Forest Ecology and Management 382 (2016) 236–243

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A little disturbance goes a long way: 33-year understory successional responses to a thin tephra deposit

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ARTICLE INFO

Article history:
Received 11 July 2016
Received in revised form 4 October 2016
Accepted 7 October 2016
Available online 15 October 2016

Keywords:
Disturbance
Mount St. Helens
Old-growth forests
Recovery
Succession
Tephra
Understory

ABSTRACT

Large volcanic eruptions can alter forest plant communities through a variety of mechanisms, including direct destruction of forests and changes to forest soils through tephra (aerially transported volcanic ejecta) deposits. While many studies have examined succession following direct destruction of forests, impacts to plant communities through tephra effects are less obvious, especially where the tephra depth is less than plant height. We used a 33-year experiment in an old growth forest that received shallow tephra deposition in the 1980 eruption of Mount St. Helens (WA, USA), to examine plant communities. We determined if community differences between plots with and without tephra: (1) were detectable, and (2) changed over time. We found that plant communities differed significantly between plots with and without tephra after 33 years. Further, differences were stronger after 33 years than at two years following the eruption. Species richness increased over time in both plots with and without tephra, but live cover was largely stable after two years. Nevertheless, communities shifted in different directions over time, where the changes in species composition and abundance immediately following tephra deposition were inconsistent with net changes that occurred over 30 years afterwards. These results suggest that widespread and apparently minor deposits of tephra, usually interpreted to be of transient importance if any, may induce long-term modifications of understory plant communities.

1. Introduction

The temperate rainforests of the Pacific Northwest (USA) experience frequent and large volcanic eruptions that alter forest plant communities, as dramatically illustrated by the recent and repeated eruptions of Mount St. Helens (Mullineaux, 1986; Dale et al., 2005). Volcanic eruptions can have a wide variety of effects on forest ecosystems, ranging from complete devastation of plant communities to minor ash fall and temporary disruption of air quality (Lipman and Mullineaux, 1981; Turner et al., 1997; Dale et al., 2005; Efford et al., 2014). Vegetation in areas strongly affected by volcanic activity has received substantial study, but comparatively few studies (e.g., Mack, 1981) have examined the effects of minor amounts (<25 mm) of tephra, which can cover larger areas (Zobel and Antos, 1997; del Moral and Grishin, 1999; Bonadonna et al., 2015). Trees can survive tephra deposits of up to 2 m (Antos and Zobel, 1987; Turner et al., 1997), implying that overstories could remain intact while understory populations are strongly diminished. Volcanic tephra deposition does not usually remove overstory biomass (but see Swanson et al., 2013), and therefore increase light availability or diurnal temperature fluctuations, but it does immediately affect edaphic conditions (Zobel and Antos, 1991a; Ayris and Delmelle, 2012). Thus, tephra deposition provides a useful opportunity to examine forest understory successional patterns in response to disturbance, but with an intact forest canopy.

Long-term studies in tephra impacted forests adjacent to Mount St. Helens have resulted in several lessons about the nature of this disturbance type. Effects of tephra on understory communities may differ from more intense disturbances, which can nearly, or completely, reset succession (Turner et al., 1998; del Moral and Grishin, 1999), and may take time to be realized (Antos and Zobel, 2005). For example, species richness is expected to be decreased by more severe volcanic disturbance (mud flows, deep tephra), but not necessarily in shallow tephra (del Moral and Grishin, 1999). Consistent with this expectation, richness declined more in deep than in shallow tephra immediately after the May, 1980 Mount St. Helens eruption, and returned to pre-disturbance values in 4.5 cm, but not 15 cm tephra deposits (Zobel and Antos,

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http://dx.doi.org/10.1016/j.foreco.2016.10.018
0378-1127/

2017). For bryophytes, and for vascular growth forms at some sites, percent cover was still expanding 20–30 years after tephra deposition (Antos and Zobel, 2005; Zobel and Antos, 2017; also see Tsuyuzaki, 2009). Given the decline in effects between sites with 15 vs 4.5 cm tephra, it is likely that sites with still less tephra will show limited, and different, effects (Zobel and Antos, 1997, 2017; Antos and Zobel, 2005). Sites receiving less tephra were generally at lower elevations (Waitt and Dzurisin, 1981) and did not have snowpack, which significantly modified tephra effects at higher elevations (Antos and Zobel, 1982, 2005). Nevertheless, some lasting effects might occur even with thin tephra (<2.5 cm) via the effects of tephra on soils, given that long-term plant growth can be inhibited by the nitrogen-poor tephra layer that is added to the soil profile (del Moral and Clampitt, 1985). In other systems, manipulative experiments adding shallow tephra have both decreased growth and altered community succession trajectories (Gómez-Romero et al., 2006; Hotes et al., 2010). Following deposition, physical and chemical weathering of the tephra and formation of a new soil layer may continue to change the substrate plants grow in (Dahlgren et al., 1999), providing opportunity for long term community changes (del Moral and Clampitt, 1985; Antos and Zobel, 2005).

