Forest Succession and Nutritional Carrying Capacity of Elk since the 1980 Eruption of Mount St. Helens

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

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ABSTRACT

There has been increasing concern over declines in habitat quality for elk (*Cervus elaphus*) on industrial timber lands west of Mount St. Helens due to canopy closure and the loss of nutritional resources related to succession of early seral stands created by the 1980 eruption. Vegetative recovery across the landscape has varied due to the range in severity of the initial disturbance and different management practices on industrial lands vs. in the Mount St. Helens National Volcanic Monument. In this thesis, I assessed the 5-year changes in the nutritional carrying capacity (NCC) for elk (elk days/ha) within a core area of the Mount St. Helens elk population since the 1980 eruption based on digestible energy of preferred forage species using the Forage Resource Evaluation System for Habitat model (FRESH). I constrained estimates of NCC by considering only areas with a minimum amount of biomass where an elk could forage profitably (150 kg/ha), species that met digestible energy requirements of a reproductive elk in late summer (2.9 kcal/g), the maximum amount that a species could contribute to the diet (40%), and the maximum amount that a species could be consumed (100%). I also limited the contribution of an area by its relative use derived from a resource selection function ($NCC_{constrained}$), which was developed from movement data of 23 GPS-collared elk monitored in 2009-2011 in this region. I tested whether the advancing forest succession of highly disturbed areas of the Monument was offsetting the broad-scale decline in elk summer range on industrial timber lands. From 1980-1995 the NCC was higher outside than inside the Monument due to low tephra and ash, active salvage logging and replanting, and rapid forest succession on industrial forest lands typical of this region. From 2000-2010 the NCC on industrial lands declined due to canopy closure and broad-scale application of operational herbicides and their associated reduction in preferred forages, whereas inside the Monument the NCC increased, showing partial support for my hypothesis. The resource selection function indicated elk selection was most strongly influence by available digestible energy, followed by distance to forage-cover edge, distance to a public road and slope. Constraining the NCC by relative use resulted in 2-49% decrease across study years with the greatest declines on industrial lands from 1980-1990 and inside the Monument from 2000-2010. We discussed trends in estimates of elk carrying capacity to trends in the elk summer distribution, body condition, probability of pregnancy, and overwinter elk mortality across a portion of the study area and found a general correspondence. Results from this study allowed us to anticipate the consequences of current forest succession trends and provide an approach to assess future trends in elk habitat quality under alterative management scenarios.

ACKNOWLEDGEMENTS

I am grateful to the Rocky Mountain Elk Foundation, the U.S. Forest Service, the University of Alberta, and NSERC Discovery Grant program, which provide both funding and in-kind support that made my research possible. I want to thank all of those who contributed data to this project, including Dr. Roger del Moral, Charlie Crisafulli and the United States Forest Services, Dr. John Cook, Dr. Rachel Cook, Dr. Evelyn Merrill, Andrew Geary, and Daren Hauswald and the Washington Department of Fish and Wildlife. A special thanks goes to Dr. Virginia Dale not only for her data contribution to this project but for allowing us to join her camp during sampling of the debris avalanche deposit. A special thanks goes to Charlie Crisafulli for sharing his vast knowledge of Mount St. Helens, for his recommendations and discussion of my work, for allowing me to be apart of The Pulse, and for making my experience in the field so enjoyable by being apart of his team. I would also like to thank the United States Forest Service field crew for their long hours in the field helping collect data, in particular, Elizabeth Schyling, Kerri Wheeler, Mark Roes, Tara Blackman, Pilita Carrera, Romi Melson, David Tange, and Summer Schlageter. I am extremely grateful for the contributions of Andrew Geary to this project, for providing me with data to analyze and for his readiness to help me understand the data.

I am grateful for the efforts of the people at Weyerhaeuser and the Department of Natural Resources that facilitated Andrew's research, and have therefore made my project possible. I would also like to recognize all of those who have helped me obtain data to analyze, Robert Kennedy with remote sensing and Jeff Essic with historical road maps. I would also like to give a special thank you to Hassan Muhammad for helping me with my data analysis, and for his patience and readiness to help. I would also like to give a special thank you to Dr. Harriet Allen

in allowing me to stay with her and for being a friend to me during my time in Olympia, and Connie Harrington at the Pacific Northwest Research Station for allowing me to use their laboratory for vegetation drying and weighing.

