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**The Spread of Exotic Plant Species at Mount St
Helens: the Roles of a Road, Disturbance Type and
Post-Disturbance Management**

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The Spread of Exotic Plant Species at Mount St Helens: the Roles of a Road, Disturbance Type and Post-Disturbance Management

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Environmental Sciences and Management**

ABSTRACT: The landscape of Mount St Helens was dramatically transformed when it erupted on May 18, 1980, creating an outstanding opportunity for ecologists to study succession following a large, intense, natural disturbance. Within the expansive (600 km²) blast area there is varied ownership and a mix of management objectives for the post-eruption landscape. On lands administered by the U.S. Forest Service, there are portions of the blast area that have been designated as a National Volcanic Monument, where the primary management objective is to allow for natural succession to proceed substantially unimpeded. In other areas outside the Monument, salvage logging and replanting of tree seedlings occurred and multiple-use is the designated management objective. Even within the Monument, activities such as road, trail, and visitor center construction has occurred. Such activities stand to increase the potential plant invasibility of the area through increased vectors and dispersal corridors. This study looks at the spatial pattern of exotic plant species richness and abundance along a road that traverses a volcanic disturbance gradient consisting of two distinct zones: a tephra impacted forest and three different vegetation types in the blow-down zone, as well as along a pedestrian trail in the roadless Pyroclastic flow zone. Plant communities were sampled along 20 replicate transects (70 m) in each of five different disturbance/management/succession areas. Transects were positioned perpendicular to the road axis to assess how exotic plant species richness, abundance, and relative abundance varied with distance from the road. Linear regression was used to determine whether the road influenced exotic plant richness and abundance. In the Pumice Plain, where primary succession is occurring, minimal amounts of two wind-dispersed, exotic species, *Hypochaeris radicata* and *Rumex acetosella*, were observed. In the blowdown zone, where the eruption destroyed vegetation, exotic plants in the replanted and shrub-dominated areas significantly decreased moving away from the road, while exotic plants did not significantly decrease away from the road in the forb-dominated blowdown area. Exotic plant species were restricted to within five meters of the road in the intact late seral forest that was disturbed by the deposits of 12 - 15 cm of cool tephra consisting of silt to gravel-sized particles. My research demonstrates an overall low abundance of exotic plants at Mount St. Helens, that exotic plant species are more prevalent along the roadsides, but that natural forest and shrubs slow their spread to the interior landscape.

Keywords: Mount St. Helens, non-native species, exotic species, road, management, volcanic disturbance

1 INTRODUCTION

1.1 Context and Definitions

The landscape surrounding Mount St Helens was dramatically disturbed during the May 18, 1980 eruption, creating an outstanding opportunity for ecologists to study natural succession. In 1982, Congress designated 44,550 ha as the Mount St. Helens National Volcanic Monument, with the purpose of protecting the land to allow for natural succession to proceed substantially unimpeded (Dale et al. 2005, Titus and Householder 2007). Some areas are closed to the public, while other areas are intended to attract visitors. Despite efforts to preserve the area for natural processes and scientific study, anthropogenic disturbances such as roads and other management decisions have amplified the invasibility of the already naturally disturbed landscape to exotic plants (Forman et al. 2003). Some of these anthropogenic disturbances occur within the Monument, but they occur to a much larger extent in areas adjacent to the Monument where the primary management objective is multiple-use (Dale et al. 2005). Roads and active management (e.g. timber production), have created opportunities for the introduction and spread of exotic plant species (Parendes and Jones 2000, Titus et al. 1998, Trombulak and Frissell 2000)). Understanding how both natural and anthropogenic disturbances are affecting the spread of exotic plant species across the Mount St. Helens landscape is important for both land managers and scientists.

Exotic species are well known to have high costs for ecosystems and economies. Exotic invasive plants are known to compete with native species, interrupt food webs, alter fire regimes, decomposition, hydrology and nutrient cycling (Mack et al. 2000, Vitousek et al. 1997). Humans have been intentionally and accidentally introducing exotic plants for centuries and the spread of

these species is reducing the differences between unique floral and faunal communities across the globe (Vitousek et al. 1997 Stohlgren et al. 2011). In the Pacific Northwest, typical exotic species are shade-intolerant and are often found in recently disturbed habitats (Gray 2007, Trombulak and Frissell 2000). In a systematic review of exotic plant species, Lozon and MacIsaac (1997) found that 86% of established exotic species were connected with disturbance.

Titus et al. (1998) conducted a thorough inventory of vascular plants in areas disturbed by the 1980 eruption in 1993 and 1994 and exotic plant species comprised 57 of 341 plant species. Twenty years after this survey, these exotic species continue to influence natural succession (Schoenfelder et al. 2010, Dale and Adams 2003, Titus et al. 1998). For example, on the debris avalanche area of Mount St. Helens, sites that were heavily invaded by exotic species had one fourth less conifers than uninvaded sites (Dale and Adams 2003)

I used the Natural Resources Conservation Science (NRCS) to define an exotic plant species as one that is not native to the study area (www.plants.usda.gov, May 2014). They are likely to become invasive as they lack the natural enemies and competitors from their home ranges (www.plants.usda.gov, May 2014). While the focus of this study is on exotic plants, some cited research looks at exotic invasive plants, which are introduced species that have invaded and are currently or “likely to cause economic or environmental harm to human health” (Clinton, 1999). It is best to control exotic plant populations while they are small as it is more economically efficient than waiting for them to cause a problem (Moody and Mack 1988). It is also quite difficult to predict when and where a plant will become invasive (Lockwood et al. 2007). Therefore, I looked at all exotic plant species, rather than just invasive plants.

1.2 Exotic Plant Concerns in Different Volcanic Disturbance Zones

The 1980 eruption created several different disturbance zones, and the Pyroclastic flow zone was the most drastically affected area. This landscape experienced a sequence of volcanic disturbances throughout a ten hour period that commenced with a gigantic rock fall avalanche as the north slope of the volcano failed and careened downslope; followed by a powerful, hot, gas-driven lateral blast; and culminated in numerous superheated incandescent pyroclastic flows (flowing masses of hot and dry rock), resulting in a primary succession situation (Swanson and Major 2005). A portion of the Pyroclastic zone, named the Pumice Plain, is an area of intensive scientific study and is the site where I conducted my research (Figure 1). The Pumice Plain is closed to camping, off-trail travel, dogs, and bicycles to minimize anthropogenic impacts to this sensitive area. Shortly after the eruption, land managers felt pressured by the public to do something to aid restoration of the disturbed landscape, yet little was known about how large, infrequent disturbances affected ecosystems (Dale et al. 1998, Turner et al. 1997). With concerns of erosion, \$50,000 was spent on intentional seeding on the debris avalanche, just west of the Pumice Plain, introducing at least six exotic plant species: *Trifolium repens*, *Lotus spp*, *Melilotus officinalis*, *Lolium perenne*, *Dactylis glomerata*, and *Festuca arundinacea* (Dale et al. 1998, Dale and Adams 2003). These plants did not solve the erosion problem, and yet provided source populations of seed with the potential to disperse into the Monument through wind and animals where they might establish populations in the Pumice Plain and other areas (Dale and Adam 2003, Franklin et al. 1988). In an extensive survey of Mount St Helens area in 1993 and 1994, Titus et al. (1998) found all but one of the initially seeded exotic species, *Melilotus officinalis*.

The most common exotic species they observed on the Pumice Plain were *Cirsium arvense*, *Gnaphalium uliginosum*, *Hypochaeris radicata*, *Senecio sylvatica*, and *Sonchus asper*.

Extending out from the Pumice Plain, the lateral blast killed all mature trees across more than 550 km² of land, either knocking them over, snapping them off, or leaving them standing, but dead (Halpern et al. 1990, Dale et al, 2005). However, some seedlings and saplings were buried under snow or protected on leeward slopes leading to quicker tree and shrub regeneration (Halpern et al. 1990). The eruption also covered the blast area with tephra deposits which are nutrient poor, especially in nitrogen and carbon (Halvorson et al. 1991). Dead trees and other coarse woody debris provide nutrients, shade, water storage, erosion reduction and a seed bed for young trees (Harmon et al. 1986). Despite these benefits of dead trees, extensive salvage logging and replanting efforts were made in the blast area forests outside the National Volcanic Monument from 1980 to 1987 (Foster et al. 1998, Titus and Householder 2007). Vast plantations of *Pseudotsuga menziesii* and *Pinus monticola* (<1000 m) and *Abies procera* (>1000 m) now dominate the landscape just outside the Monument (Titus and Householder 2007). In a study by Titus and Householder (2007), the canopy cover of trees in salvaged/replanted plots was five times higher than in unsalvaged/unplanted plots. They also found that unsalvaged/unplanted sites had greater diversity, richness, herb and shrub cover, downed woody debris, and litter depth. Furthermore, Titus and Householder (2007) found no differences in exotic cover between the two areas, although exotic species were present in every 200 m² plot. The exotic species found have varying individual responses to disturbance, were species that do not typically become dominant, and are plants frequently found in disturbed areas of the region

Beyond the blast area, coniferous forest overstory species were left largely intact, but understory plant communities were dramatically altered over 100 km² by various amounts of tephra ejected from the volcano. Antos and Zobel (2004) found that tephra fall in forests resulted in the death of many understory plants and shrubs, largely depending on microsite conditions such as snowpack, pre-existing flora, and depth of tephra. Where tephra was less than 4.5 cm, most herbaceous plants were able to survive. However, when tephra was deeper, many herbaceous plants were not able to push through the mantle of tephra and perished. Furthermore, when areas were covered in deep snow, plants were covered in thick ash, and as the snow melted, they became plastered to the forest floor and did not survive. Except for bryophytes, species not present in the pre-eruption forest had not invaded the tephra impacted forest by the year 2000 (Antos and Zobel, 2004). Despite the lack of invasive plants in Antos and Zobel's (2004) study, proximity to a road could introduce exotic plants to previously uninvaded forests.

1.3 Road Impacts on Exotic Plant Spread

The eruption created a stunning landscape that provided unprecedented scientific, education, and opportunities and roads and facilities were needed to allow visitors to experience Mount St. Helens. In 1983, Windy Ridge Viewpoint opened for visitors at the end of National Forest Road (NFR) 99, only four miles from the crater (USGS). This road travels through the tephra-fall forest, blast area, and to the edge of the Pumice Plain, and attracts many visitors every year. In studies of global patterns of plant invasions, Lonsdale (1999) and Usher (1988) both found that exotic plant species richness increased with the average number of visitors in nature reserves, most likely because tourists and their vehicles increase accidental introductions.

