Community development by forest understory plants after prolonged burial by tephra

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Abstract Several processes bury plants, but sediment can also be subsequently removed, often by delayed erosion. Thus, the ability to survive multiple years of burial and to respond when released are important to vegetation changes and population dynamics. We experimentally evaluated the effects of delayed removal of tephra (aerially transported volcanic ejecta) in an old-growth forest understory near Mount St. Helens, using 1-m^2 plots assigned to three treatments: tephra removed 4 months after deposition (50 plots), tephra removed 28 months after deposition (the delayed erosion treatment, 50 plots), and undisturbed, natural tephra (100 plots). Prior to tephra removal, species density, cover, shoot density, and shoot size in the delayed erosion treatment were all similar to values in natural plots and significantly less than values in plots cleared initially, indicating that 24 months of additional burial adversely affected understory plants. However, all attributes eventually approached pre-eruption values for shrubs and herbs, indicating that erosion greatly facilitated vegetation recovery. Responses varied substantially among species and growth forms. Overall, our experimental results indicate that some plants of most species can respond effectively after release from burial of at least three growing seasons. In addition, the delay of erosion retards ecosystem recovery relative to early erosion, facilitates recovery relative to no erosion, and modifies the trajectory of post-disturbance vegetation change.

Keywords Burial of plants · Forest understory · Mount St. Helens · Succession · Tephra · Volcano ecology

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Introduction

Many environmental situations bury plants, including wind deposits, accumulations of alluvium near streams, and ejecta from volcanoes (Antos and Zobel 1987; Kent et al. 2001). Study of plant burial is of relevance to several disciplines, but is emphasized by few investigators. Most study of plant burial has emphasized individual plant responses, but

community-level changes can be pronounced (Maun and Perumal 1999; Bach 2001; Dech and Maun 2005). For example, tephra (aerially transported volcanic ejecta) deposits modify vegetation (Griggs 1918; Antos and Zobel 2005; Hotes et al. 2010; Egan et al. 2016; Fischer et al. 2016, 2019; Zobel and Antos 2017). Debris falling from the canopy buries understory plants (Gillman and Ogden 2001; Gillman et al. 2003; Zobel et al. 2021). Burial in sand dunes, by wind-blown dust, by exceptionally late snow melt, and from alluvium along streams is restricted to a limited range of habitats, but volcanic tephra deposits, occur throughout the range of Earth's vegetation types (Swanson and Crisafulli 2018) along with human activities that can bury plants.

Plant response to burial is a major aspect of volcano ecology (Swanson and Crisafulli 2018), studied around the world for more than a century (e.g., Griggs 1918, 1919; Eggler 1948; Hotes et al. 2004; Efford et al. 2014; Swanson et al. 2016; Eddudóttir et al. 2017; Allen and Huntley 2018; Swanson and Crisafulli 2018; Hintz et al. 2021). Such study has recently focused on the 1980 eruption of Mount St. Helens, Washington State, USA (Kent et al. 2001; Dale et al. 2005; Cook and Halpern 2018; Crisafulli and Dale 2018; Chang et al. 2019), which damaged plants in many ways. The 1980 deposit of Mount St. Helens tephra was wide-spread, variable in depth, fairly uniform chemically, and mostly deposited within hours (Waitt and Dzurisin 1981).

Biotic effects of burial varied with tephra depth and texture, and the nature and environment of the vegetation (e.g., Antos and Zobel 1987; Harris et al. 1987; Kent et al. 2001; Zobel and Antos 1997, 2017). Even 2-cm deep tephra had long-term effects on forest understory communities (Fischer et al. 2016). At Mount St. Helens we have demonstrated substantial variation among understory species in morphological plasticity, flowering and seedling establishment, and major changes in plant density and cover over more than three decades (summarized by Antos and Zobel 2005; Zobel and Antos 1997, 2009, 2016, 2017; Fischer et al. 2019). Generally, recovery has been slowest where tephra was deepest and for bryophytes, morphologically inflexible herbs, and woody plants that were trapped prostrate beneath snow when the tephra fell. Mechanisms of recovery for individual species have included emergence from tephra and vegetative spread of survivors, establishment from seeds, and

survival until erosion exposed the shoots (Antos and Zobel 1985a, b, 1986, 1987; Zobel and Antos 2009).

Sediments that bury plants can be removed or thinned during sand dune movement, redistribution of alluvium, or erosion of tephra. Often, tephra erodes soon after its deposition (Ayris and Delmelle 2012; Zobel et al. 2021), but erosion can be delayed, for decades. Timing of erosion is important; understory plants buried three seasons in tephra from Katmai volcano in Alaska grew less well than plants released after one season of burial (Griggs 1919). At Mount St. Helens, erosion that removed tephra in 1980 allowed plants to recover rapidly (Zobel and Antos 1997). Experimental tephra removal two to four months after deposition in four old-growth forests near Mount St. Helens allowed full plant survival and an estimate of pre-disturbance vegetation (Zobel and Antos 1997; Fischer et al. 2019). However, as time before experimental erosion increased, survival and shoot size declined after 28 and again after 87 months in one forest (Zobel and Antos 1986, 1992, 1997; Antos and Zobel 2005). By the end of the third growing season after burial there was little potential for herbaceous plants to grow through intact tephra, although shrubs continued to emerge for up to a decade.

Erosion of tephra had the potential to alter long-term community development. Our early results from experimental tephra removal showed that after 28 months of burial, shrub density remained unchanged, but cover was only 21% of estimated pre-eruption values while herb density was 55% and cover 13% of pre-eruption values; bryophytes retained 18% of pre-eruption cover (Zobel and Antos 1986). During years 2–7 after release, plant cover exceeded that in plots on natural tephra but cover remained depressed compared to plots cleared of tephra two years earlier (Zobel and Antos 1997). By 18 years after tephra removal, total herb cover no longer differed from plots cleared in 1980 (Antos and Zobel 2005). Our previous analyses have noted the performance of different growth forms and major species after experimental erosion but did not address community compositional change after delayed erosion: to what degree will it eventually approach composition before the eruption? Our goals for this paper are to extend our results (Zobel and Antos 1986, 1997; Antos and Zobel 2005) to 34 years following the plants' release, and expands analysis to address community composition and less common species. We compare

trajectories of community change among three treatments (un-eroded, erosion after four months, and erosion after 28 months) and seek to identify plant attributes (Zobel and Antos 2009, 2016) that contributed to differences among species and treatments.

Our overall hypothesis was that delayed erosion would have a major impact on vegetation (Griggs 1919), but we wished to understand how specifically tephra removal would affect plant recovery and community change. Under this general hypothesis we consider five questions: (1) How do ordination patterns of treatments differ through time? (2) Which growth form(s) and taxa contribute to community differences? (3) Do important differences reside in diversity or cover or both? (4) If cover differs, does the difference in cover reside in its components of shoot density or of shoot size, or both? (5) Which aspects of plot treatment and plant properties may lead to the important changes in community properties?

