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**Secondary disturbance following a deposit of volcanic tephra:
A 30 year record from old-growth forest understory**

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Abstract: Forest disturbance is usually described by effects on trees, and small disturbances to forest understory are seldom studied. Nevertheless, effective analyses of succession need to consider both stand-replacing and subsequent “secondary” disturbances in both canopy and understory. We estimated characteristics of 13 types of secondary disturbance in old-growth forest understory, and of canopy cover, after the 1980 tephra (aerially transported volcanic ejecta) deposition from Mount St. Helens, Washington. We sampled 100 1-m² plots at each of four sites for vegetation change and types of disturbance at ten times from 1980-2010; we sampled tree canopy above each plot in 1980 and 2016. The number of canopy gaps increased 23 % and mean gap dimension 68 % during 36 years, mostly from loss of *Abies amabilis*. Secondary disturbance in understory affected 1.4 % of stand area per year. The areas affected by soil disturbance and effects of woody litter were similar. Erosion, greater in deep than in shallow tephra, peaked in 1981, whereas most litter-caused disturbances increased after 2000. Less frequent litter-based disturbances covered greater area. Our results differ from conclusions about non-volcanic understory disturbances. Secondary disturbances are variable, need more study, and are likely to affect many other systems.

Key words: erosion, forest understory, litter fall, Mount St. Helens, succession

Introduction

Vegetation change following disturbance has been a major topic for plant ecology for over a century (McIntosh 1980). Many types and scales of disturbance have been considered in detail (e.g., Pickett and White 1985; Gill et al. 2017). Interpreting results of such vegetation sampling requires a thorough understanding of the nature of the disturbance, which is often not described in detail (Roberts 2004; Swanson and Crisafulli 2018). Disturbances differ in type, spatial scale, frequency, and their effects, making disturbance sometimes a difficult concept to define, but it is clear that disturbance is a major factor controlling ecosystem dynamics and services relevant to humans (Thom and Seidl 2016).

In the forest understory, disturbance has an important influence on succession, population dynamics, and diversity of plants (Rydgren et al. 2004; Fourrier et al. 2015). For understanding succession in an understory herb layer, Roberts (2004) suggested judging the severity of disturbance by the proportion of the plant layer removed or damaged. He also noted that severity should be determined for the forest canopy, for understory vegetation, and for the forest floor and soil. Many sources of understory disturbance have been studied and analyzed, and the differences in their effects predicted (Peterson et al. 1990; Roberts 2004; Fourrier et al. 2015).

In many temperate forest landscapes, it has been assumed that most stands are even-aged, resulting from a disturbance that initiated a successional sequence; however, subsequent lower intensity disturbances are often important, producing a complex disturbance history (Bergeron and Fenton 2012; Petritan et al. 2017). Even old forests that appear “stable” are subject to repeated and often frequent disturbances of a lesser intensity than necessary to reset succession (Nagel et al. 2014; Khakimulina et al. 2016). Forest canopy gaps are a widely known example of small scale, frequent disturbance (e.g., Spies and Franklin 1989; Nagel and Svoboda 2008;

Després et al. 2017). Several types of intermediate disturbance can modify succession and stand dynamics, including windstorms (Woods 2004; Nagel and Diaci 2006), insect outbreaks (Sibold et al. 2007; Campbell and Antos 2015), and ice storms (Takahashi et al. 2007; Lloren et al. 2020). Even low intensity disturbances may modify future vegetation. For example, we reported significant effects of small-scale, low intensity disturbance in changing the 30 year re-development of understory vegetation following a large infrequent disturbance (Zobel and Antos 2017).

Such “secondary” disturbances in forests involve many of the processes that can initiate succession (e.g., Sibold et al. 2007); for example, wind can destroy the canopy or cause only minor burial or breakage of understory plants by falling debris (Girard et al. 2014); fire can destroy all aboveground vegetation or be confined to patches of understory (Agee 1993); and volcanoes can destroy forests throughout a landscape, or produce tephra that kills only understory plants (Swanson and Major 2005; Chang et al. 2019). Details of small scale, ongoing disturbances are available for some situations (e.g., Pickett and White 1985): tree mortality produces forest canopy gaps (Spies and Franklin 1989), modifying microenvironment and producing large woody litter that falls on plants or acts as future substrate; burrowing animals consume plants, and disturb and re-distribute soil, organic matter and microorganisms (Allen et al. 2018); and uprooted trees produce pit/mound microtopography that strongly influences plant distribution (Peterson et al. 1990; Kern et al. 2019). For disturbances that affect forest understory plants, details about the nature, size and frequency of canopy gaps exist (e.g., Nagel and Svoboda 2008; Després et al. 2017). Understory vegetation often varies at a small scale (e.g., Chudomelová and Zelený 2020), suggesting that small-scale disturbances influence forest understory structure. The effects of small-scale experimental disturbances in forest understory

have been reported (Rydgren et al. 2004), whereas specific information on natural forest disturbances at similar small (e.g., 1 m²) scales seems to be sparse.