Exotic species are not only common along roadsides, but have been found to be restricted to roadsides in some forests (Forman et al. 2003, Parendes and Jones 2000, Hansen and Clevenger 2005). Some species, such as Purple Loosestrife (*Lythrum salicaria*) can form dense roadside monocultures (Wilcox 1989). Tyser (1992) found exotic species richness to be high along a National Park road, and low 100 m away from the road. Tyser (1992) also found that hiking trails generally had less of an affect on the spread of invasion compared to roads. Hansen and Clevenger's (2005) study showed that frequency of exotic plants decreased significantly with increasing distance from both a road and railway. Their study also showed that distance was significant only in forests, and not in grasslands. Roadsides can also store seeds in their soil for future invasions. Parendes (2000) found that out of almost 2000 seeds that germinated from soil samples, 85% were from samples at distances 0 m from a road, 10% were from distance at 5 m from the road and 5% were from the 50 m locations.

Road construction disturbs roadside environments, which stresses native plants and creates a microhabitat suitable for many exotic plants (Hansen and Clevenger 2005, Parendes and Jones 2000, Trombulak and Frissell 2000). The construction process typically creates bare earth, which ruderal and wind-dispersed annuals often colonize first (Forman et al. 2003). Roads can increase soil moisture, nutrient runoff, sunlight and temperature, which can all aid the establishment of exotic invasive species (Flory and Clay 2009). At the same time, the increased sunlight and wind can easily dry out these soils (Forman et al. 2003). Exotic plants that successfully invade are often the ones that can respond well to increased light conditions and disturbance (Newsome and Noble 1986, Parendes and Jones 2000, Gray 2007).

Common roadside management techniques of mowing and thinning can also benefit certain types of exotic plants. Species such as *Hypochaeris radicata*, *Taraxacum officinale*, *Cirsium arvense*, and *Plantago lanceolata* grow from rosettes and have the advantage because they do not die when mowed and can continue to photosynthesize, thus allowing them to grow deeper roots and be less likely to be swept away with roadside erosion (Forman et al. 2004). Roadside trees are often thinned for increased driver visibility, but this can aid many ruderal exotic species because of the increased and continuous source of light (Mortensen et al. 2009).

Not only do roadsides create a microhabitat for exotic species, they can also serve as a dispersal corridor for seeds (Parendes and Jones 2000, Trombulak and Frissell 2000). Roads can serve as a point of introduction, as well as a facilitator to dispersal (Tyser 1992). Vehicles from tourism and maintenance can disturb roadsides, increase wind, and can bring in exotic seeds and vegetative propagules on their tires (Lonsdale and Lane 1993, Hansen and Clevenger 2005). Wind, water, birds and other animals may also use the road as a path, and thus further spread seeds (Flory and Clay 2009).

1.4 Questions and Hypotheses

The disturbance zones at Mount St Helens created a variety of conditions with potentially different levels of invasibility to exotic plants. Conveniently, NFR 99 runs through the tephra-fall forest and the blast area, providing an ideal “transect” to assess patterns of exotic plant spread. This study asks questions of how these different volcanic disturbance zones, post-disturbance management, and the road are affecting the richness and abundance of exotic plant species at Mount St. Helens (Figure 7 in the Appendix). I first asked which species have

established in the NFR 99 area of Mount St. Helens. I hypothesize that (1) there will be an increase in richness, abundance, and relative abundance of exotic plant species in areas closer to the road and (2) there will be an increase in richness, abundance, and relative abundance of exotic plant species in zones with greater volcanic disturbance intensity. Furthermore, I hypothesize that (3) the spread of exotic species from the road will change, depending on unique characteristics of these zones. More specifically, (3a) exotic plant species will spread from the road least in the forest outside the blast area that was affected by the tephra fall (3b) sites within the blowdown zone with low canopy cover will have increased exotic richness and abundance at distances further from the road, compared to blowdown zone areas with increased canopy cover. Finally, I hypothesize that (4) the Pumice Plain will have lower richness and abundance of exotic plants compared to areas adjacent to the road.

Hypothesis (1) is expected because of the important role roads have played in the dispersal of seeds, habitat disturbance, and increased light (Forman et al. 2008, Tyser 1992, Parendes and Jones 2000, Hansen and Clevenger 2005). Because disturbance facilitates invasion (Lockwood et al. 2007), I expect areas with higher disturbance to have greater richness and abundance of exotic species (Hypothesis 2). Light also plays an important role in facilitating the establishment of exotic species (Newsome and Noble 1986, Parendes and Jones 2000, Gray 2007) and thus, I expect areas with lower canopy cover to have increased richness and abundance (Hypothesis 3b). The late seral forest is outside the blast area, experienced the lowest amount of volcanic disturbance and also has the highest canopy cover and is thus expected to have the least richness and abundance of exotic plants compared to the other areas (Hypothesis 3a). As the Pumice Plain does not have a road traversing through it, but rather a trail, I expect it

will have decreased exotic plant richness and abundance compared to other areas that are next to the road (Hypothesis 4).

2 METHODS

2.1 Study Area

The 1980 eruption of Mount St. Helens created multiple zones of disturbance, and this study includes four zones on the north and northeast sides of the volcano: the pyroclastic flow zone, blowdown zone, scorched zone, and tephra fall zone (Figure 1). The study area includes 70 m on each side of National Forest Road 99 (NFR-99), and 70 m on each side along the first 2.3 km of the Truman Trail, trail 207 (Figure 1). The road travels through the forest affected by tephra fall and the Scorched and Blowdown Zones. This 26 km paved road contains various viewpoints and trailheads along the way and is open for tourism and recreation from July until snow covers roads in the autumn (USDA, 2013).

To eliminate potential variation in plant communities related to elevation differences across sites, data were collected between six km and 26 km (from 46°18'34" N, 122°01'46" W to 46°15'03" N, 122°08'07" W). Data were also collected along Trail 207 between 46°13'49" N, 122°09'05" W and 46°14'33" N, 122°09'53" W. Slopes ranged from 0° to 37°.

The Pumice Plain covers 15km² and is directly north of the crater. This landscape was covered by over 100 m of debris avalanche, blast deposits and pyroclastic flows during the main eruption event in 1980, and received subsequent pyroclastic flows in 1980 and a few mudflows afterward (Swanson and Major 5005). Two years after the eruption, isolated individuals of *Lupinus lepidus* marked the first plant colonization (Halvorson et al. 1991). During my study,

the Pumice Plain upland vegetation was dominated by ruderal forbs and graminoids, namely *Agrostis pallens*, *Castilleja miniata*, *L. lepidus* and *Penstemon cardwellii*, often forming dense and expansive patches, punctuated by scattered *Salix sitchensis* and *Alnus viridis* ssp. *sinuata* shrubs and occasional conifer saplings. Dissecting the upland communities are springs, seeps, and small streams that frequently support dense riparian shrub communities.

The blowdown zone is the largest disturbance zone within the blast area covering an area of 370 km² where overstory trees were leveled or snapped off, though some seedlings and saplings survived under snow or on leeward slopes (Swanson and Major 2005). Some areas outside the Monument were salvage logged and replanted in 1980 - 1987, and while lower elevation areas were replanted with *Pseudotsuga menziesii* and *Pinus monticola*, areas near NFR 99 were replanted with *Abies procera*. In these managed portions of my study area, commercial thinning has occurred within the last few years (Charlie Crisafulli, *personal communication*) so there are many canopy openings, and while frequent species are *A. pallens*, *Anaphalis margaritacea*, *H. radicata*, *Rubus lassiococcus*, and *Vaccinium spp*, bare substrate was also common. Other areas were not salvage logged and in pre-eruption clear-cuts, can be characterized by many stumps, and in pre-eruption forests, by and decaying logs. (Titus and Householder 2007). During my study, unmanaged blowdown areas could generally be characterized as two habitat types. Some unmanaged habitats consisted of low canopy cover and many ruderal forbs and graminoids, often *A. pallens*, *Anaphalis margaritacea*, *H. radicata*, *P. cardwellii*, and *Pteridium aquilinum*, with occasional shrubs or conifers. Other unmanaged habitats were densely vegetated with shrubs (*S. sitchensis* and *A. viridis* ssp. *sinuata*). For the

purpose of my study, the scorched zone was included in the blowdown zone as the ground vegetation in the scorched zone was similar to the blowdown zone vegetation.

Beyond the blowdown and scorched zones, 15 kilometers from the crater, forests were left largely intact, but vast areas were affected by cool tephra deposits (Antos and Zobel 2004). Tephra fall in forests resulted in the death of many understory plants and shrubs, largely depending on microsite conditions such as snowpack, preexisting flora, and depth of tephra (Antos and Zobel 2004). Forest stands are dominated by large late seral conifer trees as well as many *Abies amabilis*, *Tsuga mertensiana*, *Tsuga heterophylla*, and *Pseudotsuga menziesii* saplings in the understory (Antos and Zobel 2004). During 2013, the understory could be characterized by scattered *Vaccinium spp.* and *Menziesia ferruginea*, while the ground cover consisted of high amounts of conifer needle litter.

FIGURE 1. Map of Disturbance Zones, National Forest Road (NFR) 99 (in blue), Trail 207 (in red).

FIGURE 2. Photographs of five different site types. Pumice Plain (a), Replanted Blowdown Zone (b), Shrub-dominated Blowdown Zone (c), Forb-dominated Blowdown Zone (d), Tephra Fall Forest (e).

2.2 Data Collection

To test the hypotheses, a stratified random sampling method was used to reduce bias of transect site selection and to ensure data were gathered within each site type (Michalcov 2011). To aid in studying light regime and post-disturbance management effects, three disturbance intensities (pyroclastic flow (Pumice Plain), blowdown zone, tephra fall zone) were delineated using images available from Google Earth. Within the blowdown zone, the area was further delineated into three vegetation types, creating five total site types: Pumice Plain (PP), Forb-dominated Blowdown Zone (FBZ), Shrub-dominated Blowdown Zone (SBZ), Replanted

Blowdown Zone (RBZ), and Tephra Fall Forest (TFF) (Table 1). Twenty transect sites were randomly selected within each site type and located and marked on the ground with the aid of a hand-held Global Positioning System (Garmin Oregon 450). Alternative random transect sites within each site type were selected, for use in the event that some of the originally selected sites could not be sampled safely or were otherwise inappropriate. Sites were considered unsafe to sample when the slope was too steep or unstable to walk on without serious risk of injury and inappropriate when there was a visitor center, parking lot or culvert present. The Gifford Pinchot National Forest office provided data on areas previously receiving herbicide treatment, and these locations were excluded from this study. Furthermore, forest areas with evidence of recent logging activity were also not included.

