KEYSTONE HERBIVORES AND THEIR IMPACT ON VEGETATION AND SUCCESSIONAL DYNAMICS WITHIN THE DEBRIS AVALANCHE DEPOSIT AT MOUNT ST. HELENS NATIONAL VOLCANIC MONUMENT

by

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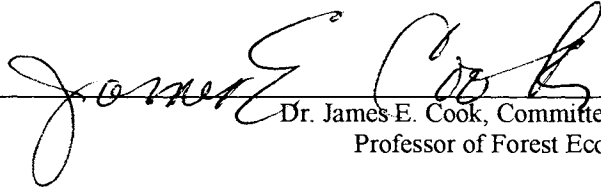requirements of the degree

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ABSTRACT

The debris avalanche at Mount St. Helens National Volcanic Monument has provided researchers with an important template in which to study various geological and ecological processess. This thesis describes the impact of two keystone herbivores on vegetation and successional dynamics within a small portion of the debris avalanche ecosystem. Chapter 1 addresses important background information pertinent to herbivory, disturbance ecology, and successional dynamics. Chapter 2 describes the role of elk (*Cervus elaphus roosevelti*) herbivory within a plant community and the subsequent changes in assemblage composition from 1992 to 1999. Finally, Chapter 3 concerns the relationship between sitka willow (*Salix sitchensis*) morphology and infestation of the exotic weevil, the willow stem borer (*Cryptorhynchus lapathi*).

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INTRODUCTION

Research at Mount St. Helens National Volcanic Monument

Researchers have studied the geological and ecological repercussions of the May 18, 1980 eruption of Mount St. Helens over the last 21 years. Ecological research has primarily focused on the recovery and colonization of areas affected by the eruption (Antos and Zobel 1982, Frenzen and Franklin 1985, Morris and Wood 1989, Halpern et al. 1990, del Moral and Bliss 1993). However, recent work has addressed the importance of biological disturbance agents within recovering populations and communities (Bishop 1996, Bishop and Schemske 1998, Fagan and Bishop 2000).

This study addressed the effect of biological disturbance on debris avalanche vegetation across several spatial and temporal scales. The effect of elk (*Cervus elaphus roosevelti*) herbivory on community succession from 1992-1999 was studied with an exclosure/control study design. The relationship between willow architecture and an exotic beetle, the willow stem borer (*Cryptorhynchus lapathi*), was addressed at population and organism levels. Implications of these biological disturbances, and potential interactions between willows, elk, and the willow stem borer, are addressed within.

Pre-eruption Environment

Mount St. Helens, located in southwestern Washington state (46° 16' N, 122° 09' W), was surrounded Gifford Pinchot National Forest and patches of state and private lands. The vegetative and physiographic features of area were typical of the Cascade Mountain

Range of southern Washington (Foxworthy and Hill 1982). The landscape was characterized by variable terrain with slopes ranging from 0% to more than 60% (Halpern et al. 1990). Dense, coniferous forests dominated the region. Douglas-fir and western hemlock forests typically occupied areas below 1,200 meters, whereas pacific silver fir, noble fir, and mountain hemlock forests occurred at higher elevations (Iverson and Martinson, 1986). However due to the 1857 eruption, the north slope of the mountain supported a unique assemblage of conifers and alpine species (Kruckeburg 1987). Clearcuts, averaging 20 ha in size, were dispersed throughout the area.

Historically, forests of the Washington Cascade Mountains have been subjected to disturbances including fire, insect outbreaks, landslides, and volcanic activity (Miles and Swanson 1986, Halpern and Franklin 1990, Johnson et al. 1994). Due to the volcanic nature of the Cascade Range, vegetation communities experience volcanic disturbances in the form of eruptions, debris flows, gas discharges, and seismic activity, on average every 60 years (Foxworthy and Hill 1982, Johnson et al. 1994). Mount St. Helens and the Cascade Range form a chain of volcanically active mountains that run parallel to the Pacific Coast. Few of the major Cascade Range volcanoes are considered extinct, as many peaks display signs of residual volcanic heat in the form of hot springs, patches of hot ground, and fumaroles (holes in the ground that emit hot gas and vapor) (Foxworthy and Hill 1982). Eruptions of Cascade Range volcanoes are typically explosive in nature because of high concentrations of gas and silica in the underlying magma (Foxworthy and Hill 1982). Four major Mount St. Helens eruptions, each depositing at least one km^3 of debris, have occurred within the last 515 years with the 1480 eruption estimated as being 5 times larger than the 1980 blast (Foxworthy and Hill 1982). The return interval

associated with Mount St. Helens eruptions is approximately 100 years (Kruckeburg 1987).

Eruption

On May 18, 1980, an earthquake measuring 5.1 on the Richter scale, and the subsequent landslide of 1.8 km³ of the northeast face of Mount St. Helens, initiated a variety of other destructive disturbances (Foxworthy and Hill 1982). A lateral blast to the northeast destroyed over 500 km² of forested land. A debris flow hurled down the North Fork Toutle river valley and eventually covered 7,100 ha (Pincha 1987). The eruption caused pyroclastic flows and numerous mudflows to scour the mountainside and sent volcanic ash more than 19 km into the air; Ash eventually fell across 57,000 km² of the western United States (Brantley 1994). Within 10 km northeast of the crater, virtually all vegetation was destroyed and buried; Forests were damaged up to 20 km away (Carpenter et al. 1987). Debris flows affected local hydrological patterns by choking and re-routing streams (Foxworthy and Hill 1982). In addition, a layer of tephra, or volcanic ejecta, (<5 cm to over 100 cm thick) covered herbaceous species, killing plants that could not grow through the material (Turner et al. 1997, Zobel and Antos 1997). Disturbance characteristics, topographic heterogeneity, colonization, and residual species life-histories affected the re-establishment of plant assemblages throughout the area affected by the blast (Turner et al. 1997).

Debris Slides

Shallow, abrupt landslides are common disturbances of forests in the Pacific Northwest (Miles and Swanson 1986). Removal of surface soil and plant biomass, and subsequent downslope deposition of those materials, redistributes resources and provides a source of plant species variability within an ecosystem (Miles and Swanson 1986).

Landslides may subsequently disrupt plant establishment on newly exposed surfaces (Miles and Swanson 1986). Adams and Dale (1987) compared the characteristics of the volcanic debris slides to those of glaciers: (1) Both events leave behind similar deposits. Glaciers carry materials as they advance and produce a terminal deposit (moraine). Similarly, debris slides carry materials as they move. Furthermore, lateral terraces and hummocks left by debris slides are similar to lateral moraines. Both processes leave substrates that are low in nitrogen and phosphorus. (2) Species composition is similar on debris slides and glacial debris. Surviving individuals are rare in most cases, and revegetation is greatly influenced by the invasion of plants from surrounding sites.

Disturbance-Succession Relationship

Disturbance can be defined as "*a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established*" (Sousa 1984). Disturbances also spatially and temporally displace resources (Chaneton and Facelli, 1991). The extent to which a disturbance has an effect on a plant community is dependent on its size, intensity, duration, and frequency (Westman 1978, Sousa 1984). Furthermore, community resistance and resiliency is influenced by internal (e.g., composition) and external (e.g., weather) factors (Westman 1978, Halpern 1988). By creating spatial and temporal variations in environmental gradients, disturbances allow species to partition environments according to their life-history traits, or adaptive strategies (Grime 1977, Tilman 1985, 1993, 1997; McCook 1994). Thus, disturbances profoundly influence shifts in species composition, or succession. (Drury and Nisbet 1973, Connell and Slatyer 1977, Halpern 1988, Kotanen 1997).

Compositional shifts are not only affected by disturbance regimes, but by initial floristic composition, interspecific interactions, environmental factors, and random events (Halpern 1989, Cook 1996). The initial floristic composition determines the spatial distribution of affected species, the potential resistance to disturbance, and composition of refugia remaining after disturbance (Halpern and Franklin 1990, Burke and Grime 1996). Although specific mechanisms are poorly understood, competition, inhibition, and facilitation between species play important roles in how species vie for resources (Connell and Slatyer 1977, Tilman 1993). Environmental factors such as climate and the availability of resources influence the presence and distribution of species (Tilman 1985, 1997; Halpern et al. 1990). Chance, or random, events such as colonization, precipitation, and herbivory play significant roles in succession (Frenzen and Franklin 1985, Dale 1989, Halpern et al. 1990). Finally, successional mechanisms may interact across spatial and temporal scales (McCook 1994), and potentially produce multiple endpoints in species composition (Cook 1996).

Successional dynamics are grouped into two categories, primary and secondary. Primary succession occurs on newly created surfaces where soil has not developed and where vegetation does not exist. Secondary succession describes shifts in species composition that occur after new sites are colonized and populations are established. Primary succession research tends to focus on factors that influence the dispersal, establishment, and survival of colonizing plants (Frenzen and Franklin 1985, Wood and del Moral 1988, del Moral 1998). Whereas, secondary succession research delves into those factors that influence competition, recruitment of species, and responses to

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subsequent disturbances (Tilman 1985, 1997; Halpern et al. 1990, Burke and Grime 1996, Kotanen 1997).

Herbivory

The relationships between herbivores and the plants they feed on are thought to be the products of diffuse coevolution (Pollard 1992). The term *diffuse* is used to mean that the interactions did not evolve on species-to-species basis. That is, multiple species of herbivores interacted with multiple species of plants over a long period of time (Pollard 1992). Plants with characteristics that rendered them less attractive to herbivores or that were able to compensate for tissue removal became better represented over time (Karban and Baldwin 1997).

Some general characteristics of plant-herbivore interactions are described by Pollard (1992) - 1) The time a herbivore spends feeding on a single plant is small relative to the lifespan of herbivore. Similarly, the time during which a plant is fed upon is small relative to the lifespan of the plant. 2) The effect of herbivory on a plant is greater than the effect of the plant on the herbivore. 3) Large herbivores tend to be generalist, while insects and other small herbivores are often specialists. 4) Relative to specialist herbivores, generalists consume large amounts of plant material and are inefficient at digesting. 5) In grazed plant communities, herbivory-tolerant plant species become more common; more sensitive species are suppressed and tolerant species are released from competition. Directly or indirectly, mammalian herbivores influence plant dispersal, reproduction, chemistry, morphology, and growth wherever the two lifeforms co-exist (Lindroth 1989). In turn, plant characteristics influence the diet selection, digestive physiology, and morphology of herbivores (Lindroth 1989).

Mammalian Herbivory

Grazing herbivores consume grasses and forbs (forage), while browsers consume leaves and shoots of woody plants; however, many animals exhibit both feeding modes (Southwood 1985, Pollard 1992). Many ungulates (hoofed animals) are browsers that are generalists in their food selection, though preferences do occur (Danell et al. 1991). The use of browse and forage by ungulates is affected by temporal and spatial variations in plant assemblage composition and structure (Lindroth 1989). In many systems, levels of browse consumption change with the seasons, and thus browsing tends to increase as forbs and grasses senesce and become less available (Merrill 1994). Jenkins and Starkey (1993) suggest that elk prefer forage species to browse. Nutrition quality (e.g. crude protein) typically drops as plants become dormant in the winter. However, concentrations of soluble digestion inhibitors (e.g. tannins and phenolic compounds) decrease in dormant plants. The seasonal distribution of ungulates can therefore be influenced by the distribution of food sources (Lindroth 1989, Merrill 1994).

Insect Herbivory

In contrast to mammalian herbivores, many insect–plant relationships appear to have wvolved on a species-by-species basis (Weis and Berenbaum 1989). Accordingly, many insect herbivores are species-specific or are restricted to using plants within certain genera, although generalist behavior does exist (Southwood 1985). Unlike large herbivores, the size differential between insects and host plants allow herbivores to specialize in utilizing particular plant organs and tissues (e.g., leaves, shoots, phloem, and roots) (Southwood 1985, Weis and Berenbaum 1989). In general terms, the more complex the architecture, the greater the number of insect species capable of feeding on a given plant (Weis and Berenbaum 1989).

Despite their small size, insect herbivores are capable of substantially impacting plant populations and communities. Periodic outbreaks of spruce bark and southern pine beetles are powerful disturbance agents that can kill hundreds of trees at a time and impact thousands of hectares (Knight and Heikkenen 1980). However, outbreaks are usually associated with ecological disturbances such as windthrow and drought, as weakened and stressed trees are more vulnerable to attack (Kozlowski et al. 1991, Rasmussen et al. 1996). Within a population, insect herbivory can noticeably alter flowering phenology and seed production (Sacchi and Price 1992, Bishop 1996). At the plant level, insect herbivores can defoliate an entire plant, modify architecture, alter nutrient concentrations, and suppress sexual reproduction (Crawley 1983, Craig et al. 1986, Sacchi and Price 1992, Stein and Price 1995)

Plant Responses to Herbivory

The response of plants to herbivory has been a popular and important area of research for ecologists (Crawley 1983, Abrahamson 1989, Stein and Price 1995, Martinsen et al. 1998). Because herbivory may result in loss of tissues, decreased vigor, and/or less sexual reproduction, plants respond to herbivory through various mechanisms which have been categorized as avoidance, escape, and defense (Lindroth 1989, Weis and Berenbaum 1989, Kozlowski et al. 1991).

Avoidance and Escape

The timing of growth and reproduction may allow plants to avoid herbivores, particularly animals with periodic and short life-cycles (e.g., insects) (Crawley 1983, Abrahamson 1989). Accordingly, the longer plant tissues are available for consumption, the greater the chance of herbivory. Variation in phenology within a population increases

the chance that at least a few individuals will either avoid or experience relatively little herbivory.

Many species respond to herbivory with rapid growth of tissues after attack (e.g., compensatory growth) (Paige 1992, Singer et al. 1998). If a plant has adequate stored resources and dormant buds subsequent to a herbivory event, compensatory growth may result in a net increase in flower and seed production (Paige 1992). Morever, Tuomi et al. (1994) noted that in the absence of herbivores, production of dormant buds may actually constitute an increased metabolic cost for a plant. Increases in biomass can reduce future impacts of low to moderate levels of herbivory on a single plant, as the proportion of biomass removed during subsequent attacks may be less than previous events. Rapid vertical growth can place tissues out of reach of many mammalian herbivores (Singer et al. 1998).

Defense

Plant defenses have been grouped into two major types, constitutive and induced (Lindroth 1989, Karban and Baldwin 1997). Constitutive defenses are traits normal occurring in plants (e.g., thorns and sap) that interfere with herbivory (Lindroth 1989). Induced defenses are modifications in plant morphology and/or physiology that occur after herbivory and that deter subsequent attacks (Karban and Baldwin 1997).