Most forest disturbance literature focuses on tree mortality as the disturbance and tree regeneration as the biotic response (Roberts 2004; Gill et al. 2017), although some studies do emphasize the response of understory plants (e.g., Halpern 1989; Rydgren et al. 2004; Fourrier et al. 2015). However, understory plants are a major component of forest ecosystems, contain much of the plant diversity in temperate forests, and can be strongly affected by disturbances, including small-scale secondary disturbances (Roberts 2004). For example, tree canopy gaps can influence understory other than tree seedlings (Roberts 2004; Kirchner et al. 2011). In turn, understory plants can influence tree reproduction (Spies and Franklin 1989; George and Bazzaz 1999; Gafta and Peet 2020), and thus the composition and dynamics of the tree canopy.

During the 1980 eruption of Mount St. Helens, deposition of tephra (aerially transported volcanic ejecta) provided a large infrequent disturbance (Waite and Dzurisin 1981). Tephra deposition was widespread, severely damaging forest understory vegetation and initiating successional understory change (e.g., Antos and Zobel 1985; Zobel and Antos 1997, 2017; Fischer et al. 2019). Effects of environment, including small scale disturbances, were significantly related to cover of all understory growth forms and several dominant species before, just after, and 30 years after the eruption. Here we describe change in canopy tree cover and 13 types of post-eruption understory disturbance, including their size and frequency, based on repeated sampling of small permanent plots during a 30-year period. Sampling sites represented two levels each of tephra depth and herb richness. We describe disturbance as suggested by Roberts (2004) and discuss the ways in which study of this volcanic disturbance and the smaller post-eruption disturbances contradict conclusions drawn for several non-volcanic disturbances.

Methods

Study sites

Mount St. Helens erupted May 18, 1980, spreading tephra across heavily forested slopes of the southern Cascade Range of Washington State, USA (Swanson and Major 2005). Tephra deposition was the only effect of the eruption at our sites; it left the forest canopy intact, but buried the forest floor and many small plants, severely modifying understory vegetation (Antos and Zobel 1985). We studied damage to and re-development of understory vegetation at four densely forested sites, which differed in tephra depth and richness of the herb layer (Table 1). All sites supported old-growth forests with trees > 600 yr old and representative of the *Abies amabilis* vegetation zone of Franklin and Dyrness (1973). Each site had approximately 100 1-m² permanent plots with intact tephra, arrayed at 3 m intervals along four or five transects established two to four months after the eruption. The fine surface layer of tephra developed into a hard crust (Waite and Dzurisin 1981; Zobel and Antos 1991) (Fig. 1a). The crust, which was only slowly permeable to water, developed after wetting and drying, but before plot establishment.

At site DR (Table 1), several old trees died in the decade after the eruption, apparently from effects of a heavy deposit of a localized fine, sticky tephra layer (Segura et al. 1994). Their decomposition increased the woody litter at this site (Fig. 2a). Damage from wind or from snow loads falling from large trees damaged trees of the lower canopy periodically at all sites.

Data collection

Our description of disturbance generally fit Roberts' (2004) suggestions: within each of our vegetation sampling plots, we measured the proportion "that is occupied by each set of disturbance conditions and the range of patch sizes in each condition" (p. 1281). Cover of vegetation and disturbance was sampled at intervals: 1980-1983, 2000, 2005, and 2010 at all sites plus 1984, 1987 and 1990 in deep tephra and 1989 in shallow tephra. During plot establishment, we recorded plot environmental variables, including percent cover by wood and by eroded tephra, and the species of all trees with foliage > 1.5 m above each plot; this tree foliage census was repeated only in 2016. During each vegetation sampling, we recorded the extent of environmental changes that may have affected resident plants or the establishment and growth of plants in the future. These "secondary disturbances" were assessed by their percentage cover in each 1-m² plot. Field recording of disturbance ignored cases that involved < 1 % of a plot's surface (i.e., < 1 dm²).

Defining post-eruption disturbances

We quantified all three locations of disturbance that Roberts (2004) suggested: canopy, understory vegetation and forest floor and soil. For the canopy layer, the species of all trees with any amount of foliage over a plot was assessed by eye at the time of plot establishment and in 2016. The observer in 1980 (JAA) was present in 2016 and trained additional observers. The change in canopy was assessed as the difference between number of plots with a canopy tree species above it in 1980 and 2016. A plot with no tree foliage above it was considered to be in a canopy gap. Thus canopy disturbance was assessed once over a period of 36 years, different from the multiple assessments over 30 years for other disturbances described below. We determined the change in number of plots with a species above it, and the number of individual

plots in which the species appeared between 1980 and 2016 and the number of plots from which a species had disappeared by 2016. We assumed that a plot without overhead canopy foliage represented a gap 3 m in dimension (plots being at 3 m intervals); thus, we estimated numbers and sizes of gaps in the canopy by counting consecutive single-plot gaps along the sampling transects.

For understory vegetation and forest floor and soil disturbance, we determined the effects of soil (usually tephra) disturbance, litter fall, and fire. Values analyzed for each plot and sampling date were equal to the difference in area of each disturbance category between the previous and current sampling date, with one exception. The influence of fallen branches with intact needles was primarily from the dense coverage of thick layers of needles attached to branches; when the needles fell off, after about two years in our experience, that influence was greatly reduced. Thus, we analyzed the area of those branches with needles attached that were currently on the plot surface.