To determine species richness, abundance, and spread of exotic species from the road into the adjacent landscape, vascular plant species were identified along 70 m transects, positioned perpendicular to the road and > 20 m away from the nearest transect. Quadrats 1 m x 1 m were placed along each transect, beginning at the first established plant, at distances of 0 m, 2 m, 5 m, 10 m, 20 m, 30 m, 50 m and 70 m (following Amor and Stevens 1975). At each quadrat, all vascular plant species < 1.5 m in height and their percent cover values were recorded. Species were identified to the lowest taxonomic level possible and percent cover was visually estimated in increasing increments. Cover less than 1% was estimated at 0.25 or 0.5%, cover between one and 15% was estimated in 1% increments, and cover between 15 and 100 % was estimated at 5% increments (adjusted from Abella et al. 2012). Unknown plants were collected, pressed, and later identified using Hitchcock and Cronquist (1973) or Kozloff (2005). Shrub species in the genera *Salix* and *Vaccinium* were identified to the genus level, as all species in those genera in the

Mount St Helens areas are native. Plants were also placed into lifeform categories: (1) forb, (2) graminoid, (3) shrub, and (4) tree. The forb category included herbaceous flowering plants, as well as crawling and prostrate shrubs, ferns and horsetails. Graminoids included grasses, rushes and sedges (Poaceae, Juncaceae, Cyperaceae). Shrubs included upright woody species typically less than 1.5 m, including member species of the genera: *Arcostaphylos*, *Gaultheria*, *Menziesia*, *Pachystima*, *Ribes*, *Rubus*, and *Vaccinium*. Larger, tree-like shrub species of *Acer*, *Alnus*, *Amelanchier*, *Salix*, *Sambucus*, and *Sorbus* function more as canopy and were thus excluded from ground cover and were instead treated as “canopy” species. Canopy cover was visually estimated and placed into four categories: (1) zero, (2) low (1 to 30%), (3) medium (31 to 70%), and (4) high (71 to 100%) (Parendes and Jones 2000). Elevation at the road was later determined using data available from Google Earth. Vegetation and physical site data were gathered over a 5 week period at peak biomass and flowering season beginning in August and extending into early September, 2013.

TABLE 1. Site types and descriptions along NFR 99 in the Gifford Pinchot National Forest.

Site Type	Volcanic features	Description
Pumice Plain (Pyroclastic Flow Zone)	Debris avalanche, pyroclastic flows, mudflows	Area affected by 1980 debris avalanche, lateral blast, pyroclastic flows (flowing volcanic hot rock and gas), and occasional subsequent mudflows. Open landscape with mostly forbs and sparse shrubs/trees. Characterized by primary succession.
Forb-dominated Blowdown Zone	Scorch/blowdown, tephra deposits	Area where trees were scorched, snapped off or blown down by the 1980 blast. Open landscape with mostly forbs and sparse shrubs (<i>alnus</i> , <i>salix</i> , <i>vaccinium</i>) and trees.
Shrub-dominated Blowdown Zone	Scorch/blowdown, tephra deposits	Area where trees were scorched, snapped off or blown down by the 1980 blast. Landscape with many dense shrubs (<i>alnus</i> , <i>salix</i> , <i>vaccinium</i>) and some trees.
Replanted Blowdown Zone	Scorch/blowdown, tephra deposits	Managed forest outside the National Volcanic Monument. Trees were blown down, snapped off or scorched by the 1980 blast, and replanted by the USFS. Mostly <i>Abies procera</i> .
Tephra Fall Forest	Cool tephra deposits	Unmanaged forest outside the blast zone, with cool tephra (silt to gravel-sized) deposits from the 1980 eruption.

2.3 Data and Statistical Analysis

Taxonomic species names follow the Integrated Taxonomic Information System (www.itis.gov, April 2014) and were identified to be either native or exotic according to National Resources Conservation Service (NRCS) Plants Database (www.plants.usda.gov, April 2014). There is some debate about whether *Phalaris arundinacea* is native. The species is native to North America, but is also listed as a class C noxious weed by the Washington State Noxious Weed Control Board (www.nwcb.wa.gov, April 2014). There is debate concerning its genetic diversity and whether some European strains have been introduced (Nelson, 2014). The NRCS and this study classify *P. arundinacea* as native.

For exotic plant species occurring in more than three quadrats, frequency was calculated by summing the number of quadrats in which a species occurred at each distance within all site types except the Pumice Plain. To characterize canopy cover within each site type, median values from the four categories (zero, low, medium, high) were used to calculate median canopy for each site type. Canopy cover values for distances of 50 m and 70 m from the road (or trail) were used to better characterize the site type with less influence from the road (or trail).

For each quadrat, the total richness (number of species) and abundance (percent cover) was summed for native, exotic and total understory plants. Relative abundance of exotic species within each quadrat was calculated by dividing the exotic percent cover by the total percent cover for each quadrat. Means of percent cover and richness at each transect distance, within each site type was calculated.

Significant differences between the interior distances (50 m and 70 m) of the three blowdown zone site types were determined using the Kruskal-Wallis Rank Sum Test and the Wilcoxon Pairwise Rank Sum Test. The blowdown zone site type data met the equal variance assumption (Levene's Test), but could not be transformed to meet the normality assumption, so these non-parametric tests were used. Pumice Plain data were not included, as those transects were perpendicular to a trail, rather than a road, and are not comparable. Furthermore, the Tephra Fall Forest data were also excluded because at the 50 and 70 m distances, only one quadrat out of 40 contained an exotic plant at only 1%. The other 39 quadrats had zero values which did not allow data to meet equal variance assumptions.

To determine whether the road significantly influenced exotic plant richness, abundance and relative abundance within each site type, I used linear regressions. A negative slope, significantly different from zero, would mean that plant richness, abundance or relative abundance was decreasing as distance from the road (or trail) increased. A non-significant slope would mean that exotic plant richness, abundance, or relative abundance remained the same regardless of the distance from the road (or trail).

3 RESULTS

3.1 General Exotic Species Patterns

I identified 152 plant species (Table 9, Appendix A). Apart from *Salix spp.* and *Vaccinium spp.*, 13 additional taxa were identified to the genus level, though some of them are the same as the 152 identified species (for example, several *Maianthemum* spp. specimens could not be distinguished between *M. racemosum* or *M. stellatum*). These specimens could not be identified to the species level because the plants were juvenile, lacking fruits or flowers, or had been damaged

by herbivory. Twenty-two exotic species were recorded from the quadrats, all of which were forbs or grasses (Table 2). Fourteen of those species were found in more than three quadrats (Figure 8, Appendix). Three additional exotic species, *Cytisus scoparius* (shrub), *Tragopogon dubius* (forb), and *Verbascum thapsus* (forb), were observed outside of quadrats and noted in the species list (Table 2), but not included in analyses. The three blowdown zone site types contained the most exotic species (Table 2). The most abundant exotic species overall, in descending order, were *Hypochaeris radicata*, *Rumex acetosella*, *Anthoxanthum odoratum*, *Leucanthemum vulgare*, *Hypericum perforatum*, *Mycelis muralis*, and *Lotus corniculatus*. *H. radicata* was the most abundant exotic plant species in every site type (Table 2).

Overall, exotic species richness, abundance and relative abundance was low with highest mean values of 6 (at 5 m in the replanted zone, Figure 3), 6.5% (at 0 m in the Forb-dominated Blowdown Zone, Table 3) and 41% (at 2m in the Shrub-dominated Blowdown Zone, Table 4), respectively. Near the road, mean values of exotic plant abundance and relative abundance varied a lot, whereas at 20 m and beyond, exotic plant abundance and relative abundance hold a fairly steady pattern (Figure 4). For both the Replanted Blowdown Zone and the Shrub-dominated Blowdown Zone, mean exotic plant abundance and relative abundance were higher at 2 m than at 0 m (Figure 4). The Tephra Fall Forest had a very distinct pattern, with higher abundance and relative abundance at 0 m and 2 m, and almost no exotic plants at distances of 10 m and beyond (Figure 3, Figure 4).

TABLE 2. Exotic species in each site type. PP = Pumice Plain, FBZ = Forb-dominated Blowdown Zone, SBZ = Shrub-dominated Blowdown Zone, RBZ = Replanted Blowdown Zone, TFF = Tephra Fall Forest. Values are mean percent cover averaged across all distances within each site type. 1 = 0 to 0.09 percent cover, 2 = 0.1 to 0.39 percent cover, 3 = 0.4 to 1.85 percent cover. The letter “W” indicates species is on the Washington State Noxious Weed List (www.nwcb.wa.gov, April 2014)

Latin Binomial	PP	FBZ	SBZ	RBZ	TFF	Roadside only species: Furthest Observed Distance from Road
<i>Agrostis capillaris</i>				1		
<i>Anthoxanthum odoratum</i>		3	2	2		
<i>Cirsium arvense</i> (W)		1	1			
<i>Digitalis purpurea</i>		1				
<i>Euphrasia officinale</i>		1	1	1		2 m
<i>Holcus lanatus</i>		1				
<i>Holcus mollis</i>					1	2 m
<i>Hypericum perforatum</i> (W)		2	3	2		
<i>Hypochaeris radicata</i> (W)	2	3	3	3	2	
<i>Jacobaea vulgaris</i> (W)		1		1		
<i>Lepidium campestre</i>		2	1	1		
<i>Leucanthemum vulgare</i> (W)		2	2	3	1	
<i>Linaria vulgaris</i> (W)			1			10 m
<i>Lotus corniculatus</i>		2	1	2		
<i>Mycelis muralis</i>		1	2	2	2	
<i>Plantago lanceolata</i>		1		1		10 m
<i>Poa compressa</i>		1	1	2		10 m
<i>Rumex acetosella</i>	1	3	3	2	1	
<i>Rumex crispus</i>			1			10 m
<i>Spergularia rubra</i>			1			
<i>Taraxacum officinale ssp. officinale</i>			1		1	2 m
<i>Trifolium repens</i>					1	5 m
<i>Tragopogon dubius</i> *						2 m
<i>Cytisus scoparius</i> *						2 m
<i>Verbascum thapsus</i> *						
TOTAL SPECIES	2	15	15	13	7	

* Species were observed outside of study plots

FIGURE 3. Boxplots showing exotic richness values for the five site types. Distances are from the road for the Forb-dominated Blowdown Zone, Shrub-dominated Blowdown Zone, Replanted Blowdown Zone, and Tephra Fall Forest. Pumice Plain distances are from a trail.

TABLE 3. Exotic species mean abundance (percent cover $\pm$ 1 standard error) at each distance within each site type.