Methods

Study site and field methods

The study site was in an old-growth forest (trees > 600 years old) at 1240 m elevation 22 km NE of the vent of Mount St. Helens; during the 18 May 1980 eruption, the site received tephra (aerially transported volcanic ejecta) that covered the original soil surface to a depth of 12–15 cm. The tephra deposit consisted of a thin, fine-textured basal layer, a coarse-textured, single-grained pumice layer that comprised most of the deposit, and a fine-textured surface crust (Waitt and Dzurisin 1981; Zobel and Antos 1991); it fell on snow over 89% of the study site. The site was not affected by other volcanic disturbances besides tephra fall, and the tree canopy remained intact. The forest was typical of the *Abies amabilis* vegetation zone of Franklin and Dyrness (1973); dominant trees were *Abies amabilis* and *Tsuga mertensiana*. The understory had a prominent shrub layer dominated by *Vaccinium* spp. and rich herb and bryophyte layers (Zobel and Antos 1997). The site is cool and wet with much of the precipitation falling as snow; a deep snowpack regularly accumulates, and snow cover persists from fall until early, sometimes mid- to late, summer.

We followed the change in understory vegetation using 100 1-m^2 plots on undisturbed tephra (natural plots, abbreviated "Nat", Zobel and Antos 1997, 2017). For comparisons with natural plots and to estimate pre-disturbance vegetation, we also established 50 1-m^2 experimental plots (1980-cleared treatment, Cl) from which tephra was removed in 1980, four months after the 18 May 1980 eruption (Fischer et al. 2019). Early values in Cl plots were used to estimate pre-eruption vegetation composition. To test the effects of delaying erosion, the subject of this paper, tephra was also removed in September 1982, 28 months after the eruption, from 50 additional plots (1982-cleared treatment, Cl82). Tephra was removed using small excavating tools, taking care to minimize damage to plants. Minor amounts of the thin, sticky basal layer were left where its removal would have caused excessive damage to plants. The Cl82 plots alternated with plots of the Cl treatment at 3-m intervals along six transects. Transects of cleared plots alternated at ∼ 3–4 m spacing with five transects with natural plots, which were also at 3 m intervals within a transect.

For each vascular species, cover was estimated, and the number of shoots was counted at their point of emergence from the soil (density) in each Nat and Cl plot annually from 1980 to 1984 and periodically thereafter. For bryophytes, total cover was estimated along with cover of a few prominent taxa (Waxwing et al. 2021). For the Cl82 treatment, plots were sampled immediately before the experimental tephra removal in September, 1982. Subsequently all three types of plots were generally sampled at the same times and in the same way. Details of sampling were discussed by Zobel and Antos (1997). During 2010 sampling of Cl plots, only cover of vascular plants was measured. Plant nomenclature followed Hitchcock and Cronquist (1973) to be consistent with our earlier publications.

Understory vegetation was very sparse in September 1982 except in eroded areas and the Cl plots. Most plants failed to grow through the tephra, even though summer temperature and moisture conditions in the buried soil were favorable for growth (Zobel and Antos 1986, 1992). Cover of shrubs and of small trees was low because stems bent over beneath snowpack were effectively buried by tephra (Antos and Zobel 1982). However, a dense layer of conifer seedlings established on the tephra in 1983 (Zobel and Antos

1997); conifer cover averaged 53% in Nat plots and 37% in Cl plots by 2016. The sampling of the Cl82 plots in 1983 allowed determination of survival and initial growth (Zobel and Antos 1986). Results from 1984, 1987, and 1990 were reported by Zobel and Antos (1997), and Antos and Zobel (2005) included data from 2000. Further sampling in 2010 and 2016 allows the response of plants to delayed erosion to be extended over a long period, 36 years after the initial tephra disturbance. After 36 years the total cover of herbs at this site was no longer significantly reduced compared to the estimated pre-disturbance values, whereas shrub and bryophyte cover remained lower (Fischer et al. 2019). Among the six tephra deposition sites we have studied at Mount St. Helens, this site had the greatest and most persistent effects of tephra on understory plants (Antos and Zobel 1985c; Fischer et al. 2019), making it an ideal location to study the effects of a treatment that simulated delayed erosion.

Data analysis

All three plot treatments were assumed to have had the same type of original vegetation; differences among treatment means, therefore, are assumed to represent treatment effects. Differences between Nat and Cl plots represent the effects of tephra removal. Differences between Cl and Cl82 plots (cleared after 4 and 28 months of burial, respectively) represent the effects of burial for the additional 24 months.

For non-metric multidimensional scaling ordination plots, data were summed for each treatment type and then ordinations were created with a single datum for each year and treatment combination. All ordinations used Bray–Curtis distance measures and two-dimensional solutions based on stress-plots with a final ordination stress of < 0.2, and 100 iterations to determine the final solution. To determine community differences through time, we used a PERMANOVA approach, where year and treatment, and year x treatment were all treated as factors. Individual plot identification codes were also included as a factor to account for variation associated with repeatedly sampling the same plots through time. We used 1000 permutations to determine significance based on Bray–Curtis distance measures. All analyses were conducted using the *vegan* package (Oksanen et al. 2020) in R (R Core Team 2019).

Plot-level species richness was determined as species density within shrub and herb growth forms, equal to number of species per 1-m² plot. Shoot size for each plot and species was calculated as cover/density; cover is recorded as percent of plot surface ($1\% = 1$ decimeter^2).
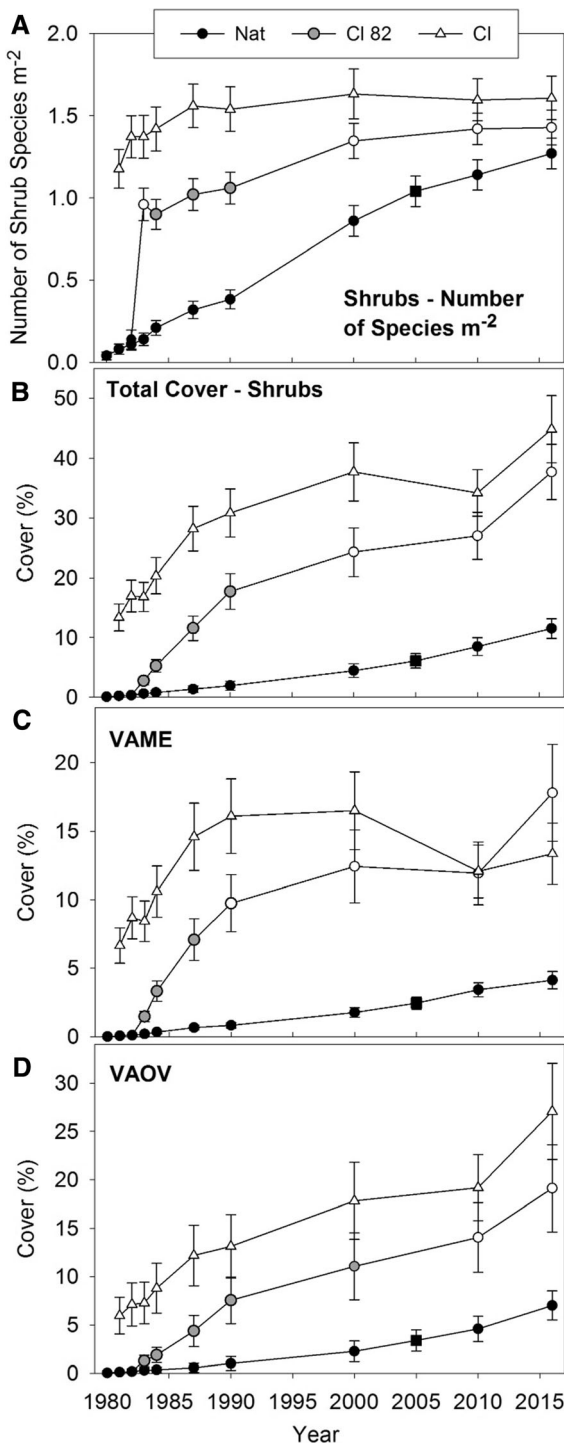
In univariate analyses, all response variables (species density, cover, shoot density, and shoot size) were analyzed using a repeated measured REML model approach with treatment and year as fixed effects while plot number nested within plot type was treated as a random effect. For cover and shoot density, models were created separately for each species and growth form. For shoot size, models were created separately for each species. The *lme4* package in R (R Core Team 2019) was used for all REML models. Following significant results, the *emmeans* package in R was used to perform contrasts to determine pairwise differences. Response variable data were log transformed, when non-normal, for all analyses.