Plants employ several constitutive defense mechanisms to ward off herbivores (Lindroth 1989, Weis and Berenbaum 1989). The evolution of trichomes, thorns, and toxins allows plants to prevent animals from consuming tissues and reduce the number of herbivore species capable of feeding on their tissues (Southwood 1985, Lindroth 1989). Tissue moisture and texture, and chemical and nutrient concentrations can be highly variable within a single plant and among many individuals within a population (Suomela

and Ayres 1994). Variation in chemical concentrations prevents herbivores from habituating to a specific toxin level and increases energy requirements of digestion, thereby reducing foraging efficiency (Pollard 1992, Karban and Baldwin 1997). And like variation in phenology, variation of chemical concentrations among individuals aid in defense within a population or community.

While induced defenses have been reported by several authors, the specific mechanisms governing induced responses are not clearly understood (Palo 1984, Häjltén et al. 1993, Halulinen et al. 1995, Karban and Baldwin 1997). An induced response occurs when plants subjected to herbivory increase the concentrations of secondary metabolites (e.g., phenolics, alkaloids, and terpenes) in remaining tissues and in tissues produced subsequent to herbivore attack (Karban and Baldwin 1997). While many herbivores are deterred by these defensive compounds (Palo 1984, Weis and Berenbaum 1989, Stein and Price 1995, Karban and Baldwin 1997), other authors have cited positive responses in ungulates and insects (Danell and Huss-Danell 1985, Southwood 1985, Lindroth 1989, Martinsen et al. 1998).

Role of Herbivory in Succession

As a persistent ecological disturbance, herbivory plays an important role in successional dynamics (Drury and Nisbet 1973, Knight and Heikkenen 1980, Hobbs 1996). The influence of herbivory in succession is strongly influenced by initial floristics, size of the plant community, herbivore behavior, and indirectly by interactions with other ecological factors (e.g., precipitation and soil nutrients) (Hanley and Taber 1980, Hobbs 1996).

Species composition, selective herbivory, and plant responses to herbivory interact to influence successional pathways (Hobbs 1996). For example, Hanley and

Taber (1980) found that elk selectively grazed various forb species. Clonal, grazing-tolerant species thrived under grazing, whereas intolerant species declined in cover in comparison to exclosure populations. Defoliation and/or death of dominant tree species by insect herbivores can release subdominant species, and thus accelerate successional changes (Knight and Heikkenen 1980). Through deposition of urine and feces, trampling, and browsing of woody plants, gregarious ungulates can increase N input within an community, create new microsites, and delay canopy closure (Hanley and Taber 1980, Hobbs 1996). In turn, these modifications interact with plant life-histories to affect competition and colonization and thus, affect species turnover.

OBJECTIVES

This thesis describes the impact of two categories of herbivores on debris avalanche vegetation. Although elk are keystone species throughout the Pacific Northwest (Hanley and Taber 1980), the effect of elk herbivory on community succession has never been addressed within MSHNVM. Chapter 2 looks at the impact of elk herbivory on a community over 7 years and focuses on the role of species life-history traits in determining community responses to site treatments. Chapter 3 addresses the relationships between willow architecture and the willow stem borer at the genet, ramet, and shoot levels. The relationship between boring and shoot nitrogen concentrations was also studied to assess plant responses to borer attack. It is hoped that these studies will help to generate hypotheses about successional dynamics within MSHNVM.

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Chapter 2: The Effects of Ungulate Exclusion on Species Composition within a Debris Avalanche Community in Mount St. Helens National Volcanic Monument.

ABSTRACT

In 1992 personnel at Mount St. Helens National Volcanic Monument placed an ungulate exclosure and a corresponding control plot on the debris avalanche. Cover of plant species was visually estimated in 1992, 1994, and 1999 with 1m² microplots. Unfortunately the 1994 data could not be included in analyses because the time of sampling was much earlier than in other years. From 1992 to 1999, cover in both study plots increased greatly: 17.8 to 102.6% in the control and 29.8 to 116.7% in the exclosure. While the absolute increase in mean microplot cover was similar for both sites, the degree of change was markedly different. Cover increased by nearly 500% in the control, but by only about 300% in the exclosure from 1992 to 1999. Species density (# of species per 1m² microplot) differed between sites and years. Mean species density increased from 8.3 to 9.4 in the control plot, but decreased from 10.3 to 7.7 in the exclosure. From 1992 to 1999, mean cover of exotic species increased from 1.4 to 14.5% in the control and from 1.3 to 4.3% in the exclosure. In contrast, mean cover of modal forest species increased from 0.2 to 1.4% in the exclosure and was negligible in the control plot in 1992 and 1999 (0.3 and 0.2%, respectively). As expected, cover of grasses increased in the control plot from 0.4 to 1.8%, while cover of the same group declined from 0.4 to 0.2% in the exclosure. Cover of woody species was not influenced by site treatment as much as other studies suggest, but its treatment was complicated by large initial differences between the two plots. Shrub cover increased by similar amounts in both sites, whereas tree cover was greater in the exclosure in both sampling years. Detrended Correspondence Analysis of species presence (n=90) indicated that both sites were following moderately different successional trajectories. However, when species with frequencies ☐5% were excluded from the DCA, a more pronounced divergence in the relative frequency of the 43 most common species was observed. The proliferation of exotic species in the control site can be explained by the initial colonization of the debris avalanche by weedy species and by elk herbivory and trampling. Moreover, the greater litter cover and shading in the exclosure may have facilitated the establishment and growth of modal forest species. While elk herbivory has influenced the composition of herbaceous species, the increase of woody cover in both sites suggest that elk herbivory is not intense enough to impede the development of a red alder/willow-dominated community on the debris avalanche.

INTRODUCTION

The role of ungulate herbivory in successional dynamics has been studied in many ecosystems (Hanley 1984, Jenkins and Starkey 1993, Hobbs 1996). Researchers have addressed how ungulates interact with plants across various temporal and spatial scales (Hobbs 1996, Singer et al. 1998). Hobbs (1996) noted that ungulates may affect plants directly via herbivory or indirectly by interacting with ecosystem processes such as interspecific competition, nitrogen cycling, and community structure. This chapter addresses the impact of Roosevelt elk (*Cervus elaphus roosevelti*) on vegetational dynamics within two sites on the debris avalanche of Mount St. Helens National Volcanic Monument (MSHNVM) from 1992 to 1999. The focus is on the role that elk and plant life-history interactions may play in shaping successional trends in this environment.

Role of Plant Strategies in Succession

Changes in species composition over time reflect complex interactions between individual plants, populations, resources, stochastic events, and disturbance regimes (Connell and Slatyer 1977, Grime 1977, Tilman 1985, Halpern 1989). Species have been grouped by growth form and by ecological traits by many workers to better understand successional mechanisms (Curtis 1959, Grime 1977, Halpern 1988, 1989; Tilman 1993, 1997; McIntyre et al. 1995, Thomas et al. 1999). Plant shape and size influence how competion for resources and the partitioning of resources that results (Tilman 1993, McIntyre et al. 1995). Furthermore, morphological characteristics may play important roles in successional dynamics (Whittaker 1993, del Moral 1998). The effect of nucleation, or the facilitation of colonization through spatial proximity to a larger plant, has been cited in rangeland studies of secondary succession (Blundon et al. 1993). In primary succession too, seedling establishment is thought to be enhanced by shading and

other site amelioration by established plants. Blundon et al. (1993), reported that shading and nitrogen-fixation by shrubs aided herbaceous colonization on a glacial foreland. Ofcourse, facilitation was likely non-obligate, as herbs were able grow without the presence of shrubs, albeit, less vigorously.

Life-history traits, largely determine how individual plants react to biological stimuli and fluctuations in environmental processes (Grime 1977, Halpern 1989, McIntyre et al. 1995, Tilman 1997). However, plants are often constrained by trade-offs in the allocation of carbohydrates and nutrients (Tilman 1985, Tilman 1993). Modes of dispersal, reproduction, defense, and resource acquisition suggest how different species may respond to disturbances and shifts in species composition, and thus affect patterns of spatial and temporal heterogeneity within communities (Sousa 1984, Halpern 1988, McIntyre and Lavorel 1994, Parendes and Jones 2000).

Plant Strategies and Invasive Species

The colonization of disturbed sites is influenced by residual plants, seed sources, seed dispersal, and biological and environmental barriers to dispersal (Dale 1989, Parendes and Jones 2000). Many invasive species are characterized by rapid growth, the ability to reproduce sexually and vegetatively, the production of numerous, wind-borne seeds, and the ability to thrive under high levels of resources (e.g. light and nitrogen) (McIntyre and Lavorel 1994, Kotanen 1997). Plants that are capable of rapid, clonal growth are often able to dominated sites after they become established. However, these species often decrease in abundance over time as site conditions change and new species colonize and compete for resources (Halpern 1988, Dale 1989, McCook 1994). Rapid, clonal growth allows some invasive species to persist under frequent disturbances such as herbivory and localized trampling (Chaneton and Facelli 1991, Hobbs 1996).

Effect of Ungulate Herbivory on Plant Communities

Herbivory is obviously a common and important biological agent of disturbance. The extent to which a disturbance affects on a plant community is dependent on its size, intensity, duration, and frequency (Sousa 1984). Herbivore effects are complicated by interactions with environmental gradients (e.g., moisture, light, and soil productivity) and plant life-history traits (Hobbs 1996).

Herbivores may preferentially feed on individual species, deplete carbohydrate reserves over time, and effectively remove preferred species from an assemblage (Hobbs 1996). Gregarious grazers frequently disturb substrates, and thus facilitate colonization of invasive species and clonal spread into new microsites (Chaneton and Facelli 1991). Persistent herbivory can prevent plants from accumulation the resources necessary for sexual reproduction and thus, stimulate vegetative growth (Abrahamson 1989). Thus, reproductive patterns of species within an assemblage may be affected over time. The culmination of these interactions is an increase in the abundance of grazing-tolerant species (e.g., many graminoids), the suppression of woody species, and the reduction of dead material and litter biomass (Coughenour 1991, Hobbs 1996, Singer and Harter 1996).

Nitrogen mineralization rates may be increased if N returns to the soil in a more readily decomposable form as feces and urine rather than organic litter (Mattson 1980, Coughenour 1991). Deposition of feces and urine is concentrated to where ungulate congregate and increases N heterogeneity within the substrate of a community (Hobbs 1996).

Exclosure Studies

Researchers have been able to document the effects of ungulate herbivory by excluding ungulates from areas and comparing species composition and growth to unprotected vegetation. The strongest trends identified have been short-term increases in species richness, increases in grass cover and other grazing-tolerant species, and decreases of woody cover outside of exclosures (Hanley and Tabor 1980, Chaneton and Facelli 1991, Case and Kauffman 1997, Singer et al. 1998). Case and Kauffman (1997) reported suppression of shrub growth rates and sexual reproduction in plots open to browsing. Some evidence suggests that the presence and spread of disturbance-adapted species (e.g. ruderals and invasives) is facilitated by grazing, as herbivores disturb microsites and reduce vigor of competitive species (Grime 1977, Chaneton and Facelli 1991). Hanley and Tabor (1980) studied ungulate exclusion over 8 years and reported significant increases in graminoid cover and decreases in shrub cover outside of exclosures. They attributed the differences to tolerance to trampling of certain species and selective grazing.

Exclusion of herbivory involves more than preventing the removal of plant biomass. Exclosures remove many indirect impacts associated with ungulate herbivory, such as changes in N inputs and cycling rates, trampling disturbances, physiological and architectural responses to tissue removal, interspecific plant interactions, and processes involving other herbivores (Mattson 1980, Coughenour 1991, Hobbs 1996).

Finally, the underlying question behind ungulate exclosure work is often to determine the role of ungulate herbivory changing community composition. Singer et al. (1998) suggest that intense elk browse since the late 19th century has dramatically decreased the distribution and abundance of willow communities in Yellowstone

National Park through consistent, intensive browsing. Whereas under moderate browsing intensities, Case and Kauffman (1997) reported an increase in shrub growth over two years in areas excluded from cattle use, despite the presence of native ungulates. Furthermore, information from exclosures may be obscured by compositional differences prior to exclusion, substrate differences, and edge effects along exclosures (Coughenour 1991, Lepš 1991, Case and Kauffman 1997). Thus, vegetation may differ independently of ungulate herbivory, and yet still be strongly influenced by the frequency, intensity, and consistency of herbivory.

METHODS

Study Area

Mount St. Helens National Volcanic Monument (hereafter MSHNVM) is located in southwestern Washington (46° 16' N, 122° 09' W) and is surrounded by Gifford Pinchot National Forest and patches of state and private lands. The climatic and physiographic features of MSHNVM are typical of the Cascade Mountain Range of southern Washington (Foxworthy and Hill 1982). Cool, wet winters and hot, dry summers characterize the regional climate. Temperatures may range from –4.2 °C to 0.5 °C in January and 7.3 °C to 22.2 °C in July (mean minimum and maximum values). Precipitation averages 237 cm annually, with only 7% falling between June and August (Halpern et al. 1990, Franklin and Dyrness 1973). The region receives approximately 75% of its annual precipitation between October and March, with persistent snowpacks forming above 1,000 meters (Franklin and Dyrness 1973).

Debris Avalanche

During the May 18, 1980 eruption, approximately 2 million m^3 of rock, glacial ice, water, soil, and vegetation was propelled down the North Fork Toutle river valley at

an initial speed of 100 to 110 m per second (Pincha 1987). The deposit eventually covered more than 7,000 ha and extended 22.9 km west of the crater (Pincha 1987). North-south flowing streams were impounded, forming and new bodies of water, such as Coldwater and Castle lakes (Meyer and Sabol 1989). The new surface was devoid of vegetation and was composed primarily of hummocks (mounds of unconsolidated material) of varying shapes and sizes (Meyer and Sabol 1989, Pincha 1987). Samples taken at the southern edge of the debris avalanche near Castle Lake primarily of rock (>2mm in diameter) interspersed with finer material that averaged 62% sand, 33 % silt and 4% clay. Aeration was suitable for plant growth, but water percolation was high and nitrogen and phosphorus levels were found to be lower than local soils (Adams and Dale 1987, Dale 1989). West-flowing stream channels became heavily braided and were subjected to seasonal variations in channel morphology (Meyer and Sabol 1989). Seeps, fed by impounded water sources and buried streams, developed in depressions and on eroded hummock slopes and stream channels (Meyer and Sabol 1989).

Although the debris deposit was seemingly devoid of vegetation, regrowth was influenced by plants emerging from root stocks buried in the debris as well as by wind-dispersed seeds from the valley slopes (Dale 1989). In general, species with close seed sources, high seed production, and long distance seed dispersal dominated the initial revegetation of the avalanche. Colonizers such as thistle (*Cirsium* spp.), fireweed (*Epilobium angustifolium*), and willow produce light, wind-borne seeds that are capable of traveling long distances; lupine (*Lupinus* spp.) and willow are capable of producing new stems from rhizomes (Dale 1989). By 1981, several thousand willow ramets were observed on the avalanche deposit (Adams and Dale 1987). At present, red alder and

willows are the dominant woody species, while forbs and grasses constitute the majority of species on the deposit (Peter Frenzen, Monument Scientist, *personal communication*). Conifer establishment has been hampered by unfavorable site conditions (direct sunlight and poor nutrient content of the substrate), poor seed dispersal, and intense winter browsing by the resident elk herd (Frenzen and Franklin, 1985).