Distance from road (or trail for Pumice Plain) (m)	Tephra Fall Forest (% cover)	Forb-dominated Blowdown Zone (% cover)	Shrub-dominated Blowdown Zone (% cover)	Replanted Blowdown Zone (% cover)	Pumice Plain (% cover)
0	2.61 $\pm$ 0.57	6.50 $\pm$ 1.00	4.44 $\pm$ 1.69	4.68 $\pm$ 1.28	0.04 $\pm$ 0.03
2	1.53 $\pm$ 0.44	4.11 $\pm$ 0.85	6.20 $\pm$ 1.53	5.95 $\pm$ 1.62	0.10 $\pm$ 0.06
5	0.30 $\pm$ 0.16	4.70 $\pm$ 1.69	3.08 $\pm$ 0.68	6.10 $\pm$ 2.55	0.38 $\pm$ 0.21
10	0.13 $\pm$ 0.10	5.50 $\pm$ 1.21	3.59 $\pm$ 0.97	4.05 $\pm$ 1.52	0.23 $\pm$ 0.09
20	0.10 $\pm$ 0.07	4.30 $\pm$ 0.81	2.50 $\pm$ 0.60	3.25 $\pm$ 0.80	0.25 $\pm$ 0.09
30	0.00 $\pm$ 0.00	4.23 $\pm$ 0.74	1.55 $\pm$ 0.48	1.70 $\pm$ 0.52	0.33 $\pm$ 0.16
50	0.00 $\pm$ 0.00	3.78 $\pm$ 0.90	2.33 $\pm$ 0.53	2.73 $\pm$ 0.85	0.78 $\pm$ 0.35
70	0.05 $\pm$ 0.05	4.28 $\pm$ 1.04	1.65 $\pm$ 0.45	1.70 $\pm$ 0.38	0.31 $\pm$ 0.14

TABLE 4. Exotic species mean relative abundance (percent cover $\pm$ 1 standard error) at each distance within each site type.

Distance from road (or trail for Pumice Plain) (m)	Tephra Fall Forest (% cover)	Forb-dominated Blowdown Zone (% cover)	Shrub-dominated Blowdown Zone (% cover)	Replanted Blowdown Zone (% cover)	Pumice Plain (% cover)
0	0.07 $\pm$ 0.02	0.37 $\pm$ 0.05	0.31 $\pm$ 0.07	0.00 $\pm$ 0.00	0.26 $\pm$ 0.07
2	0.09 $\pm$ 0.05	0.33 $\pm$ 0.06	0.41 $\pm$ 0.07	0.01 $\pm$ 0.00	0.29 $\pm$ 0.05
5	0.01 $\pm$ 0.01	0.27 $\pm$ 0.06	0.34 $\pm$ 0.07	0.02 $\pm$ 0.01	0.21 $\pm$ 0.04
10	0.00 $\pm$ 0.00	0.37 $\pm$ 0.07	0.23 $\pm$ 0.05	0.03 $\pm$ 0.01	0.18 $\pm$ 0.04
20	0.00 $\pm$ 0.00	0.34 $\pm$ 0.07	0.24 $\pm$ 0.05	0.02 $\pm$ 0.01	0.13 $\pm$ 0.03
30	0.00 $\pm$ 0.00	0.22 $\pm$ 0.04	0.22 $\pm$ 0.06	0.03 $\pm$ 0.01	0.08 $\pm$ 0.03
50	0.00 $\pm$ 0.00	0.24 $\pm$ 0.05	0.24 $\pm$ 0.06	0.05 $\pm$ 0.02	0.17 $\pm$ 0.05
70	0.00 $\pm$ 0.00	0.25 $\pm$ 0.04	0.17 $\pm$ 0.05	0.03 $\pm$ 0.01	0.07 $\pm$ 0.02

FIGURE 4. Line graphs showing mean transect abundance (a) and relative abundance (b) for five site types. Distances are from the road for the Forb-dominated Blowdown Zone, Replanted Blowdown Zone, Shrub-dominated Blowdown Zone, and Tephra Fall Forest. Pumice Plain distances are from a trail.

3.2 Canopy Cover

Median canopy cover differed among the site types (Figure 5). Both the Pumice Plain and Forb-dominated Blowdown Zone is characterized by a median of zero canopy cover. The Shrub-dominated and Replanted Blowdown Zones had low median canopy cover (1 to 30%), while the Tephra Fall Forest had the high median canopy cover (71 - 100%). Before the recent commercial thinning of the Replanted Blowdown Zone, the canopy cover was much higher than current levels.

FIGURE 5. Median canopy cover for interior habitats (50 and 70 m) among site types.

3.3 Differences Among Site Types

Significant interior (50 and 70 m) differences existed among the three blowdown site types in richness ($\chi^2 = 11.6351$, $p = 0.0030$), abundance ($\chi^2 = 8.2192$, $p = 0.0164$), and relative abundance ($\chi^2 = 8.1827$, $p = 0.0167$) of exotic plant species at $\alpha < 0.05$ (Table 5) using the Kruskal-Wallis Rank Sum Test. Pairwise Wilcoxon Rank Sum Tests were used to determine significant differences between interior distances of blowdown site type pairs (Table 5). The Forb-dominated and Shrub-dominated Blowdown Zones were significantly different in richness

($W = 1036.5$, $p = 0.0176$), abundance ($W = 1058.8$, $p = 0.0123$), and relative abundance ($W = 1104.5$, $p = 0.0032$). The Forb-dominated and Replanted Blowdown Zones were significantly different in richness ($W = 1129.5$, $p = 0.0009$) and abundance ($W = 1049.5$, $p = 0.0154$). The Shrub-dominated and Replanted Blowdown Zones were not significantly different in richness, abundance, or relative abundance.

TABLE 5. Kruskal-Wallis Rank Sum and Wilcoxon Pairwise Rank Sum Test results showing differences in richness, abundance and relative abundance for interior distances (50 m and 70 m) within three blowdown zone site types. FBZ = Forb-dominated Blowdown Zone, SBZ = Shrub-dominated Blowdown Zone, RBZ = Replanted Blowdown Zone. Boldface numbers are significant at $\alpha < 0.05$.

	Richness		Abundance		Relative Abundance	
	$\chi^2 = 11.6351$ p = 0.0030		$\chi^2 = 8.2192$ p = 0.0164		$\chi^2 = 8.1827$ p = 0.0167	
	W	p value	W	p value	W	p value
FBZ vs. SBZ	1036.5	0.0176	1058.5	0.0123	1104.5	0.0032
FBZ vs. RBZ	1129.5	0.0009	1049.5	0.0154	961	0.1198
SBZ vs. RBZ	716.5	0.3994	796	0.9724	904	0.3061

3.4 Differences Across Distances Within Site Types

On the Pumice Plain, where transects were perpendicular to a trail, rather than a road, only two exotic species were observed, *H. radicata* and *R. acetosella* (Table 2). *R. acetosella* was only observed once and *H. radicata* was observed at most distances from the trail at low cover amounts. The maximum percent cover (6%) for *H. radicata*, was observed once. Linear regression across distances from the trail showed slope was not significantly different from zero for richness (Table 6), while slopes were slightly positive, yet significant at $\alpha = 0.05$, for abundance (slope = 0.0053, $p = 0.0415$, Table 7) and relative abundance (slope = 0.0004, $p =$

0.0383, Table 8). The most abundant species were *Lupinus lepidus*, and *Penstemon cardwellii*, both native forbs (Table 9, Appendix).

In the Forb-dominated Blowdown Zone, 15 exotic species were observed, with *A. odoratum*, *H. radicata*, and *R. acetosella* being the most abundant (Table 2). Linear regression across distances from the road showed that slope was not significantly different from zero for richness, abundance or relative abundance at the $\alpha = 0.05$ significance level. *Pteridium aquilinum* was the most abundant species in the Forb-dominated Blowdown, with *H. radicata*, an exotic, as the second most abundant (Table 9, Appendix A).

In the Shrub-dominated Blowdown Zone, 15 exotic plant species were observed and *H. radicata*, *R. acetosella*, and *H. perforatum* were the most abundant exotic species (Table 2). Linear regression across distances from the road showed that slope was negative and significantly different from zero for exotic plant richness (slope = -0.0110, $p = 0.0021$, Table 6), abundance (slope = -0.0449, $p = 0.0028$, Table 7), and relative abundance (-0.0024, $p < 0.0001$, Table 8). Aside from *Salix* spp. and *A. viridis* ssp. *sinuata* species, *Vaccinium* spp. and *Rubus lasiococcus* were the most abundant plants in the Shrub-dominated Blowdown Zone (Table 9, Appendix A).

In the Replanted Blowdown Zone, 13 exotic plant species were identified (Table 2). The two most abundant exotic species found were *H. radicata* and *L. vulgare* (Table 2). Linear regression across distances from the road showed that slope was negative and significantly different from zero for richness (slope = -0.0167, $p < 0.0001$, Table 6), abundance (slope = -0.0562, $p = 0.0052$, Table 7) and relative abundance (slope = -0.0023, $p = 0.119$, Table 8).

Vaccinium spp. and *H. radicata*, were the most abundant plants in the Replanted Blowdown Zone (Table 9, Appendix).

In the Forest, seven exotic plant species were observed, three of which were restricted to 10 m of the roadside (Table 2). The two most abundant exotic plant species were *H. radicata* and *Mycelis muralis* (Table 2). Quadrats at distances 5 m through 70 m rarely contained an exotic plant (Figure 3, Figure 4), with no observations of exotic plants at 30 m or 50m, and only one observation of *H. radicata* of 1% at 70 m. Linear regression across distances from the road showed that slope was significantly different from zero for richness (slope = -0.0118, $p < 0.0001$, Table 6), abundance (slope = -0.0222, $p < 0.0001$, Table 7), and relative abundance (slope = -0.0008, $p = 0.0044$, Table 8). Overall, the understory was sparsely vegetated, and the most abundant plants were *Vaccinium* spp. and *Anaphalis margaritacea*, though *A. margaritacea* was mostly along the roadside (Table 9, Appendix A).

TABLE 6. Exotic species linear regression values for richness within each site type. Boldface numbers are significant at $\alpha < 0.05$.

Site Type	Coefficient	Estimate	Std. error	T-value	p-value
Pumice Plain	Intercept	0.2110	0.0489	4.3140	< 0.0001
	Slope	0.0022	0.0015	1.4950	0.1370
Forb-dominated Blowdown Zone	Intercept	1.9184	0.1271	15.0960	< 0.0001
	Slope	-0.0043	0.0038	-1.1150	0.2670
Shrub-dominated Blowdown Zone	Intercept	1.5955	0.1171	13.6300	< 0.0001
	Slope	-0.0110	0.0035	-3.1330	0.0021
Replanted Blowdown Zone	Intercept	1.8779	0.1363	13.7790	< 0.0001
	Slope	-0.0167	0.0041	-4.0710	< 0.0001
Tephra Fall Forest	Intercept	0.6073	0.0691	8.7840	< 0.0001
	Slope	-0.0118	0.0021	-5.6740	< 0.0001

TABLE 7. Exotic species linear regression values for abundance within each site type. Boldface numbers are significant at $\alpha < 0.05$.

Site Type	Coefficient	Estimate	Std. error	T-value	P-value
Pumice Plain	Intercept	0.1763	0.0856	2.0600	0.0411
	Slope	0.0053	0.0026	2.0550	0.0415
Forb-dominated Blowdown Zone	Intercept	5.1268	0.5270	9.7280	< 0.0001
	Slope	-0.0194	0.1586	-1.2230	0.2230
Shrub-dominated Blowdown Zone	Intercept	4.2147	0.4900	8.6010	< 0.0001
	Slope	-0.0449	0.0148	-3.0430	0.0028
Replanted Blowdown Zone	Intercept	5.0828	0.6726	7.5570	< 0.0001
	Slope	-0.0562	0.0203	-2.7770	0.0062
Tephra Fall Forest	Intercept	1.1074	0.1528	7.2470	< 0.0001
	Slope	-0.0222	0.0046	-4.8210	< 0.0001

TABLE 8. Exotic species linear regression values for relative abundance within each site type. Boldface numbers are significant at $\alpha < 0.05$.