Results

Major aspects of vegetation change in plots with delayed erosion showed a similar pattern (Figs. 1, 2, 3, 4, 5, 6, 7, and 8): Initially, Cl82 plots were not
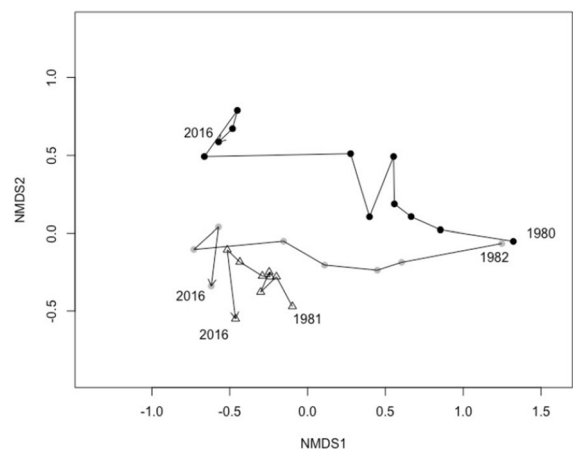
Fig. 1 NMDS ordination of community change through time following tephra deposition from Mount St. Helens during the 1980 eruption for three treatments: plots cleared of tephra 4 months after the 1980 eruption (Cl treatment, open triangles); plots cleared of tephra in 1982 after 28 months of burial (Cl82 treatment, gray circles); and natural plots with unaltered tephra (Nat plots, black circles)

vascular plant cover and density. Bryophyte cover and vascular shoot size had different patterns, as did all variables for some individual species. Below we refer to relationships of Cl82 plots to time and to other treatments; comparisons between Cl and Nat plots are given in Fischer et al. (2019) and citations therein.

Trajectories of community composition

The three plot treatments at our site (Nat, Cl, Cl82) produced three distinct trajectories of community change (Fig. 1). Year and treatment, along with year by treatment interactions, were significant factors throughout the duration of our study based on our PERMANOVA analysis (all effects $P < 0.001$, $F_{year(10,1725)} = 52.9$, $F_{treatment(2,1725)} = 148.3$, $F_{interaction(15,1725)} = 13.25$). Cleared treatments (Cl) and natural tephra plots (Nat) were initially dissimilar and remained so through time ($P < 0.001$). While the Cl82 treatment (before clearing in 1982) was initially similar to the Nat treatment, by 1990 the Cl82 treatment was similar to the Cl treatment, and dissimilar from Nat treatments ($P < 0.001$). The Nat and Cl82 centroids began at the same point in ordination space; both initially had minimal plant cover. These two treatments subsequently moved in parallel along ordination axis NMDS1 but diverged along NMDS2, with Nat moving to higher values along NMDS2 while Cl82 moved very little along this axis but moved toward the Cl treatment along NMDS1 (Fig. 1). In contrast, the Cl treatment moved little along either axis, remaining within a small area in ordination space. The Cl82 treatment converged on the Cl treatment by 1990, and these two treatments remained in a similar location on the ordination subsequently; the Cl and Cl82 treatments made a

significantly different from Nat plots but subsequently diverged, becoming not significantly different from Cl plots after seven to 30 years. This pattern was clear for community composition, vascular plant diversity and
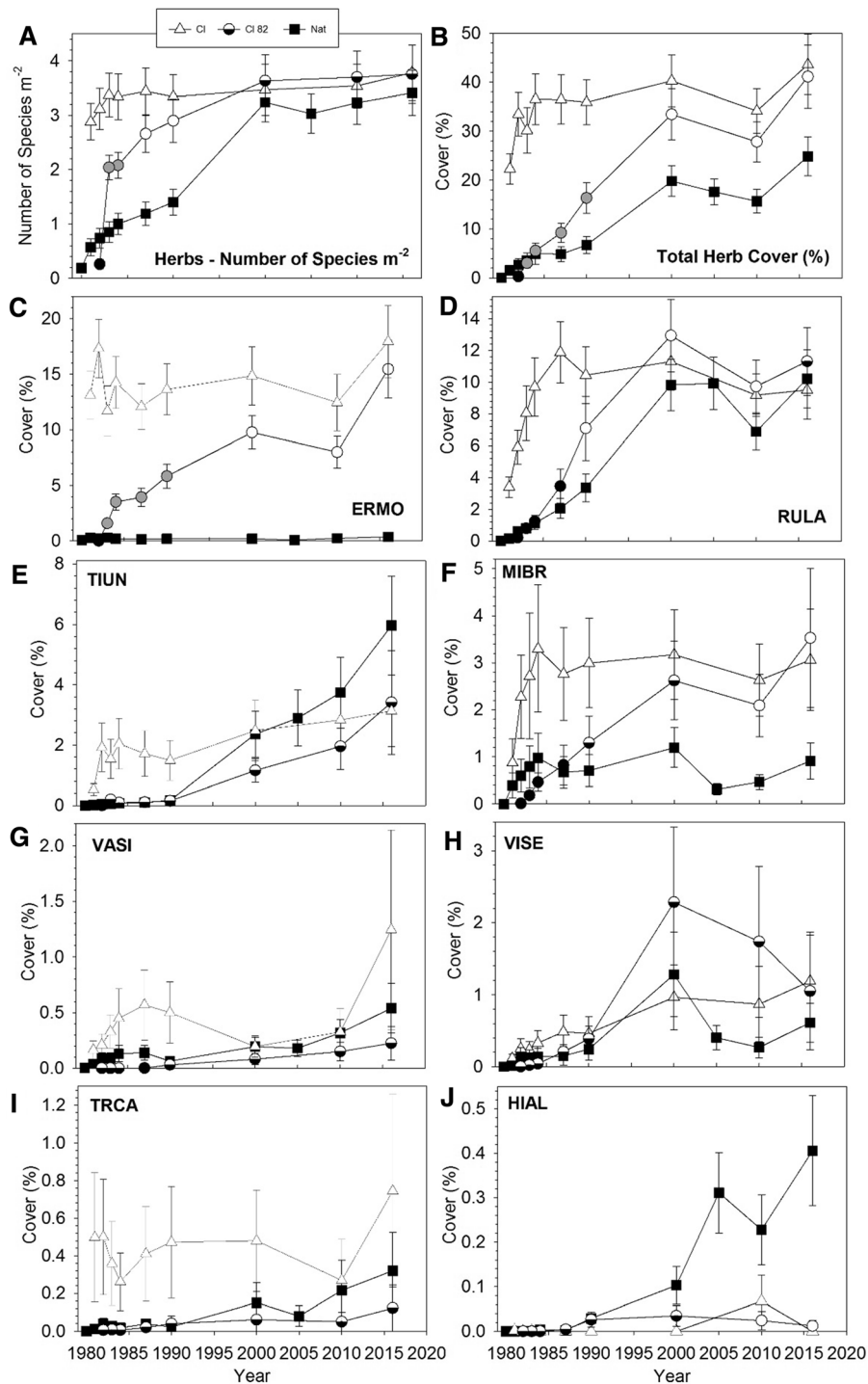
substantial parallel change in trajectory along axis NMDS2 from 2010 to 2016. In summary, the Cl82 treatment converged on the Cl treatment while