Castle Lake Exclosure and Control Sites

The Castle Lake exclosure and its associated control plot, are located on the southern portion of the debris deposit near Castle Lake. The deposit in this region consists of hummocks and shallow depressions. Subsurface water continuously seeps from the Castle Lake impoundment and moves northwest into Castle Creek and the North Fork Toutle River. Thus, the areas affected by seepage tend to be more mesic than other portions of the generally xeric debris deposit. Stands of red alder are encroaching from the edge of the deposit, increasing shade and contributing nitrogen-rich litter to the substrate.

Although deer (*Odocoileus hemionus*) have been observed on the debris avalanche, elk are the most abundant ungulates in MSHNVM (Peter Frenzen, Monument Scientist, *personal communication*). Thus, elk are presumed to be the dominant herbivore on the debris avalanche.

Elk

The American elk, or wapiti, is a keystone species in various plant communities of the Pacific Northwest (Merrill et al. 1986). Historically the Roosevelt subspecies inhabited the vast forests of western Washington. Distribution was sparse, with populations tending to concentrate in riparian and disturbed zones (Washington Dept. of Fish and Wildlife, 1997). Settlement of the region in the late 1800's largely extirpated

the species from much of its range (Washington Dept. of Fish and Wildlife, 1997). The herd in the Mount St. Helens region (hereafter, the St. Helens herd) probably declined to less than 500 in the early 1940's. The remnant herd is believed to have inhabited the headwaters of the Green, Toutle, and Kalama rivers (Merrill et al. 1986). By the 1960's the population was stable enough for regulated harvesting by hunters. Before the 1980 eruption, the St. Helens herd was estimated at 16,000 individuals (Washington Dept. of Fish and Wildlife, 1997). Recent estimates (1996) place the St. Helens herd near pre-eruption levels.

The St. Helens herd historically used the North Fork Toutle river valley as a corridor between calving in high elevations and wintering in lowlands west of Mount St. Helens (Merrill et al. 1986). However, Merrill et al. (1986) found no definitive seasonal migrations within the northwest portion of MSHNVM. They suggested that abundant forage along the river valley, combined with low forage abundance at higher elevations and human recreation outside of the monument, may be influencing elk to reside within the North Fork Toutle drainage.

The 1980 eruption of Mount St. Helens killed approximately 1,600 elk (Washington Dept. of Fish and Wildlife, 1997). Merrill et al. (1986) assessed the initial recovery of elk populations within the northwest portion of MSHNVM. They found a 12% and 27% increase in the spatial distribution of elk in 1982-1983 and 1983-1984, respectively. The Washington Dept. of Fish and Wildlife recently estimated that 200 elk reside year-round on the debris deposit. As many as 600 elk may migrate throughout the 1012 ha of the North Fork Toutle river valley affected by the debris avalanche (Washington Dept. of Fish and Wildlife, 1997).

Seasonal variations in the availability and quality (e.g., crude protein content) of forage strongly influence ungulate feeding behavior (Merrill et al. 1995, Molvar et al. 1993). Merrill (1994) found that elk exhibit a seasonal pattern of forage selection within the northwest portion of MSHNVM. From June to August forbs are the primary food source. From September to November grasses are selected and the browsing of shrubs increases. From December to early spring, the primary food source is shrub and conifer browse (Merrill 1994).

Experimental Design

A 70.75 x 70.75m exclosure was constructed on a randomly selected vegetated area of the debris avalanche deposit in 1992. A companion site of the same site was identified to serve as a control. Within each site, workers randomly placed 125, 1m² microplots and 15, 15m line intercepts. All intercepts and microplots were placed 5m from the exclosure fenceline to account for edge effects, so the effective sample area was 60 X 60m. Data were collected from the exclosure and control plots in August 1992, July 1994, and August 1999. Species were recorded and cover visually estimated in the microplots. Cover of woody species not emerging from within microplots, but that extended over microplot perimeters was included. Within each site, 115 plots were consistently measured in the three sampling years. Ten microplots were not measured in all sampling years. Additional woody cover was recorded along line intercepts. Species were divided into growthform codes consistent with previous work within the monument (Halpern et al. 1990): 1) grasses, 2) rushes and sedges, 3) forbs, ferns, and fern allies, 4) shrubs and woody vines, and 5) trees (Appendix).

Analysis

Because the treatment units were the exclosure and control sites, microplots and line transects within each site were not considered to be independent, treatment replicates (e.g., pseudo-replication). Therefore, statistical testing of cover and frequency values was deemed to be inappropriate, as significant results would merely implicate differences between locations and not treatments (Heffner et al. 1996). Mean species density, site richness, and diversity (Shannon-Weiner index) were calculated for each sampling year. The similarity of species composition between sites and between sampling years was calculated with Sorensen's coefficient of community:

$$C = 2j /(2j + a + b)$$

Where: j = # of species found in both communities
a = # of species unique to sample a
b = # of species unique to sample b

Mean microplot cover of all species was calculated for each site-year combination. The mean microplot cover and frequency of occurrence of growthform classes was also analyzed. In addition to growthform codes, exotic and modal forest species (e.g., species typical of local coniferous forests, *sensu* Curtis 1959) were identified for analyses (n=22 and n=11, respectively). Classifications were derived from habitat and life-history descriptions, historical information, and prior classifications presented in publications (Franklin and Dyrness 1973, Hanley 1984, Halpern et al. 1990, Jenkins and Starkey 1993, Pojar and MacKinnon 1994, Thomas et al. 1999, McKenzie et al. 2000). Because pre-treatment site differences existed, the percent change of the aforementioned values was calculated for 1992-1999.

Species presence and frequency data were analyzed with Detrended Correspondence Analysis (DCA) to place sites in ordination space by year (Hill and

Gauch 1980). DCA measures species and site frequency data simultaneously and position sites using a Chi-squared distance metric based on compositional dissimilarity (Hill and Gauch 1980, Michin 1987). Detrended correspondence analysis is similar to reciprocal averaging, but removes (*detrends*) the spurious arch-effect associated with basic correspondence analyses. Rare species are downweighted to decrease their effects on spatial distancing. As recommended by Hill and Gauch (1980), species with frequencies of occurrence ≤5% were excluded from analyses. Thus, 43 of 90 species were used for analyses. The process of detrending and rescaling data changes the meaning of axis eigenvalues, such that they no longer represent the amount of variation explained by axes. Instead, each axis is divided into standard deviation units that separate sites by their relative dissimilarities in species composition. Although DCA has been strongly criticized (Michin 1997), it remains a popular ordination technique for species abundance data due to its availability and general interpretability (Halpern 1988).

RESULTS

Anomolous results of 1994 data analyses suggested that the early July sampling of 1994 data did not capture the full number, nor the maximum cover, of species present. Therefore, 1994 data were excluded from analyses.

Species Abundance Patterns

In 1992 mean species density was greater in the exclosure site (control = 8.3, exclosure = 10.3), whereas richness and diversity values were similar (Table 1). Species richness increased from 46 to 62 in the control, and from 44 to 65 in the exclosure, from 1992 to 1999 (Table 1). Species density increased by 1.1 in the control, whereas, exclosure species density decreased by 2.6. Species diversity increased overall from 1992 to 1999, whereas between-site differences were negligible. However, dissimilarity

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in species composition between sampling years were greater than site differences (Table 1). This suggested that colonization, interspecific interactions, and environmental factors affected changes in species composition more strongly than ungulate herbivory.

Microplot Cover and Species Functional Groups

Mean microplot cover in the exclosure (29.8%) was almost double the value in the control site (17.8%) in 1992 (Table 2). Over the next seven years, the absolute change in cover was early equal in both sites (85% in the control and 87% in the exclosure). However, the degree of change in mean microplot cover in the control was practically twice that of the exclosure (477% and 292%, respectively). Distinct site differences were detected when species were grouped by life-history attributes. In 1992, mean cover of exotic species was similar in both sites (1.4% in the control and 1.3% in the exclosure) (Table 2). By 1999, cover of exotic species was three times greater in the control (14.5% and 4.3%, respectively). Overall, the percent change in exotic cover in the control was nearly four times that in the exclosure. Mean microplot cover of modal forest species was less than 2% in all site-year combinations (Table 2). The decrease of mean cover from 0.3 to 0.2 in the control was negligible. However, cover of modal forest species increased from 0.2 to 1.4 in the exclosure. Thus, while cover increased over sampling years, species life-history traits appeared to have interacted with site treatments.

Cover and Frequencies of Growthform Classes

Initial site differences and temporal changes appeared to obscure effects of herbivory on growthform cover and abundance patterns (Tables 3 and 4). Whereas cover of grasses and forbs in the two sites was similar in 1992, cover of sedges, rushes, and woody plants was greater in the exclosure site (Table 3). By 1999, mean cover of all species was greater in exclosure microplots (Table 2). However, the relative

Table 1. Species density (# species in 1m², n = 115) with standard error values, site richness, and diversity (Shannon-Weiner Index) in 1992 and 1999 at the Castle Lake control and exclosure sites on the debris avalanche at Mount St. Helens Volcanic Monument. Compositional similarity was calculated with Sorensen's community coefficient. Similarity values were calculated for site comparisons within each sampling year and for comparisons between years using all species from both sites.

Year	Species Density		Richness		Diversity		Similarity
	Control	Exclosure	Control	Exclosure	Control	Exclosure	
1992	8.3 (0.3)	10.3 (0.4)	46	44	3.133	3.171	0.89
1999	9.4 (0.3)	7.7 (0.3)	62	65	3.346	3.368	0.80

	Absolute Change						
	Species Density		Richness		Diversity		
Interval	Control	Exclosure	Control	Exclosure	Control	Exclosure	
1992-1999	1.1	-2.6	16	21	0.213	0.197	0.64

Table 2. Mean microplot cover (1m², n = 115) with standard error values and percent change of values for all species (n=90), exotic species (n=19), and modal forest species* (n=11) in 1992 and 1999 in the Castle Lake control and exclosure sites on the debris avalanche at Mount St. Helens National Volcanic Monument.

	Mean Cover					
	All Species		Exotic Species		Modal Forest Species	
Year	Control	Exclosure	Control	Exclosure	Control	Exclosure
1992	17.8 (2.3)	29.8 (3.0)	1.4 (0.2)	1.3 (0.2)	0.3 (0.1)	0.2 (0.1)
1999	102.6 (4.6)	116.7 (4.7)	14.5 (1.9)	4.3 (0.8)	0.2 (0.1)	1.4 (0.4)

	Absolute Change					
	All Species		Exotic Species		Modal Forest Species	
Interval	Control	Exclosure	Control	Exclosure	Control	Exclosure
1992-1999	84.8	86.9	13.1	3.0	-0.1	1.2

	Percent Change					
	All Species		Exotic Species		Modal Forest Species	
Interval	Control	Exclosure	Control	Exclosure	Control	Exclosure
1992-1999	476.4	291.6	935.7	230.8	-7.1	761.1

*modal forest species identified as those species most likely to be present in regional mid- to late-successional hemlock and douglas-fir forests (*sensu* Franklin and Dyrness 1973, Halpern 1988, Thomas et al. 1999, McKenzie et al. 2000)

Table 3. Mean cover with standard error values and changes in mean microplot ($1m^2$, n = 115) cover of lifeform classes in 1992 and 1999 in the Castle Lake control and exclosure sites on the debris avalanche at Mount St. Helens National Volcanic Monument.

Growthform Classes	Mean Cover				Absolute Change		Percent Change	
	1992		1999		1992-1999		1992-1999	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
1) grasses	0.4 (0.1)	0.4 (0.1)	1.8 (0.2)	0.2 (0.1)	1.4	-1.6	216.2	-45
2) sedges and rushes	1.6 (0.4)	3.0 (0.4)	1.9 (0.4)	0.9 (0.2)	0.3	-1.0	16	-70
3) forbs, ferns, and allies	6.3 (1.2)	6.4 (0.8)	26.5 (2.4)	22.7 (1.9)	20.2	16.3	318.3	254.6
4) shrubs and woody vines	9.0 (1.4)	18.2 (2.3)	25.5 (2.6)	33.3 (3.6)	16.5	15.1	183.1	82.9
5) trees	0.5 (0.1)	1.8 (0.9)	47.5 (4.0)	59.6 (4.1)	47.0	57.8	10012.8	3191.2

Table 4. Mean frequency of occurrence and percent change in mean microplot (1m², n = 115) frequency of growthform classes in 1992 and 1999 in the Castle Lake control and exclosure sites on the debris avalanche at Mount St. Helens National Volcanic Monument.

| | Mean Frequency | | | | Percent Change | |
| | 1992 | | 1999 | | 1992-1999 | |
Growthform Classes	Control	Exclosure	Control	Exclosure	Control	Exclosure
1) grasses	0.44	0.53	0.64	0.21	45.5	-60.4
2) sedges and rushes	0.64	0.82	0.48	0.38	-25.0	-53.7
3) forbs, ferns, and allies	0.99	0.98	1.00	0.99	1.0	1.0
4) shrubs and woody vines	0.94	0.95	0.82	0.67	-12.8	-29.5
5) trees	0.54	0.60	0.76	0.87	40.7	45.0

increase was greater in the control. In contrast, by 1999 all growthform frequencies, except trees, were greater in the control site (Table 4). As anticipated, mean cover of woody species (lifeforms 4 and 5) was greater in the exclosure by 1999 (73% and 93%, respectively). However, this was true when sites were first measured in 1992 (9.5% and 20%, respectively). The absolute increase in shrub cover was similar in the control and the exclosure (16.5 and 15.1, respectively). However, tree cover increased by 57.8% in the exclosure, and by only 47% in the control. By 1999 grass cover in the control was almost ten-times that of the exclosure (1.8% and 0.2%, respectively). Moreover, cover of sedges and rushes was twice that of the exclosure in the control. Similarly, the frequencies of occurrence for grasses, sedges, and rushes was greater in the exclosure in 1992, but by 1999, was greater in the control (Table 4). By 1999, forb cover and frequency was similar between sites (Table 3, 4). Because forbs made up the majority of all species observed (52%), the impact of ungulate herbivory on forb species turnover was analyzed. However, species turnover patterns in the forb class were similar within sites from 1992 – 1999 (Table 5).

Species Ordination

DCA results of presence data indicated that species composition was similar within sites in 1992 (Fig. 1). However, dissimilarity between sites steadily increased from 1992 to 1999. A greater divergence of species composition between sites was observed when species frequencies of occurrence were analyzed (Fig 2). The increasing frequencies of common species separated sites by sampling year along DCA axis 1. By 1999, sites were separated by the greater proportions of grazing-tolerant (e.g., grasses) and exotic species such as *Hypochaeris radicata* and *Trifolium repens* in the control, and

Table 5. Species turnover for forb growthform class in the Castle Lake control and exclosure sites on the debris avalanche at Mount St. Helens National Volcanic Monument. Sorensen's community coefficient was used to measure species similarity between sites and between time periods within sites. a = # species unique to first year or site, b = # species unique to second year or site, and j = # species in common.