I thank my committee members Dr. Scott Nielson and Dr. Edward Bork for their time and expert opinion on my work. Most importantly, I am extremely grateful for having Dr. Evelyn Merrill as a supervisor, I could not thank her enough for taking a chance on me by taking me on as a master's student. I would like to thank Evie for her continual patience, guidance, and contagious passion for research that has inspired me greatly in the last three years. Lastly, I would like to thank Evie for being a role model to me prior to becoming a student of hers, for mentoring me while I was her student, and for being a friend to me during this whole process. It was a true honor to be one of her graduate students. I would also like to thank the members of the Merrill lab for their readiness to provide me with feedback on all of my presentations, specifically, Kerri Krawchuk, Eric Spilker, Kara MacAulay, Kayla Deasley, and Jodi Berg. A special thank you to Joshua Killeen for going above expectations in editing my work.

Finally, I would like to offer thanks to my friends and family for being supportive and understanding during my time as a graduate student. I would especially like to thank my fiancé, Nicholas Carels, for always knowing exactly what I needed and for making my life as a master's student so enjoyable. This sum of work wouldn't have been possible without his reminders to take time to enjoy the small things in life, and to not wish any days away during times of peak stress because each day is an opportunity for something great to happen. I would also like to give thanks to my father, Gordon Sparkes, for leading by example that hard work will always pay off, and to my mother, Dolena Sparkes, for encouraging me to push through the stressful times and make sure to always remain positive. I hope my work has made all of you proud.

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CHAPTER 1

GENERAL INTRODUCTION

The change in forest management in the Pacific Northwest of the United States from a continuous supply of timber to the conservation of old-growth forests has been attributed to the increased use of wood aggregate products, competition with foreign markets, and conservation of species that depend on late-succession and old-growth forests, such as the Northern Spotted Owl and the Marbled Murrelet (Miller and McCorquodale 2006, Washington Department of Natural Resources 2009). This change has led to about a 40% decrease in timber harvest from 1990 to 2008 (Washington Department of Natural Resources 2009), which has raised concerns about declining carrying capacity for ungulates due to the loss of early-succession forests. Further, increasing use of herbicides in the first 1-2 years following timber harvest since the mid 1990s has added to this concern because of the approximately 77% decrease in total forage in the first two years after herbicide application (Geary 2013).

Early studies in the western hemlock (*Tsuga heterophylla*) and the Pacific silver fir (*Abies amabilis*) forest communities in Oregon and Washington show a distinct pattern in ungulate forage dynamics after timber harvest in the Pacific Northwest (Witmer et al. 1985, Jenkins and Starkey 1996, Hanley 1984, Alaback 1982). Cook et al. (*in press*) reported that total abundance of forage peaks at 3000-4500 kg/ha in 8 to 10-year-old stands, beginning with grass and forbs followed by an abundance of shrubs and tree seedlings. As the forest canopy closes, herbaceous understory rapidly decreases to 100-300 kg/ha in 20 to 50-year-old stands, and ~160 years after timber harvesting when the trees begin to form natural gaps within the canopy and forage begins increasing again to 151-600 kg/ha (Cook et al. *in press*). These general patterns of forage dynamics have been the basis of ungulate management for the past several decades (Witmer et al. 1985, Cook et al. 2002, Cook et al. 2001, Hanley 1982, Pyke et al. 1977). However, ungulates have not shown consistent relationships between forage abundance and habitat use (Hanley 1982, Hanley 1997, Jenkins and Starkey 1993), which indicates forage quality may be equally important in assessing habitat quality for ungulates (Starkey et al. 1982, Happe et al. 1990, Parker 2003, Cook et al. *in press*).

Recent work relating abundance of types of forages to dietary energy (DE) levels of elk in this region has improved the approaches being used for assessing the value of forest stand to habitat quality based on forage nutrition (Cook et al. *in press*). Based on foraging trials with tame elk in late summer, Cook et al. (*in press*) showed that nutritional quality of a forest stand in western hemlock and the Pacific silver fir stands (1 year to 650 years) could be assessed based on the availability of *selected*, *neutral* or *avoided* forages that elk consumed less, equal to or greater than their available biomass, respectively. They showed that levels of DE were related to the availability of *accepted* (selected plus neutral) biomass in a stand, and that when accepted biomass dropped to below 150 kg/ha DE intake declined. Geary (2013) showed that biomass of avoided, but not accepted biomass, was strongly related to total biomass. As a result, DE levels in early seral forests can be highly variable but often approaches lactating elk maintenance needs (2.68 kcal/g) while in closed canopy forests, DE levels were found to consistently be below 2.68 kcal/g. Low DE intake can result in inadequate summer nutrition in lactating elk leading to poor body condition. Cook et al. (2004) reported that a 13% decline in summer DE (2.75 to 2.40 kcal/g) will result in a 50% reduction in body fat of a lactating elk and a 20% decline in the probability of pregnancy.