We defined 13 categories of secondary disturbance below the canopy, first based on the three mechanisms of influence on small plants: soil disturbance, litter fall, and fire. Within each mechanism, we defined categories as follows; names are short for convenience in data presentation:

A. Soil disturbance

1. Elk: Individual elk hoof prints in tephra, elk trails, or more diffuse breakage of tephra crust and stirring or compaction of the underlying layer of coarse, single-grained pumice.

2. Dig: Holes and loose tephra related to animal digging or burrowing. Some were made by mountain beaver (*Aplodontia rufa*). Gophers and other mound-builders were absent from these old-growth forest sites.
3. Erode: Tephra washed or sloughed into or away from a plot (Fig. 1a).
4. Loose: Tephra that is loose atop the plot surface, but with no obvious cause. This was recorded beginning in 2000, by which time most of the tephra surface was covered with litter. Because of this short record, we omit it from some analyses.
5. Rootwad: Disturbance of the soil surface adjacent to where a tree had tipped or blown over, as in pit-and-mound microtopography

B. Litter fall

6. Wood: Logs or slabs from broken or blown down trees lying on the surface (Fig. 1c, d, Fig 2).
7. Suspend: Logs or slabs above the surface in the plot that would reach the surface as decomposition occurred (Fig. 1b, c).
8. Bark: pieces of bark > 10 cm in dimension, on the surface.
9. Branch: Major branches without needles, > 3 cm diameter (Fig. 1c, d, Fig. 2b).
10. FWD: "Fine woody debris": a dense covering of small pieces of wood, bark, rotten wood or twigs (Fig. 1c, d).
11. Rot: masses of rotted wood fallen from snags or decomposing logs.
12. BrNe: Branches with needles attached, only recorded if $\geq 5\%$ of the plot (Fig. 1b, d).

C. Fire

13. Char: An area affected by a ground fire, indicated by charred wood or vegetation or by soil disturbance associated with fire suppression.

We calculated values for combined disturbance types affecting soil (Soil-all, the sum of types 1-5) and associated with woody litter (Wood-all, types 6-11). We also refer to all litter-associated disturbances, i.e., Wood-all plus BrNe.

The fire-induced disturbance was encountered only in one plot at site SP in 2003. A non-sampling visit to the site revealed effects from a lightning strike on a tree, which set fire to an adjacent tree, and fire had spread in a narrow tongue across the forest floor for perhaps 10 m before it had been extinguished, causing charring and some soil disturbance. Fire-related disturbance is not considered further.

Each disturbance type at each site was described by three properties, to indicate how large it was and how often it occurred:

1. Total area (**TA**) for a site during a sampling year is the sum of all cover values for a disturbance type for all individual plots in that year (or for all sampling years). One value of TA can be calculated for each disturbance type at each site for each sampling year.
2. Frequency (**N**) is the number of plots in which the disturbance type was recorded at a site during a sampling year, or for all sampling years. As sites had slightly different numbers of plots and sites with different tephra depths were sampled different numbers of times, we calculated an overall Relative Frequency (RF), which is N across all years divided by the total plot-years sampled at that site, for comparisons among sites. The total plot years for a site for the whole study was approximately 100 plots times the number of sampling

years for a site (7 for shallow tephra, 9 for deep tephra). RF values were converted to percentage; one value was available for each disturbance type at each site.

3. Area per incident, or size (**A/I**). Values of cover recorded in the field were used as the size of each disturbance incident in a plot in a sampling year. For a year or years, mean A/I at a site is the sum of percentages of plot covered by the disturbance type in all plots (TA), divided by the number (N) of plots in which that type was recorded. Individual plot values of A/I were available for analysis. Multiple occurrences of a disturbance type in a plot in one year were included in a single A/I value for that plot.

Statistical analysis

Plot values of A/I were analyzed using a mixed effects Restricted maximum likelihood (REML) model to determine significance among tephra depths, herb richness levels and years. In each model, tephra depth, herb richness and year were treated as fixed effects while individual plot identity nested within site was treated as a random effect to account for the repeated measures of individual plots through time. All such analyses were conducted in R (version 3.6.1; R Core Team 2019) using the package *lme4*, and R Studio (version 1.2.5001). Type III analysis of variance tables from each REML model were constructed using Satterthwaite's method.

Analysis of site-level means for each year utilized regression to relate, for each disturbance category: 1) RF to A/I using means of disturbance types across years, 2) all plot values of A/I to sampling year for each site, and 3) all-site values of TA and N to sampling year. Linear or polynomial models were chosen based on appropriate distribution of residuals.

Results

Tree canopy change

The prevalence of canopy gaps increased at all sites over the 36 years between measurements (Table 1). Most of the canopy reduction was due to a decrease in *Abies amabilis* at all sites (Table 1). No other species consistently lost or gained coverage. At three sites, relative importance shifted from *A. amabilis* toward *Tsuga heterophylla*. The pattern of change was dynamic: overall, 36 % of plots either gained or lost a species from overhead. For *A. amabilis*, which made up most of the small tree cohort, 4.7 % of total plots gained this species while 15.7 % lost it. *Tsuga heterophylla* appeared in 4.2 % of plots but was lost from only 2.4 % of plots. Change for other species was less consistent.

