



6-20-2007

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Recommended Citation

Titus, J. H. and Householder, E. (2007) "Salvage logging and replanting reduce understory cover and richness compared to unsalvaged-unplanted sites at Mount St. Helens, Washington," *Western North American Naturalist*: Vol. 67 : No. 2 , Article 5.

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SALVAGE LOGGING AND REPLANTING REDUCE UNDERSTORY COVER AND RICHNESS COMPARED TO UNSALVAGED-UNPLANTED SITES AT MOUNT ST. HELENS, WASHINGTON

J.H. Titus¹ and E. Householder²

ABSTRACT.—The 1980 eruption of Mount St. Helens killed trees in a broad 600-km² swath north of the crater. Over most of the blast zone, dead trees were salvage logged and *Abies procera* was planted, except in areas within the Mount St. Helens National Volcanic Monument. We compared salvage-replanted sites and unsalvaged sites in 1 area of the blast zone where the sites were adjacent by using twenty-five 200-m² plots for each treatment. Salvaged-replanted plots had significantly lower herb and shrub cover, richness, diversity, litter depth, downed woody debris, nitrate, and phosphate. Salvaged-replanted sites also had significantly more stumps, bare area, and moss cover than unsalvaged plots. Soil organic matter and nonnative species cover did not differ. Nonnative species were not important components of any plots. Nitrate, total nitrogen, organic matter, and litter were correlated with the major patterns of species distribution in a canonical correspondence analysis of the salvaged-replanted plots. In the unsalvaged plots, slope, downed woody debris, and elevation were correlated with the major patterns of species distribution.

Key words: volcano, succession, punice, noble fir.

The massive 1980 lateral eruption of Mount St. Helens, Washington, destroyed or altered forests within the blast zone and blanketed vast areas with airborne tephra. Beyond the zone of complete destruction, trees were knocked down and killed by the eruption, but some seedlings and saplings survived under snow and were able to emerge through the deposited tephra. Still further away from the crater, trees were killed by the eruption but remained standing. In 1982 the 44,550-ha Mount St. Helens National Volcanic Monument was established to preserve the effects of the eruption of Mount St. Helens and to allow natural successional processes to occur. However, the majority of the impacted landscapes were outside of the monument. Those lands that were unlogged at the time of the eruption were subsequently salvage logged in 1980–1982 and planted in *Abies procera* at higher elevations and in *Pseudotsuga menziesii* and *Pinus monticola* at lower elevations between 1981 and 1987. The unsalvaged sites on Mount St. Helens compose a large, slowly reforesting area, which is important for bird, amphibian, and mesopredator biodiversity (Dale et al. 2005). Recently, naturally disturbed, unplanted-unsalvaged forest that is undergoing natural

succession has been considered the rarest condition on forest lands in the Pacific Northwest (Franklin et al. 2000). The proximity of unsalvaged sites and salvaged-replanted sites provides a unique opportunity to observe differences in forest development under these 2 management options.

Large-scale natural disturbances that impact forests are common worldwide. The recouping of economic losses due to large-scale forest disturbance is usually attempted by salvaging the timber; for example, salvage logging has ensued following large wildfires and windstorms in southeastern Asia, Australia, and North America (van Nieuwstadt et al. 2001, Lindenmayer et al. 2004, Donato et al. 2006). The ecological consequences of salvage logging and whether it actually helps forests recover are debated (McIver and Starr 2000, Lindenmayer et al. 2004, Donato et al. 2006, Stokstad 2006). Forest managers must decide to salvage-log and replant, to leave disturbed areas to recover on their own, or to possibly replant without salvage logging. Under the recently passed federal Healthy Forests Restoration Act (available from: <http://www.fs.fed.us/projects/hfi/field-guide/>), much more salvage logging is planned for federal forest lands that

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have been disturbed by fire, wind, insects, disease, and so forth. Thus, it is important to understand how these management choices impact disturbed forested ecosystems.

Summer temperatures in soils of unsalvaged areas are 5°C cooler than in soils in salvage-logged areas (Rumbaitis-del Rio 2006). Trees downed by storms provide shade to vegetation, including surviving tree seedlings; salvage logging removes these downed trees. Likewise, trees killed by wildfire and left standing provide shade, which slows heating of the soil surface (Amaranthus et al. 1989). Thus, snags and downed woody debris (DWD) modify surface microenvironmental conditions. Dead trees are also a source of large woody debris for streams (Amaranthus et al. 1989).

Post-fire salvage logging in southwestern Oregon reduced natural conifer regeneration due to soil disturbance and burial, and increased downed woody fuel loads thereby possibly raising reburn risk (Donata 2006). Salvage logging caused high seedling mortality in a coniferous subalpine forest damaged by a windstorm in Colorado (Rumbaitis-del Rio 2006). The unsalvaged sites had greater herb and shrub cover and diversity than salvaged sites, which showed a shift towards graminoid dominance (Rumbaitis-del Rio 2006). Eleven years after logging, shrub cover was higher and forb cover was lower on unsalvaged sites than on salvaged sites (Stuart et al. 1993, Sexton 1994). In northwestern California, community composition in Douglas-fir forests was strongly affected by post-fire salvage logging, including marked differences in life-forms of the dominant species; however, species diversity was not affected. Hardwood dominance on salvaged sites may continue for a long time to come because hardwoods inhibit establishment of Douglas-fir and thereby prevent succession to open-canopy Douglas-fir forest, which occurs on post-burn unsalvaged sites (Stuart et al. 1993).

