relationships present before the eruption all disappeared in year 1, with at least one relationship lost from each site. Species turnover is not required by widely used definitions of succession (e.g., "Directional change in community composition and structure through time"; Gurevitch et al. 2006:528). Thus, we will consider vegetation change at all our sites to represent succession.

There was substantial evidence of community divergence from pre-eruption conditions on the same site. Although some attributes clearly were converging upon the pre-eruption conditions (near or at pre-eruption abundance), others were not. At no site did all growth forms regain pre-eruption levels; mosses failed to do so at all sites (Fig. 3) along with herbs in deep tephra and shrubs at site DR (Figs. 4–6). In a second pattern, divergence occurred as attributes exceeded their pre-eruption levels (Figs. 2, 4–6, Tables 2, 3). In a third pattern, a previously dominant species became rarer after 30 yr than it was just after the eruption (*E. montanum* at site DR; Fig. 4c). Both patterns 2 and 3 represent some level of movement away from pre-disturbance conditions, whereas the divergence in the first pattern may simply reflect inadequate time to reach the pre-disturbance state. Patterns of convergence and divergence in overall understory species composition relative to the pre-eruption community are clear in NMS ordination results (Fig. 8). The dramatic impact of disturbance and the major trajectory back toward pre-eruption conditions are clear for all sites, especially site DR (Fig. 8a). Sites DR and SR still remain far from their pre-eruption ordination coordinates—reflecting pattern one—even though large changes have occurred during succession. Divergence patterns of types two or three are represented on ordinations: the trajectory of site DR toward a point below pre-eruption conditions, the continuation of the DP trajectory past a near coincidence with its original coordinates, and the recent movement of site SP's trajectory away from its pre-eruption status. The pattern in which communities diverge or converge during succession, compared to pre-disturbance conditions, is a topic of major theoretical and practical relevance for evaluating long-term community development; apparently minor factors can sometimes have substantial influence on the trajectory of succession (Fukami et al. 2005, Matthews and Spyreas 2010). For example, even very thin tephra can produce long-term changes in communities that perhaps indicate divergence in trajectories of change (Fischer et al. 2016). Our observations underscore that disturbances, even less severe ones, can set systems onto alternate trajectories (Beisner et al. 2003, Suding et al. 2004, Ratajczak et al. 2014), which in some cases may result in alternate stable states (Schröder et al. 2005, Fukami and Nakajima 2011).

Growth forms differed greatly in their patterns of convergence and divergence from pre-eruption conditions. The differences between ordinations for herbs and shrubs (Fig. 8b, c, respectively) from the all-species result, and from each other, are striking. The two growth forms differed in their degree of change and convergence, herbs differing mostly between tephra depths and shrubs with snow coverage. Both growth forms showed clear examples of convergence and divergence, differing among study sites. This implies that focusing on the whole community or on a single growth form can obscure important differences among growth forms in trajectories of temporal change. In addition, the occurrence of divergence vs. convergence can differ between species composition and trait attributes (Fukami et al. 2005, Götzenberger et al. 2016), indicating the importance of clearly specifying the attributes being studied.

The nature and properties of plant communities have been a focus of study for many decades (Oosting 1956, Daubenmire 1968); however, conceptual ideas about communities still remain controversial (Vellend 2016). Among ecologists, opinions differ widely about what characteristics of a piece of vegetation are required to confirm its status as a community. At one extreme, Odum (1959:245) states that "...any assemblage of organisms living in a prescribed area..." is a community. If we accept this, any question about loss of community status is moot. On the other hand, Whittaker (1975:2) states that a biotic community is more than a random collection of organisms: It is "...a distinctive living system, with its own composition, structure, environmental relations, development, and function." Here, we will accept and discuss Whittaker's more restrictive definition of community. Some relevant questions include the following:

1. How much loss of relationships, or importance, or diversity will allow us to say that these co-occurring populations of plants no longer meet the criteria to be called a community?
2. What criteria can we use to identify the conversion of a fragmentary community remnant to a functioning community and how long does it take to re-establish those criteria?
3. What level and type of change in community properties, compared to pre-disturbance conditions, will change the type of community that we recognize?

The degree of integration is an important community property, reflected by the number and type of significant relationships between the importance of a plant group and environmental factors or the importance of other plants. In our study, disturbance disrupted the interrelationships among organisms and environment that help confer the status of "community," when all pre-eruption relationships disappeared with tephra emplacement and did not re-appear during our thirty-year study. In addition, many relationships with other types of plants were lost, although most did re-appear with time. New relationships in year 1 were primarily associated with factors controlling the degree of tephra damage to plants, most of which disappeared with time. Such a loss of the pre-eruption relationships and their replacement by factors associated with damage can be interpreted to mean that no community existed in year 1, simply a collection of plants whose properties depended on the local details of tephra emplacement and the damage it caused. We believe that may be a defensible conclusion, especially in deep tephra with snow, site DR, where plant importance in year 1 was minimal. The effect of such initial conditions may influence vegetation for years after disturbance (Zobel and Antos 1997, *in press*). Other relationships reflected secondary disturbances, such as erosion of tephra and increases in large woody debris. With time, relationships with tephra disturbance that first appeared in year 1 faded, whereas new relationships of types similar to those before the eruption increased, indicating an increase in the level of integration and the existence of a community in the sense of Whittaker (1975). At 30 yr, the number of new relationships was increasing rapidly.