We estimated the numbers of canopy gaps of different size (Table 2) by assuming that one plot lacking overhead tree foliage represented 3 m of transect beneath a canopy gap, and then counting consecutive plots along a transect without a tree overhead. Most gaps included only a single plot (i.e., have a 3 m dimension), 50 including data from both 1980 and 2016; other size/number combinations were: 6 m, 19; 9 m, 15; 12 m, 6; 15 m, 4; 21 m, 2; and 27 m, 1. The overall mean dimension was 3.75 m in 1980, 6.3 m in 2016; assuming circular gaps, the corresponding mean gap areas would be 11.0 and 31.2 m² for the two years, respectively.

Disturbance in the understory

At all sites, understory plant cover increased for the 30 year study period, responding to the substantial cover lost during tephra deposition. The secondary disturbances, which we summarize here, had the potential to modify the trajectory of that response. We recorded disturbance for 41.3 % of the total plot area of 400 m² (or 1.4 % of the area per year); 1981 was highest at 11.3 %, while other years ranged from 0.5-1.7 %.

Summarizing our secondary disturbances by mechanism showed equivalence of the importance of soil- and woody litter-based disturbances: overall means of relative frequency (RF) and size (A/I) of Soil-all were similar to those variables for Wood-all (Table 3).

Overall, the fall of branches with needles (BrNe) and wood debris (Wood) were the most frequent secondary disturbance types, followed by erosion (Erode) and deposition of bark (Bark) (Table 3). Development of loose tephra with unknown cause (Loose), assessed only during the last three sampling dates, would have been among the most frequent if the record had been longer.

Area per incident (A/I) differed in relation to tephra depth, herb-richness of the habitat and year, depending on the disturbance type (Table 4). Soil-all and four of its component disturbance types differed significantly among tephra depths and years, but not with herb-richness. Erode, Elk and Loose had larger A/I in deep tephra, while Rootwad had larger values in shallow tephra. Interactions of tephra depth x year were significant for Soil-all, Erode and Rootwad. The disturbance type Elk showed interactions with herb richness. Disturbance type Dig had no significant differences. Woody litter disturbance types had more diverse patterns of significance than soil-related types (Table 4). All types (except Rot) differed among years. Only Wood-all, Suspend and Fine Woody Debris (FWD) differed with tephra depth, the latter two more important in shallow tephra. Wood and FWD were more important in herb-poor communities. Wood-all, Suspend and FWD showed multiple interactions. Rot had no significant differences in this analysis. Branches with needles (BrNe) differed with year but not with tephra depth or herb richness, although year showed a significant interaction of depth and richness (Table 4). A/I was higher for Rot, FWD, Branch and Erode than for other disturbance types.

The relationship of A/I to RF was highly variable (Table 3). Among the seven litter-based disturbances, the less frequent categories produced larger incidents ($r^2 = 0.95$, $p = 0.002$), although for some categories some sites provided exceptions. Suspended wood (Suspend) had consistently high A/I in all sites, probably because it often involved large diameter logs (Fig. 1b). The five soil-based categories showed no relationship between RF and A/I ($p = 0.27$).

A/I of all except two secondary disturbance types varied among years (Table 4). Regressions of individual plot A/I values versus year for each disturbance type that varied significantly among years were significant for Wood-all and five individual disturbance types ($n = 6$ to 372, all p -values < 0.037): A/I increased with time for Elk, Erode (after 1981), Wood-all, Wood, Bark and BrNe; no type declined. Soil-all after 1981 showed no significant relationship with year.

Total area (TA) per site and number of incidents per site (N) varied greatly among sampling years (Table 5). The highest values for TA and N occurred in 1981 for Soil-all (Table 5). The largest change with time was the sharp drop in N and TA of Soil-all from 1981 to 1982 (Table 5). The major contributor to this pattern was Erode; from 1981 to 1982, TA declined from > 1000 to 25 dm^2 and N dropped from > 30 to < 1 incidents per site. This disturbance had < 2 incidents/site from 1982 to 1990, and 2.8/site after 1990. Other disturbance groups and types did not show such an abrupt change in importance; Wood-all did not have a strong peak year. With only ten values for TA and N, one for each of ten sampling years, no disturbance type or combination of types was significantly related to sampling year at $p < 0.050$ using several regression models. Erode, however, had a p -value for N of 0.051.

Discussion

Measuring disturbance

Studies addressing disturbance effects on forest understory layers are sparse, especially for herbs and bryophytes (e.g., Jonsson and Esseen 1990; Rydgren et al. 2004; Fourrier et al. 2015, Waxwing et al. in press). Study of understory layers has often been hampered by inadequate description of disturbances (Roberts 2004). Most study of forest disturbance is focused on woody plants and disturbances are described to fit that goal. Roberts (2004) emphasized the herbaceous layer, and stressed that ecologists considering forest understory need to describe the degree of damage from disturbance for three categories: canopy trees, understory plants themselves, and the forest floor and soil. In addition, prompt study is critical (Swanson and Crisafulli 2018): for example, delayed description of our plots would have missed the importance of snow beneath tephra (Antos and Zobel 1982) and the early importance of erosion (Fig. 1a) and its subsequent reduction.