Documented effects of salvage logging on soil erosion and soil nutrient loss have been variable. For example, several studies (Chou et al. 1994a; 1994b; Helvey et al. 1985) found that erosion increased with salvage logging, whereas others found no difference between logged and unlogged sites (Marston and Haire 1990, Maloney et al. 1995). These disparate findings may arise because of the wide array of environmental conditions, forests, salvage-

logging techniques, and research methods. Vegetation removal and soil disturbance caused by post-fire salvage logging may have created the conditions for colonization by nonnative ruderal plant species in Florida scrub (Greenberg et al. 1995). Likewise, nonnative-species cover and richness were slightly higher on salvage-logged sites in Oregon (Sexton 1994).

Thus, salvage logging after fire can reduce vegetation biomass, increase nonnative plant species cover, increase graminoid cover, reduce overall plant species richness, and decrease the growth of post-disturbance tree regeneration in the 1st years after logging. At present, information on the environmental effects of salvage logging remains scanty (McIver and Starr 2000, Donato et al. 2006). We are still far from detecting similar responses to the impacts of salvage logging across systems. All species have evolved in the presence of disturbance, and frequent disturbances such as fire and wind should not result in a long-term change to the fundamental character of a system. However, more serious consequences may possibly result from compounded perturbations within the normal recovery time of a community (Paine et al. 1998, van Nieuwstadt et al. 2001). Thus, after multiple perturbations communities may be deflected into alternative stable states. This study addresses differences in herb and shrub vegetation and soils in 1 area of the blast zone between adjacent salvaged-replanted sites and unsalvaged sites 23 years after the eruption of Mount St. Helens. Differences between the 2 treatments are due to the combined influence of salvage logging and replanting in comparison to unsalvaged-unplanted sites.

METHODS

The lateral eruption on 18 May 1980 created a wide range of disturbance, primarily to the north of Mount St. Helens (46°12'N, 122°11'W; Fig. 1). Climate is maritime, with cool, wet winters and warm, dry summers. Annual precipitation fluctuates widely around a mean of 237 cm; drought is common during July and August; and mean temperatures range from a -4°C minimum to a 0°C maximum in January and a 7°C minimum and a 22°C maximum in August (Swanson et al. 2005).

The area near Meta Lake was used for this study because salvaged-replanted and unsalvaged areas are adjacent, with the most distant

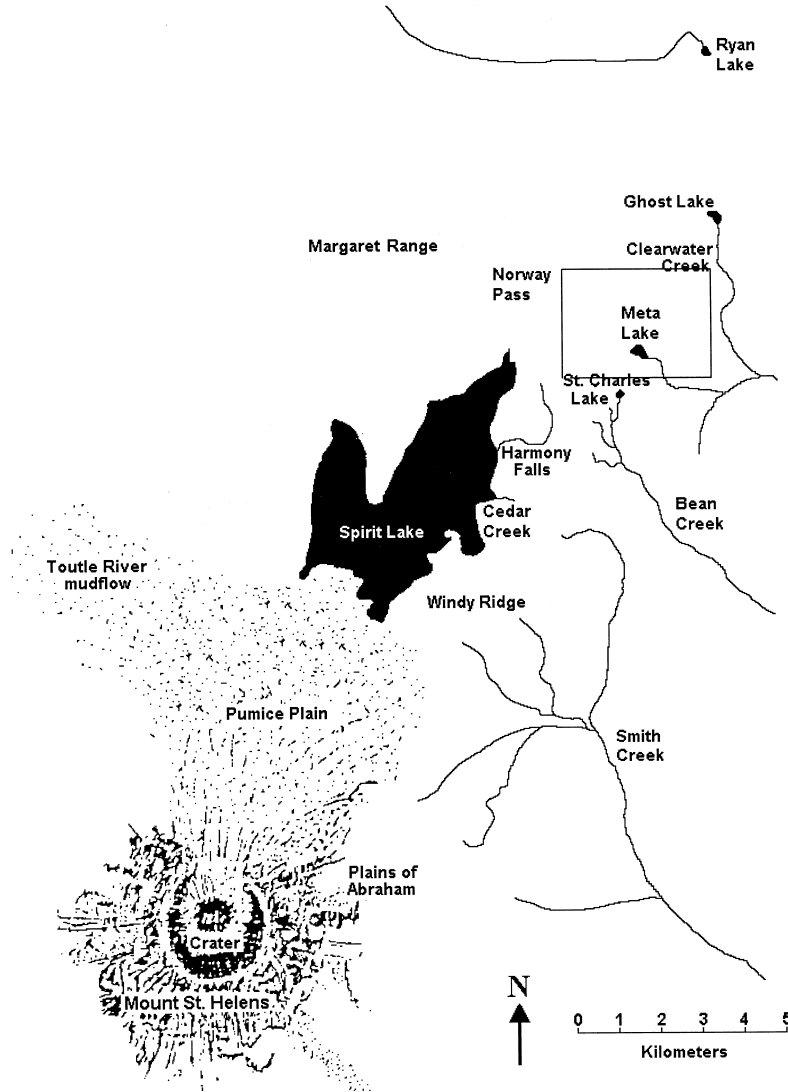


Fig. 1. Study area on Mount St. Helens, Washington. The square drawn on the map approximates the study area with unsalvaged plots on the west side and salvaged-replanted plots to the east.

plots being <3 km apart (Fig. 1). Thus, pre-eruption differences between plots were presumably not large. We sampled only sites believed to have been old growth before the eruption. Stumps and logs blown down in the direction of the blast were used as evidence. However, some plots, or portions of some plots, may have been clearcut prior to the eruption. Tephra approximately 15–30 cm deep was deposited over the study area by the eruption. Tephra deposits are extremely nutrient poor and contain very low concentrations of carbon,

nitrogen, and phosphorus (Titus unpublished data). This area was ground-salvaged in 1981–1982 and planted in *Abies procera* in 1982–1984. Planting density and survival of planted seedlings are not known.