In less disturbed areas, and perhaps throughout our study area, a community may continue to exist after disturbance but differ from the original. Even though all pre-eruption relationships with environment were lost in both deep and shallow tephra, the importance of most vascular plants remained high in sites with shallow tephra, making removal of their status as communities untenable. However, the degree of loss of the original organisms required before we recognize a new type of community is problematic. Overall, the heavily damaged communities no longer fit any community described in local classifications of vegetation types (Franklin 1966, Franklin et al. 1988).

The pattern of community re-development differed from most disturbances. In many successional situations, original species are replaced by early seral species after disturbance; these early seral specialists persist until environmental change and time for immigration allow later seral species to re-invade. Such situations have been described in our region, both at Mount St. Helens and for other types of disturbance (Halpern 1988, 1989, Agee 1993, Dale et al. 2005, Carey et al. 2006, del Moral 2007, Swanson et al. 2011, del Moral et al. 2012, Halpern and Lutz 2013). In our case, however, most differences in composition occurred in the relative abundance of the same suite of species that occupied the site before the eruption.

Community development in tephra as a model for other disturbances

Succession in our situation contrasts strongly with that after disturbances that kill overstory trees, as described by Swanson et al. (2011). In our case, the tree canopy remained intact (Fig. 1a, b; although some old trees at site DR died after a decade or so, perhaps attributable to tephra; Segura et al. 1994). However, the understory was damaged and almost obliterated where deep tephra fell on a snow pack, forming a new substrate with very low N content that covered existing vegetation and organic matter. The intact tree canopy meant that understory microclimate and root competition in the buried soil were altered little. Tree litter input and root and fungal colonization from the buried soils modified tephra chemistry and biology (Zobel and Antos 1991*a*, *b*) and allowed development after 30 yr of a consolidated forest floor with substantial root colonization. Species from the original forest dominated the re-developing vascular vegetation, and few of the survivors lost vigor after the disturbance. Other disturbances to forest can produce somewhat similar conditions to those caused by tephra: under-burning and sediment deposition during flooding (which primarily damage understory plants but not canopy trees), both of which affect substantial areas (Stone and Vasey 1968, Agee 1993).

The situation described for volcanic eruptions by Swanson et al. (2011, their table 1) applies only to a minority of the area affected by volcanism. The most frequent and widespread (but least destructive) volcanic disturbance is from tephra like that which affected our sites (Griggs 1918, Zobel and Antos 1991*a*, Swanson and Major 2005, Ayris and Delmelle 2012). Tephra deposits can extend across continents, occur repeatedly over millions of years, and apparently have widespread effects on biogeography and evolution (Axelrod 1981, Morony 2010, Ayris and Delmelle 2012). Tephra disturbance in our region has been extensive and frequent (Shipley and Sarna-Wojcicki 1983, Egan et al. 2016).

Despite their differences from most disturbances affecting forest understory, several aspects of our results illustrate generalities pertinent for ecologists who study succession and managers who seek to accelerate or manipulate its path; they are listed here and discussed below:

1. Apparently similar species may differ in their responses,
2. apparently minor environmental differences associated with the disturbance may induce major, long-term changes in vegetation,
3. routine events ("secondary disturbances"), after the major disturbance under study, may modify the pathway of succession, and
4. successional trajectories may diverge from that which would return to the community present before disturbance.

Our early analyses of this succession relied primarily upon growth form composition. Individual taxa, however, often responded differently from the mean for their growth form and from other taxa of the same growth form (Figs. 3–5, Tables 3, 6, 7, and Appendices S2, S3; Zobel and Antos 2007, 2009, 2016, *in press*). Although analyses based on growth form can simplify studies and lead to effective generalizations, caution needs to be exercised when making interpretations, given that in many situations species within a growth form differed greatly in response (Halpern 1988, 1989).

Conditions at the time of the eruption (presence of snow pack) or soon after (tephra erosion in the first winter) produced vegetation differences that remained significant (Tables 6, 7), and in places still dominant, 30 yr later. Measurement of such initial environmental differences required rapid initiation of studies before evidence was lost. For instance, evidence of locations where tephra fell on snow (cracks in the tephra surface; Fig. 1c) disappeared during the first winter (Antos and Zobel 1982), and identification of erosion patterns required pre-erosion data on tephra depth. In another example, a series of events early in succession may modify vegetation development for centuries: At the beginning of a series of relatively wet years (Major 2004), a large 1982 conifer seed crop fell on an unoccupied mineral seedbed (the tephra) which lay atop a buried soil with mycorrhizal fungi that rapidly colonized new seedling roots in the tephra (Zobel and Antos 1991*b*). At site DR, this led to very high survival of the new conifers, producing a dense layer of healthy seedlings that dominated the site in year 30. This seedling cohort may produce stands unlike any that we sampled. However, stands with an unusually dense conifer sub-canopy were present elsewhere NE of Mount St. Helens (J. A. Antos, *personal observation*, 1979) and had apparently developed on tephra from the 1800 eruption. Long-lasting consequences of nuances of disturbance events and initial post-disturbance conditions, which could easily be overlooked, are critical to understanding the course of succession or restoring vegetation on degraded sites; such a situation is common in many types of ecosystems and with many types of disturbance (Kayes et al. 2010, Brown et al. 2015, Fukami 2015, Gibson et al. 2016).