diverging from the Nat plots, indicating that delayed erosion facilitated compositional resilience (recovery to the original state) but that understory composition is

◄**Fig. 3** Herb diversity (species density) and cover through time following the 1980 eruption of Mount St. Helens. Symbols represent three treatments: plots cleared of tephra in 1980 (Cl; open triangles), plots cleared of tephra in 1982 (Cl82; circles), and tephra impacted natural plots (Nat; filled squares). Symbols for Cl82 plots are either filled in black (not significantly different from Nat plots), open (not significantly different from Cl plots), filled in gray (significantly different from both Nat and Cl plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** Species density (number of herb species per m^2); **B** total herb cover; **C** *Erythronium montanum* (ERMO) cover; **D** *Rubus lasiococcus* (RULA) cover; **E** *Tiarella unifoliata* (TIUN) cover; **F** *Mitella breweri* (MIBR) cover; **G** *Valeriana sitchensis* (VASI) cover; **H** *Viola sempervirens* (VISE) cover; **I** *Trautvatteria caroliniensis* (TRCA) cover; **J** *Hieraceum albiflorum* (HIAL) cover. 1982 values for Cl82 plots were taken before tephra was removed

still divergent (after 36 years) from the pre-disturbance vegetation if tephra is not removed.

Diversity

In plots cleared 28 months after the eruption (Cl82), shrub richness (i.e., species density, number of species per m^2) rose rapidly after tephra was removed and then more slowly approached the species density of Cl plots (Fig. 2A). Shrub species density of Cl82 plots became statistically different from Nat plots and similar to Cl plots between 10 and 20 years after the eruption. Herb species density of Cl82 plots rose rapidly and was not significantly different from that of Cl plots in just five years (1987; Fig. 3A). After 20 years, all three treatments had similar herb diversity, indicating that delayed clearing accelerated but did not alter the long-term result for local herb diversity at the m^2 scale.

Cover

Total cover of shrubs in Cl82 plots initially did not differ from values in natural tephra, rose rapidly after tephra removal, and became statistically equivalent to
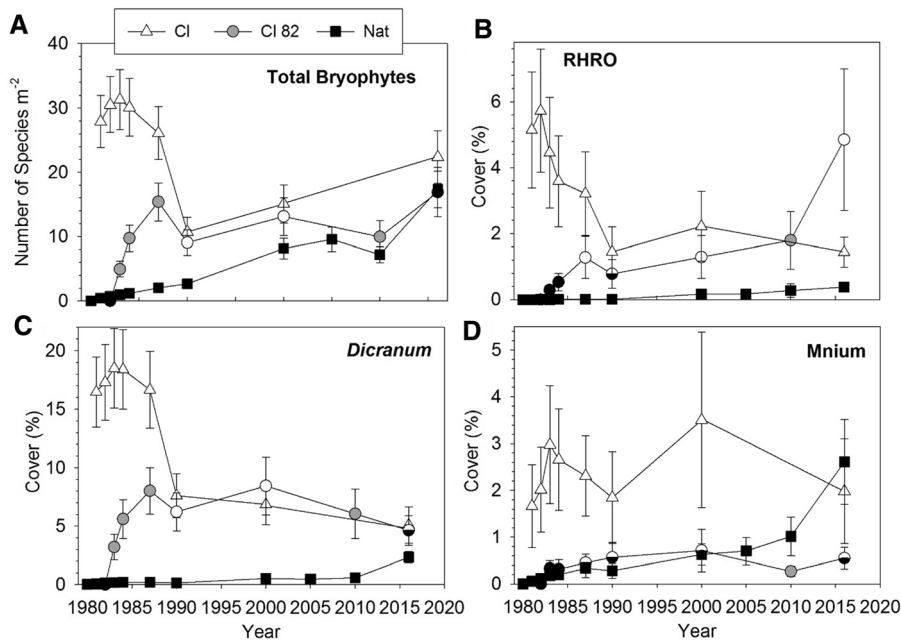
Fig. 4 Bryophyte cover through time following the 1980 eruption of Mount St. Helens. Symbols represent three treatments: plots cleared of tephra in 1980 (Cl; open triangles), plots cleared of tephra in 1982 (Cl82; circles), and tephra impacted natural plots (Nat; filled squares). Cl82 symbols are either filled in black (not significantly different from Nat plots), open (not significantly different from Cl plots), filled in gray (significantly different from both Nat and Cl plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** Total cover; **B** cover of *Rhytidiopsis robusta* (RHRO); **C** cover of *Dicranum* spp.; **D** cover of *Mnium* and related taxa. 1982 values for Cl82 plots were taken before tephra was removed. The Cl treatment was not sampled for bryophytes at 30 years and thus could not be compared to the Cl82 treatment at that time
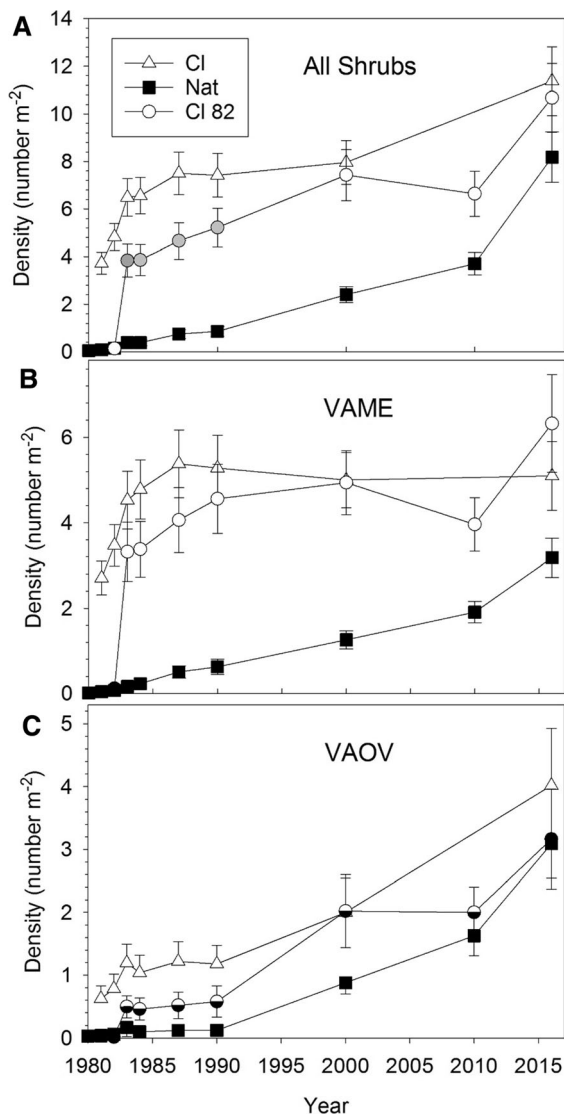
Fig. 5 Shoot density (number of stems/m²) of shrubs through time following the 1980 eruption of Mount St. Helens. Symbols represent three treatments: plots cleared of tephra in 1980 (Cl; open triangles), plots cleared of tephra in 1982 (Cl82; circles), and tephra impacted natural plots (Nat; filled squares). Symbols for Cl82 plots are either filled in black (not significantly different from Nat plots), open (not significantly different from Cl plots), filled in gray (significantly different from both Nat and Cl plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** Density of all shrubs; **B** *Vaccinium menbranaceum* (VAME); **C** *V. ovalifolium* (VAOV). 1982 values for Cl82 plots were taken before tephra was removed. Density for the Cl treatment was not sampled at 30 years and thus could not be compared to the Cl82 treatment at that time