Plots were located between 1096 m and 1177 m in elevation. Although many plots were located at similar elevations, the mean elevation of unsalvaged plots was slightly higher. All plots were located on south- to west-facing slopes so that we could reduce variation in aspect and assess sites that caught the brunt of

the blast. Slopes were not different between salvaged-replanted and unsalvaged plots, and many sites were quite steep.

Twenty-five 200-m² circular plots in both salvaged-replanted and unsalvaged areas were assessed in July 2003. Slope and aspect were determined with compass and clinometer. Elevation and location were determined by a GPS (Garmin eTrex[®] Legend; UTM, NAD 1927). Percent cover and density of each plant species in each plot was estimated. A gridded 1-m² frame aided cover estimates. Height of each woody plant, including seedlings, was also measured. Density of clonal species was estimated. We identified species by referring to Hitchcock and Cronquist (1973) and Hickman (1993). Nomenclature was current in 2005 (Integrated Taxonomic Information System [ITIS]).

To obtain a coarse estimate of the quantity of downed woody debris (DWD), we used the line-intercept method on a randomly selected 16-m transect across each plot (van Wagner 1968), with diameter measured on each DWD diameter >10 cm. Diameters and numbers of snags, tip-ups, and stumps in each plot were also recorded. In each plot, soil was collected from the top 10 cm of 4 randomly selected sites and aggregated for a total of 500 mL of soil. Because of slopes, depth to pre-eruption soils varied dramatically (Titus personal observation). It appeared that on many of the sites pre-eruption soils were close to the surface. If loose, unconsolidated pumice was present at the sampling site, the soil samples were collected from below the loose pumice. Larger plants would most likely have their roots in pre-eruption soils, which could differ from the soils of the top 10 cm. At each soil collection site, litter depth was recorded. Litter depth refers to the depth of the L, F, and H horizons (Agriculture Canada Expert System on Soil Survey 1987). The F and H horizons were poorly represented, and the L horizon composed the majority of the depth. Litter depths from the 4 sites were averaged to yield a mean plot litter depth.

Soil samples were analyzed for total nitrogen, nitrate, phosphorus, soil pH, cation exchange capacity (CEC), and soil organic matter (TOC) at the Soil, Water, and Plant Analysis Laboratory in the Department of Soil, Water, and Environmental Science, University of Ari-

zona. Total nitrogen was determined by the Kjeldahl method (McGill and Figueiredo 1993). Exchangeable nitrate levels were determined by cadmium reduction in 2.0 N KCl extract (Maynard and Kalra 1993, Miller et al. 1998). Available phosphorus was determined by Olsen's procedure (Miller et al. 1998). Soil pH was determined by saturated paste (Miller et al. 1998), CEC by ammonium replacement (Miller et al. 1998), and TOC levels by loss on ignition (Miller et al. 1998). Although measured nitrate levels are not clear indicators of actual nitrate availability or flux rates (Stark and Hart 1997), the measured nitrate levels may at least illustrate overall trends in nitrate availability.

For salvaged-replanted and unsalvaged sites, we calculated mean percent plant cover, mean species richness, and mean diversity (Shannon-Wiener index, base_e). For analysis, the aspect was converted to an exposure scale. This scale ranged from 1 for north-facing sites to 10 for exposed south-facing sites (Whittaker 1960).

We used detrended correspondence analysis (DCA) to obtain indirect ordinations of plots (Hill and Gauch 1980). The best plot and species spread in ordination space was achieved without data transformations and without down-weighting the influence of rare species.

The relationships between measured environmental variables and the species-plot relationships were explored by canonical correspondence analysis (CCA), a constrained ordination method (ter Braak and Smilauer 1998). The correlation of each variable to canonical axes provided insights into factors that may control community structure. In general, the longer the environmental vector, the stronger the relationship of that variable with the community. The position of a species relative to an environmental vector can be used to interpret the relationship between various species and the measured environmental variables. We performed Monte Carlo permutation tests to determine if observed patterns differed from random. CANOPOST graphics were used (Smilauer 1993). Salvaged-replanted and unsalvaged treatments were passive in the analysis. In this way, patterns observed in the diagrams are not affected by the treatments; rather the patterns are due to measured environmental variables and species distributions in the plots. In the biplot, axis 1 represents the direction of the

TABLE 1. Mean, standard deviation, and range of environmental variables in salvaged and unsalvaged plots on Mount St. Helens ($n = 25$). Salvaged and unsalvaged plots were contrasted by independent samples t tests at $\alpha = 0.5$.