Site & Year	a / b	j	Similarity
a) Control			
1992 - 1999	4 / 18	16	0.59
b) Exclosure			
1992 - 1999	4 / 20	16	0.57
c) Control vs. Exclosure			
1992	4 / 4	16	0.80
1999	5 / 7	29	0.83
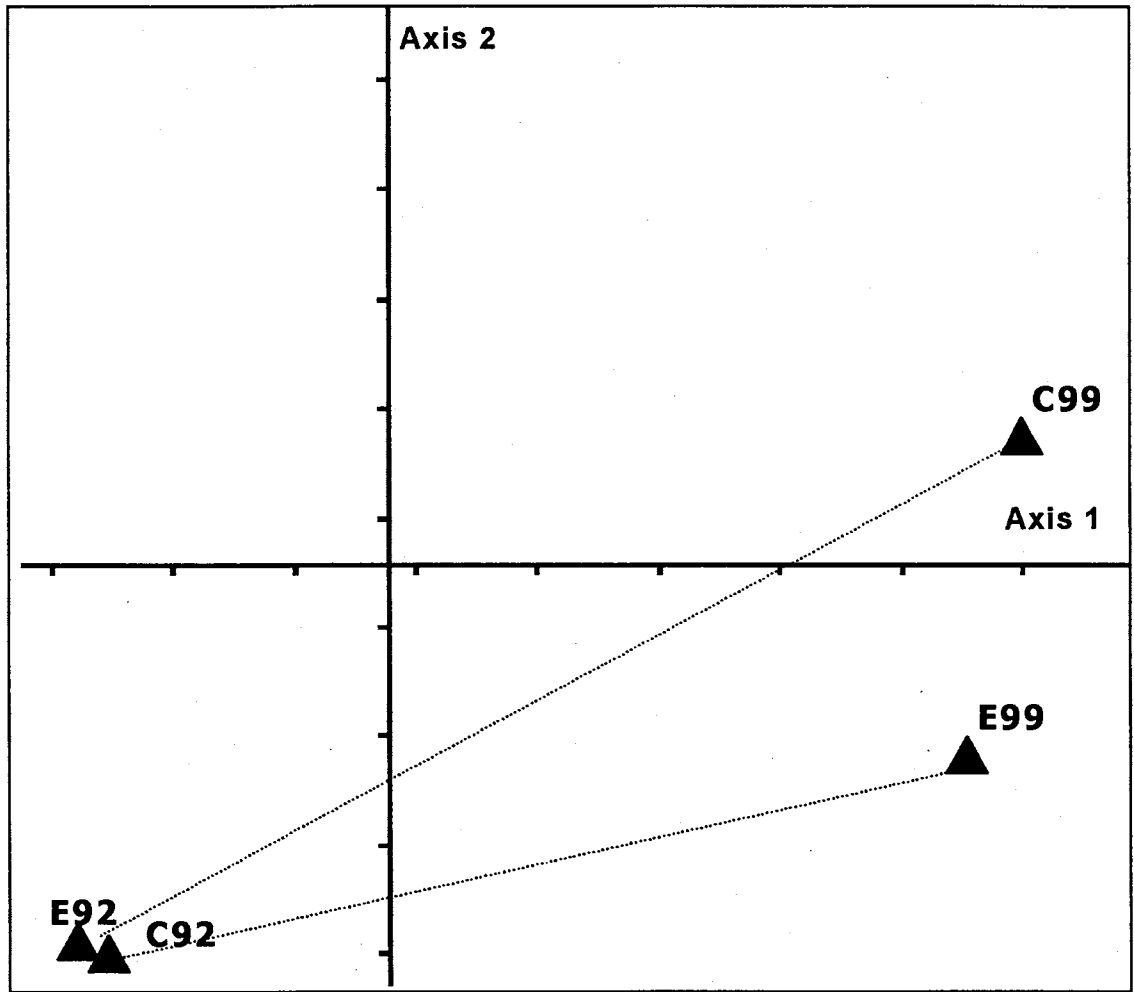
Fig. 1. Divergence of species composition from 1992 to 1999 as determined by detrended correspondence analysis of presence/absence data of 90 species. Axis 1 represents increases in site richness after 1994, whereas Axis 2 represents initial site differences and the effects of site treatment. *C* = Castle Lake control site, *E* = Castle Lake exclosure site, Mount St. Helens National Volcanic Monument.
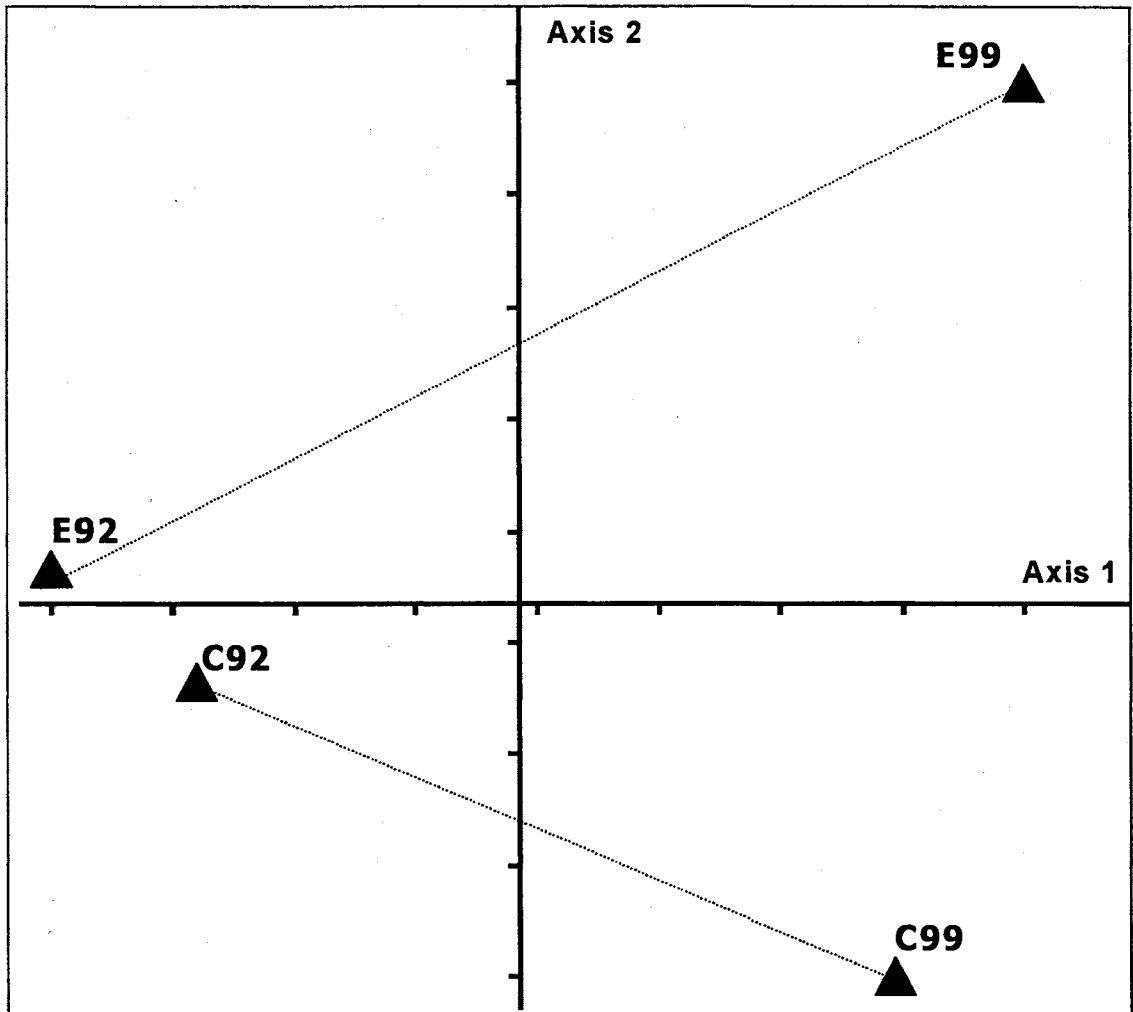
Fig. 2. Divergence of the relative frequencies of species from 1992 to 1999 as determined by detrended correspondence analysis of 43 species using frequency of occurrence data (species with frequencies of occurrence ≤5% were excluded as recommended by Hill and Gauch, 1980). Axis 1 represents increasing differences in relative species frequencies over time, whereas Axis 2 represents initial site differences and the subsequent effects of ungulate herbivory on species frequencies. *C* = Castle Lake control site, *E* = Castle Lake exclosure site, Mount St. Helens National Volcanic Monument.

modal forest species such as *Gaultheria shallon* and *Adenocaulon bicolor* in the exclosure site.

DISCUSSION

Changes in Species Richness and Density

Increases in richness in both sites indicated that herbivory was not limiting species recruitment (Table 1). Similarity of species composition was greater between sites than between sampling periods. This suggests that recruitment, site characteristics (e.g., light availability) and species interactions (e.g., competition, facilitation, or inhibition) played a greater role in compositional shifts than ungulate herbivory.

While richness increased to similar levels in both sites, species densities differed within treatments. Mean species density values increased in the control from 1992-1999, while it decreased in the exclosure over the same period (Table 1). The early colonization of the debris avalanche was strongly influenced by the haphazard distribution of suitable microsites and refugia (Adams and Dale 1987, Dale 1989). Thus, early debris avalanche communities were heterogeneous and consisted of discrete vegetated patches. The decline of species density in the exclosure may reflect a continuation of environmental partitioning by species and suggests that microsite conditions are still heterogeneous within the site. However, it is possible that subcanopy closure, shading, and development of a litter layer within the exclosure will lead to microsite homogeneity.

The increase in species density within the control site was consistent with previous studies (Chaneton and Facelli 1991, McIntyre et al. 1995), and may reflect consistent disturbance of microsites by elk. Trampling may homogenize microtopographic features and physically created open space for colonization (Hanley

and Taber 1980, Hobbs 1996). Herbivory can reduce the competitive abilities of plants as resources are allocated to tissue repair (McIntyre et al. 1995). Consistent grazing may also reduce plant size, and allow more species to reside within any 1m² in the control than in the exclosure. Thus, herbivory may facilitate colonization of sites by fast-growing, clonal species and effectively exclude grazing-intolerant species (Chaneton and Facelli 1991, McIntyre et al. 1995).

Invasive and Modal Forest Species

Life-history attributes affected vegetative cover patterns within both sites. The increase of exotic species cover in the control was nearly four times that of the exclosure (Table 2). However, no increase in modal forest species cover occurred within the control, whereas cover of these species marginally increased in the exclosure. The increase in exotic species cover in the control was largely driven by *Hypochaeris radicata* and *Trifolium repens*, two highly palatable forage species that exhibit rapid, vegetative growth (Hanley and Taber 1980).

Invasion of exotic species in the Castle Lake area may be effected by several processes. The initial colonization of the debris deposit was dominated by species with light, wind-dispersed seeds and the ability to propagate vegetatively (Dale 1989). As vegetation expanded across the deposit, elk movement and herbivory provided a consistent source of disturbance. Both trampling and herbivory have been reported to facilitate invasions of exotic species (Chaneton and Facelli 1991). Because many exotic species are highly competitive in high-resource environments (Tilman 1993, Kotanen 1997), the greater availability of nitrogen in the control due to deposition of elk feces and urine may facilitate invasions of these species. Finally, invasive exotics may be inhibited from establishment within the exclosure as litter accumulates and prohibits the germination of

relatively small seeds (Table 6) (Burke and Grime 1996, Tilman 1997). Data from the 15m line transects (Table 7) and microplot data (Table 3) suggest that canopy cover was greater in the exclosure site. Shading in the exclosure may be excluding fast-growing species that require high-to-moderate light intensities for rapid carbohydrate production (Tilman 1985, Parendes and Jones 2000).

Growthform Patterns

Changes in growthform cover and frequency of occurrence suggest that ungulate herbivory has not dramatically affected abundance of growthforms, but rather, has modified the degree of change over seven years (Table 3, 4). As expected, cover of grasses increased noticeably in the control and declined in the exclosure over the seven year period (Table 3). The frequency of grasses followed the same pattern (Table 4). Grazing tolerance and trampling may have facilitated the vegetative spread of these species (Hanley and Taber 1980, Jenkins and Starkey 1993). However, patterns of woody lifeforms did not conform to previous exclosure studies (Case and Kauffman 1997, Singer et al. 1998). The absolute increase in shrub cover was similar in the control and the exclosure (16.5 and 15.1, respectively). And while shrub cover was greater in the exclosure by 1999, then same held true in 1992. increased Shrub cover increased at a greater rate in the control site (Table 3). Furthermore, tree cover increased dramatically in the control site (9813%) from 1992 to 1999. Initial site conditions influenced rates of increase, as shrub and tree cover was lower in the control in 1992. Furthermore, the relative unpalatable nature of red alder compared to willow browse (Case and Kauffman 1997), may have prevented elk from impeding the growth and spread of the dominant canopy species.

Table 6. Litter and light intensity (micromoles/m²/sec) readings from the debris avalanche at Mount St. Helens National Volcanic Monument. Mean litter values were recorded in August, 1999 from the Castle Lake control (n=115) and exclosure (n=115) 1m² plots. Light intensity values were collected at a height of 1.5m in August, 2000 from the Castle Lake exclosure and from a dense willow stand (open site) within 150m of the Castle Lake control site.

	Exclosure	Control	Open Site
a) litter cover			
mean and standard error	63.7 (3.4)	33.0 (3.5)	-
b) light intensity			
mean maximum	585	-	1912
mean minimum	17	-	137

Table 7. Mean woody cover along 15m line intercepts in the Castle Lake control and exclosure sites and changes in cover from 1992 to 1999 on the debris avalanche at Mount St. Helens National Volcanic Monument. n = 15 in each site.

	Mean Intercept Cover			Absolute Change	
Year	Control	Exclosure	Interval	Control	Exclosure
1992	17.1	22.9	1992-1999	86.8	111.9
1999	103.9	134.8			

An analysis of species turnover among forbs revealed that elk herbivory had little effect on similarity in this growthform between treatments (Table 5). A larger change in composition of the forb assemblage occurred within each treatment due to recruitment of species over the seven years.

Successional Trajectories

DCA results suggest that elk herbivory and species recruitment have influenced species composition to diverge between sites from 1992 to 1999 (Fig. 1). And while compositional differences between sites increased steadily from 1992-1999, successional trajectories of sites appeared to be similar. This may be due to the large proportion of early seral species observed in both sites. However, an analysis of species frequencies suggested that site treatments affected the relative frequencies of species within site microplots (Fig. 2). Ungulate herbivory and trampling in the control may be creating a suitable environment for invasive species. Herbivory can suppress the growth and spread of established plants, and trampling may create microsites suitable for colonization by invasive plants (Chaneton and Facelli 1991, McIntyre et al 1995, Hobbs 1996). Shading and litter accumulation in the exclosure (Table 6) may be facilitating the colonization of sites by modal forest species. Typically, these species do not require high light-intensities and their relatively larger seeds are better suited for survival in litter (Halpern 1989, McKenzie et al. 2000).