There is an increase in concern for elk in the Pacific Northwest due to the decline in early seral stands coupled with elk population declines in several elk herds across western Oregon and Washington (Miller and McCorquodale 2006). Cook et al. (*in press*) measured autumn ingesta-free body fat (%) of 21 different elk herds across Washington and Oregon. It was found that the percent body fat of these herds were highly variable ranging from 5.5% to 15% body fat (Cook et al. *in press*). Percent body fat was linked to the probability of pregnancy, timing of birth, and overwinter fat utilization (Cook et al. *in press*). With an autumn body fat greater than 12% there were few or no summer nutritional limitations, but with an autumn body fat of less than 6% there was a high probability of reproductive pause, suggesting inadequate summer nutrition (Cook et al. *in press*). The Mount St. Helens elk herd had some of the lowest autumn body fat scores among these 21 elk herds (~5.5%). The body fat levels at Mount St. Helens were between 30-75% of those observed within captivity being fed a high quality diet, indicating the potential for reduced pregnancy rates, later conception dates, and reduced calf survival (Cook et al. 2004), suggesting that the Mount St. Helens elk herd is faced with very poor forage conditions.

The Mount St. Helens elk herd is one of the most important herds in Washington. Thirty-six years after the volcano eruption, proportions of the elk herd population appear to be in poor nutritional condition and this has been attributed to forest succession since the eruption and the possible influence of broad-scale use of herbicides (Miller and McCorquodale 2006, McCorquodale et al. 2014, Cook et al. *in press*). After the Mount St. Helens eruption, the elk population recovery was rapid due to immigration (Raedeke et al. 1986), attributable to the natural rapid recovery of forage, initial restrictions on human access and harvest, and seeding of Douglas fir trees (*Pseudotsuga menziesii*) on industrial lands and grass-legume mixes on the wildlife management area because of its importance for elk winter range (Merrill 1987; Merrill et al. 1995). By the late 1990s periodic elk winter mortality became apparent along the north fork of the Toutle River in 1990-1999 (79 elk), 2005-2006 (63 elk), 2007-2008 (158 elk, McCorquodale et al. 2014).

Contributing to this decline may be a decrease in the highly nutritious plant understory after ~20 years of forest succession and associated closure of the canopy, in combination with the increased use of herbicides and high herbivory within the area (Miller and McCorquodale 2006, McCorquodale et al. 2014). However, recovery has been variable across the landscape due to the variability of the severity in the initial disturbances, different management practices on industrial lands vs. in the Mount St. Helens National Volcanic Monument, and gradient of growing season conditions related to elevation. In general, the higher elevation close to the Mount St. Helens areas have recovered much more slowly, and today may provide high quality forbs and grasses for elk with little to no canopy cover. In contrast, in low elevation areas that were quickly replanted after the eruption, forest succession has advanced quickly and today more than 35 years after the eruption this area is now a mid-seral forest stand with closure of the tall canopy (McCorquodale et al. 2014). As a result of the differences in vegetation recovery across the landscape, it is unclear how the summer carrying capacity has changed for various portions of the Mount St. Helens elk herd.

Washington Department of Fish and Wildlife's current elk management is directed at increasing harvests to reduce the current Mount St. Helens elk population because of the presumed decline in carrying capacity. Population health has been evaluated primarily through monitoring populations with aerial estimates of population size, and body fat and reproductive studies (Geary 2014, Cook et al. *in press*, McCorquodale et al. 2014), and recent hoof disease studies (Washington Department of Fish and Wildlife 2011). However, no large-scale assessment of changes in habitat conditions for elk has been performed.

In this thesis, I assessed the changes in the nutritional carrying capacity for elk since the 1980 eruption of Mount St. Helens. Nutritional carrying capacity is defined as the number of animals that can be supported by an area based on the forage available and quality (Wallmo et al. 1977, Hobbs and Hanley 1990, DeYoung et al. 2000). Early models were based on the total available biomass and the quality of biomass available to an animal (Wallmo et al. 1977, Hobbs and Swift 1985, Irby et al. 2002, Coughenour et al. 1996). The theoretical calculation of animal nutritional carrying capacity is confounded because forage quantity and quality may not be substitutable for one another (Hobbs and Hanley 1990, Wallmo et al. 1977) because of digestive constraints of low quality forages in ruminants due to an increase in time to digest low quality forage (Hanley et al. 2012). We used the Forage Resource Evaluation System for Habitat (FRESH) developed by Hanley et al. (2012) to address this issue. The model is able to account for nutritional and foraging constraints in estimating nutritional carrying capacity using a linear programming model that maximizes the amount of forage biomass while meeting the minimum constraints of DE, the minimum amount of biomass available for an elk to forage profitably within a habitat, and the maximum amount that a species can contribute to the diet (Hanley et al. 2012).