	Salvaged plots		Unsalvaged plots		Statistics	
	Mean	Range	Mean	Range	t -value	P
Elevation (m)	1135 \pm 18	1096–1168	149 \pm 19	1118–1177	–1.961	0.056
Aspect ($^{\circ}$) ^a	231 \pm 33	160–290	204 \pm 35	148–264	–1.557	0.126
Slope (%)	37 \pm 12	16–60	34 \pm 12	17–62	0.649	0.519
Litter depth (cm)	0.3 \pm 0.4	0–1.8	2.2 \pm 1.9	0–6.5	–4.851	<0.001
% litter cover	29 \pm 17	2–65	38 \pm 26	5–75	–1.454	0.154
% downed woody debris ^b	3.9 \pm 3.3	1–12	20.4 \pm 11.2	6–50	–7.092	<0.001
No. DWD \cdot 16 m ⁻¹ c	2.3 \pm 1.8	0–6	8.1 \pm 3.0	5–13	–8.257	<0.001
Average DWD diameter (cm) ^d	29 \pm 19	0–65	48 \pm 11	28–68	–4.432	<0.001
No. tip-ups	0.8 \pm 1.4	0–4	2.4 \pm 1.8	0–8	–3.578	0.001
Snags	0.04 \pm 0.2	0–1	0.08 \pm 0.3	0–1	–0.586	0.561
Stumps	5.0 \pm 3.4	0–17	0.08 \pm 0.4	0–2	6.480	<0.001
% bare area cover	47 \pm 17	14–75	20 \pm 12	4–50	6.420	<0.001
% moss cover	8 \pm 6	1–30	3 \pm 2	1–10	4.192	<0.001
% understory plant cover	14 \pm 8	4–32	29 \pm 15	8–68	–4.332	<0.001
Understory richness ^e	11 \pm 3	6–17	21 \pm 5	8–29	–8.444	<0.001
Understory diversity ^e	1.48 \pm 0.32	0.86–2.07	1.97 \pm 0.44	0.64–2.60	–4.566	<0.001
% nonnative species cover	2.0 \pm 2.4	0.1–10.0	1.2 \pm 1.2	0.1–4.0	1.242	0.223
% total nitrogen	0.016 \pm 0.0091	0.0077–0.038	0.021 \pm 0.010	0.0097–0.046	–1.846	0.071
Nitrate ($\mu\text{g} \cdot \text{g}^{-1}$)	0.50 \pm 0.77	0.15–3.45	4.33 \pm 5.18	0.15–18.50	–3.657	0.001
Phosphate ($\mu\text{g} \cdot \text{g}^{-1}$)	7.38 \pm 3.08	2.00–15.66	15.20 \pm 4.85	7.28–26.18	–6.809	<0.001
% soil organic matter	0.50 \pm 0.32	0.18–1.62	0.56 \pm 0.25	0.17–1.07	–0.667	0.508

^aAspect converted to Whittaker (1960) exposure classes for statistical analysis.

^bPercent of the plot covered by downed woody debris >10 cm in diameter.

^cAverage number of downed woody debris >10 cm in diameter encountered in a 16-m transect across each plot.

^dAverage diameter of downed woody debris in a 16-m transect across the plot. Only diameters >10 cm are included. If none are present then a “0” is achieved.

^eThese analyses were conducted without the coniferous species *Abies procera*, *Abies amabilis*, *Picea engelmannii*, *Pinus monticola*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*. Broad-leaved trees (*Populus balsamifera*, *Salix sitchensis*, and *Alnus viridis*) were present as saplings and were included in the analysis.

greatest amount of variation, and axis 2 represents the 2nd-greatest amount of variation in the data set.

RESULTS

Salvaged-replanted and unsalvaged sites were significantly different for most of the measured variables (Table 1). Unsalvaged plots had overall more DWD. Unsalvaged plots had more tip-ups than salvaged-replanted plots and salvaged-replanted plots had, as expected, more stumps. Unsalvaged plots had deeper litter, whereas salvaged plots had a greater percentage of bare soil and moss cover. Unsalvaged plots had more herb and shrub cover and were richer and more diverse than salvaged-replanted plots. A total of 90 species were found in all of the plots (Appendix); 52 species were found in salvaged-replanted plots and 78 species were found in unsalvaged plots. Along with the greater cover of herbs and shrubs in unsalvaged sites, herb and shrub richness and diversity were also higher. Collectively, unsalvaged plots contained more species in

various life-form groups than did salvaged-replanted plots (Table 2). All of the species detected are common species of the region (Hitchcock and Cronquist 1973, Franklin and Dyrness 1988, Titus et al. 1998).

Chamerion angustifolium, *Hieracium albiflorum*, *Anaphalis margaritacea*, *Hypochaeris radicata*, and *Vaccinium membranaceum* were found in more than 80% of the salvaged-replanted plots, and the last 3 species were found in every plot (Table 3). *Hypochaeris radicata*, *Hieracium albiflorum*, *V. membranaceum*, *A. margaritacea*, and *C. angustifolium* were found in more than 80% of unsalvaged plots, and the last 2 species were found in every plot. *Abies procera* was found in 22 of the 25 salvaged-replanted plots and in none of the unsalvaged plots (Table 4). The 3 salvaged-replanted plots without *A. procera* canopy cover did not differ from other salvaged-replanted plots in terms of herb and shrub composition or soil characteristics. *Abies amabilis* was found in 14 of the 25 unsalvaged plots and was not found in salvaged-replanted plots, whereas

TABLE 2. Number of species in life-form groups in salvaged and unsalvaged plots on Mount St. Helens ($n = 25$). The nonnative species are all forbs, except for 1 grass, and are included in both their respective categories.