Cl plots at 20 years (Fig. 2B). Both species of *Vaccinium*, which formed most shrub cover, had patterns similar to the total, although *V. membranaceum* became similar to Cl plots and different from Nat plots at 10 years, while *V. ovaliforlium* required 30 years (Fig. 2C, D).

Total herb cover in the Cl82 plots increased similarly to shrubs but more linearly until 20 years after the tephra disturbance, by which time values were not significantly different from the Cl treatment (Fig. 3B). Herb species differed greatly in their response to delayed clearing (Fig. 3C–J); two of eight herbs (Fig. 3C, F) had patterns resembling total cover with no significant difference from Cl plots but significantly higher cover in Cl82 than in Nat plots by the end of the study. Other species had a diversity of patterns, but for most of these species cover in Cl82 plots at the end of the study was not significantly different from that in either of the other treatments (Fig. 3D, E, G–I). *Hieracium albiflorum* (Fig. 3J) differed from the other species in that it was absent before the tephra disturbance but subsequently established from seed, primarily on tephra.

Delayed erosion initially facilitated the recovery of total bryophyte cover (Fig. 4A); values in the Cl82 treatment were equivalent to Cl values at 10 and 20 years. Patterns for three bryophytes varied considerably. The two most abundant forest groups, *Rhytidiopsis robusta* and *Dicranum* spp. (Fig. 4B, C) increased abruptly in the Cl82 plots after tephra removal and soon did not differ significantly from Cl plot values. In contrast, cover of the moss group *Mnium* (Fig. 4D) remained low in Cl82 plots.

Shoot density

Shoot density can be viewed as a second measure of plant abundance or, along with shoot size, as a component of plant cover. Total shoot density of shrubs and herbs in treatment Cl82 rose rapidly after plots were cleared, becoming equivalent to Cl values but different from Nat values by years 20 for shrubs and the end of the study for herbs (Figs. 5A, 6A). Patterns of density in the Cl82 treatment differed between the two shrub species (Fig. 5B, C). Herb species (Fig. 6B–I) differed substantially in temporal patterns of shoot density among treatments. The pattern for *Mitella breweri* density resembled the pattern for all herbs, but the density in the Cl82
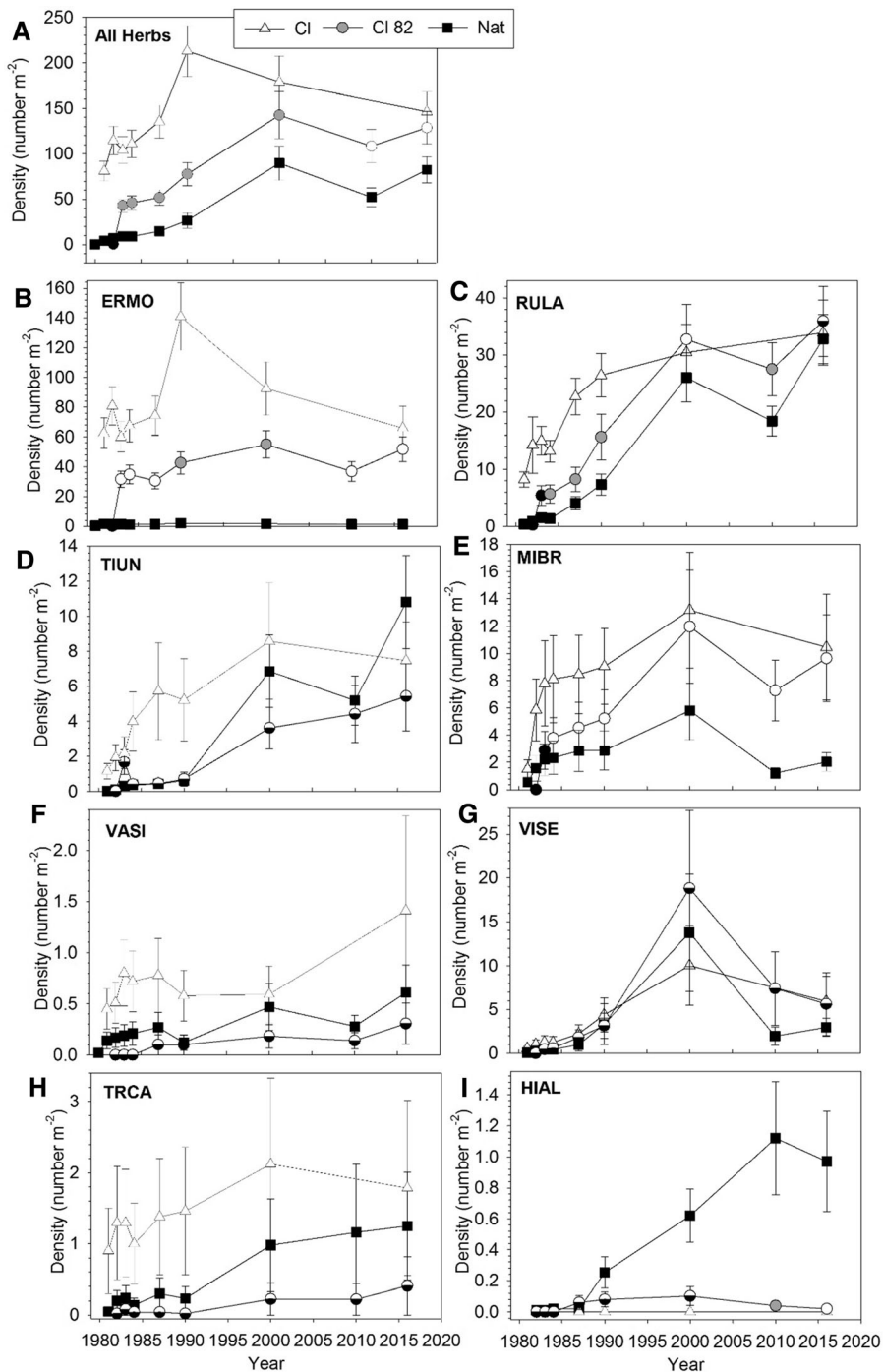
treatment converged on Cl treatment density sooner (Fig. 6A–E). Density of *Erythronium montanum* (Fig. 6B) increased abruptly in 1983, after clearing, subsequently increasing slightly, but did not differ