Our data, here and from studies of understory plant cover (e.g., Antos and Zobel 1985; Zobel and Antos 1997, 2017), constitute an appropriate measurement of disturbance to a forest understory. We began two months after the eruption and included damage to canopy trees, understory plants and soil and forest floor, using sites across a wide range of disturbance severity and species composition (Table 1). We also measured additional environmental factors, as Roberts (2004) suggested: tephra depth, soil-surface light, microtopography, and presence of snow beneath the tephra deposit (Table 1) and, for a few years, soil temperature and water potential. Such thorough measurements are rare (Roberts 2004). We measured disturbance repeatedly over 30 years, more frequently just after the eruption when disturbance was most frequent, and long enough to allow three sites to reach pre-eruption shrub cover and two to do so for herbs. Roberts (2004) also called for elucidation of mechanisms of understory recovery. We

have studied such mechanisms, including survival of buried plants, structural and chemical change of buried plants that emerged from tephra, flowering and seedling establishment, and long-term expansion of plants released by both immediate and delayed erosion (see citations in Zobel and Antos 1997, and Zobel and Antos 2007, 2009, 2016, 2017).

Sampling of disturbance could be done several ways. Our methods, periodic sampling of disturbances in small plots, is a reasonable way to delineate the types, relative numbers and relative sizes of small disturbances. It does, however, introduce differences from what one would measure by an annual census of disturbances as entire individual events, measuring the size of each new erosion channel and area impacted by each newly fallen tree, for example. We measured annually through 1984, but periodically afterward, at intervals of three to eleven years. For cases that are obviously a single event, like the fall of a tree or a branch system, that affect a single plot, our counts will be correct. However, our counts may underestimate other disturbances that develop as a series of episodes, adding up to what we recorded: examples are erosion, elk disturbance, and fall of bark or rotten wood from a decomposing snag. Sizes of individual episodes will be unknown, but their cumulative area should be accurately measured, which presumably is what will affect organisms. For branches with needles (Fig. 1b, d), which fall off after two years, we would have recorded only events that occurred during final two years of our 3- to 11-year intervals between measurements. The size of many events will be underestimated by our methods that measure proportion of area of a 1-m² plot, given that many events cross the plot boundary (Fig. 1b, c, d). Some erosion channels and tree falls were tens of m long (Fig. 1b, 2). Depending on their orientation relative to sampling transects, such events may affect from one to several plots, and our counts will overestimate the number of events when one event affects > 1 plot.

Even so, viewing our 100 plots per site as sampling points within the larger stand should allow a reasonable estimate of the proportion of the stand affected by that type of disturbance in that year (or series of years) and of canopy gap dimensions. Although we added measurement of disturbance to a system designed for sampling vegetation change, what we present here should give a reasonable estimate of timing and relative importance of individual disturbance types, and a good estimate of the proportion of stand area affected by each type. There appear to be few or no similar descriptions of secondary understory disturbance available.

Topography will affect some types of disturbance. Our study sites were less steep than most of the surrounding landscape, chosen to minimize erosion and thus allow effective study of the influence of intact tephra. Most erosion in our plots occurred downhill from steeper slopes outside our sites, where erosion seemed to be more common. This would result in more removal or thinning of tephra in some steeper areas and accumulation of disturbed tephra in others.

Describing our disturbances

A complete description of disturbance involves identifying the types of conditions producing disturbance, the conditions disturbance produces and how they impact plants, and the patch sizes, frequency and total area for each type. We identified two major mechanisms, soil modification and litter-fall, with several types in each. Data presented here about post-eruption disturbances indicated that: (1) canopy disturbance involved primarily the loss of the late-seral dominant, *Abies amabilis*; (2) combined soil- and litter-associated disturbances had similar frequency and size, each mechanism affecting about 20 % of the area of about 11 % of the plots; (3) erosion and the sum of soil disturbances peaked the first year after the eruption; (4) some other disturbance types were also not uniform through time (Table 5); (5) for wood-associated

disturbances, less frequent types were larger (Table 3), and (6) post-eruption disturbances in the understory affected an average of 1.4 % of stand area each year.

The most obvious significant change of disturbance frequency and size through time was the abrupt reduction of erosion after the first year following the eruption. We documented erosion as a frequent event in 1981, but not later. This pattern probably reflects the early development of a rill network in the tephra (Fig. 1a); settling of tephra under the meters-thick winter snowpack; and the accumulation of litter and, later, development of a forest floor. The initial erosion removed some of the low-infiltration, cemented tephra surface crust (Zobel and Antos 1991) and produced rills. The reduction of erosion of tephra soon after its emplacement is common (Ayrís and Delmelle 2012), especially after development of a rill network. In our case, water flowing off the crust entered the loose, coarse lower tephra layer exposed in rills (Fig. 1a), which provided a high infiltration pathway, reducing the accumulation of surface flow that produced the initial erosion of crust.

Size (A/I) of four other disturbance types (Elk, Wood, Bark and Branches with needles) and of the combined type for woody litter all increased significantly with time. Elk populations increased through time (McCorquodale et al. 2014) and elk probably lingered longer in the forest as understory foliage expanded. Increase of incident size for wood, bark, and all woody litter reflected the delayed mortality of several old-growth canopy trees (Segura et al. 1994) at site DR (Fig. 2a), the lightning strike at site SP, and high mortality among smaller *Abies amabilis* trees at sites SR, DR and DP, perhaps stemming from wind throw or snow breakage. The obvious increases in wood, bark and branches with needles occurred after 2000. Sloughing of large branches, segments of trunk, bark and other woody debris from snags followed mortality by a decade or more (Fig. 2a).