While ordination analyses have been used to interpret successional trajectories of sites in the Pacific Northwest (Halpern 1988, Halpern et al. 1990), the unique disturbance history of the debris avalanche, the variety of species present, and the limited time frame of analyses, constrain the predictive value of DCA results. Interpretation is limited

further by the exclusion of 47 species with frequencies of occurrence ≤5% from analyses (Fig. 2).

Because red alder and sitka willow dominate canopy layers in both sites, it would appear that the communities would be best classified as *riparian* (Franklin and Dyrness 1973). Franklin and Dyrness (1973) noted that the understory composition of regional riparian communities was highly variable, and ranged from little to dense vegetation. However, pre-eruption vegetational communities and the presence of conifers throughout the debris avalanche suggest that a mixed douglas-fir - western hemlock forest may eventually return to the North Fork Toutle River valley (Peter Frenzen, Monument Scientist, *personal communication*). Furthermore, modal conifer forest species have been present (e.g., *Tsuga heterophylla*) since at least 1992.

CONCLUSION

Successional trends often result from complex interactions between disturbance characteristics, initial species composition, life-history traits, and environmental gradients (Connell and Slatyer 1977, Sousa 1984, Tilman 1985, Halpern 1988). Furthermore, the relative importance of factors may be dependent on the spatial and temporal scales in which interactions are observed (McCook 1994).

The applicability of Castle Lake data are limited in scope. The debris avalanche is a highly heterogeneous environment in terms of below-ground resources, species composition, and microsite characteristics (Dale 1989; Peter Frenzen, Monument Scientist, *personal communication*). Thus, data from the Castle Lake sites should not be interpreted as representative of the entire debris avalanche environment. Results were complicated further by initial site differences, lack of replication, and poor

documentation of elk abundance and behavior within the debris avalanche. Limitations notwithstanding, important trends were identified.

Increases in mean microplot cover and species richness were best explained as temporal trends. However, important herbivory-driven patterns were identified when species were separated by gross life-history traits. The increase in exotic species cover and abundance in the control site relative to the exclosure, suggests direct and indirect facilitation by elk. Elk may be disturbing microsites and facilitating clonal expansion or colonization by wind dispersed seeds, and herbivory may reduce the abundance of grazing-intolerant species. The low abundance of modal forest species may be related to the lack of nearby seed sources (Dale 1989, Peter Frenzen, Monument Scientist, *personal communication*). However, modal forest species should eventually disperse into the debris avalanche as the recovery of disturbed forest communities continues throughout the monument (Halpern et al. 1990, del Moral 1998).

Elk may be impacting debris avalanche vegetational dynamics across various temporal and spatial scales (Hobbs 1996). Fine scale, short-term effects include removal of plant biomass, stimulation of lateral growth, inhibition of sexual reproduction, creation of exposed microsites, and changes in C/N ratios in soil organic material (Mattson 1980, Chaneton and Facelli 1991). Over longer temporal scales, plant resources may be depleted as stored carbohydrates are allocated for tissue regeneration. Competition with nearby plants may be increased or decreased depending on grazing intensities, preferential selection by elk, and changes in utilization of above- and below-ground resources (Tilman 1985, 1993; McIntyre et al. 1995). At coarser spatial scales, because herbivores congregate in preferred grazing patches, species heterogeneity may be

sustained in an already heterogeneous environment, though plant diversity within patches may decrease (Hanley 1984, Jenkins and Starkey 1993). This may be accentuated by patchy deposition of N in feces and urine (Hobbs 1996). Potential long-term, coarse scale effects include increases in grazing-tolerant species, indirect interactions with other herbivores, amelioration of soil N conditions, and the suppression of woody species. Elk are shaping the recovery of communities on the debris avalanche, and will continue to play an important role in successional dynamics throughout Mount St. Helens National Volcanic Monument.

Species Observed in the Castle Lake Control and Exclosure Sites, 1992-1999.

Binomial & Lifeform Code	Exotic Species	Modal Forest Species
Growthform 1 - graminoids		
Agrostis spp. (A. scabra & A. exerata)		
Aira caryophyllea	X	
Deschampsia elongata		
Elymus glaucus		
Festuca bromoides		
Festuca rubra		
Festuca spp.		
Gramin spp.		
Holcus lanatus	X	
Growthform 2 - sedges & rushes		
Carex spp.		
Carex mertensiana		
Eleocharis palustris		
Juncus acuminatus		
Juncus arcticus		
Juncus bolanderi		
Juncus brachyphyllus		
Juncus bryoides		
Juncus bufonius		
Juncus effusus		
Juncus ensifolius		
Juncus mertensianus		
Juncus oxymeris		
Juncus regelii		
Juncus tenuis		
Scirpus acutus		
Scirpus lacustris		
Scirpus microcarpus		
Growthform 3 - forbs, ferns, & horsetails		
Adenocaulon bicolor		X
Anaphalis margaritacea		
Aruncus dioicus		X
Castilleja miniata		
Centaurium umbellatum		
Cerastium spp.		
Cirsium spp.	X	
Crepis capillaris		

Epilobium angustifolium		
Epilobium minutum		
Epilobium paniculatum		
Epilobium watsonii		
Equisetum arvense		
Equisetum hyemale		
Equisetum palustre		
Equisetum telmatiea		
Fragaria spp.		
Gnaphalium chilense	X	
Gnaphalium microcephalum	X	
Hieracium albiflorum		
Hypochaeris radicata	X	
Lactuca muralis	X	
Lactuca serriola	X	
Lotus purshiana	X	
Lupinus lepidus		
Madia spp.		
Mimulus guttatus		
Myosotis laxa	X	
Parentucellia viscosa	X	
Petasites frigidus		
Plantago major	X	
Polystichum munitum		X
Rumex acetosella	X	
Saxifraga ferruginea		
Sagina procumbens		
Sagina spp.		
Senecio jacobaea	X	
Senecio sylvaticus	X	
Senecio vulgaris	X	
Sonchus asper		
Spergularia macrotheca		
Spiranthes romanzoffiana		
Stellaria calycantha		
Stellaria longifolia		
Taraxacum officinale	X	
Trifolium pratense	X	
Trifolium repens	X	
Typha latifolia		
Veronica spp.		

Growthform 4 - shrubs & woody vines

Alnus sinuata		
Gaultheria ovatifolia		X
Gaultheria shallon		X

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Menziesia ferruginea	X
Rubus spp.	
Salix lasiandra	
Salix sitchensis	
Vaccinium spp.	X

Growthform 5 - trees

Abies amabilis	X
Abies procera	X
Alnus rubra	
Populus trichocarpa	
Pseudotsuga menziesii	X
Tsuga heterophylla	X

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Chapter 3: Interactions Between Sitka Willow (*Salix sitchensis*) and the Willow Stem Borer (*Cryptorhynchus lapathi*) on the Debris Avalanche of Mount St. Helens National Volcanic Monument

ABSTRACT

In July, 2000, sitka willow genets were sampled in a mesic (n=50) and a hydric site (n=50) on the debris avalanche at Mount St. Helens National Volcanic Monument to address relationships between sitka willow and the willow stem borer. Initial analyses indicated that site conditions affected willow morphology. Thus, subsequent analyses were performed within each site group. I tested for differences in genet, ramet, and current annual growth (CAG) morphology between treatments (bored by stem borer and not selected by the borer). Bored genets were taller, had more ramets, more shoots per ramet, and greater mean ramet diameters than unaffected genets in the mesic site (T^2 test, p<0.001). However, bored genets only had greater mean ramet diameters in the hydric site (T^2 test, p = 0.02). There was no significant difference in unbored ramet morphology across genet level treatments in either site (p>0.3). Tests of ramet morphology within bored genets indicated that bored ramet diameters were significantly greater than unbored ramets in both sites (paired t-tests, p<0.001 for both sites). ANCOVA results indicated that total Kjeldahl nitrogen concentrations were significantly greater in CAG shoots from bored ramets than in unbored ramets from unbored genets in both site types (p=0.03, mesic site; p<0.01, hydric site). The relationship between mean CAG shoot diameters and the number of sister ramets for mature unbored ramets (basal diameters >1.31cm) differed in genet treatment groups. Pearson correlation coefficients were significant for both ramet groups (p=0.03). However, while the relationship was positive in unbored genets (0.38), the relationship was negative (-0.44) in bored genets. The difference in relationships suggests that genet level boring affects resource sharing among ramets. Results indicated that willow stem borer larvae have specific morphological requirements and may induce chemical defenses in sitka willows. Moreover, genet-level boring may divert resources from mature unbored ramets to bored ramets for compensatory growth or chemical defense.

INTRODUCTION

The broad goal of this study was to describe relationships between the willow stem borer and a population of Sitka willow on the debris avalanche in Mount St. Helens National Volcanic Monument (MSHNVM) across three distinct scales: willow genet, ramet, and current annual growth (CAG) shoot. Several hypotheses were addressed – 1) Availability of soil moisture influences borer-willow relationships. 2) Willow selection by the stem borer is mediated by willow morphology. 3) Larval boring affects nitrogen concentrations in new shoots. 4) Elk browsing intensity interacts with larval activity.

Effects of Herbivory on Woody Plant Physiology and Morphology

The most common interaction that effects plant physiology and morphology is herbivory (Crawley 1983, Karban and Baldwin 1997). Herbivory can reduce plant vigor or initiate compensatory growth, stimulate clonal expansion, modify plant architecture, and facilitate seed dispersal. The impact of herbivory on plants is dependent on the amount and type of tissues affected, the timing of the interaction relative to plant development and health, the amount of carbohydrate reserves, the herbivory history of the plant, and environmental factors (Crawley 1983, Kozlowski et al. 1991). Plant growth is directly affected by the complete or partial consumption of photosynthetic structures (e.g. leaves), storage structures (e.g. roots), transportation structures (e.g. xylem and phloem), and reproductive structures (e.g. flowers and fruits) (Crawley 1983). Thus, herbivory can influence photosynthetic capability, carbohydrate balances, water and nutrient uptake, and structural integrity. The phenological state of a plant influences how the consumption of tissues affects the plant. For example, consumption of leaves near the end of a growing season is less detrimental to a plant than if the same leaves are

consumed shortly after emergence, as the plant is able to produce carbohydrates with those leaves for most of the growing season (Crawley 1983).

Many shrubs and trees exhibit induced chemical responses to herbivory (Karban and Baldwin 1997). Secondary compounds such as alkaloids, phenolics, and terpenes are metabolic by-products that are thought to play an important role in plant-herbivore interactions (Palo 1984, Kozlowski et al. 1991). The ability of a secondary compound to deter or attract herbivory appears to be herbivore-specific (Danell and Huss-Danell 1985). Ungulate herbivores often prefer shoots high in nitrogen-rich secondary compounds (Southwood 1985), whereas defoliating and sucking insects are often deterred by the presence of similar chemical compounds (Stein and Price 1995, Kearsley and Whitham 1997).

Plant shape is determined by the amount and distribution of branching (Crawley 1983). Typically, the terminal bud of a leading stem suppresses branching at lower nodes (Crawley 1989, Kozlowski et al. 1991). Removal of a terminal bud releases lower nodes from apical dominance and allows shoot development, or branching, to occur (Crawley 1989, Kozlowski et al. 1991). In open areas, clipping of shoots often results in plants developing relatively low, bushy shapes. Thus, photosynthetic productivity can be enhanced (Crawley 1983). Consumption of tissues can stimulate plants to allocate carbohydrates to vegetative reproduction in lieu of production of reproductive structures. Similarly, many plants have evolved rapid growth responses to tissue damage. Herbivory often stimulates the growth of new ramets in clonal species as apical dominance is removed. However, herbivore attack in closed canopies does have, in cases, detrimental effects on a plant. Removal of elongated apical shoots that allow a plant to compete for

light would not necessarily promote lower shoot development, and would impede the competitive ability of the plant (Crawley 1983, Kozlowski et al. 1991).

Environmental Conditions and Physiological Responses to Herbivory

Resistance to herbivory is constrained by environmental conditions during periods of plant-herbivore interactions, and also by phylogenetics and evolutionary history (Knight and Hekkenen 1980, Kozlowski et al. 1991). Extremes in moisture availability can modify plant physiology, availability of soil nitrogen, and thus, plant nitrogen concentrations (Kozlowski et al. 1991, Bowman and Conant 1994). In turn, nitrogen concentrations in plants influence availability and concentrations of chemical defensive compounds (Stein and Price 1995, Karban and Baldwin 1997).

Drought conditions lead to increased hydrolysis of proteins and thus, increased concentrations of soluble nitrogen and secondary compounds (Mattson and Haack 1987). Furthermore, flooding, or soil saturation, can lead to nitrification of ammonium and loss of nitrate via denitrification (Kozlowski et al. 1991). Loss of soil nitrogen and reductions in photosynthesis associated with soil saturation, may reduce nitrogen concentrations in plants subjected to consistent flooding (Regehr et al. 1975).

Willow Response to Herbivory

The effects of herbivory on willows, and other members of the *Salicaceae*, have been well documented (Tahvanainen et al. 1985, Craig et al. 1986, Sacchi and Price 1992, Hakulinen et al. 1995). Willows often respond to herbivory by rapid, compensatory growth of new tissues (Singer et al. 1998). New and larger shoots are produced within ramets subjected to insect and ungulate heribivory (Southwood 1985, Elmqvist et al. 1987). Genet-wide browsing can induce genets to produce new ramets

(Ottenbreit and Staniforth 1992). Overtime, herbivory can drastically alter genet architecture (Singer et al. 1998).

A trade-off exists between allocating resources for clonal growth and sexual reproduction (Lindroth 1989, duToit et al. 1990). Singer et al. (1998) reported that persistent browsing of reduced the occurrence of flowering in two willow species. Insect herbivory can also interfere with the production of reproductive structures (Stein and Price 1992).

Willows have exhibited induced chemical responses to sucking insects and browsing mammals (Palo 1984, Elmqvist et al. 1987, Bowman and Conant 1994). Nitrogen-rich secondary compounds, typically alkaloids such as salicin and salicortin, are released in tissues affected by herbivory (Palo 1984). Although induced responses can stimulate an increase in browsing by ungulates, chemical defenses have been shown to deter further insect herbivory, although exceptions do occur (Mattson 1980, Stein and Price 1992, Karban and Baldwin 1997).