significantly from Cl plots by the end of the study. In contrast, patterns in density of *Rubus lasiococcus* (Fig. 6C) were similar through time among treatments, and density was almost identical among

◀**Fig. 6** Shoot density (number of shoots/m^2) of herbs through time following the 1980 eruption of Mount St. Helens. Symbols represent three treatments: plots cleared of tephra in 1980 (Cl; open triangles), plots cleared of tephra in 1982 (Cl82; circles), and tephra impacted natural plots (Nat; filled squares). Symbols for Cl82 plots are either filled in black (not significantly different from Nat plots), open (not significantly different from Cl plots), filled in gray (significantly different from both Nat and Cl plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** All herbs; **B** *Erythronium montanum* (ERMO); **C** *Rubus lasiococcus* (RULA); **D** *Tiarella unifoliata* (TIUN); **E** *Mitella breweri* (MIBR); **F** *Valeriana sitchensis* (VASI); **G** *Viola sempervirens* (VISE); **H** *Trautvatteria caroliniensis* (TRCA); **I** *Hieraceum albiflorum* (HIAL). 1982 values for Cl82 plots were taken before tephra was removed. Density in the Cl treatment was not sampled at 30 years and thus could not be compared to the Cl82 treatment at that time


treatments by the end of the study. Density of *Tiarella unifoliata* (Fig. 6D) increased slowly for CL82 plots, but values usually did not differ from other treatments. Density of *Valeriana sitchensis, Viola sempervirens,* and *Trautvatteria caroliniensis* (Fig. 6F–H) in Cl82 plots generally did not differ from that in the other plot types, whereas *Hieraceum albiflorum* remained very low except in Nat plots.

Shoot size

Shoot size (cover/density) of both *Vaccinium* species dropped in 1983 (the first measurement after clearing) but then increased, and Cl82 plots did not significantly differ from other treatments (Fig. 7). Three of eight herb species in Cl82 plots also showed the initial size reduction (Fig. 8A, B, D); size then rose, consistent with size increases in many species through time (Fig. 8). While initial values in CL82 plots for six species were similar to values in Nat plots, seven species were indistinguishable from both other treatments by 2016, and one species (*Hieraceum albiflorum*) was indistinguishable from the Nat treatment, but comparisons with the Cl treatment were not available (Fig. 8).

Discussion

Our study provides a well-developed example of an under-appreciated phenomenon. Plant burial has several causes and a substantial literature (e.g., Kent et al.
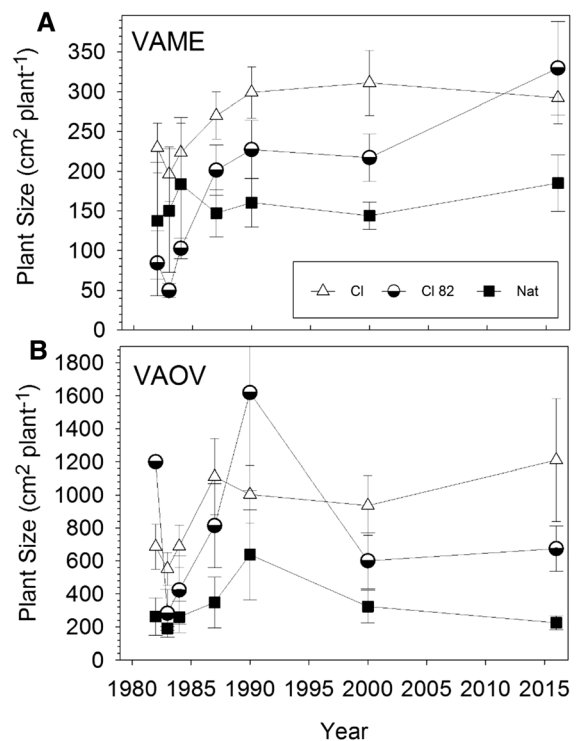
Fig. 7 Shoot size (cover/density) of shrubs through time following the 1980 eruption of Mount St. Helens. Symbols represent three treatments: plots cleared of tephra in 1980 (Cl; open triangles), plots cleared of tephra in 1982 (Cl82; circles), and tephra impacted natural plots (Nat; filled squares). Symbols for Cl82 plots are either filled in black (not significantly different from Nat plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** *Vaccinium menbranaceum* (VAME); **B** *V. ovalifolium* (VAOV). 1982 values for Cl82 plots were taken before tephra was removed. Density in the Cl treatment was not sampled at 30 years and thus shoot size could not be calculated and compared to the Cl82 treatment at that time

2001; Gilbert and Ripley 2010), although some reviews of phenomena that can bury plants (e.g., dust, Field et al. 2010) and others about understory disturbance (e.g., Roberts 2004) hardly mention plant burial. Although the ecological consequences of tephra emplacement have been studied in several localities (Griggs 1919; Antos and Zobel 1987; Kent et al. 2001; Ayris and Delmelle 2012; Swanson and Crisafulli 2018) and rapid erosion of volcanic tephra is common, ecological consequences of the secondary disturbances that remove tephra are seldom reported (Zobel and Antos 2017; Zobel et al. 2021). The changes induced by delay of erosion are worthy of more recognition: naturally occurring erosion does modify