Relating disturbance to plant cover

Our previous work quantified the degree of damage to the understory itself caused by tephra deposition (Antos and Zobel 1985; Zobel and Antos 1997, 2017). Damage to bryophytes was severe with > 2 cm tephra (loss of 97-99 % of pre-eruption cover), low to moderate to herbs with 4.5 cm (0-41 %) and severe with >12 cm (99 %), and moderate to severe to woody plants only where tephra fell on snow (66-99 % contrasted to 21-30 % with little snow). Re-development of cover has been variable (Zobel and Antos 2017).

In our analysis of relationships between secondary disturbances and plant cover (Zobel and Antos 2017), we used three disturbance categories: all soil disturbances combined, branches with needles, and all other woody litter combined (Soil-all, BrNe and Wood-all as defined here). Soil disturbance was most often significant in modifying plant cover just after the eruption, whereas biological variables (e.g., fall of woody litter, species of canopy tree) were more important before the eruption and 30 years afterwards. Plant cover of all growth forms was higher where soil (usually only tephra) was disturbed in 1981. In seven of 13 instances with a significant correlation, the soil-disturbance effect lasted 25 or 30 years. The only negative effect of soil disturbance was a decrease in herb cover associated with movement of roots of fallen trees. Cover of woody litter often increased bryophyte cover but occasionally reduced herb and tree seedling cover. In some cases where woody litter covered a plot, causing near-total loss of plants, cover did recover years or decades later as the litter decomposed. Branches with needles reduced herb and tree seedling cover in year 30.

Tephra deposition: a contrast to other disturbances

Ecological response to volcanic disturbance has been studied for over a century and in detail, but secondary disturbances have received limited attention and disturbances are often poorly described (Swanson and Crisafulli 2018), similar to Roberts' (2004) conclusions about other disturbances. Volcanic disturbance types differ widely, as do ecosystem responses to them (Chang et al. 2019).

Here we compare understory plant responses in tephra to Roberts' (2004) review of responses of herbs to several non-volcanic disturbances. It is remarkable how often and how distinctly tephra deposition and subsequent secondary disturbances act differently, often opposite, from the several types of disturbance that Roberts reviewed. Roberts (2004, p. 1281) states that, although some disturbances caused by people will do so, no natural disturbance will leave a canopy intact, but seriously impact the forest floor and soil. But these are precisely the effects of many tephra deposits. Although tephra falls are often widespread and relatively uniform, the potential impact of their size is mitigated by secondary disturbance of the types we described (e.g., Fig. 1a): distance to a propagule source is reduced by the propensity of new tephra to erode (Ayrís and Delmelle 2012), which allows formerly buried survivors to expand and reproduce. Although the major impact of tephra on understory plants is burial, and ecologists have studied plant burial in many situations (Antos and Zobel 1987), Roberts (2004) mentions only that floods can bury plants, without reference to how plants react. On his 3-axis diagram (Fig. 1 of Roberts 2004), tephra deposition of the type we studied would be located near the minimum on the canopy damage axis, at the maximum on the forest floor damage axis, and highly variable, depending on tephra depth and properties, on the understory damage axis, a position partly overlapping with floods on his diagram, but with more consistently high forest

floor and low canopy damage. Deeper and denser types of tephra may also severely damage or destroy the canopy.

Some of Roberts (2004) conclusions about how a particular disturbance type will affect the understory contrast with our findings. He concluded that soil disturbance reduced understory cover, but we found almost all disturbances of tephra increased understory cover (Fig. 1a), as tephra removal and breakage of crust allowed buried plants to expand when exposed, the effect lasting for years after burial (Zobel and Antos 2017). Roberts (2004) concluded that woody debris and pit and mound microtopography, caused by tree fall, were important because they will increase the future variety of substrate; in our systems, woody debris sometimes significantly reduced vascular plant cover on impact, while soil disturbance by roots of fallen trees reduced herb cover. Bryophyte cover, in contrast, increased with cover of wood. Roberts (2004) viewed the increase of light caused by canopy damage as leading to greater competition among understory species. In contrast, in our sites (Zobel and Antos 2017) there were only three significant negative correlations between cover of different understory strata or species, but 27 positive correlations, indicating that tree seedlings, shrubs, herbs and bryophytes generally did well in the same microenvironments. We did find, however, that correlations of understory cover with individual canopy tree species were more often negative than positive, as Roberts suggests; correlations with canopy gaps were mostly positive.