Release of resins in damaged tissues has been documented in conifer species affected by insects (Knight and Hekkenen 1980). The flow of resins is thought to flush-out phloem-consuming insects (e.g., bark beetle). Although this defense mechanism has not been documented in willows, copious flow of resin and sap is characteristic associated with fast-growing trees. Flows of sap were observed extruding from boring wounds in willows affected by the willow stem borer in MSHNVM (*personal observation*). Excavation of willow stem borer wounds reveal dark purple staining of affected tissues (*personal observation*). Staining of tissues often indicates abrupt changes in chemical concentrations (Kozlowski et al. 1991), and in this case, may indicate the use

of chemical defenses to repel larvae or compartmentalize wounded tissues (Kolowski et al. 1991).

Phloem-Boring Insects

Meristematic insects, bark beetles and phloem borers, typically enter cracks or fissures in bark, consume phloem in early larvae stages, and eventually move past meristematic tissues into secondary phloem and xylem to either feed or pupate (Knight and Hekkenen 1980). Although many species attack old and weakened trees, others prefer young, vigorous hosts (Knight and Hekkenen 1980).

Although not fully understood, infestations appear to be cyclical for many meristematic insects (Kozlowski et al. 1991). Cyclical outbreaks of bronze birch borers (*Agrilus anxius*) and southern pine bark beetles (*Dendroctonus frontalis*) have been well documented (Knight and Hekkenen 1980). While environmental stress and ecological disturbances have been blamed for massive infestations, the direct causal mechanisms likely involve complex interactions between hosts and environmental conditions (Kozlowski et al. 1991).

METHODS
Willows

Members of the genus *Salix* (*Salicaceae*) are widely distributed throughout temperate and boreal regions of the northern hemisphere. They primarily occupy moist, resource-rich sites (e.g. wetlands and riparian zones) and are considered to be early-sere species in many environments (Alliende and Harper 1989, Sacchi and Price 1992). However, in some moist boreal zones willows are a climax species (*sensu* Clements) (Bowman and Conant 1994). They are dioecious plants that range in morphology from small, prostrate woody shrubs to large, spreading trees. The typical ratio of females to

males for a given willow population is approximately 2:1, but exceptions do occur (Alliende and Harper 1989). A characteristic of most *Salix* species is a rapid growth rate (Palo 1984). Within a single growing season, a single ramet may produce over 50 new shoots or if only producing a single apical shoot, yearly growth may exceed 1 meter in length (*personal observation*). Although lifespan data for willows are scant, Ottenbreit and Staniforth (1991) reported senescence of willow shrubs after twelve years.

Adams and Dale (1987) and unpublished MSHNVM data indicate that the debris avalanche supports three species of willow: sitka (*S. sitchensis*), pacific (*S. lasiandra*), and Scouler's (*S. scouleriana*). Sitka willow is a shrub or small tree, 1-8 m tall; leaves are obovate, with satiny hairs on the lower sides (Pojar and MacKinnon 1994). Pacific willow is a tall, slender shrub or tree, 1-12 m tall. Leaves are relatively long and narrow (Pojar and MacKinnon 1994). Scouler's willow is very similar in morphology to sitka willow, but the leaves are generally ovate (Pojar and MacKinnon 1994). It should be noted that the morphology of willows is very plastic and can make field identification difficult (Palo 1984, Pojar and MacKinnon 1994). All three species are regionally found in riparian zones and clearings from low to middle elevations (Pojar and MacKinnon 1994).

Willow Stem Borer

A member of the *Curculionidae* (weevil) family of beetles, the willow stem borer was first described in Europe by Linnaeus in 1758 (Harris and Coppel 1967). The species was thought to have been inadvertently introduced to North America in the late 1800's through nursery stock (Smith and Stott 1964, Harris and Coppel 1967). The beetle attacks members of the willow, poplar, alder, and birch genera in temperate regions of the northern hemisphere (Smith and Stott 1964, Harris and Coppel 1967). However, Harris

and Coppel (1967) found that caged beetles did not feed on red alder, quaking aspen (*Populus tremuloides*), or paper birch (*Betula papyrifera*). Studies have suggested that the poplar-and-willow borer prefers willow species and black cottonwood (Smith and Stott 1964, Harris and Coppel 1967). Although distributed throughout North America, no estimates of population size and density have been reported.

Past studies have found that the lifecycle of the willow stem borer may last one to three years, with two to three years being more common (Smith and Stott 1964, Harris and Coppel 1967). From July to August, eggs (1 mm long) are oviposited into small holes that adults create in the bark of trees; holes are usually cut at damaged areas, lenticels, or branch bases within one meter of the ground (Harris and Coppel 1967). Eggs hatch in about three weeks (Harris and Coppel 1967). Harris and Coppel (1967) found that the larval stage develops through six instars, ranging form one to thirteen mm in length. The first instar frequently overwinters, but the duration of the remaining instars last two to four weeks each. After overwintering the larvae mine around the circumference of infested trees. At approximately the fourth instar, the larvae bore inward and move upward through xylem or pith to pupate (Harris and Coppel 1967). The pupal stage lasts two to three weeks with the transformation of late pupae to adults frequently occurring from July to September (Harris and Coppel 1967). Adults overwintering in trees emerge through mines created by larvae; adults may also overwinter in ground litter (Harris and Coppel 1967). Adults are oval-shaped weevils, about 8 mm long, and are both pink and black or gray and black (Harris 1981). Mating occurs one to two days after emergence with eggs developing in mated females within

two weeks. Ovipositing follows egg development by approximately one week (Harris 1981, Harris and Coppel 1967).

Adults feed on bark during the evening and early morning and return to bark crevices or litter during the day (Harris 1981). Adults rarely fly, but a flight distance of 6m was observed by Smith and Stott (1964). Thus, movement is usually restricted to crawling (Smith and Stott 1964).

Borer-Willow Dynamics

The willow stem borer currently infests willows and black cottonwoods on the debris avalanche (Peter Frenzen, Monument Scientist, *personal communication*). The density and distribution of the organism on the debris avalanche, and the monument at large, is unknown. However, the borer appears to be common where willows are located throughout the debris avalanche and pumic plain (Peter Frenzen, Monument Scientist, *personal communication*). Preliminary data suggest that the borer selects willow ramets that are greater than 0.7 cm in diameter (*personal observation*); Previous work has suggested a larger diameter requirement of 2.24cm (Baker 1972). Larvae bore around stems in cambial tissues and then tunnel inward and upward to pupate. Although some girdling of cambium does occur, most ramets are not killed this way. Rather, they suffer structural damage and become susceptible to windthrow (Baker 1972).

Study Area

Mount St. Helens National Volcanic Monument is located in southwestern Washington (46° 16' N, 122° 09' W) and is surrounded by Gifford Pinchot National Forest and patches of state and private lands. The climatic and physiographic features of MSHNVM are typical of the Cascade Mountain Range of southern Washington (Foxworthy and Hill 1982). Cool, wet winters and hot, dry summers characterize the

regional climate. Temperatures may range from –4.2 °C to 0.5 °C in January and 7.3 °C
to 22.2 °C in July (mean minimum and maximum values). Precipitation averages 237 cm
annually, with only 7% falling between June and August (Franklin and Dyrness 1973,
Halpern et al. 1990). The region receives approximately 75% of its annual precipitation
between October and March, with persistent snowpacks forming above 1,000 meters
(Franklin and Dyrness 1973).

Debris Avalanche

During the May 18, 1980 eruption, approximately 2 million m³ of rock, glacial
ice, water, soil, and vegetation was propelled down the North Fork Toutle river valley at
an initial speed of 100 to 110 m per second (Pincha 1987). The deposit eventually
covered more than 7,000 ha and extended 22.9 km west of the crater (Pincha 1987).
North-south flowing streams were impounded and new bodies of water, such as
Coldwater and Castle lakes, were formed (Meyer and Sabol 1989). The new surface was
devoid of vegetation and was composed of hummocks (mounds of unconsolidated
material) of varying shapes and sizes (Pincha 1987, Meyer and Sabol 1989). Samples
taken near Castle Lake (southern edge of the debris avalanche) indicated that the debris
substrate was primarily rock (particles > 2mm in diameter) with smaller particles
consisting of approximately 62% sand, 33 % silt and 4% clay. Aeration was suitable for
plant growth, but water percolation was high and nitrogen and phosphorus levels were
found to be lower than local soils (Adams and Dale 1987, Dale 1989). West-flowing
stream channels became heavily braided and were subjected to seasonal variations in
channel morphology (Meyer and Sabol 1989). Seeps, fed by impounded water sources
and buried streams, developed in depressions and on eroded hummock slopes and stream
channels (Meyer and Sabol 1989).

Although initially devoid of vegetation, regrowth on the debris avalanche was influenced by plants emerging from buried root stocks in the debris and wind-dispersed seeds from the valley slopes (Dale 1989). In general, species with close seed sources, high seed production, and adequate seed dispersal mechanisms dominated the initial revegetation of the avalanche. Colonizers such as thistle (*Cirsium* spp.), fireweed *(Epilobium angustifolium)*, and willow produce light, wind-borne seeds that are capable of traveling long distances; lupine (*Lupinus* spp.) and willow are capable of producing new stems from rhizomes (Dale 1989). By 1981, several thousand willows were observed on the avalanche deposit (Adams and Dale 1987). To date, red alder and willows are the dominant woody species, whereas forbs and grasses constitute the majority of species on the deposit (Peter Frenzen, Monument Scientist, *personal communication*). Conifer establishment has been hampered by unfavorable site conditions (xeric amd nutrient-poor substrates), poor seed dispersal, and intense winter browsing by the resident elk herd (Frenzen and Franklin, 1985).

Willow Community

A large expanse of willow shrubs (hereafter, Castle Lake willow community) was selected to address willow-borer relationships. The area was selected because of its close proximity to the Castle Lake control and exclosure sites, and thus when coupled with the elk exclosure study, would help to address the broad impact of herbivory in the area. A large subsurface seep is located below the community (Peter Frenzen, Monument Scientist, *personal communication*). Water flows northwest from the Castle Lake blockage to the North Fork Toutle river (Meyer and Sabol 1989). General morphological characteristics of the terrain suggest that water comes to the surface intermittently. A

large portion of the willow community was inundated by up to 10cm of water from at least July to late August, 2000 (*personal observation*).

Field Methods

Preliminary data were collected from the Castle Lake elk exclosure and control sites in late August, 1999 (Appendix *A*). Within each site, 1m² microplots that contained willow genets were randomly selected. Each genet was numbered and the number of live and dead ramets was recorded. The occurrence of browsing and boring was noted. To assess willow ramet characteristics, 31 ramets in the exclosure and 26 in the control were randomly selected and tagged. Basal stem diameters were measured to the nearest mm, and ramet heights and the lengths of the longest and the shortest CAG (current annual growth) shoots were measured to the nearest cm. The number of browsed and unbrowsed CAG shoots and the number of dead shoots (previously browsed) were recorded and the presence of the willow borer was noted.

Two areas were arbitrarily selected in the Castle Lake willow community in July, 2000. To address apparent site differences, a population was selected in a mesic site and a wet site. The hydric area had up to 10cm of standing water into late August, whereas the mesic site had no standing water (*personal observation*). Five random compass directions were selected for sampling transects from the center of each area. Genets were divided into two herbivory treatments. Bored genets (*BO*) were defined as shrubs with at least one ramet showing signs of willow borer infestation. A borer wound was considered to be active if frass and/or sap was extruding from wounds when genets were selected in July. Unbored genets (*NS*) showed no signs of boring. However, all genets had been browsed by elk over the previous fall and winter. Five bored and five unbored genets were identified along each transect, such that each genet was ≥ 3m from each

other to ensure biological independence (*sensu* Ottenbreit and Staniforth 1992, n = 100).

An unbored ramet ≥0.75 cm in diameter was randomly selected within each genet (n = 100). The diameter requirement was used to select ramets that could support borer larvae. Additionally, a bored ramet was randomly selected within each bored genet (n = 50). Finally, a CAG shoot was randomly selected and removed from a subsample of the selected ramets for nitrogen analyses (n = 120). Kozlowski et al. (1991) suggested that yearly shoot growth of members of the *Salicaceae* can continue into late summer. Accordingly, all measurements were performed in August, 2000.

To help delineate site differences, vegetation data were collected from 3, 50m transects randomly placed on each substrate site. Presence of species was observed in 10, 1m² quadrats spaced by 5m increments along each transect (n=60, Appendix *B*).

<u>Genet Level</u>

All ramets within a genet were counted and their diameters measured. Diameters were consistently measured where ramets began to noticeably swell at stem bases. Genet heights were measured from ground level to the highest reach of the tallest CAG shoot. The number of CAG shoots was counted on five randomly selected ramets with diameters ≥0.75cm. Because of consistent and distinct color differences in shoot bark, shoots from the previous year were easily identified. An ungulate browse intensity index was produced by dividing the number of browsed 1999 CAG shoots by the total number of 1999 shoots on the five selected ramets. The number of active borer holes was counted for each genet. Finally, the density of willow shrubs within 1.5m of the centers of each selected genet was measured. Genets were counted >50% of the genet was located within the circle. Because sampled genets were within 3m of each other, the 1.5m radius discouraged repetitive sampling of neighboring willows.

Ramet Level

Height (mm), number of CAG shoots, and browse intensity was measured on each ramet. Additionally, basal diameters of three randomly selected CAG shoots were measured on each ramet to estimate the mean diameter of CAG shoots (mm). The number of active borer wounds was counted on each bored ramet to develop a boring intensity index.

Shoot Level

In late August, one CAG shoot was randomly selected on each sampled ramet and removed for shoot level analyses. Basal diameter, length, and dry weight was measured for each shoot.

Analyses

Analyses were split into two components to separate herbivore treatments from potentially confounding influences of several ecological factors. Initial analyses were performed to help delineate differences in vegetative associations, genet density, and elk browsing between genet populations. Analyses were then performed within each willow population to address herbivore treatments (Fig. 1). Tests were run with PC-ORD, SYSTAT 9.0, and NCSS 97 software packages.