The 1980 events were not the last effective disturbance of our sites. Erosion was episodic and substantial in early decades. Tree mortality occurred occasionally with important local effects, which changed the light and soil competitive environment, sometimes disturbed the soil surface, and covered vegetation with branches, wood, and bark. The effects of both erosion and tree fall were statistically significant in our data (Table 6); both were partially induced by the eruption, as most erosion was of new tephra and tephra probably contributed to the demise of old trees at site DR (Segura et al. 1994). Minor disturbances following a major disturbance are important in modifying successional trajectories in many situations (e.g., the survival of shrubs in erosion channels in the tree-fall zone at Mount St. Helens; Swanson and Major 2005); our results add to this generalization.

The idea that convergence on the characteristics of pre-disturbance vegetation occurs during succession has a long history (Clements 1916), and although convergence often does occur during succession (Christensen and Peet 1984, Leps 1991), divergence has also been frequently documented (Romme et al. 2016). However, a distinction needs to be made between convergence/divergence among sites during succession and convergence/divergence relative to pre-disturbance conditions on a given site; the former is usually emphasized in part perhaps because of the lack of pre-disturbance data. Because we have good evidence of vegetation prior to disturbance, we can address the latter situation. We found that there was pronounced convergence toward the pre-disturbance state irrespective of the extent to which the understory was deflected from that state initially (Fig. 8). However, there were limits to this convergence and now some understory vegetation (in total, or some growth forms) is diverging from the pre-disturbance community. At Mount St. Helens, this appears to be occurring even with a very thin tephra deposit (Fischer et al. 2016). Multiple successional pathways have been commonly documented following disturbance (Donato et al. 2012); these may ultimately result in convergence, but continued divergence is likely in many cases (Harvey and Holzman 2014, Brown et al. 2015, Romme et al. 2016). Such divergence emphasizes the importance of initial conditions and could ultimately result in alternate states that may be stable (Beisner et al. 2003, Schröder et al. 2005, Fukami and Nakajima 2011, Ransijn et al. 2015).

Advantages of long-term, permanent plot studies

Study of vegetation change has been a staple for plant ecologists. In this case involving a rare natural event, we were able to study change through time on the same sites, rather than using chronosequences, which have well-known disadvantages (Bakker et al. 1996, Foster and Tilman 2000, Gurevitch et al. 2006). Studies that use the same site through time differ in their length, frequency of sampling, and use of permanent plot locations. Most studies last less than three decades. Many long-term studies involve a single re-sampling of locations that had been initially sampled long ago, often for purposes other than extended studies (Rogers et al. 2008, Damschen et al. 2010, McCune and Vellend 2013, Kopp and Cleland 2014). Both two- and repeated-sample studies may either use permanent plots (Fischer et al. 2016) or may relocate later samples (Kopecký and Macek 2015, Li and Waller 2015, Bretfeld et al. 2016).

Our study offers several advantages that most successional studies lack:

1. a good estimate of pre-disturbance vegetation before a major, unpredictable natural disturbance;
2. measurements of initial conditions while signs of disturbance intensity and mechanisms of damage were still obvious;
3. measurement of environmental factors at the scale of individual small plots, which are applicable both before and after the disturbance;
4. consideration of the changes in plant–environment relationships during succession;
5. a long time span with several re-measurements;
6. consistency in methods: using permanent plots, with the same investigators involved in virtually all determinations of cover and density;
7. focused study of the reactions of many species to burial and of mechanisms of reproduction and growth in tephra (summarized by Zobel and Antos 1997, 2007, 2009, 2016) that could be used to develop causal hypotheses.

Because of these properties, we were able to examine thoroughly disturbance effects and successional changes in ancient forests resulting from tephra deposition—a widespread, frequent disturbance in some regions where the soil falls out of the sky. More generally, our results mirror and reinforce conclusions from studies of succession elsewhere and following other types of disturbance (Walker and del Moral 2003). Succession is a fundamental but often slow ecological process that can span centuries, and is thus poorly suited to short-term study. Long-term, permanent plot studies, although often logistically difficult, offer great promise in unraveling the complexities of the successional process.

ACKNOWLEDGMENTS

Funding for this research came from the U.S. National Science Foundation (DEB-8020866 and DEB-8109906), USDA Science and Education Administration (59-2411-1-2-009-0), National Science and Engineering Research Council of Canada, Global Forest, USDA Forest Service, and Oregon State University. We thank the following persons for their contribution to data collection: Matt Blakely-Smith, Susan Seyer, Ray Yurkewycz, Tom Hill, Erica Wheeler, Heidi Guest, Joanna Smith, Mike Ryan, Debbie Brinckman, and Dylan Fischer.

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