There are a number of reasons why some of our conclusions differ from those reached by Roberts (2004). Soon after tephra deposition, secondary disturbance of tephra can remove the impact of tephra on plants, rather than further damaging plants. Differences also could reflect time scales: Roberts (2004) considered an eventual result (woody litter turning into substrate, for example), whereas our data often represent an immediate effect (plants destroyed when a log

falls on them). Of most importance is that tephra emplacement and subsequent secondary disturbances differ from the types of disturbance that are usually considered. Our work contradicts Roberts' (2004, page 1274) assertion that his review considered "the full range of natural disturbance agents". Tephra fall and volcanic disturbance in general are frequent and widespread on a global scale (Swanson and Crisafulli 2018), and need to be considered when ecological generalizations and successional models are developed (Chang et al. 2019). Similarly, the complexity of understory performance is complicated beyond the variability among herbs, which Roberts (2004) emphasized; tree seedlings behaved differently than herbs; and, especially, forest floor bryophytes were more sensitive to disturbance than herbs, took longer to regain cover, and, in our system, were the only understory layer in which ruderal species were important (Zobel and Antos 1997). Discussion of "forest disturbance" and succession should refer to more than the canopy species, and consider all the plant growth forms present in the understory.

Although secondary disturbances following tephra deposition differ from those in other situations, the variation among secondary disturbances does not detract from their widespread importance, but indicates that generalization may be difficult. Secondary disturbances need to be considered when examining vegetation changes in many situations. There is a tendency to assume that major disturbances, especially ones that initiate new stands, are of primary importance in controlling vegetation change. However, secondary or intermediate disturbances can modify trajectories of vegetation change substantially (e.g., Woods 2004; Sibold et al. 2007; Bergeron and Fenton 2012; Gill et al. 2017; Martin et al. 2019). This is the case for both the forest understory and the tree canopy. Thus, a fuller understanding of both forest canopy

dynamics and understory changes requires acknowledgement and thorough examination of the role of secondary disturbances.

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Draft

Table 1. Site characteristics at the time of the eruption and frequency (% of 1 m² plots) with a given canopy tree species overhead or no tree species (canopy gap) for 1980/2016.

Property	Site code ^a			
	SP	SR	DP	DR
Distance to crater (km)	58	58	22	22
Elevation (m)	1245	1290	1160	1240
Tephra depth (mm)	42.9	46.1	134.3 ^b	139.1
Herb diversity (species/m ²)	1.56	3.60	0.98	2.90
Herb cover (%)	23.2	20.4	4.8	22.3
Light intensity (% of open)	14.0	16.3	9.2	23.4
Average slope of plot (degrees)	1.9	3.6	3.3	1.6
Cover by snow pack, 1980 (%)	27.5	92.0	11.0	89.3
Cover by large wood, 1980 (%)	10.7	3.7	5.4	4.3
<i>Abies amabilis</i> canopy ^c	76/64	61/49	81/64	56/55
<i>Chamaecyparis nootkatensis</i> canopy ^c	4/3	55/61	5/5	0/0
<i>Pseudotsuga menziesii</i> canopy	4/3	0/0	10/10	0/0
<i>Tsuga heterophylla</i> canopy	53/53	16/20	56/60	1/1
<i>T. mertensiana</i> canopy	4/0	3/3	3/4	18/19
Canopy gap	3/13	12/19	4/8	33/36

^aSite codes: S = shallow tephra, D = deep; P = herb-poor, R = herb-rich

^bTephra depth was not measured at each plot at site DP; the depth value is the mean depth (10 measurements) in 1987.

Nomenclature follows Hitchcock and Cronquist (1973) to be consistent with earlier publications. The name of *C. nootkatensis* has been changed to *Callitropsis nootkatensis*.

Note: Environmental factors differ among sites ($p \leq 0.007$) based on a Kruskal-Wallis test.

Draft

Table 2. Size and number of canopy gaps in each study site in 1980 (year 0) and 2016 (year 36) based on number of consecutive plots in a transect without tree foliage above the plot.

Site	SP		SR		DP		DR	
Year	0	36	0	36	0	36	0	36
Gaps/300 m transect	0	5.3	8	8	4.1	6.8	13.4	11.4
Median dimension (m)	0	7.5	3	6	3	3	6	6
Mean dimension (m)	0	7.5	4.5	6.9	3	3.3	7.5	7.5
Maximum dimension (m)	0	12	9	21	3	6	21	27

Note: Plots are 3 m apart, and we assume that each plot counted represents 3 m of gap dimension. Number of gaps is expressed per 100 plots (300 m of transect), because sites differ in number of plots.

Table 3. Relative frequency (RF, %) and mean size of incidents (A/I, dm²) of secondary disturbance types in plots with natural tephra in four old-growth forests northeast of Mount St. Helens from 1981 to 2010.

Site (n)	SP (714)		SR (700)		DP (891)		DR (900)		All (3205)	
Property	RF	A/I	RF	A/I	RF	A/I	RF	A/I	RF	A/I
Soil-all	6.4	24.3	7.1	22.7	8.2	22.3	18.0	20.5	10.6	22.0
Elk	0.4	47.0	0	0	1.7	4.1	7.8	18.9	2.7	18.0
Dig	0.4	9.7	0	0	0	0	0.6	1.0	0.2	3.2
Erode	6.3	27.0	6.1	24.6	5.2	31.8	2.7	49.5	4.9	32.3
Loose	1.4	3.8	1.0	1.1	1.5	6.0	7.7	10.9	3.2	9.5
Rootwad	0.4	25.0	0.4	15.0	0.2	0.5	0	0	0.2	20.2
Wood-all	13.3	25.0	7.4	15.9	10.8	9.4	10.6	19.7	11.6	19.6
Wood	6.6	16.1	5.9	13.1	5.6	7.8	6.1	14.0	6.9	13.8
Suspend	2.1	24.8	1	25.7	0.4	18.8	0.8	23.1	1.1	25.0
Bark	4.6	19.4	1.3	23.3	4.8	7.0	3.4	15.7	3.7	16.0
Branch	1.4	31.9	0.6	6.5	0.6	13.0	2.1	29.4	1.2	30.8
FWD	1.5	43.5	0.4	13.3	0.2	17.5	0.2	5.0	0.7	37.6
Rot	0.4	40.0	0	0	0.2	50.0	0.2	4.0	0.2	41.3
BrNe	8.8	9.3	4.6	9.8	10.9	9.0	4.8	14.0	7.7	10.9