Initial Analyses

Prior to genet-level analyses, genets were grouped by substrate type – mesic and hydric. Hotelling's T^2 procedure was used to test differences in genet morphology. The T^2 procedure is identical to a MANOVA, but tests for differences between two populations. Conceptually, the MANOVA procedure was deemed to be inappropriate as multiple populations were not tested. Although the T^2 statistic was unavailable within software packages at my disposal, Zar (1999) reported that both procedures yield
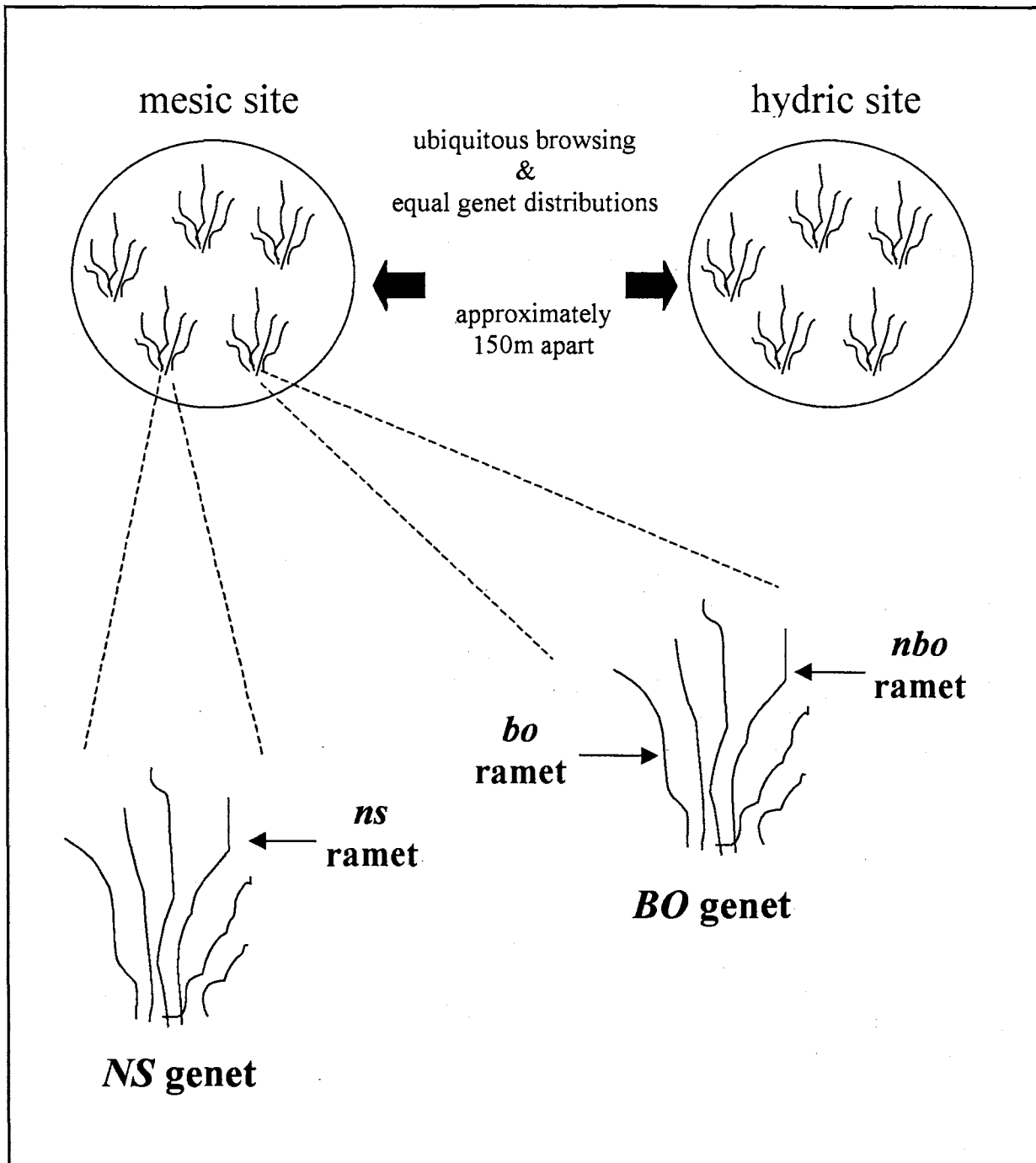
Fig. 1. Schematic of study design and willow treatments.

identical results. Thus, the Pillai trace statistic was substituted for the T^2 statistic. It was assumed that the T^2 procedure held assumptions of homoscedasticity and equality of covariances as required by MANOVA (Zar 1999). However, Zar (1999) reported that the Pillai trace statistic was robust to departures from these assumptions.

Detrended Correspondence Analysis (DCA) was used to illustrate compositional differences associated with substrate groups using species presence data (Hill and Gauch 1980). DCA measures species and site frequency data simultaneously and position sites using a Chi-squared distance metric based on compositional dissimilarity (Hill and Gauch 1980, Michin 1987). The process of detrending and rescaling data changes the meaning of axis eigenvalues, such that they no longer represent the amount of variation explained by axes. Instead, each axis is divided into standard deviation units that separate sites by their relative dissimilarities in species composition.

Herbivory Analyses

Within each population, genets and ramets were identified by herbivore treatments:

Table 1. Willow genet and ramet treatment categories and the corresponding treatment symbols.

Genet Symbol	Ramet Symbol	Treatment
BO		actively bored by *C. lapathi* larvae
	bo	actively bored by *C. lapathi* larvae
	nbo	not bored by *C. lapathi* larvae
NS		not selected by *C. lapathi*
	ns	not selected by *C. lapathi*

Genet Level

Hotelling's T^2 procedure was used to test for morphological differences between genet types (*BO* vs. *NS*). Morphological characteristics used in the analysis were:

maximum ramet height to the nearest cm, number of live ramets, mean live ramet diameter, and an estimate of the number of CAG shoots per ramet.

To meet assumptions of normality, data were transformed when necessary. Ramet height and the number of CAG shoots per ramet were $\log_{10}$ transformed, while the number of live ramets required a square-root transformation.

Ramet Level

The impact of genet-level boring on unbored ramet morphology was assessed by comparing morphological characteristics between unbored ramets (*nbo* vs. *ns*), within each population, with Hotelling's T^2 test. Metrics used for the composite morphology variable were: ramet diameter, number of CAG shoots per ramet, mean CAG shoot diameter, and browse intensity. No data transformations were necessary for either population.

Morphological characteristics of ramet treatments within bored genets (*bo* vs. *nbo*) were compared with multiple paired t-tests. As recommended by Zar (1999), α was adjusted to 0.005 to account for α inflation due to interdependence of the data. Metrics tested were: ramet diameter, number of CAG shoots per ramet, mean CAG shoot diameter, and browse intensity. The number of CAG shoots and ramet height were $\log_{10}$ transformed in the hydric population, whereas the number of CAG shoots was square-root transformed in the mesic population.

CAG Shoot Level

Shoots were dried and ground for chemical analyses, and then digested and distilled via the macro-Kjeldahl method (Soil Science Society of America, 1990). The Kjeldahl process extracts nearly all ammonium (NH_4) from samples. Therefore nitrogen concentrations were expressed as total Kjeldahl nitrogen, or TKN. Due to sampling

procedures, CAG shoots from *bo-nbo* ramet pairs were not considered to be biologically independent. Accordingly, CAG TKN levels were analyzed between *ns* and *nbo* ramets, and between *ns* and *bo* ramets within genet substrate populations using separate ANCOVA procedures.

Covariates differed between shoot populations for both ANCOVA's. Within the *ns-nbo* ANCOVA, CAG shoot dry mass (log_{10}) was identified as the most significant covariate in the mesic population, whereas ramet basal diameter (log_{10}) was selected for the hydric population. The *nbo-bo* ANCOVA used CAG shoot dry mass (log_{10}) for the mesic population and the sum of sister ramet diameters for the hydric population. The impact of genet-level boring on CAG shoot N concentrations was addressed through the *ns* and *nbo* ANCOVA. Whereas, comparisons between *ns* and *bo* ramets addressed the combined impact of genet-level and ramet-level boring on CAG shoots.

Herbivore Interaction

A 2-Factor ANOVA was performed on all bored genets (n = 50) with boring intensity as the dependent variable, and genet density and browsing intensity as fixed factors. Factor levels were defined prior to analysis to meet assumptions of equal replication (Zar 1999). Boring intensity data were log_{10} transformed to meet assumptions of normality and heteroscadasticity (Zar 1999). Genet density level was defined as: low = <7 genets within 1.5m (n = 19) and high = ≥7 genets within 1.5m (n = 21). Browse intensity was defined as: low = 17-70% (n = 13), moderate = 71-77% (n = 13), and high = >77% (n = 14).

Potential Resource Sharing

Pearson correlation coefficients between the mean diameter of CAG shoots selected for N-analyses and number of sister ramets for unbored ramets (*ns* and *nbo*) were

calculated to address potential resource sharing within genets. Data were $\log_{10}$ transformed to produce a linear relationship (Zar 1999). Significant differences in correlation coefficients might suggest that genet-level boring was affecting the source-sink dynamics of resource sharing between ramets for CAG shoot growth.

RESULTS

Population Comparisons

Substrate conditions separated genets by affecting morphological traits independent of herbivory. T^2 results indicated that genets on hydric substrates were morphologically distinct from genets on mesic substrates (p = <0.001, Table 2). Genets within the hydric population had more and taller ramets than mesic population genets. In contrast, mean ramet diameters and the average number of CAG shoots were greater in the mesic population. However, genet densities and browsing intensities were similar between populations (p = 0.57). DCA of vegetation associated with substrate moisture conditions suggested that sites were compositionally distinct (Fig. 2).

Genet Morphology

T^2 results showed that genets selected by the willow borer (*BO*) were morphologically distinct from unselected genets (*NS*) in the hydric (p = 0.02) and mesic (p = <0.001) site (Table 3). Bored genets had more and larger ramets in the mesic substrate population. However, the difference was only expressed by greater average ramet diameters within bored genets in the hydric population.

Ramet Morphology

Unbored ramet morphology did not significantly differ between genet types in either site (p = 0.77, hydric; p = 0.29, mesic; Table 4). Bored ramets (*bo*) were larger in diameter and had more CAG shoots than unbored ramets (*nbo*) in both substrate

Table 2. Morphological and ecological comparisons between willow populations (mesic and hydric sites) on the debris avalanche at Mount St. Helens National Volcanic Monument. Comparisons performed with Hotelling's T² procedure, α = 0.05. Sites were delineated by the presence of standing water in the hydric site throughout July and August, 2000.

Variables	means		p-value
	mesic	hydric	
a) genet morphology	mesic ≠ hydric		< 0.001
max. ramet height, cm	158	164	
# live ramets	9	15 *	
mean live ramet diameter, cm	1.36	1.19 *	
# CAG shoots per ramet	26	23	
b) ecological conditions	mesic = hydric		0.57
genet density (# genets within 1.5m radius)	6.2	7.3	
browse intensity (% CAG shoots browsed over winter)	0.72	0.71	

* indicates statistical difference between sites, $p \leq 0.05$.
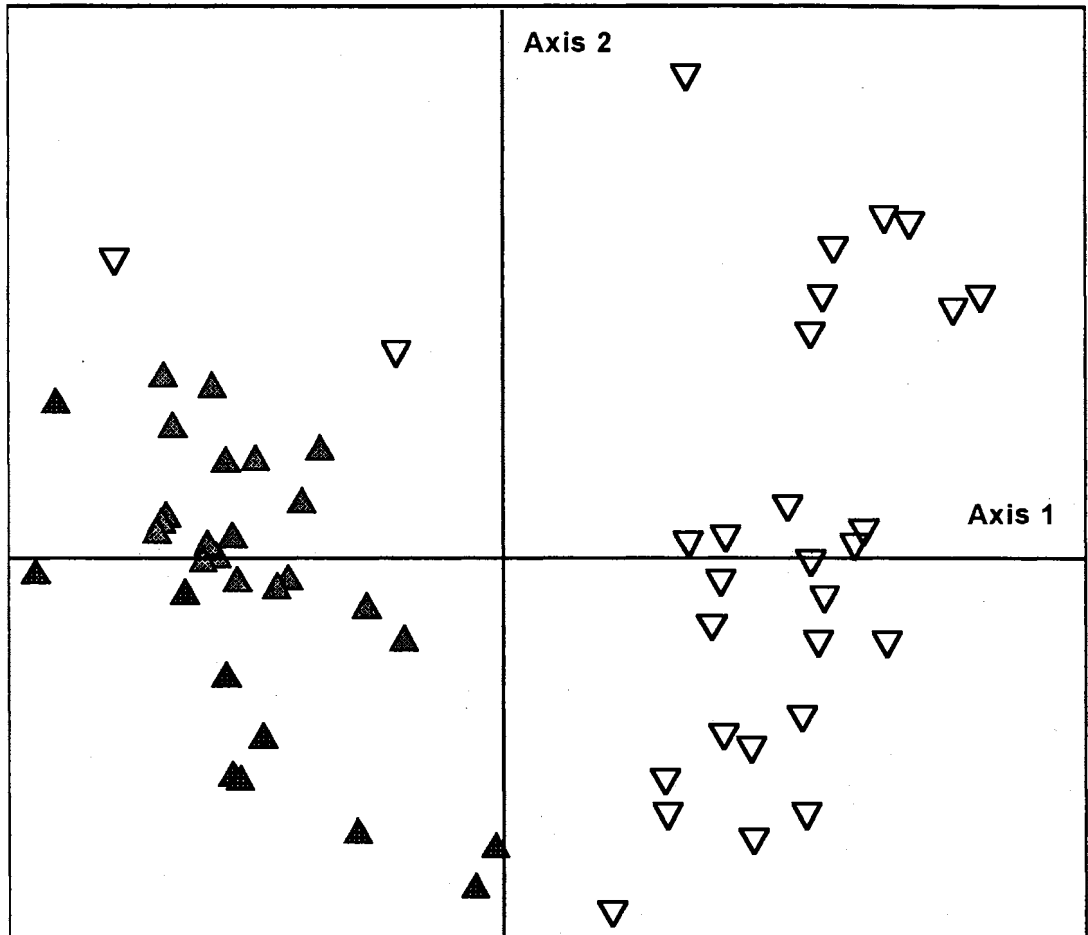
Fig. 2. Detrended correspondence analysis of species composition associated with two willow populations located on hydric and mesic sites. Analyses were performed on presence data of 28 species observed in 60, 1m² plots. Dark triangles (n = 30) represent plots in the hydric population. White triangles (n = 30) represent plots located in the mesic population.

Table 3. Morphological comparisons between bored (*BO*) and unbored (*NS*) willow genets by population type on the debris avalanche at Mount St. Helens National Volcanic Monument. Bored genets were infested with willow stem borer larvae. Comparisons performed with Hotelling's T² procedure. $\alpha = 0.05$.

	means		
morphological variables	NS	BO	p-value
a) hydric population			
genet morphology	NS ≠ BO		0.02
max. ramet height, cm	*165*	*176*	
# live ramets	*15*	*16*	
mean live ramet diameter, cm	*1.09*	*1.28 **	
# CAG shoots per ramet	*23*	*27*	
b) mesic population			
genet morphology	NS ≠ BO		< 0.001
max. ramet height, cm	*143*	*175 **	
# live ramets	*7*	*11 **	
mean live ramet diameter, cm	*1.27*	*1.44 **	
# CAG shoots per ramet	*23*	*31 **	

* indicates statistical difference between treatments within sites, $p \leq 0.05$.

† populations delineated by presence of standing water in hydric site in August, 2000.