Site Type	Coefficient	Estimate	Std. error	T-value	P-value
Pumice Plain	Intercept	0.0141	0.0061	2.3130	0.0220
	Slope	0.0004	0.0002	2.0890	0.0383
Forb-dominated Blowdown Zone	Intercept	0.3383	0.0282	11.9900	< 0.0001
	Slope	-0.0017	0.0008	-1.9590	0.0518
Shrub-dominated Blowdown Zone	Intercept	0.2304	0.0220	10.4690	< 0.0001
	Slope	-0.0024	0.0007	-3.5820	0.0005
Replanted Blowdown Zone	Intercept	0.3221	0.0298	10.8260	< 0.0001
	Slope	-0.0023	0.0009	-2.5450	0.0119
Tephra Fall Forest	Intercept	0.0409	0.0095	4.3220	< 0.0001
	Slope	-0.0008	0.0003	-2.8880	0.0044

4. DISCUSSION

4.1 Habitat Invasibility and Roads

Different disturbance types resulting from the 1980 eruption of Mount St. Helens have created a highly variable landscape, and NFR 99 has provided a pathway for exotic plant species to increase in both richness and abundance. Results showed that proximity to the road increased the richness, abundance, and relative abundance of exotic plants in the Tephra Fall Forest, Shrub-dominated Blowdown Zone and Replanted Blowdown Zone, which supports hypothesis (1) that exotic plants will increase near the road (Table 6, Table 7, Table 8). However, in the Forb-dominated Blowdown Zone, exotic species did not decrease with distance from the road. These results agree with other studies that have shown roads promote the dispersal and establishment of exotic species, and that these species spread further when canopy cover decreases (Parendes and Jones 2000, Hansen and Clevenger 2005, Birdsall et al. 2012, Mortensen et al. 2009).

Roads provide a point of introduction, as well as a seed dispersal corridor by which cars, wind, water, animals, and birds can spread seeds (Flory and Clay 2009, Parendes and Jones 2000, Trombulak and Frissell 2000). One of the largest factors in whether a habitat becomes invaded is simply whether it is exposed to enough propagules (Lockwood et al. 2007) and roads are providing a pathway for exotic propagules to be introduced and to disperse. Six out of seven of the most frequent species (*H. radicata*, *R. Acetosella*, *A. odoratum*, *L. vulgare*, *H. perforatum*, and *M. muralis*) have lightweight seeds and/or appendages that suggest wind as a primary dispersal mechanism (Parendes and Jones 2000). As vegetation can reduce dispersal distances (McEvoy and Cox 1987) roads may increase distance seeds can travel and cars may increase

roadside wind (Hansen and Clevenger 2005). Seeds, especially grasses, can also attach to vehicles to be carried even further distances (Lonsdale and Lane 1993).

While vehicles do carry seeds of exotic plants, sometimes over 250 km, the seed density is typically low, and therefore resources are better spent on early detection and eradication efforts than on removing seeds from cars (Lonsdale and Lane 1993, Taylor et al. 2012). As exotic plant abundance is higher along roads than interior habitats (except for the Forb-dominated Blowdown zone where abundance remained consistent throughout the transects) those roadside areas also serve as a seed source for spread along the roadsides and into interior lands (Forman et al. 2003). Detection and eradication efforts should be focused on roadside areas, especially those with more traffic, such as view points. Windy Ridge viewpoint, with its proximity to the Pumice Plain should be given extra consideration.

Roadside habitat can also alter the nutrient conditions, and this could be another reason for increased richness and abundance of exotic plants near the road. Vehicle runoff can change the chemistry and pH of roadside habitats. In particular, nitrogen and phosphorus can increase, and these changes can stress or kill native plants, leaving unused resources that provide opportunities for introduced plants to establish (Trombulak and Frissell 2000, Mortensen et al. 2009, Myers and Bazely 2003).

Despite the increased richness and abundance of exotic plants near the road, it should be noted that the richness and abundance in all areas at all distances from the road was relatively low (Figure 4). One possible explanation for this relates to the elevation and climate at Mount St Helens. In my study, the elevation ranged from 1100 to 1320 m, and thus, during the wetter months of October through May, much of the precipitation falls as snow. The summer growing

period is typically dry and volcanic tephra substrate is porous and does not retain water well (Reynolds and Bliss 1986, del Moral and Wood 1993). Thus many plants are not able to establish, and this is especially true for the small seeded wind-dispersed plants typical of successful exotic plants because they dry out quickly (Fuller and del Moral 2003). Larger seeds are better able to withstand the stressful conditions typical at Mount St. Helens (Fuller and del Moral 2003). This relates to Wood and del Moral's (1987) finding that many species with high dispersal traits are typically not able to establish on the stressful sites of open volcanic areas, and also to Grime's (1979) conclusions that ruderal, successful dispersers do not typically establish at high elevations. Roads may be providing the additional moisture and nutrients that exotic plants need to establish along the roadsides, but the overall abundance remains low.

One noticeable spatial pattern was that exotic plant richness, abundance and relative abundance was higher at two meters than zero meters from the road in both the Shrub-dominated Blowdown Zone and Replanted Blowdown Zone (Figure 4). The reason for this may be due to canopy cover. Shoulders along NFR 99 in the Blowdown Zone are often lined with *Alnus viridis* ssp. *sinuata* and *Salix* spp. Traveling away from the road, canopy openings often occurred after the initial dense roadside lining of shrubs (*personal observation*, Figure 6). *Alnus* and *Salix* spp. are common riparian trees in Washington and their increased presence along roadsides could be attributed to the increased runoff from the impervious road surfaces (Forman et al. 2003, Balian and Naiman 2005). Perhaps this lining of roadside shrubs is slowing the spread of exotic plants. A second reason for the increase in exotic plant abundance at 2 m is that when the immediate roadside was not vegetated with shrubs, the ground substrate right next to the pavement may be too disturbed for many plants to grow (Forman et al. 2003). Ullmann

(1998) found similar results, though the increase in exotic plants a few meters from the road was more likely due to the presence of a roadside ditch that provided increased moisture. As the interior areas of the Shrub-dominated and Replanted Blowdown Zones had significantly less exotic plant richness and abundance than the Forb-dominated Blowdown Zone (Table 5, Figure 4), this suggests that roadside shrubs in any area may restrict the spread of exotic plants. This idea is also supported by Parendes and Jones' (2000) findings that dense canopy cover can serve as a barrier to exotic plant establishment and dispersal.

FIGURE 6. Example of the lining of shrubs along NFR-99. Image is from Google Earth.

4.2 Habitat Invasibility and Canopy Cover

While some exotic species are able to establish as a result of their own life history traits (rapid growth, small seeds, persistent seed bank) (Rejmanek and Richardson 1996), many plant invasions have also been linked to habitat characteristics such as canopy cover. For example, both Parks et al. (2005) and Hansen and Clevenger (2005) found that forests had significantly fewer invasive plants than grasslands. In my study, areas with lower canopy cover had higher exotic plant richness and abundance, which supports hypothesis (3b). The interior Forb-

dominated Blowdown Zone (median canopy = 0) contained significantly higher richness and abundance than the interiors of the Replanted and Shrub-dominated Blowdown Zones (median canopy cover = low) (Figure 4, Table 5). The interior Tephra Fall Forest, with the highest canopy cover (median canopy cover = high) had no exotic plants, with the exception of a 1% observation (0.01 m²) of *H. radicata*, which supports hypothesis (3a) that exotic plants will spread from the road least in the Tephra Fall Forest (Figure 5, Figure 4). Blowdown areas were less disturbed by the eruption than the Tephra Fall Forest and contained higher exotic plant richness, abundance, and relative abundance, which supports Hypothesis (2), although it would be difficult to tease apart whether this is due to the disturbance intensity, canopy cover, or both as the two are closely related (ie. The Tephra Fall Forest has higher canopy cover than the Blowdown Zone because it only received tephra fall, rather than the force of the lateral blast).

The sharp decline in exotic species richness and abundance in the Tephra Fall Forest is a clear example of edge effect. A study on *Pseudotsuga menziesii* forests of the U.S. Pacific Northwest found interior forest light levels were < 15% of edge levels (Chen et al. 1995). In addition to light, Chen et al. (1995) also found that edges differ in humidity, wind, soil moisture, and air temperature, and these differences are greatly affected by aspect, season, and time of day. Another study of forest edge effect in a laurel and pine forest found that interior forest conditions reappear at 6 to 10 m from the road (Delgado et al. 2007). These studies and others (Chen et al. 1993, Alignier and Deconchat 2013, Harper et al. 2005) show that roadside habitats are considerably different from interior forests, which suggests a likely reason for why quadrats at zero and two meters from the road had up to four exotic species, while quadrats at 30, 50 and 70

m from the road had no exotic species (except for one observation of *H. radicata* at 70 m) (Figure 3).

While exotic species abundance and richness differences between site types may be partly due to other factors besides canopy cover, the Forb-dominated Blowdown Zone and Shrub-dominated Blowdown zone site types were largely delineated based on vegetation cover, and thus their differences are tightly linked to canopy cover. However, canopy differences between Shrub-dominated and Forb-dominated Blowdown Zone transects were not always clear cut. Transect in the Shrub-dominated Blowdown Zone were mostly covered with shrubs, but 26% of quadrats still had no canopy. Likewise, in the Forb-dominated Blowdown Zone, 3.8% of quadrats had medium canopy and 5% had high canopy. Despite this, the dense areas of shrubs in the Shrub-dominated Blowdown Zone may be preventing further spread of exotic plants within the site type and to other areas.

Despite the relationship between increased exotic plant abundance and areas with greater light, some exotic species do well in shaded areas. *M. muralis* was often found under high or medium canopy cover in the Shrub-dominated Blowdown Zone (Figure 8). This supports the findings of Parendes and Jones (2000). They found that five out of six of the most frequent exotic species (*H. perforatum*, *L. vulgare*, *C. vulgare*, *H. radicata*, and *T. repens*) were present significantly more in areas with greater disturbance and greater light, while *M. muralis*, which occurred frequently, was found at both high and low light and disturbance levels.