Note: Sites are described in Table 1. Categories of disturbance are defined in Methods.

n = number of plot x year cases in the sample.

Table 4. Significance (*p*-values) from Type III analysis of variance table computed from REML models of individual plot values of A/I in relation to three fixed effects: tephra depth (D), herb-richness of the community (R), and year (Y).

Disturbance	Fixed Effects				Interactions		
	D	R	Y	DxR	DxY	RxY	DxRxY
Soil-all	<0.001	0.12	<0.001	0.12	0.002	0.81	0.95
Elk	0.008	0.087	<0.001	<0.001	0.24	0.079	<0.001
Erode	0.018	0.80	<0.001	0.34	0.15	0.98	0.61
Loose	<0.001	0.34	<0.001	0.095	0.004	0.81	0.71
Rootwad	0.008	0.81	0.007	0.78	0.001	0.99	0.90
Wood-all	0.012	0.56	<0.001	0.020	0.022	0.027	0.52
Wood	0.11	0.042	0.001	0.78	0.48	0.53	0.72
Suspend	0.023	0.10	<0.001	0.56	0.009	0.023	0.29
Bark	0.14	0.45	<0.001	0.34	0.003	0.14	0.79
Branch	0.40	0.69	0.002	0.067	0.55	0.33	0.11
FWD	0.004	0.046	0.020	0.020	0.002	0.067	0.006
BrNe	0.26	0.36	<0.001	0.037	0.058	0.20	0.010

Note: The disturbances Dig and Rot had no significant fixed effects or interactions.

Bold values are significant at $p < 0.050$.

Table 5. Means per site-year for each sampling period (Year) of the total area recorded (TA, dm²), number of plots impacted (N), and mean size (A/I, dm²) for Soil-all, Wood-all and BrNe.

Type	Soil-all			Wood-all			BrNe		
Year (n)/Item	TA	N	A/I	TA	N	A/I	TA	N	A/I
1 (4)	1084	34.0	31.9	34	2.8	12.3	7	1.5	4.5
2 (4)	67	1.5	44.7	46	1.5	30.5	53	5.5	9.6
3 (4)	40	1.5	26.7	38	2.5	15.1	69	6.5	10.6
4 (2)	4	1.0	4.0	21	3.5	6.0	26	2	13
7 (6)	25	5.5	4.6	63	10.3	6.1	18	2.8	6.5
9 (12)	0	0	0	45	2.3	19.2	47	6.5	7.2
10 (6)	7	3.0	2.4	87	5.7	15.4	51	6.3	8.2
20 (42)	12	0.4	32.4	54	3.0	17.9	127	12.9	9.9
25 (20)	71	3.2	22.1	29	1.1	26.7	7	0.3	29
30 (20)	26	2.9	8.9	108	3.2	36.1	34	0.9	38.4

Note: n = number of site-years represented by the means for each sampling year; for BrNe, the number is fewer for periods longer than 2 years (2 x number of sites included in the sample). Year 1 = 1981. Numbers of plots per site are: SP, 102; SR, 100; DP, 99; DR, 100.

Figure captions:

Fig. 1. Understory secondary disturbance types near and within our sites. Painted bars on the plot frames are 1 dm (10 cm) long. a) Erode: Rill erosion that occurred in early summer 1980 in tephra 12-15 cm deep, allowing substantial re-development of herbs during 1980, whereas intact tephra allowed few herbs to penetrate. Note the intact crust atop the tephra and the single-grained, coarser lower layer in the sides of the rill beneath. (In a meadow adjacent to site DR). b) BrNe, Suspend: A branch with intact needles, sparser than most BrNe we counted, lies atop the suspended log (site SP, 2005). The metal plot frame extends beneath the log. With time, the bark will be shed (disturbance type Bark), causing further damage to plants, and eventually the rotting log will reach the surface (disturbance type Wood). c) Fine woody debris (FWD), Branch, Wood, Suspend, listed from upper left toward lower right, (Site SP, 2005). d) BrNe suspended above a plot (which would not be counted), Wood (site SP, 2020).

Fig. 2. Two examples of major woody litter fall. a) Dead old-growth trees at site DR, 2005, which died during the decade after the eruption, with some still standing as snags, others fallen. b) Many types of woody litter, site SP, 2020. The left log was on the ground before the eruption; tephra atop the log hastened its decomposition from the top. Logs to the right fell after the eruption.

Figure 1.

Figure 2.