It is traditionally accepted that understory succession follows changes in overstory structure, and stabilizes as forest canopies close (Franklin and Dyrness, 1973; Oliver and Larson, 1990). Early theoretical and empirical work (e.g., Bormann and Likens, 1979; Alaback, 1982) indicated that understory biomass peaked before the canopy closed, then remained consistently low following canopy closure. After canopy closure, changes in understory communities are typically related to canopy gaps (Van Pelt and Franklin, 2000; Rankin and Tramer, 2002; Grandpré et al., 2011). Nevertheless, some understory successional trends can be difficult to summarize and predict (Pickett et al., 1987). Understory communities should remain stable in old-growth forests over long temporal scales, but recent studies have found a significant decline in species richness through time (Woods et al., 2012; Murphy and McCarthy, 2014), or a lack of relationship between understory metrics and overstory structure (Halpern and Lutz, 2013). Understory plants may respond more to underground competition than light level (e.g., McCune, 1986; Lindh and Gray, 2003), but it seems likely that stability of canopy structure would result in rather stable conditions belowground. Long-term datasets in temperate forests of the Pacific Northwest, such as those near Mount St. Helens (Zobel and Antos, 2017), provide a unique opportunity to revisit models of succession because they are paired with disturbance studies. Furthermore, these long term studies provide many advantages over chronosequence studies (Bakker et al., 2002; Halpern and Lutz, 2013), and also allow field-based evaluation of stable states in old growth forest communities, which represent a significant gap in the literature (Schröder et al., 2005).

Our study examines changes in understory community composition after 33 years in a site with shallow tephra (2.3 cm) from the 1980 eruption of Mount St. Helens in Washington State, USA. We assess understory community changes with (tephra plots) and without tephra (cleared plots), by taking advantage of experimental tephra removal that occurred less than three months after the eruption. For initial post-disturbance response, we re-analyze data from 1980 and 1982 (Antos and Zobel, 1985b) and to evaluate long-term changes we use a re-measurement of the same plots in 2013. We use a variety of community analysis techniques to address three hypotheses: (1) tephra plots will show more long-term change than cleared plots as they "recover" from the tephra disturbance; (2) the species composition of tephra plots will converge on that of the cleared plots and following 33 years there will be no significant differences in community metrics between treatments given limited initial effects from this minor disturbance and the long recovery period; and (3) cleared (control) plots will have changed very little if any in this old-growth forest. In contrast to these hypotheses based on general ideas about minor disturbance and old-growth forests, significant temporal changes in both cleared and tephra plots would highlight dynamism in understory communities, and unique changes in the tephra-impacted plots alone could reflect a legacy effect of tephra deposition 33 years after disturbance.

2. Methods

2.1. Study design

Our study took place at 550 m elevation in an old growth stand typical of the *Tsuga heterophylla* vegetation zone (Franklin and Dyrness, 1973; Swanson et al., 2005). The site was described by Antos and Zobel (1985b, 1987). It is located 39 km northeast of Mount St. Helens, and received approximately 2.3 cm of tephra deposit from the 1980 eruption, a low amount compared to areas closer to the volcano or more centrally located in the tephra plume.

In 1980, Antos and Zobel (1985b, 1987) delineated a 1-ha homogeneous stand at the site. All trees >10 cm DBH were permanently tagged and measured for diameter in 1980; the trees (primarily *Pseudotsuga menziesii* and *T. heterophylla*) were remeasured in 2011 by the HJ Andrews Experimental Forest research program (Pabst et al., unpublished data).

Within the 1-ha tree stand, Antos and Zobel (1985b) established 150 1-m^2 understory plots along six evenly spaced transects using a stratified random sampling approach with plots located every 3 m along each transect. Tephra was removed from 50 of the 1-m^2 plots during August 2–6, 1980. These cleared plots were located along transects that alternated with transects containing undisturbed tephra plots. Tephra was carefully removed using a variety of hand tools, including small excavating implements and brushes, along with a small vacuum cleaner. Most tephra was removed but some sticky tephra was left if removal would have damaged plants. The set of plots resulting from this gentle removal of tephra provided a baseline description of pre-eruption vegetation, allowing comparison of the effects of tephra deposit with a control. Accordingly, statistical differences in 1980 between cleared and tephra plots were initially interpreted as evidence of the immediate impact of the tephra on plant communities.

Vegetation was first measured on September 4 and 5 following the May 1980 eruption of Mount St Helens, and again between July 21 and 29 in 1982. In September, 2013, we relocated and measured 87 of the 1-m^2 plots along five transects from the original sampling of 150 plots. Of the 87 relocated plots, 20 were cleared of tephra in 1980 and 67 were original uncleared plots (hereafter referred to as "tephra" plots). Only plots that could be confidently located and identified as matching the original 1980 plot locations were used, hence the discrepancy between the original 150 and current number of plots. We deemed this sampling most appropriate for comparisons because: (1) using the exactly located same plots is critical to effective comparisons, and other plots could not be relocated with confidence, and (2) we chose tephra plots closest to the cleared plots to maximize the relevance of comparisons, abandoning a previously measured transect located down-hill and distant from the other plots. With these data we were able to compare cleared vs tephra treatments using the same plots measured in 1980, 1982 and 2013. At each sampling, all vascular plants were identified to species and the cover determined after all plants have fully grown, but before leaf senescence. In each 1 m^2 plot, cover was estimated for each vascular plant species and for major bryophyte taxa, along with total bryophyte cover (Antos and Zobel, 1985b). Nomenclature follows Hitchcock and Cronquist (1973);