4.3 The Pumice Plain

While altered nutrient conditions along roads may increase invasibility in the Blowdown Zones by stressing native plants, the nutrient conditions of the Pumice Plain may be preventing exotic plant establishment. Only two wind-blown exotic plant species (*H. radicata* and one observation of *R. acetosella*) were found in this study (but see Titus et al. 1998) and the vegetation was dominated by native plants which, aside from the Tephra Fall Forest, supports hypothesis (4) that the Pumice Plain would have the lowest exotic plant richness and abundance. The pyroclastic volcanic material lacks nitrogen (Halvorson et al. 1991, del Moral and Clappitt 1985), which prevents the establishment of plants that cannot supply their own nitrogen. *Lupinus lepidus*, a native plant that fixes nitrogen through *rhizobium*, was the first plant to establish on the Pumice Plain (Halvorson et al. 1995, del Moral and Clappitt 1985). The growth and death of both *L. lepidus* and *L. latifolius* provide important sources of carbon and nitrogen, which in turn support soil formation and habitat for other plants, as well as microbes (Halvorson 1995). *H. Radicata* has been found to have rapid nitrogen uptake abilities, which could allow it to take advantages of small pulses of nitrogen on the Pumice Plain (Schoenfelder et al. 2010). It is quite possible that exotic plant seeds are being blown in by the wind, carried by animals, or hiked in by people. However, as other studies (Fuller and del Moral 2003, Braatne and Bliss 1999) have found, the wind dispersed seeds characteristic of the exotic plants found at Mount St Helens typically dehydrate before they can establish, whereas *Lupinus* spp. have heavier seeds with higher food reserves and are able to establish deeper roots more quickly in order to survive on the stressful volcanic substrate.

Other possible reasons for the low abundance of exotic plants on the Pumice Plain include the lack of a road, less visitors, or because of the severe disturbance. The 1980 eruption removed or buried all vegetation on the Pumice Plain and it is isolated from other areas of vegetation (del Moral & Bliss 1993, Tsuyuzaki 1997). Despite the potential spread of seeds via wind, animals, water and people, 33 years after the eruption, the richness and abundance of exotic plants is very low. These results support Tyser's (1992) study that showed hiking trails contribute less to exotic plant spread than roads.

4.4 Actively Managed Forest (Replanted Blowdown Zone)

Patterns in Figure 4 shows the Replanted Blowdown Zone was similar to the Shrub-dominated Blowdown Zone in exotic plant abundance, but similar to the Forb-dominated Blowdown Zone in relative abundance. In the interior (50 and 70 m) areas, the Replanted Blowdown Zone had significantly less exotic plant abundance than the Forb-dominated Blowdown Zone, however, the two zones did not differ in exotic plant relative abundance (Table 5, Figure 4). This means that the Replanted Blowdown Zone had less total plants than the Forb-dominated Blowdown Zone, but the same ratio of exotic plants to total plants. Fewer total plants could be a result of the thick forest canopy prior to the recent thinning operation, causing light limitations, in combination with the poor nutrient status of volcanic substrate (Halvorson et al. 1991). Similar ratios of exotic to total plants could mean that the replanted forest does not prevent the spread of exotic species any better than the forb-dominated area. When looking at linear regression results across distances from the road, if relative abundance did not significantly decrease, that would indicate exotic plant that abundance simply decreased as a

result of a total decrease in plants. However, in the Replanted Blowdown Zone, Shrub-dominated Blowdown Zone, and Tephra Fall Forest, both the abundance and relative abundance decreased as distance from the road increased meaning that not only did exotic plant abundance decrease, but they decreased relative to the total plant abundance (Table 7, Table 8).

Salvage logging changes the nutrient cycles of a landscape (Harmon et al. 1986). Since 1980, several studies have focused on learning more about the ecological importance of dead trees (Harmon et al. 1986, Harmon and Hua 1991). Along with being less effective against the spread of exotic plants, the removal of dead trees has negative impacts on forest ecosystems. Dead trees can provide habitat for microbes, invertebrates, vertebrates, as well as native plants, and they can also hold water, provide shade, and thus reduce temperatures (Harmon et al. 1986, Titus and Householder 2007). Furthermore, while decomposition may be slow, they are also important for nutrient and energy cycling (Harmon et al. 1986). The importance of dead trees suggests that change in nutrient cycling by salvage logging would also stress native plants and create opportunities for exotic plant establishment seen in the Replanted Blowdown Zone.

The lack of downed wood in the Replanted Blowdown Zone will most likely cause the understory to develop slowly because of the lack of organic matter, causing nutrients to build up more slowly, making it difficult for understory plants, including exotic plants, to establish (Harmon and Hua 1991, Maranon-Jimenez and Castro 2013). As a result of the commercial thinning operation, the remaining trees should grow larger, and without another large disturbance, the canopy will eventually close in, thus creating a light barrier to the establishment of the shade intolerant, ruderal exotic species.

4.5 Management Implications and Conclusions

Of the fourteen species occurring in more than three quadrats, ten are perennials, two are annuals (*Euphrasia officinale*, *Mycelis muralis*), and two are either annuals or biennials (*Jacobaea vulgaris* and *Lepidium campestre*). Several species appear to be more frequent near roadsides: *Leucanthemum vulgare*, *Poa compressa*, *Lotus corniculatus*, *E. officinale*, *Trifolium repens*, *Taraxacum officinale*, and *Linaria vulgaris* (Figure 8). With the exception of *M. muralis*, the shade tolerance of most of these species is intermediate to intolerant according to the NRCS (www.plants.usda.gov, May 2014). According to the Washington State Noxious Weed List (www.nwcb.wa.gov, April 2014), five of the more frequent species from my study are listed as noxious weeds: *L. vulgaris*, *J. vulgaris*, *Hypericum perforatum*, *H. radicata*, and *L. vulgare*. Considering the widespread abundance of *H. radicata* at Mount St. Helens (Schoenfelder et al. 2010), it seems resources would not be well spent on this species. I suggest initial control and/or eradication of species that are on the Washington State Noxious Weed List and appear more frequently near the road: *L. vulgaris*, *L. vulgare*, *J. vulgaris*, and *H. perforatum*.

The results of this study showed that quadrats nearer to the road in the Tephra Fall Forest, Shrub-dominated Blowdown and Replanted Blowdown Zones contained higher exotic plant species richness, abundance and relative abundance than quadrats far from the road (Table 6, Table 7, Table 8). The tephra-impacted forest canopy seems to be providing an efficient barrier to exotic plant spread into interior areas, and thus, roadsides in the Shrub-dominated, Forb-dominated and Replanted areas should become more of a focus for detection and control than the Tephra Fall Forest. However, as succession proceeds over time, the Forb-dominated Blowdown Zone will become more vegetated with shrubs, and the canopy cover of both the Forb-dominated

and Shrub-dominated Zones will slowly close in as trees establish and grow in the area. The decrease in exotic plant richness and abundance in blast areas with less canopy cover suggests that perhaps natural succession may be the most effective method of preventing the establishment of exotic plants at Mount St Helens.

5. ACKNOWLEDGEMENTS

Many thanks to the volunteers that helped with data collection: Sara Copp, Charlie Crisafulli, Abi Groskopf, Kate Rhodes, and most especially, Jessica Camp. Thank you to the Mount St. Helens Institute for providing me with living arrangements while in the field. I could not have identified hundreds of pressed plant specimens without the help of Bill Becker, John Bishop, Sara Copp, Charlie Crisafulli, Tim Elder, Ed Guarrant, Richard Halse (and the Oregon State University Herbarium), Dominic Maize, Ashley Smithers, Duncan Thomas and Anthony Wenke. I would also like to thank Sara Copp, Mat Dorfman, Tim Elder, Yangdong Pan and Jill VanWinkle for their statistical expertise. Finally, I would like to thank my advisor, Jeff Gerwing, and my community partner, Charlie Crisafulli, for their help in many steps along the way.

6. REFERENCES

- Abella S.R., E.C. Engel, J.D. Springer, and W.W. Covington. 2012. Relationships of exotic plant communities with native vegetation, environmental factors, disturbance, and landscape ecosystems of *Pinus ponderosa* forests, USA. *Forest Ecology and Management* 271:65-74.
- Alignier, A. and M. Deconchat, M. 2013. Patterns of forest vegetation responses to edge effect as revealed by a continuous approach. *Annals of forest science* 70(6):601-609.
- Amor R.L. and P.L. Stevens. 1975. Spread of weeds from a roadside into sclerophyll forests in Dartmouth, Australia. *Weed Research* 16:111-118.
- Antos, J.A. and D.B. Zobel. 2005. Plant responses in forests of the tephra-fall zone. Pages 47 - 58 in V.H. Dale, F.J. Swanson, and C.M. Crisafulli, editors, *Ecological Responses to the 1980 eruption of Mount St. Helens*. Springer, New York.
- Balian, E.V. and R.J. Naiman. 2005. Abundance and production of riparian trees in the lowland floodplain of the Queets River, Washington. *Ecosystems* 8:841-861.
- Birdsall, J.L., W. McCaughey, and J.B. Runyon. 2012. Roads impact the distribution of noxious weeds more than restoration treatments in a lodgepole pine forest in Montana, U.S.A. *Restoration Ecology* 20(4):517-523.
- Braatne, J.H. And L.C. Bliss. 1999. Comparative physiological of lupines colonizing early successional habitats on Mount St. Helens. *Ecology* 80(3): 891-907.
- Chen, J., J.F. Franklin, and T.A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219-237.
- Chen, J., J.F. Franklin, and T.A. Spies, T. A. 1995. Growing season microclimatic gradients from clearcut edges into old-growth Douglas fir forests. *Ecological Applications* 5(1):74-86.
- Clinton, W (1999). U.S. Presidential Executive order 13112 re: Invasive species February 3, 1999. *Federal Daily Register* 64 (25):6183-6186.
- Dale, V. H., A.E. Lugo, J.A. MacMahon, and S.T.A. Pickett. 1998. Ecosystem Management in the context of large, infrequent disturbances. *Ecosystems* 1:546-557.
- Dale, V.H. and W.M. Adams. 2003. Plant reestablishment 15 years after the debris avalanche at Mount St. Helens, Washington. *Science of the Total Environment* 313(1-3):101-113.
- Dale, V.H., C.M. Crisafulli, and F.J. Swanson. 2005. 25 years of ecological change at Mount St. Helens. *Science* 308:961-962.

Delgado, J.D., N.L. Arroyo, J.R. Arevalo, and J.M. Fernandez-Palacios. 2007. Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape and Urban Planning* 81:328-340.

del Moral, R. and C.A. Clampitt. 1985. Growth of native plant species on recent volcanic substrates from Mount St. Helens. *American Midland Naturalist*, 114(2):374-383.

del Moral, R. and L.C. Bliss. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. *Advances in Ecological Restoration* 24: 1-66.

del Moral, R., L.A. Thomason, A.C. Wenke, N.L., and M.D. Abata. 2012. Primary Succession trajectories on pumice at Mount St. Helens. *Washington Journal of Vegetation Science* 23:73–85.

del Moral, R. and D.M. Wood. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *American Journal of Botany* 80(9):981-991.

Flory, S. L. and K. Clay. 2009. Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation* 142:2531-2537.

Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F. J. Swanson, T. Turrentine, and T.C. Winter. 2003. *Roadsides and vegetation in Road Ecology: Science and Solutions*. Island Press, 2003 Washington, D. C.

Foster, D.R., D.H. Knight, and J.F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1:497-510.

Franklin J.F., P.M. Frenzen, and F.J. Swanson. 1988. Re-creation of ecosystems at Mount St. Helens: contrasts in artificial and natural approaches Pages 1 - 37 *in* J. Cairns, editor, *Rehabilitating Damaged Ecosystems*. Lewis Publishers, Boca Raton.

Franklin F.J., D.B. Lindenmayer, J.A. MacMahon, A. McKee, J. Magnuson, D.A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. *Conservation Biology in Practice* 1:8-16.

Fuller, R.N. and R. Del Moral. 2003. The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. *Journal of Vegetation Science* 14:637-644.

Gray, A. 2007. Distribution and abundance of invasive plants in Pacific Northwest forests, page 3 *in* *Meeting the Challenge: Invasive Plants in Pacific Northwest Ecosystems*. General Technical

Report PNW-GTR-694. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, New York, USA.

Halpern, C.B., P.M. Frenzen, J.E. Means, and J.F. Franklin. 1990. Plant Succession in Areas of Scorched and Blown-Down Forest after the 1980 Eruption of Mount St. Helens, Washington. *Journal of Vegetation Science* 1(2):181-194.

Halvorson, J.J., J.L. Smith, and E.H. Franz. 1991. Lupine eInfluence on soil carbon, nitrogen and microbial activity in developing ecosystems at Mount St. Helens. *Oecologia* 87(2):162-170.

Halvorson, J.J., J.L. Smith, and A.C. Kennedy. 2005. Lupine Effects on soil development and function during early primary succession at Mount St. Helens Pages 243 - 254 in V.H. Dale, F.J. Swanson, and C.M. Crisafulli, editors, *Ecological Responses to the 1980 eruption of Mount St. Helens*. Springer, New York.

Hansen M.J. and A.P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation* 125:249–259.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Restoration* 15:133-302.

Harmon M.E. and C. Hua. 1991. Course woody debris dynamics in two old-growth ecosystems. *Bioscience* 41(9):604-610.

Harper K.A., S.E. Macdonald, P.J. Burton, J.Q. Chen, K.D. Brososke, S.C. Saunders, E.S. Euskirchen, D. Roberts, M.S. Jaiteh, and P.A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19:768–782.

Hitchcock, C.L. and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle.

Integrated Taxonomic Information System On-line Database (ITIS). Retrieved April, 2014. <http://www.itis.gov>.

Maranon-Jiménez, S. and J. Castro. 2013. Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. *Biogeochemistry* 112:519-535.

- Kozloff, E.N. 2005. Plants of Western Oregon, Washington and British Columbia. Timber Press, Portland.
- Lockwood, J.L., M. F. Hoopes, and M.P. Marchetti. 2007. *Invasion Ecology*. Blackwell Publishing, Malden.
- Lonsdale, W.M. 1999. Global patterns of plant Invasions and the concept of Invasibility. *Ecology* 80(5):1552-1536.
- Lonsdale W.M. and A.M. Lane. 1993. Tourist vehicles as vectors of weed seeds in Kakadu National Park, Northern Australia. *Biological Conservation* 69:277-283.
- Lozon, J.D. And H.J. MacIsaac. 1997. Biological invasions: are they dependent on disturbance? *Environmental Review* 5:131-141.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* 10:689–710.
- McEvoy, P.B. and C.S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. *Ecology* 68(6):2006-2015.
- Michalcov, D., S. Lvoncik, M. Chytry, and O. Hajek. 2011. Bias in vegetation databases? A comparison of stratified-random and preferential sampling. *Journal of Vegetation Science* 22:281-291.
- Moody, M.E. and R.N. Mack. 1988. Controlling the spread of plant invasions: The importance of nascent foci. *Journal of Applied Ecology* 25(3): 1009-1021.
- Mortensen, D.A., E.S.J. Rauschert, A.N. Nord, and B.P. Jones. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management* 2:191-199.
- Myers, J.H. and D.R. Bazely. 2003. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge, United Kingdom.
- Natural Resources Conservation Service (NRCS). Plants Database. United States Department of Agriculture. <http://plants.usda.gov/java/>.
- Nelson, M.F., N.O. Anderson, M.D. Casler, and A.R. Jakubowski. 2014. Population genetic structure of N. American and European *Phalaris arundinacea* L. as inferred from inter-simple sequence repeat markers. *Biological Invasions* 16(2):353-363.

Newsome, A.E. and I.R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1 - 20 in R.H. Groves and J.J. Burton, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, United Kingdom.

Noxious Weed Control Board, Washington State. Accessed April 2014. <http://www.nwcb.wa.gov/>

Parendes, L.A. 1997. Spatial patterns of invasion by exotic plants in a forested landscape. PhD Dissertation, Oregon State University, Corvallis

Parendes, L.A. and J.A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology 14(1):64-75.

Parks, C. G., S.R. Radosevich, B.A. Endress, B.J. Naylor, D. Anzinger, L.J. Rew, B.D. Maxwell, and K.A. Dwire. 2005. Natural and land-use history of the northwest mountain regions (USA) in relation to patterns of plant invasions. Perspectives in Plant Ecology Systems 7:137-158.

Pimentel D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52(3): 273-288.

Rejmanek, M. and D.M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655-1661.

Reynolds, G. D. And L.C. Bliss. 1986. Microenvironmental investigations of tephra covered surfaces at Mount St Helens. Pages 147-152 in S.A.C. Keller, editor. Mount St. Helens: five years later. Eastern Washington University, Cheney, Washington, USA.

Schoenfelder, A.C., J.G. Bishop, H.M. Martinson, and W.F. Fagan. 2010. Resource use efficiency and community effects of invasive *Hypochaeris radicata* (Asteraceae) during primary succession. American Journal of Botany 97(11):1772-1779.

Stohlgren, T.J., P. Pyšek, J. Kartesz, M. Nishino, A. Pauchard, M. Winter, J. Pino, M. Richardson, J.R.U. Wilson, B.R. Murray, M.L. Phillips, L. Ming-yang, L. Celesti-Grapow, and X. Font. 2011. Widespread plant species: natives versus aliens in our changing world. Biological Invasions 13:1931-1944.

Swanson, F. J. and J.J. Major. 2005. Physical Events, Environments, and Geological—Ecological Interactions at Mount St. Helens: March 1980–2004 in V.H. Dale, F.J. Swanson, and C.M. Crisafulli, editors, Ecological Responses to the 1980 eruption of Mount St. Helens. Springer, New York.

Taylor, K., T. Brummer, M.L. Taper, A. Wing, and L.J. Rew. 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Biodiversity Research* 18:942-951.

Titus, J. H., S. Moore, M. Arnot, and P. Titus. 1998. Inventory of the vascular flora of the blast zone, Mount St. Helens, Washington. *Madroño* 45(2):146-161.

Titus, J. H. and E. Householder. 2007. Salvage logging and replanting reduce understory cover and richness compared to unsalvaged-unplanted sites at Mount St. Helens, Washington. *Western North American Naturalist* 67(2):219-231.

Trombulak S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14(1):18-30.

Tsuyuzaki, S., J.H. Titus, and R. Del Moral. 1997. Seedling establishment patterns on the Pumice Plain, Mount St. Helens, Washington. *Journal of Vegetation Science* 8:727-734.

Turner, M. G., V.H. Dale, and E.H. Everham III. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. *Bioscience* 47(11):758-768.

Tyser, R. W. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology* 6(2):253-262.

United States Department of Agriculture. Mount St. Helens National Volcanic Monument. Accessed May 14, 2013. <http://www.fs.usda.gov/mountsthelens>

USGS. Mount St. Helens National Volcanic Monument. Accessed May 1, 2014. <http://pubs.usgs.gov/gip/msh/monument.html>

Usher, M.B. 1988. Biological Invasions of Nature Reserves: A search for generalisations. *Biological Conservation* 44:119-135.

Ullmann, I. 1998. Lateral differentiation and the role of exotic species in roadside vegetation in Southern New Zealand. *Flora*. 193:149-164.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21(1):1-16.

Wilcox, D.A. 1989. migration and control of purple loosestrife (*Lythrum salicaria*) along highway corridors. *Environmental Management* 13:365-370.

Wood, D.M and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St Helens. Ecology 68(4):780-790.

7. APPENDIX

FIGURE 7. Conceptual diagram of Mount St. Helens road study.

FIGURE 8. Frequency graphs for exotic species occurring in more than three quadrats.

TABLE 9. List of all species found. FO = Tephra Impacted Forest, FBZ = Forb-dominated Blowdown Zone, RB = Replated Blowdown Zone, SB = Shrub-dominated Blowdown Zone, PP = Pumice Plain.

<i>Species Name</i>	TFF	FBZ	RBZ	SBZ	PP	Total
<i>Abies amabilis</i>	0.984			0.313		1.297
<i>Abies procera</i>			0.058	0.016	0.019	0.092
<i>Acer circinatum</i>	0.013					0.013
<i>Acer glabrum</i>		0.003		0.003		0.006
<i>Achillea millefolium</i>	0.006	0.191	0.141	0.406	0.108	0.852
<i>Achlys triphylla</i>	0.063					0.063
<i>Acmispon parviflorus</i>		0.363	0.030			0.392
<i>Agoseris aurantiaca/grandiflora</i>		0.006			0.003	0.009
<i>Agoseris aurantiaca</i>	0.050		0.006	0.019		0.075
<i>Agoseris grandiflora</i>		0.013		0.031	0.003	0.047
<i>Agrostis</i>			0.013			0.013
<i>Agrostis capillaris (E)</i>			0.003			0.003
<i>Agrostis exarata</i>		0.003		0.053		0.056
<i>Agrostis pallens</i>	0.716	0.922	1.148	0.680	1.597	5.063
<i>Agrostis scabra</i>	0.013	0.034	0.020	0.033	0.144	0.244
<i>Alnus viridis ssp. sinuata</i>		0.002	0.013		0.002	0.016
<i>Amelanchier alnifolia</i>						
<i>Anaphalis margaritacea</i>	3.623	1.647	1.322	1.981	0.153	8.727
<i>Anemone deltoidea</i>				0.006		0.006
<i>Anthoxanthum odoratum (E)</i>		0.583	0.336	0.303		1.222
<i>Arctostaphylos uva-ursi</i>					0.441	0.441
<i>Arnica cordifolia</i>	0.025					0.025
<i>Aruncus dioicus</i>	0.288				0.002	0.289
<i>Asteraceae</i>				0.013		0.013
<i>Athyrium filix-femina</i>	0.375	0.141	0.050	0.119		0.684
<i>Bromus</i>	0.025					0.025
<i>Bromus carinatus</i>		0.050	0.003	0.019		0.072
<i>Bromus vulgaris</i>		0.006				0.006
<i>Calamagrostis canadensis</i>		0.019	0.450	0.038		0.506
<i>Campanula scouleri</i>	0.091	0.152		0.044		0.286
<i>Carex spectabilis/mertensii</i>					0.009	0.009
	0.031	0.003	0.028		0.047	0.109
<i>Carex lenticularis</i>				0.469		0.469
<i>Carex mertensii</i>	0.025	0.063	0.016	0.358	0.059	0.520
<i>Carex pachystachya</i>	0.031	0.314	0.166	0.475	0.094	1.080
<i>Carex preslii</i>					0.013	0.013
<i>Carex spectabilis</i>					0.045	0.045
<i>Castilleja miniata</i>	0.019	0.272	0.234	0.359	0.508	1.392
<i>Chamerion angustifolium</i>	0.177	0.138	0.184	0.317	0.041	0.856
<i>Chimaphila menziesii/umbellata</i>	0.003					0.003
<i>Chimaphila menziesii</i>	0.006		0.003			0.009
<i>Chimaphila umbellata</i>	0.097		0.044	0.013		0.153
<i>Cinna latifolia</i>				0.019		0.019
<i>Circaea alpina</i>	0.006					0.006
<i>Cirsium arvense (E)</i>		0.031		0.025		0.056
<i>Cirsium edule</i>			0.513			0.513
<i>Cistanthe umbellata</i>					0.014	0.014
<i>Claytonia sibirica</i>	0.025					0.025
<i>Clintonia uniflora</i>	0.088					0.088
<i>Collomia heterophylla</i>		0.019				0.019
		0.006	0.006			0.013
<i>Corallorhiza maculata</i>	0.002					0.002
<i>Deschampsia</i>				0.013		0.013
<i>Dicentra formosa</i>	0.013					0.013