Fig. 8 Shoot size (cover/density) of herbs from 1980 to 2016 for three treatments: plots cleared in 1980 (Cl), plots cleared in 1982 (Cl82), and plots with undisturbed, natural tephra (Nat). Symbols for Cl82 plots are either filled in black (not significantly different from Nat plots), open (not significantly different from Cl plots), filled in gray (significantly different from both Nat and Cl plots), or half-filled black (not significantly different from Nat or Cl plots). Error bars represent ± 1 SE. **A** *Erythronium montanum*; **B** *Rubus lasiococcus*; **C** *Tiarella unifoliata*; **D** *Mitella breweri*; **E** *Valeriana sitchensis*; **F** *Viola sempervirens*; **G** *Trautvatteria caroliniensis*; **H** *Hieraceum albiflorum*. 1982 values for Cl82 plots were taken before tephra was removed. Density in the Cl treatment was not sampled at 30 years and thus shoot size could not be calculated and compared to the Cl82 treatment at that time
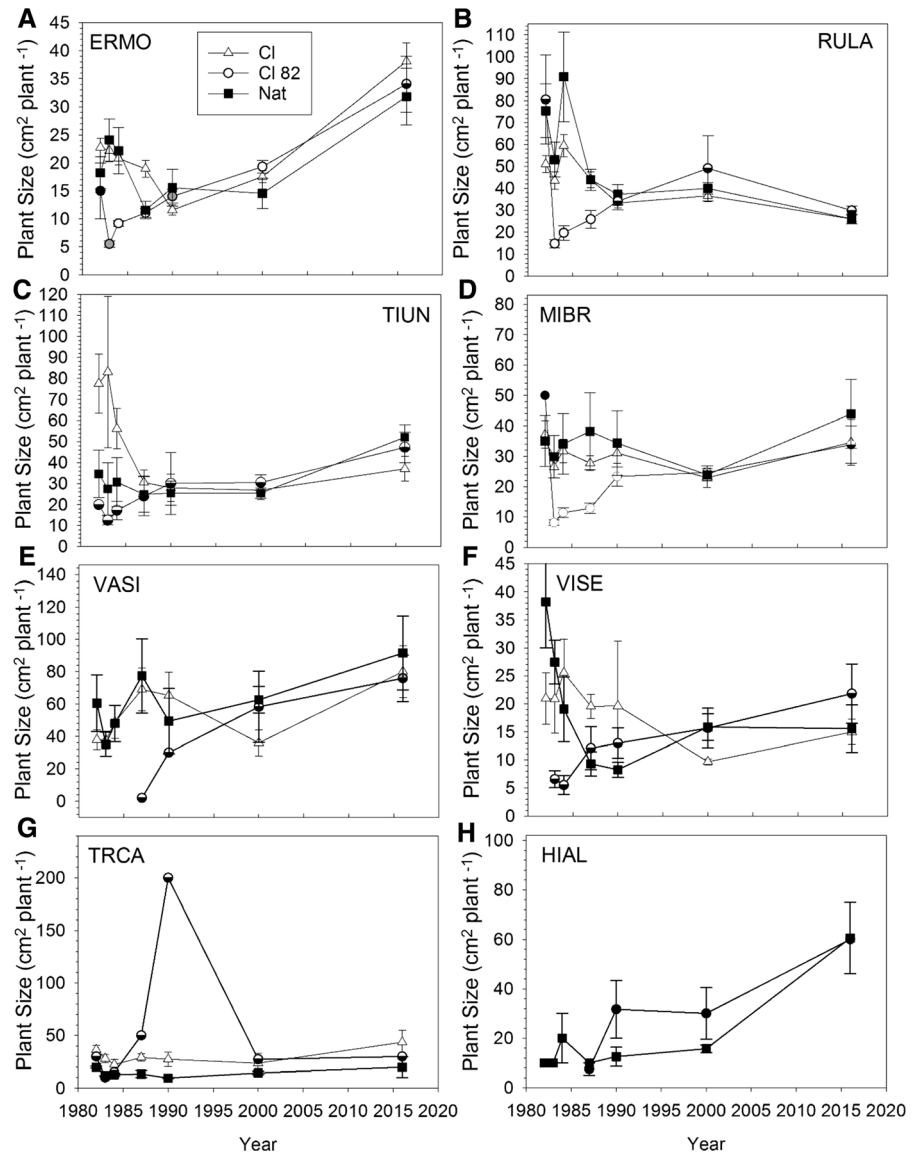
the successional trajectory in our study area (Zobel and Antos 1997), as does experimental erosion (Fischer et al. 2019), and instances of erosion have been delayed by years or decades at Mount St. Helens.

Our overall hypothesis that delayed erosion has a major impact on vegetation is strongly supported by our experimental data, but the specifics of plant response are complex and variable. We structure the following part of our discussion around the questions posed at the end of the Introduction:

(1) How do ordination patterns of treatments differ through time?—The plots cleared in 1982

started in an almost identical position as natural plots, but converged with time on the plots cleared in 1980 (a good indicator of pre-disturbance conditions; Zobel and Antos 1997, 2009, 2017; Fischer et al. 2019), indicating that delayed erosion facilitated the return of forest understory vegetation composition to the pre-disturbance condition. In contrast, they diverged to some extent from plots on natural tephra, indicating that, in the absence of delayed erosion, a return to the pre-disturbance composition is equivocal.

(2) Which growth form(s) and taxa contribute to community differences?—Herbs and bryophyte taxa differentiate our treatments more clearly than shrubs. Tree seedlings, not considered in detail here, also differed, establishing and surviving better on the tephra seedbed in natural plots than in either cleared plot treatment (Zobel and Antos 1997). In a previous analysis of community change (Fischer et al. 2019), which did not include Cl82 plots, we identified indicator taxa for 1981, 2000, and 2016 that differentiated natural plots from plots cleared in 1980. Of the nine taxa considered in that study that were also considered specifically here, three were significantly associated with natural plots (in 2000, the *Mnium* group of mosses and, in 2016, *Hieraceum albiflorum* and *Tiarella unifoliata*), whereas six taxa were significantly associated with 1980 cleared plots (in 1981, the bryophyte genus *Dicranum*; in 2000, *Vaccinium membranaceum*, *Rubus lasiococcus* and *Mitella breweri*; and, in 2016, *Erythronium montanum* and *Vaccinuum ovalifolium*). The three species associated with natural plots (Fischer et al. 2019) had their highest values in this plot type at the end of our study, but the values were not significantly different from Cl82 plots. Five of the six species associated with Cl plots (Fischer et al. 2019) had their highest values in this plot type at the end of our study, but these values were also not significantly different from Cl82 plots; cover of *Rubus lasiococcus* was very similar in all three treatments by 2016. In 2016, *Valeriana sitchensis*, *Trautvateria caroliniensis*, *Rhytidiopsis robusta*, and *Mnium* had cover values in Cl82 plots that appeared quite different from those in other plot types (Fig. 2, 4), and appear to separate Cl82 plots from Cl and Nat plots. For *R. robusta*, the late-cleared conditions were very favorable for cover values. In contrast, for the other three taxa, the low cover in Cl82 plots indicated that late clearing was detrimental to their development. For *Erythronium montanum*, the most abundant herb at the site prior to the tephra disturbance, delayed erosion was critical as both cover and density became very similar in Cl and Cl82 plots but remained very low in Nat plots even after 36 years. Overall, delayed erosion was more beneficial for herbs and bryophytes than shrubs and was beneficial for many, but not all, species.