Life-form	Number of species	
	Salvaged	Unsalvaged
Total species	52	80
Conifers	5	4
Broad-leaved trees	2	3
Shrubs	9	12
Forbs	22	38
Grasses	11	18
Ferns	3	5
Nonnative species	4	6

Pseudotsuga menziesii was found in 8 salvaged-replanted plots and in 9 unsalvaged plots. Deciduous trees, which often dominate successional forests in the region, were more common in unsalvaged plots (Table 4). Every plot contained nonnative species, mostly at low cover (Table 5). Unsalvaged plots contained 6 nonnative species overall, and salvaged-replanted plots contained 4 nonnative species. Salvaged-replanted and unsalvaged plots did not differ in nonnative species cover (Table 1).

The greater species richness and variety in species composition of unsalvaged plots is apparent in the DCA (Fig. 2). The environmental factors with the greatest difference between salvaged-replanted and unsalvaged sites are clearly seen in the CCA; this shows that the environments of salvaged-replanted and unsalvaged plots differ markedly (Fig. 3). Elevation, slope, and aspect do not appear to be important in structuring the vegetation; that is, they are not correlated with the other factors.

In the DCA analysis, 29 species that occurred in only 1 or 2 plots were excluded. These uncommon species were predominantly from unsalvaged plots and had little effect on the ordination (Fig. 2). The 2 axes in this ordination are 3.1 and 2.4 half-changes long, which are indicative of a data set with a moderate range of species composition (Table 6). In Figure 2 the salvaged-replanted plots are located below the unsalvaged plots and are more tightly clustered, showing that they exhibit less variation in species composition than do unsalvaged plots. The reduced variation of salvaged-replanted plots is evident in the smaller standard deviations of the plot scores for salvaged-replanted plots (axis 1: $s = 0.507$; axis 2:

$s = 0.335$) than for unsalvaged plots (axis 1: $s = 0.742$; axis 2: $s = 0.448$).

In Figure 2 the unsalvaged outlier plot on the far right-hand side of the horizontal axis was dominated by *Pteridium aquilinum* and the unsalvaged plot outlier at the top of the vertical axis was dominated by the ruderals *C. angustifolium* and *A. margaritacea* and by *Rubus lasiococcus*. Species that were important in unsalvaged plots occur in the top left and far right portions of the ordination diagram. Species that are common in both salvaged-replanted and unsalvaged plots occur in the central portion of the diagram.

In the CCA, the variable "number of snags" was removed because snags were infrequent (Fig. 3). The environmental attributes of salvaged-replanted plots can be seen in the lower left quadrant with the correlation between stumps and bare area, both of which had significantly higher values in salvaged-replanted plots than in unsalvaged plots. Likewise, the species mostly found in salvaged-replanted sites are in this quadrant. Most species found in unsalvaged plots are in the upper right quadrant. In addition, the majority of the infrequent species excluded from the analysis were also in unsalvaged plots. Thicker litter, higher phosphorus levels, and more DWD are associated with unsalvaged plots, along with weaker trends for higher levels of total nitrogen, nitrate, litter cover, TOC, and more tip-ups. Elevation, slope, and aspect vectors are at right angles to the other variables, indicating the lack of correlation of these 3 factors to the other site factors. Steeper slopes are correlated with higher elevations. A few species that were found in the higher elevation plots on steep slopes are located in the lower right quadrant; these were unsalvaged plots. The first 2 axes explain 55% of the relationship between species and the environment.

The nitrogen fixers (*Alnus* and *Lupinus*) are not related to the nitrogen axes in any of the analyses, meaning that these species are not found in areas of higher nitrogen. Nonnative species do not cluster in any of the analyses. The CCA was significant by the Monte Carlo test.

DISCUSSION

The differences found in environmental factors and species distributions, richness, and

TABLE 3. Non-tree species in salvaged and unsalvaged plots on Mount St. Helens with >50% frequency and >1% mean cover ($n = 25$). Mean cover is the average of all 25 plots.

Species	Salvaged plots		Unsalvaged plots	
	% frequency	% mean cover	% frequency	% mean cover
<i>Vaccinium membranaceum</i>	100	4.5	96	5.5
<i>Anaphalis margaritacea</i>	100	2.2	100	5.2
<i>Hypochaeris radicata</i> ^a	100	2.0	92	1.1
<i>Eriogonum pyrolifolium</i>	60	2.0	28	0.4
<i>Vaccinium ovalifolium</i>	52	1.5	80	2.0
<i>Menziesii ferruginea</i>	24	0.3	40	0.2
<i>Epilobium minutum</i>	48	0.5	44	0.3
<i>Hieracium albiflorum</i>	96	0.2	96	0.5
<i>Chamerion angustifolium</i>	88	0.1	100	3.4
<i>Pteridium aquilinum</i>	0	0	16	2.7
<i>Rubus lasiococcus</i>	0	0	60	0.7
<i>Polystichum munitum</i>	28	0.05	80	0.4
<i>Athyrium filix-femina</i>	12	0.01	64	0.3
<i>Sorbus sitchensis</i>	8	0.004	48	0.3
<i>Luzula parviflora</i>	12	0.02	76	0.2
<i>Agrostis scabra</i>	36	0.1	64	0.06

^aNonnative speciesTABLE 4. Frequency, mean percent canopy cover, and mean density (trees · 200 m⁻²) of tree species in salvaged and unsalvaged plots on Mount St. Helens ($n = 25$).