Table 4. Morphological comparisons of unbored ramets from unbored willow genets (*ns*) and unbored ramets from bored genets (*nbo*) within substrate populations on the debris avalanche at Mount St. Helens National Volcanic Monument. Bored ramets were infested with willow stem borer larvae. Comparisons performed with Hotelling's T2 procedure (a = 0.05).

morphological variables	means		p-value
	ns	nbo	
a) hydric population			
ramet morphology	ns = nbo		0.77
ramet diameter, cm	*1.44*	*1.52*	
# CAG shoots	*26*	*27*	
mean CAG shoot diameter, cm	*0.23*	*0.24*	
browse intensity	*0.72*	*0.74*	
b) mesic population			
ramet morphology	ns = nbo		0.29
ramet diameter, cm	*1.42*	*1.28*	
# CAG shoots	*30*	*24*	
mean CAG shoot diameter, cm	*0.22*	*0.24*	
browse intensity	*0.66*	*0.73*	

* populations delineated by presence of standing water in hydric site in August, 2000.

populations (Table 5). In contrast, average diameters of CAG shoots were significantly larger on unbored ramets in the hydric population (p = <0.001) and marginally larger in the mesic group (p = 0.006).

CAG Shoot Nitrogen Concentrations

ANCOVA results indicated that genet-level and ramet-level boring affected CAG shoot nitrogen concentrations (Table 6, 7). The *ns* vs. *nbo* ANCOVA detected significantly higher TKN concentrations in *nbo* shoots in the mesic population (p = 0.02, Table 8). Differences in the hydric population were not significant (p = 0.29). The *ns* vs. *bo* ANCOVA revealed that nitrogen concentrations were significantly higher in *bo* shoots in both populations (p = 0.03, hydric; p = 0.01, mesic; Table 8).

Herbivore Interactions

Results of the boring intensity 2-factor ANOVA showed that genet density and the interaction term were significant, indicating an interaction between the two herbivores (Table 9). The mean number of borer holes per genet increased across browsing intensity classes in the low genet density class (8.4, 10.1, and 16.9, respectively, Table 10). However, mean values decreased overall across as browse intensity increased in the high genet density class (10.6, 4.5, and 5.4, respectively, Table 10).

Resource Sharing Between Ramets

Correlation coefficients for mean CAG shoot diameter and the number of sister ramets were statistically significant (p = 0.03 for both ramet treatments), but indicated converse relationships (Table 11). Ramets from unbored genets (*ns*) showed a positive relationship (r = 0.38), whereas the relationship was negative (r = -0.43) in ramets from

Table 5. Morphological comparisons of bored (*bo*) and unbored (*nbo*) willow ramets within bored genet populations on the debris avalanche at Mount St. Helens National Volcanic Monument. Bored ramets and genets were infested with willow stem borer larvae. Comparisons performed with multiple paired t-tests. $\alpha = 0.005$.

morphological variables	means		p-value
	bbr	bobr	
a) hydric population			
ramet diameter, cm	1.52	2.14	<0.001
# CAG shoots	22	34	0.001
mean CAG shoot diameter, cm	0.24	0.21	0.006
browse intensity	0.73	0.63	0.04
b) mesic population			
ramet diameter, cm	1.28	2.09	<0.001
# CAG shoots	22	46	<0.001
mean CAG shoot diameter, cm	0.23	0.20	<0.001
browse intensity	0.73	0.80	0.14

* populations delineated by presence of standing water in hydric site in August, 2000.

Table 6. ANCOVA testing CAG shoot nitrogen concentration between willow ramet treatments *(nbo* = ramet from genet bored by willow stem borer larvae, *ns* = ramet from unbored genet) on the debris avalanche in Mount St. Helens National Volcanic Monument. α = 0.05.

Source	SS	df	MS	F	p - value
a) mesic population					
ramet treatment	0.016	1	0.016	5.656	0.023
CAG shoot dry weight	0.065	1	0.065	22.778	< 0.001
error	0.105	37	0.003		
b) hydric population					
ramet treatment	0.005	1	0.005	1.163	0.288
ramet diameter	0.028	1	0.028	6.087	0.018
error	0.169	37	0.005		

Table 7. ANCOVA testing CAG shoot nitrogen concentration between willow ramet treatments *(bo* = bored ramet from genet bored by willow stem borer larvae, *ns* = ramet from unbored genet) on the debris avalanche in Mount St. Helens National Volcanic Monument. α = 0.05.

Source	SS	df	MS	F	p - value
a) mesic population					
ramet treatment	0.031	1	0.031	5.492	0.025
CAG shoot dry weight	0.031	1	0.031	5.371	0.026
error	0.211	37	0.006		
b) hydric population					
ramet treatment	0.044	1	0.044	7.63	0.009
sum of sister ramet diameters	0.024	1	0.024	4.174	0.048
error	0.215	37	0.006		

Table 8. Mean values from ANCOVA's comparing CAG shoot TKN concentrations (%) between willow ramet treatments within genet populations on the debris avalanche in Mount St. Helens National Volcanic Monument.

Tests	means		
	ns	nbo	bo
a) Table 5 ANCOVA (ns vs. nbo)			
mesic population, shoot TKN	0.578	0.610 *	-
hydric population, shoot TKN	0.523	0.562	-
b) Table 6 ANCOVA (ns vs. bo)			
mesic population, shoot TKN	0.578	-	0.614 *
hydric population, shoot TKN	0.523	-	0.648 *

* indicates significant difference between treatments, $p \leq 0.05$.

Table 9. Two-factor ANOVA (α = 0.05) comparing the # of boring wounds created by the willow stem borer in willow genets within genet density and browse intensity classes on the debris avalanche in Mount St. Helens National Volcanic Monument.

Source	SS	df	MS	F	p - value
genet density level	0.593	1	0.593	12.47	0.001
browse intensity level	0.189	2	0.095	1.99	0.152
interaction	0.643	2	0.321	6.76	0.003
error	1.617	34	0.048		

Table 10. Mean # of wounds created by willow
stem borer larvae in willow genets within genet
density and browse intensity classes on the debris
avalanche in Mount St. Helens National Volcanic
Monument. Genet density classes: low = <7 genets
within 1.5m radius, high = >=7. Browse intensity
classes: low = <70% of CAG shoots browsed
during dormant period previous to 2000 growing
season, moderate = 71-77%, high = >77%.

interaction classes	# borer holes
a) low genet density	
Low	8.4
Moderate	10.1
High	16.9
b) high genet density	
Low	10.6
Moderate	4.5
High	5.4

Table 11. Pearson correlation coefficients between mean CAG shoot diameter and the number of sister ramets for unbored willow ramets within genet treatments on the debris avalanche in Mount St. Helens National Volcanic Monument. *ns* = ramets from unbored genets, *nbo* = ramets from genets infested with willow stem borer larvae.

ramet type	Pearson correlation coefficient	p - value
ns	0.38	0.03
nbo	-0.44	0.03

bored genets (*nbo*). However, relationships were only significant for ramets >1.31cm in diameter.

DISCUSSION

Role of Moisture

Genet morphology was strongly influenced by substrate conditions (Table 2). Although yearly patterns of soil moisture are unknown, intermittent saturation of soils could have contributed to more robust growth of willows, in comparison to willows on mesic and dry sites (Kozlowski et al. 1991). Leaves were drying and turning yellow within several genets in the mesic population by mid-August (*personal observation*). Genets in the mesic substrate group may have been suffering from water stress as debris avalanche substrates are typically low in moisture and are highly porous (Dale 1989). The apparent contradiction between water stress and the larger mean ramet diameters observed in the mesic genet population, is explained by a trade-off between ramet size and the number of ramets produced per genet.

Morphology and Borer Selection

Genets selected by the willow stem borer were morphologically distinct from unselected genets in both substrate populations. Analysis of the morphological metrics, and presumed requirements for larval feeding space (e.g., minimum ramet diameter), suggest that adult borers selected larger diameter ramets. Thus, genet-level boring may be dictated by ramet-level morphological characteristics. This implies that adult willow stem borers perceive willow populations as a collection of ramets, rather than genets. However, it is unclear how adult feeding requirements also affect selection processes. There may be important CAG shoot characteristics required for adult feeding (e.g., diameter, bark thickness, position within genet).

Finally, there may a physiological interaction between willows and adult borers. Several beetle species are attracted to pheromones released by trees (Knight and Hekkenen 1980). Perhaps adult borers are picking up chemical cues from suitable genets and ramets. Adult willow stem borers may be responding to sugar concentrations in CAG shoots they feed upon, in addition to ramet diameters (Harris 1981).

Shoot Level

Although unbored ramet morphology was similar between genet-level treatments, ANCOVA results suggested that genet-level boring influenced the higher nitrogen concentrations observed in shoots from *nbo* ramets in the mesic genet population (Table 4, 6). However, concentrations were similar in the hydric population. Higher nitrogen concentrations in shoots from bored genets would be expected if induced chemical responses played a role in borer-willow interactions (Karban and Baldwin 1997). However, saturated conditions in the hydric site, and the subsequent loss of nitrogen, may be limiting nitrogen-based defenses in bored genets (Kozlowski et al. 1991).

Nitrogen concentrations were consistently greater in *bo* shoots than in *ns* shoots, irrespective of site moisture conditions. This indicated that nitrogen-based defensive compounds were allocated to bored ramets. The inference that ramet- and genet-level boring, not differences in willow size, created the difference in TKN concentrations between treatments, was strengthened because covariates removed the influence of biomass on nitrogen concetrations. Results were further strengthened by finding significant treatment effects despite the highly variable nature of N concetrations between clones of a single willow species (Simon et al. 1990).

Potential Herbivore Interactions

ANOVA results indicated that boring frequency responded significantly to an interaction between genet density and ungulate browsing intensity (Table 9). However, this was an artifact of ramets obtaining larger diameters in areas with low competition with other genets. Furthermore, it would be expected that more borers would be concentrated on a genet if few acceptable genets were nearby.

The apparent interaction between boring intensity and elk browsing was indirect and developed over the last 20 years. Persistent browsing in the area has shaped willow densities by influencing genet morphology and clonal reproduction. In turn, ungulate browsing is thought to be strongly influenced by the spatial arrangement of food items (Lindroth 1989, Danell et al. 1991). Therefore, elk browsing intensity is strongly linked to the distribution and availability of ramets. If few ramets are available, an elk will spend longer at a given ramet and thus, browse more intensely. More borers are found on a given genet if few suitable genets exist within the immediate area. As ramet densities increase, competition for space and resources would lead to smaller ramet diameters. Thus, under high ramet densities, browsing and boring becomes diffuse across genets.

Potential Resource-Sharing

The sharing of resources among ramets of clonal plants has been addressed by numerous researchers, though seldom with woody species (Huenneke 1985, Abrahamson et al. 1991). In theory, resources, such as carbohydrates and nutrients, are distributed to optimize the health of individual ramets and the genet as a whole (Caraco and Kelly 1991). However, a balance must be made between providing the more robust ramets with resources and maintaining optimal resources levels in less-developed ramets (Abrahamson et al. 1991, Caraco and Kelly 1991). Mature ramets require resources for

sexual reproduction, while development of new ramets allows genets to increase photosynthesis and acquisition of belowground resources. Thus, genets benefit from new ramet development and the willow population is able to expand via sexual reproduction.

Results suggested that resources are shared between ramets in unbored genets. Within bored genets, resources utilized for new shoot growth may have been diverted to bored ramets for chemical defenses and/or compensatory growth. Analyses indicated that resources were contributed to mature ramets (diameters >1.31cm) in unbored genets. This relationship was assumed to be the prevailing trend, i.e., a control demonstrating that mature ramets are resource *sinks*. The reversal of the relationship within *BO* genets suggested that resources were diverted from unbored ramets to those ramets attacked by willow stem borer larvae. From the perspective of bored ramets, mature unbored sister ramets may serve as important contributors of resources needed for chemical defense or compensatory growth. Thus, willow stem borer attacks affect genets by reducing shoot development in younger ramets and may interfere with sexual reproduction in mature ramets. At the population level, genet health is compromised and the exchange of genetic material may be suppressed.

CONCLUSION

Sitka willow genets of the MSHNVM debris avalanche have been subjected to willow stem borer herbivory since at least the early 1990's (Peter Frenzen, Monument Scientist, *personal communication*). Larval activity is clearly controlled by ramet diameters, and accordingly, willow genet densities. Results provided indirect evidence of a induced chemical defensive against borer larvae and of resource-sharing among ramets. Mature ramets may be resource sinks under typical conditions, but may become resource contributors for ramets bored by the willow stem borer.

Consistent elk herbivory has shaped the architecture and distribution of willow communities over coarse spatial and temporal scales (Peter Frenzen, Monument Scientist, *personal communication*; Hobbs 1996). Ungulate browsing tends to promote clonal expansion, and over time, reduces the avaerage diameter of willow ramets. Thus, use of willows by the willow stem borer has been indirectly influenced by ungulate activity.

Entomological research suggests that wood boring and phloem-feeding outbreaks are cyclical in nature and respond positively to enivronmental stress of plants (Knight and Henneken 1980). Thus, infestations of *C. lapathi* may also be cyclical. Growing conditions on the debris avalanche have been poor to moderate for most plant species since the 1980 eruption (Peter Frenzen, Monument Scientist, *personal communication*). However, conditions are improving as plants spread throughout the debris deposit creating shade and ameliorating soil conditions. The recent outbreak of the willow stem borer may be a response to the moderately-stressed condition of willows throughout the debris avalanche. Vigorous genets may be able to repel larval attacks and dessicated genets may be unable to meet nutritional needs of larvae (Kozlowski et al. 1991). Thus, an intermediate level of stress may facilitate boring and provide needed resources for larvae and adults.

Appendix A

Summary of preliminary data collected within the Castle
Lake control and exclosure sites in 1999.

NS = not affected by elk or willow stem borer herbivory
BO = bored by willow stem borer larvae
BR = browsed by ungulates
BOBR = bored and browsed

Site	# Observed	# NS	# BO	# BR	# BOBR
a) control					
genets	183	21	0	146	16
ramets	425	21	39	365	0
dead ramets	12	0	0	7	5
b) exclosure					
genets	141	118	23	-	-
ramets	339	269	70	-	-
dead ramets	73	52	21	-	-

Minimum bored diameter observed: 0.71 cm.

Appendix B

Presence of species within 60, 1m2 plots in mesic and hydric
willow populations.

Functional Group & Binomial	# of Plots Species Observed In	
	mesic site	hydric site
Bryophytes		
bryophyte spp.	22	0
Grasses		
Agrostis exerata	9	9
Agrostis scabra	8	0
Deschampsia elongata	0	2
Holcus lanatus	24	11
Rushes & Sedges		
Carex kellogii	16	1
Eleocharis palustris	0	2
Juncus acuminatus	16	30
Juncus effusus	3	4
Juncus ensifolius	2	19
Juncus tenuis	10	7
Forbs & Horsetails		
Anaphalis margaritacea	5	0
Castilleja miniata	3	0
Cirsium spp.	0	2
Epilobium ciliatum	10	5
Equisetum arvense	6	4
Equisetum hyemale	3	28
Hypochaeris radicata	23	19
Myosotis laxa	0	30
Parentucellia viscosa	13	2
Trifolium pratense	9	0
Trifolium repens	29	18
Typha latifolia	1	9
Shrubs & Trees		
Alnus rubra	3	0
Alnus sinuata	1	0
Populus trichocarpa	5	0
Salix lasiandra	1	10
Salix sitchensis	28	30

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