(3) Do important differences reside in diversity or cover or both?—Although both diversity and cover responded positively to delayed erosion, diversity responded more quickly. In the Cl82 treatment, species density (number of species per m^2) increased more quickly and approached more closely that of Cl plots than did cover (Figs. 2A, B, 3A, B) After 2000, species density of herbs in Cl82 plots was almost identical to that in the Cl treatment. For total cover of both herbs and shrubs, Cl82 did not differ significantly from Cl plots, but values were significantly higher than in Nat plots, indicating the importance of delayed erosion in facilitating recovery from the initial tephra disturbance.

(4) If cover differs, does the difference in cover reside in its component of shoot density or of shoot size, or both?—Shoot size for most species became similar among plot types with time. Thus, most differences in cover emerged from density differences, and many species that had similar early values between Nat and Cl82 treatments switched such that Cl and Cl82 treatments were indistinguishable by 2016 (e.g., *V. membranaceum*, *E. montanum*, *R. lasiococcus*, *M. breweri*).

(5) Which aspects of plot treatment and plant properties may lead to the important changes in community properties?—The plot types differed in the presence of tephra, which provides a different rooting medium and seedbed than the old forest floor. Much of the initial chemical difference between tephra and pre-eruption topsoil declined or disappeared with time, with much of the change in the first two years, as cations and sulfur leached away, some accumulating in the pre-eruption soil (Zobel and Antos 1991). Seedling establishment on tephra was substantial but variable during 1981–1984 (Antos and Zobel 1986; Zobel and Antos 1997, 2007), but subsequently declined, probably associated with litter accumulation and development of a forest floor and perhaps with changes in seedbed chemistry. Differences between plots cleared after four and 28 months (Cl and Cl82, respectively) may include

nutrients leached into pre-eruption soil during the two-year longer residence of tephra, the two years of accelerated decomposition of forest floor while it was buried, and the two-year delay in accumulation of leaf litter on old forest floor (litter fall was heavy just after the eruption). In addition, competition differed between Cl and Cl82 treatments. Pre-eruption conifer seedlings were common in Cl plots but did not survive two years of burial and were absent from Cl82 plots. Probably the most important difference between Cl and Cl82 plots was the herb and bryophyte death and the decline of vigor of all growth forms that accompanied the 2-year's longer period of burial (Zobel and Antos 1986, 1992).

Some of our other results can be explained by previous observations, including an initial reduction in shoot size, and the behavior of some species that we have studied in detail. In the first year after clearing of Cl82 plots, shoot size dropped for shrub and many herb species, sometimes drastically, but increased in subsequent years. There are a variety of explanations, depending on conditions. In Cl82 plots, the 1982 data were pre-clearing and the few shoots measured then were large enough to protrude above tephra or to penetrate it. In 1983, after clearing, smaller shrubs were exposed along with herbs unable to penetrate the tephra, lowering the mean shoot size. Adding to this effect, and extending to other treatments, were the sprouts originating from plant parts buried by tephra or originally belowground and newly established seedlings, all with small shoots. Another shoot size reduction occurred for vegetatively spreading species, with stolons that grew rapidly from a rooted location the first year but without rooting on the new growth; in later years these stolons produced roots in several locations, reducing the size of what we defined as an individual shoot (Zobel and Antos 1997).

Our results clearly indicate that many plants survived burial for three growing seasons, although size reductions indicate that extended burial had limited their resources. Burial is a common phenomenon in some habitats, such as sand dunes, and some species are adapted to burial (e.g., Maun 1998). Although shallow deposits can stimulate growth of many species (Gilbert and Ripley 2010), most species are adversely affected by burial, especially if deep,

even if burial is frequent in such situations (e.g., sand dunes, Bach 2001, or near volcanos where tephra deposition is frequent, Zobel and Antos 1997). The depth of burial is clearly important, with shallow burial more likely to allow survival, but removal of a deposit is an alternative route to survival. Growing through a deposit is quite a different phenomenon than prolonged survival until a deposit is partially or fully removed by erosion. Perhaps it may seem surprising that we found that so many plants can survive complete burial for three growing seasons and recover to normal size within a few years after removal of the deposit. Survival in the dark, a condition of complete burial, is quite limited, although highly variable, for some species (Sykes and Wilson 1990b). However, prolonged dormancy—wherein some individuals reappear after being absent aboveground for one or more growing seasons—occurs occasionally to frequently in many species (Shefferson et al. 2018), which indicates that these species would have the ability to survive multiple years of burial without aboveground shoots.

Species with prolonged dormancy occur in many habitats (Shefferson 2009; Reintal et al. 2010; Shefferson et al. 2018), and this phenomenon has important implications for the demography and possibly the survival of these species (e.g., Kéry and Gregg 2004; Miller et al. 2012). Furthermore, plants of the forest understory may be adapted to temporary burial by falling litter or debris from the canopy. Litter has major effects on forest understory plants (e.g., Sydes and Grime 1981a, b), and debris falling from the canopy can influence understory plants substantially (Gillman and Ogden 2001; Gillman et al. 2003). Thus, the ability to survive burial in the understory for one or more years is likely to be adaptive and is consistent with the common survival of many species for two years that we found.

We propose that performance of plants after release from burial needs more attention. Although the ability of plants to grow through deposits has been investigated in a variety of situations (Antos and Zobel 1985a, b; Sykes and Wilson 1990a; Xiong et al. 2001; Hotes et al. 2004), much less attention has been devoted to survival while buried and subsequent growth after erosion. Removal or thinning of deposits that bury plants appears to be common and can be considered a reversal of the initial burial or a type of secondary disturbance (Zobel et al. 2021). In forest

understories, temporary burial by falling canopy debris that subsequently decomposes could select for plants that can both survive burial for one or a few growing seasons and have the capacity to expand after release from burial. Accordingly, we suggest that most species in the forest understory could be expected to resume growth after one or more years of burial, and our results support this expectation. There is a limit to retaining the capacity to survive and expand after erosion; the number of species and individuals surviving and their initial growth declined substantially between 28 and 87 months of burial (Zobel and Antos 1992). However, survival during burial until the covering material is removed and subsequent expansion are likely to be important phenomena in a variety of ecosystems and need to be more fully appreciated when considering the population dynamics of species and compositional changes in communities.

Declarations

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