Species	Salvaged plots			Unsalvaged plots		
	% frequency	% cover	Density	% frequency	% cover	Density
<i>Abies amabilis</i>	0	0	0	56	3.0	1.8
<i>Abies procera</i>	88	22.5	17	0	0	0
<i>Alnus viridis</i>	16	0.2	0.72	56	2.0	2.0
<i>Picea englemannii</i>	4	0.2	0.08	0	0	0
<i>Pinus monticola</i>	12	0.2	0.12	8	0.02	0.08
<i>Populus balsamifera</i>	0	0	0	12	0.06	0.21
<i>Pseudotsuga menziesii</i>	32	0.1	0.6	36	0.3	0.54
<i>Salix sitchensis</i>	40	0.2	0.64	72	1.4	2.8
<i>Tsuga heterophylla</i>	12	0.1	0.2	16	0.3	0.5

TABLE 5. Nonnative species in salvaged and unsalvaged plots on Mount St. Helens ($n = 25$). Percent cover is a mean based only on plots that contained the species.

Species	Salvaged plots		Unsalvaged plots	
	% frequency	% cover (range)	% frequency	% cover (range)
<i>Hypochaeris radicata</i>	100	1.9 (0.1–10)	92	1.2 (0.1–3)
<i>Lactuca muralis</i>	4	0.01 (0.01)	44	0.2 (0.01–0.5)
<i>Anthoxanthum odoratum</i>	12	0.2 (0.01–0.5)	48	0.4 (0.01–2)
<i>Cirsium arvense</i>	8	0.1 (0.1)	12	0.07 (0.01–0.1)
<i>Senecio jacobea</i>	0	0	4	0.1 (0.1)
<i>Spergularia rubra</i>	0	0	4	0.01 (0.01)
TOTAL	100	2.3 (0.1–10)	100	1.9 (0.1–4)

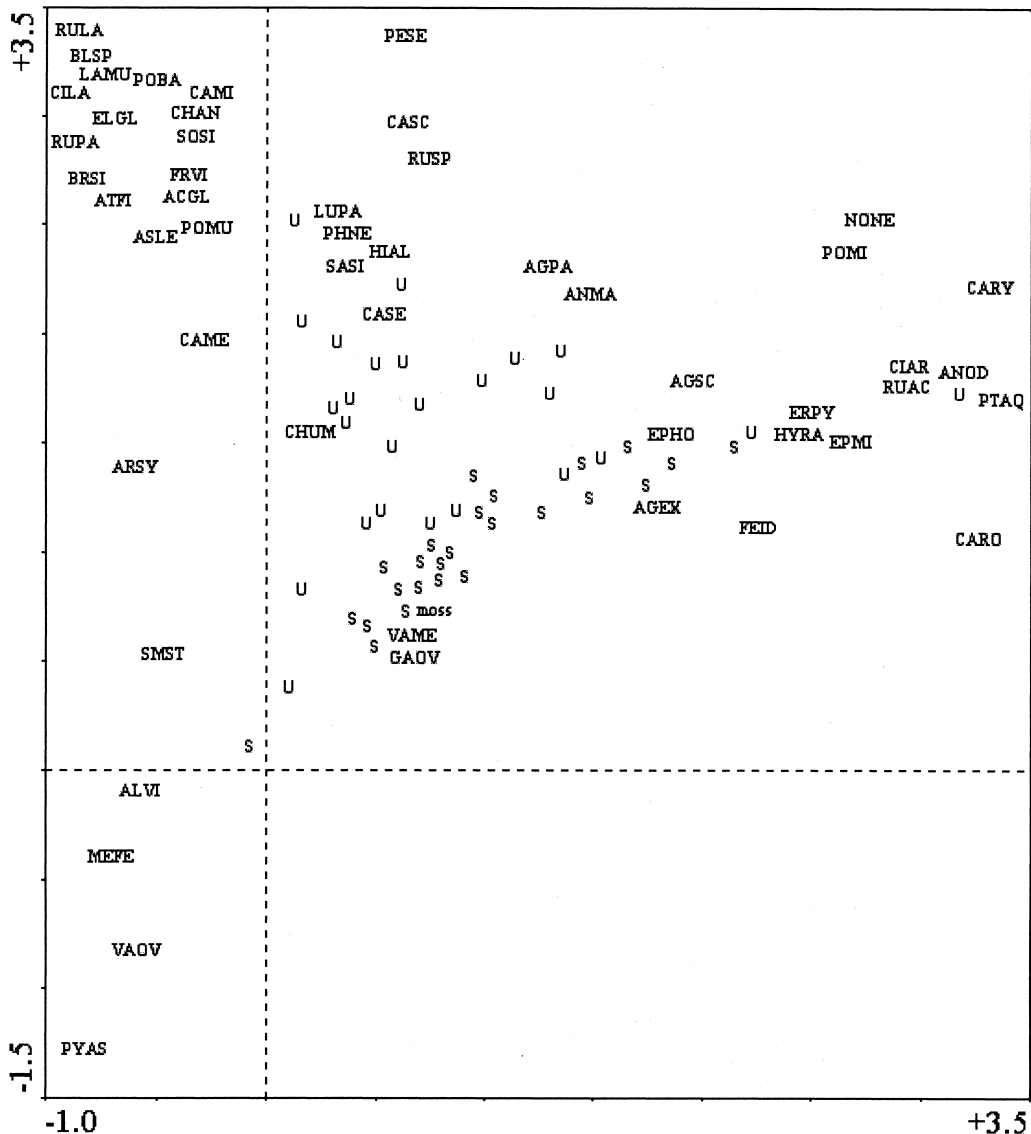


Fig. 2. Detrended correspondence analysis plot of salvaged-replanted plots (S) and unsalvaged plots (U) on Mount St. Helens. Infrequent species have been removed. The 4-letter species abbreviations are defined in the Appendix. Salvaged-replanted plots are closer to each other on the diagram, indicating that their species compositions are more similar.