TABLE 9. List of all species found. FO = Tephra Impacted Forest, FBZ = Forb-dominated Blowdown Zone, RB = Replated Blowdown Zone, SB = Shrub-dominated Blowdown Zone, PP = Pumice Plain.

Species Name	TFF	FBZ	RBZ	SBZ	PP	Total
<i>Digitalis purpurea</i> (E)		0.013				0.013
<i>Elymus glaucus</i>	0.044	0.550	0.122	0.906		1.622
<i>Epilobium</i>	0.013			0.003		0.016
<i>Epilobium anagallidifolium</i>	0.214	0.003	0.130	0.311	0.009	0.667
<i>Epilobium brachycarpum</i>		0.209	0.030	0.006	0.003	0.248
<i>Epilobium ciliatum</i>			0.006			0.006
<i>Epilobium glaberrimum</i>					0.003	0.003
<i>Epilobium hornemannii</i>		0.003				0.003
<i>Epilobium howellii</i>					0.006	0.006
<i>Epilobium minutum</i>		0.295	0.139	0.094	0.016	0.544
<i>Equisetum arvense</i>			0.006	0.028		0.034
<i>Eriogonum nudum</i>			0.006			0.006
<i>Eriogonum pyrolifolium</i>		0.248	0.044	0.044		0.336
<i>Eriophyllum lanatum</i>		0.003				0.003
<i>Eucephalus ledophyllus</i>		0.019	0.009	0.006		0.034
<i>Euphrasia officinale</i> (E)		0.003	0.008	0.006		0.017
<i>Festuca</i>	0.256	0.031		0.019		0.306
<i>Festuca rubra</i>	0.236	0.003				0.239
<i>Fragaria vesca</i>			0.288	0.175		0.463
<i>Fragaria virginiana</i>	0.075	0.022	0.006	0.050	0.002	0.155
<i>Galium triflorum</i>	0.050					0.050
<i>Gaultheria humifusa</i>	0.056					0.056
<i>Gaultheria ovatifolia</i>	0.270	0.013				0.283
<i>Gaultheria shallon</i>				0.013		0.013
<i>Glyceria striata</i>			0.094	0.006		0.100
			0.009			0.009
<i>Gymnocarpium dryopteris</i>	0.075					0.075
<i>Hieracium albiflorum</i>	0.589	0.195	0.634	0.778	0.217	2.414
<i>Holcus lanatus</i> (E)		0.006				0.006
<i>Holcus mollis</i> (E)	0.019					0.019
<i>Hypericum perforatum</i> (E)		0.188	0.322	0.456		0.966
<i>Hypochaeris radicata</i> (E)	0.294	1.850	1.803	1.089	0.298	5.334
<i>Hypericum scouleri</i>			0.003			0.003
<i>Jacobaea vulgaris</i> (E)		0.006	0.022			0.028
<i>Juncus</i>		0.013	0.003			0.016
<i>Juncus mertensianus</i>					0.008	0.008
<i>Juncus parryi</i>		0.153	0.042	0.019	0.316	0.530
<i>Lepidium campestre</i> (E)		0.194	0.003	0.006		0.203
<i>Leucanthemum vulgare</i> (E)	0.031	0.269	0.438	0.247		0.984
<i>Linaria vulgaris</i> (E)				0.081		0.081
<i>Lomatium martindalei</i>		0.003				0.003
<i>Lotus corniculatus</i> (E)		0.175	0.198	0.045		0.419
<i>Luetkea pectinata</i>					0.139	0.139
<i>Lupinus latifolius</i>	2.902	0.591	0.261	0.341	0.175	4.269
<i>Lupinus lepidus</i>			0.019		2.897	2.916
<i>Luzula</i>	0.006		0.003			0.009
<i>Luzula parviflora</i>	0.050	0.053	0.075	0.481	0.092	0.752
<i>Maianthemum racemosa/stellatum</i>	0.002	0.006				0.008
<i>Maianthemum racemosa</i>	0.063		0.006	0.006		0.075
<i>Maianthemum stellatum</i>	0.041					0.041
<i>Menziesia ferruginea</i>	2.044	0.069	0.063	0.181		2.356
<i>Mertensia paniculata</i>	0.156					0.156
<i>Micranthes ferruginea</i>				0.044	0.013	0.056
<i>Microsteris gracilis</i>		0.047	0.005			0.052

TABLE 9. List of all species found. FO = Tephra Impacted Forest, FBZ = Forb-dominated Blowdown Zone, RB = Replated Blowdown Zone, SB = Shrub-dominated Blowdown Zone, PP = Pumice Plain.

Species Name	TFF	FBZ	RBZ	SBZ	PP	Total
<i>Mitella pentandra</i>				0.031		0.031
<i>Montia parvifolia</i>		0.016	0.003	0.006		0.025
<i>Mycelis muralis</i> (E)	0.150	0.019	0.113	0.336		0.617
<i>Nothochelone nemorosa</i>	0.019	0.141	0.567	0.683		1.409
<i>Orthilia secunda</i>	0.038					0.038
<i>Osmorhiza berteroi</i>	0.053					0.053
<i>Osmorhiza occidentalis</i>	0.006					0.006
<i>Paxistima myrsinites</i>				0.094		0.094
<i>Penstemon cardwellii</i>	0.058	1.719	0.402	0.353	2.531	5.063
<i>Penstemon serrulatus</i>	0.013	0.019	0.019	0.116	0.036	0.202
<i>Phalaris arundinacea</i>		0.053	0.006	0.019		0.078
<i>Phacelia nemoralis</i>		0.297	0.402	0.273	0.056	1.028
<i>Picea sitchensis</i>						
<i>Pinus monticola</i>	0.006		0.044			0.050
<i>Plantago lanceolata</i> (E)		0.006	0.006			0.013
<i>Poa</i>				0.063		0.063
<i>Poa compressa</i> (E)		0.028	0.197	0.031		0.256
<i>Poa palustris</i>			0.025			0.025
<i>Poa pratensis</i>			0.013	0.066		0.078
<i>Polygonum douglasii</i>		0.003		0.005		0.008
<i>Polygonum minimum</i>		0.052	0.233	0.075	0.150	0.509
<i>Polystichum munitum</i>	0.100	0.063	0.059	0.069		0.291
<i>Populus trichocarpa</i>		0.031			0.044	0.075
<i>Pseudotsuga menziesii</i>	0.022		0.006		0.533	0.561
<i>Pteridium aquilinum</i>	0.531	2.681	0.344	0.044		3.600
<i>Pyrola asarifolia</i> var. <i>purpurea</i>	0.019					0.019
<i>Pyrola picta</i>	0.013					0.013
<i>Ranunculus uncinatus</i>	0.006					0.006
<i>Ribes acerifolium</i>				0.013		0.013
<i>Ribes lacustre</i>	0.063	0.063		0.263	0.002	0.389
<i>Rubus lasiococcus</i>	0.391	0.372	0.617	2.275		3.655
<i>Rubus parviflorus</i>	0.300	0.625		0.325		1.250
<i>Rubus spectabilis</i>	0.031	0.050	0.063	1.613		1.756
<i>Rubus ursinus</i>		0.188		0.069		0.256
<i>Rumex acetosella</i> (E)	0.025	1.303	0.320	0.497	0.002	2.147
<i>Rumex crispus</i> (E)				0.003		0.003
<i>Salix</i> species	0.003			0.003		0.006
<i>Sambucus racemosa</i>				0.006		0.006
<i>Sedum oregon</i>		0.009	0.025			0.034
<i>Senecio triangularis</i>	0.013					0.013
Shrub spp		0.002				0.002
<i>Sorbus scopulina</i>	0.005			0.025		0.030
<i>Sorbus sitchensis</i>			0.006	0.013		0.019
<i>Spergularia rubra</i> (E)				0.014		0.014
<i>Stellaria crispa</i>	0.019		0.006	0.319		0.344
<i>Taraxacum officinale</i> ssp. <i>officinale</i> (E)	0.050			0.025		0.075
<i>Tellima grandiflora</i>			0.025			0.025
<i>Tiarella trifoliata</i> var. <i>unifoliata</i>	0.122					0.122
<i>Trautvetteria caroliniensis</i>	0.025					0.025
<i>Trillium ovatum</i>	0.014		0.006	0.006		0.027
<i>Trifolium repens</i> (E)	0.020					0.020
<i>Trisetum spicatum</i>		0.006				0.006
<i>Tsuga heterophylla</i>	0.544			0.003	0.050	0.597
<i>Tsuga mertensiana</i>	2.356			0.006		2.363

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<i>Species Name</i>	TFF	FBZ	RBZ	SBZ	PP	Total
<i>Vaccinium</i>	10.364	0.663	3.266	6.327		20.619
<i>Valeriana sitchensis</i>	0.025					0.025
<i>Vancouveria hexandra</i>	0.006					0.006
<i>Veratrum viride</i>				0.013		0.013
<i>Veronica americana</i>				0.006		0.006
<i>Viola glabella</i>	0.014					0.014
<i>Viola palustris</i>				0.013		0.013
<i>Viola sempervirens</i>	0.002					0.002
	29.700	18.617	16.355	25.661	10.897	101.230