diversity show that salvage logging and replanting affected vegetation and to a lesser extent soils 23 years post-disturbance and 20 years post-salvage and planting. This is not only due to the overstories, which have completely different compositions because *Abies procera* has been planted in the salvaged sites and is not present in the sparse canopy of the unsalvaged sites, but also to the understories, which differ dramatically. Unsalvaged plots

have higher herb and shrub diversity and cover. Soils are also quite different between the 2 treatments. The soils of unsalvaged plots have higher levels of nitrate and phosphorus than soils of salvaged-replanted sites. It may be that less phosphorus is present in salvaged-replanted sites because of uptake by ectomycorrhizal fungi connected to the young noble fir. In addition, salvaged-replanted plots have a greater amount of unvegetated soil surface and moss

TABLE 6. Summary of the detrended correlation analysis (DCA) axes, the canonical correlation analysis (CCA) axes, and Monte Carlo significance test results. The axis-2 column is trace for Monte Carlo results.

Variable	DCA all plots		CCA all plots	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.725	0.461	0.443	0.350
Length of gradient	3.086	2.405		
Species-environment correlation			0.829	0.880
% variance of species data	23.3	9.6	14.2	11.3
% variance of spp.-env. relation		30.8	24.3	
Unconstrained eigenvalues		3.115		3.115
Constrained eigenvalues				1.440
%				46.2
Monte Carlo <i>P</i>			0.030	0.005

differences are not considered large enough to have caused any of the observed variation in vegetation and soil nutrients. We observed that nearby intact forests in the Cascades do not show vegetational differences across an elevational gradient of <100 m at this elevation. The force of the eruption may have been greater in the unsalvaged sites, as indicated by the greater number of tip-ups. In any case, most trees in the salvaged-replanted plots died standing and were subsequently logged, leaving behind a stump.

Because of the litter generated by *A. procera* on salvaged-replanted sites, litter cover did not differ between salvaged-replanted and unsalvaged sites (Table 1). However, litter was much deeper in unsalvaged sites probably because of the greater retention of litter in these sites and the greater quantity of broad-leaved species generating litter. This could potentially result in long-term differences in nutrient cycling between salvaged-replanted and unsalvaged sites.

Regardless of whether sites are salvaged, surface soils had much lower organic matter levels than soils of undisturbed forests in the region (Franklin and Dyrness 1988). This was due to the deposition of tephra. However, organic matter levels were much higher than the <0.01% soil organic matter found in primary successional sites on the Pumice Plains, where >100 m of tephra was deposited (del Moral 1999, Titus unpublished data).

In the unsalvaged plots, greater litter depth is positively correlated with phosphorus and total nitrogen, and weakly correlated with TOC (Fig. 3). Although axis 1 illustrates the strongest

patterns in species distributions, many species are also responding to the environmental factors of axis 2 and are distributed along this axis. The nitrogen fixers (*Alnus* and *Lupinus*) are not related to the nitrogen vectors in any of the CCA diagrams, perhaps because they are never sufficiently prevalent to affect nitrogen levels.

There were no differences in nonnative species between salvaged-replanted and unsalvaged plots. The nonnative species found here are common in clear-cuts throughout the region, and they invade, but do not dominate, the highly disturbed environments created by the eruption, whether or not salvage has occurred. Nonnative species do not cluster in any of the CCAs, indicating that each species is responding differently to environmental conditions. In other environments, such as Florida scrub (Greenberg et al 1995), nonnative species are prevalent in salvaged sites. This was not the case here. *Hypochaeris radicata*, the most common nonnative species in this study (Table 5), is prevalent on successional sites across the volcano. Nonnative species may alter the trajectory of succession at many successional sites (Vitousek and Walker 1989, Titus and Tsuyuzaki 2003). However, the facts that *H. radicata* cover is generally low in most plots and that it has decreased in other areas on Mount St. Helens (Titus unpublished data) reduce the probability of major changes to vegetation composition from this species.

If it was the case that some of the salvaged-replanted area was clear-cut before the eruption, then this treatment did not cause a wide

discrepancy in species cover among the salvaged-replanted plots (Fig. 2). Clear-cuts in the region are dominated by many of the species that are prevalent in the unsalvaged plots. Because both the salvage logging and the subsequent planting of noble fir occurred on all but 3 of the salvaged plots, it was difficult to separate the effects of the salvage logging from the effects of the developing noble fir. However, the 3 plots, which did not contain any *A. procera*, did not differ in terms of herb and shrub composition from those with *A. procera* cover. This result suggests that differences between treatments were likely due to logging activities rather than planting. In any case, the combination of the 2 treatments has led to reduced diversity and cover, completely different overstory species composition, and lower nutrient levels in salvaged sites at this time. We predict that salvaged and unsalvaged sites will remain very different for a long time to come. Not only will the overstories continue to have very different compositions, but understory species will struggle to establish themselves in salvaged sites when the planted noble fir achieves a closed canopy. Salvage logging will continue to be planned for post-disturbance forest lands; therefore, it is important that land managers understand the effects that this management tool will have on forest composition and structure. Because large, naturally reforesting areas are rare not only in the Pacific Northwest but worldwide, and because they are important for regional biodiversity, unsalvaged sites are an important natural laboratory for observing successional processes and are worthy of conservation interest.

ACKNOWLEDGMENTS

This work was supported by U.S. National Science Foundation grant DEB-0089843 to J. Bishop and J.H. Titus. We thank the Mount St. Helens National Volcanic Monument for permission to conduct field research and the Biosphere 2 Center for logistical support. C. Rumbaitis-del Rio provided invaluable ideas on field research and on the manuscript. The manuscript was greatly improved by comments from J. Bishop, R. del Moral, and anonymous reviewers. Thanks go to J. Seeds, S. Wills, and S. Yang for field camp support. We are grateful to P. Titus and L. Gephart for generous encouragement and support.

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Received 12 December 2005

Accepted 27 October 2006

APPENDIX. Species at salvaged and unsalvaged sites on Mount St. Helens. Species without a 4-letter abbreviation are either conifer species or infrequent and not represented on an ordination diagram.

Abbreviation	Species name
	<i>Abies amabilis</i>
	<i>Abies procera</i>
ACGL	<i>Acer glabrum</i>
	<i>Achillea millefolium</i>
	<i>Achlys triphylla</i>
	<i>Agoseris aurantica</i>
	<i>Agoseris grandiflora</i>
AGEX	<i>Agrostis exarata</i>
AGPA	<i>Agrostis pallens</i>
AGSC	<i>Agrostis scabra</i>
ALVI	<i>Alnus viridis</i>
	<i>Amelanchier alnifolia</i>
ANMA	<i>Anaphalis margaritacea</i>
	<i>Antennaria rosea</i>
ANOD	<i>Anthoxanthum odoratum</i>
	<i>Arnica latifolia</i>
ARSY	<i>Aruncus sylvestre</i>
ASLE	<i>Aster ledophyllus</i>
ATFI	<i>Athyrium filix-femina</i>
BLSP	<i>Blechnum spicant</i>
BRSI	<i>Bromus sitchensis</i>
	<i>Calamagrostis canadensis</i>
	<i>Calamagrostis purpurescens</i>
CASE	<i>Calamagrostis sesquiflora</i>
CASC	<i>Campanula scouleri</i>
CAME	<i>Carex mertensii</i>
	<i>Carex pachystachya</i>
CARO	<i>Carex rossi</i>
CARY	<i>Caryophyllacea</i> sp.
CAMI	<i>Castilleja miniata</i>
CHAN	<i>Chamerion angustifolium</i>
CHUM	<i>Chimaphila umbellata</i>
CILA	<i>Cinna latifolia</i>
CIAR	<i>Cirsium arvense</i>
	<i>Clermontia parviflora</i> (Montia)
	<i>Cystopteris fragilis</i>
	<i>Deschampsia atropurpurea</i>
	<i>Deschampsia elongata</i>
ELGL	<i>Elymus glaucus</i>
EPHO	<i>Epilobium hornemannii</i>
EPMI	<i>Epilobium minutum</i>
ERPY	<i>Eriogonum pyrolifolium</i>
FEID	<i>Festuca idahoensis</i>
FRVI	<i>Fragaria virginiana</i>

APPENDIX. Continued.

Abbreviation	Species name
GAOV	<i>Gaultheria ovatifolia</i>
	<i>Glyceria elata</i>
	<i>Gnaphalium canadensis</i>
HAL	<i>Hieracium albiflorum</i>
	<i>Holodiscus discolor</i>
HYRA	<i>Hypochaeris radicata</i>
LAMU	<i>Lactuca muralis</i>
LUPA	<i>Luzula parviflora</i>
MEFE	<i>Menziesia ferruginea</i>
	<i>Mitella breweri</i>
moss	moss
NONE	<i>Nothochelone nemorosa</i>
	<i>Orthilia secunda</i> (Pyrola)
	<i>Pachistima myrsinites</i>
	<i>Penstemon cardwellii</i>
PESE	<i>Penstemon serrulatus</i>
	<i>Petasites frigidus</i>
PHNE	<i>Phacelia nemorosa</i>
	<i>Picea engelmannii</i>
	<i>Pinus monticola</i>
POMI	<i>Polygonum minimum</i>
POMU	<i>Polystichum munitum</i>
POBA	<i>Populus balsamifera</i>
	<i>Pseudotsuga menziesii</i>
PTAQ	<i>Pteridium aquilinum</i>
PYAS	<i>Pyrola asarifolia</i>
	<i>Ribes lacustre</i>
RULA	<i>Rubus lasiococcus</i>
	<i>Rubus leucodermis</i>
RUPA	<i>Rubus parviflorus</i>
RUSP	<i>Rubus spectabilis</i>
RUAC	<i>Rumex acetosella</i>
SASI	<i>Salix sitchensis</i>
	<i>Sambucus racemosa</i>
	<i>Senecio jacobea</i>
	<i>Senecio triangularis</i>
SMST	<i>Smilicina stellata</i>
SOSI	<i>Sorbus sitchensis</i>
	<i>Spergularia rubra</i>
	<i>Trisetum spicatum</i>
	<i>Tsuga heterophylla</i>
	unkown forb species
VAME	<i>Vaccinium membranaceum</i>
VAOV	<i>Vaccinium ovatum</i>
	<i>Vaccinium parviflorum</i>
	<i>Valarian sitchensis</i>