While a step forward in modeling nutritional carrying capacity, the early versions of FRESH were designed at a plant community type level where all available forage contributed to the total biomass of the diet. More recently, the landscape-level carrying capacity model was developed to take in consideration the spatial layout of the habitat. The landscape level model is able to consider the heterogeneous mixture of habitats that an animal has access to within the area of an approximate home-range size (Hanley et al. 2012). Further, FRESH currently assumes that the habitats within an area are equally selected, and therefore it weights availability of forage in all areas equally, unless forage biomass falls below a minimum quantity. Only recently have researchers began to refine their nutritional carrying capacity models by incorporating predictions of resource selection (Beck et al. 2006). Beck et al. (2006) used habitat selection data from a reintroduced elk population in Nevada, USA to constrain a nutritional carrying capacity model based on a resource selection function (RSF) derived from 17 radio-collared cow elk. With the constrained nutritional carrying capacity model, Beck et al. (2006) found that the nutritional carrying capacity corresponded to a decrease of 18-35% of the original nutritional carrying capacity because elk avoided certain landscape features. This indicates that traditional nutritional carrying capacity models are likely biased toward a higher number of animals compared to nutritional carrying capacity models that incorporate animal habitat use. We incorporated a resource selection function into the FRESH model based on an elk radio telemetry study from 2009-2011. We use the habitat covariates that were found to be important predictors of elk habitat use in the Pacific Northwest and used to develop the West Coast Elk Habitat Model (Rowland et al. 2013). The West Coast Elk Habitat Model was designed to evaluate elk summer range conditions in western Oregon and Washington and was used as a foundation for elk management on public and private lands, and for setting direction in elk habitat restoration (Rowland et al. 2013).

In summary, we assessed the changes in nutritional carrying capacity since the eruption based on changes in forest succession using FRESH and constrained these values by a resource selection function. In chapter 2 of this thesis I assessed the change in vegetation communities and their associated nutritional resources available to elk across the Monument since 1980 at 5-year increments. Based on these modeling efforts, I addressed the following research questions:

1. Is the advancing forest succession of unmanaged highly disturbed areas inside the Monument off setting a broad-scale decline in elk summer range on forest management lands?
2. To what degree has the broad-scale use of herbicides since 1995 reduced the potential elk nutritional carrying capacity on managed lands since 1995?
3. Do factors other than nutritional resources alter the potential carrying capacity for elk more through time on managed than unmanaged lands?

In chapter 3 I summarize the results for these questions and address their importance relative to future elk management at Mount St. Helens.

CHAPTER 2

FOREST SUCCESSION AND NUTRITIONAL CARRYING CAPACITY OF ELK SINCE THE 1980 ERUPTION OF MOUNT ST. HELENS

1. Introduction

A disturbance can be defined as a discrete event in time causing substantial changes in an ecosystem, community, or population structure by an environmental stressor over a short period of time. Although ecological disturbances can occur at any spatial scale, the most devastating disturbances involve large-scale alterations such as fires, hurricanes and volcanic eruptions (Turner et al. 1997). The 1980 volcanic eruption of Mount St. Helens is one of the most extensively studied volcanic areas in the world (Dale et al. 2005). The initial eruption involved the collapse of the north face of the mountain triggered by a 5.1 earthquake and a laterally directed blast that extended to the north devastating an area of ~60,000 ha designated as the "blast zone" by the United States Geological Survey. Within the blast zone unique disturbance types exist including the pyroclastic flow and debris avalanche along the North Fork of the Toutle river, areas where trees were completely removed, blown down, or left standing but scorched, and massive mudflows that ran down the major river drainage of the North and South Toutle rivers (Fairchild 1985, Turner et al. 1997, Fig. 2.1). Because of the uniqueness of these disturbances, a 44,500-ha area of the blast zone was designated as the Mount St. Helens National Volcanic Monument (Monument) in 1982 and managed for natural recovery.

As a result of the eruption and post-eruption management inside and outside the Monument, patterns of vegetation recovery since 1980 have been highly variable across the landscape in and adjacent to the blast zone. High elevation areas near Mount St. Helens in general were more severely disturbed and vegetation recovery has been slower than in areas at low elevations farther from the mountain (Crisafulli et al. 2005). In addition to the initial volcanic impact, variability in plant succession has been related to the vegetation that existed prior to the eruption, the depth of the debris/ash/tephra deposition, the varying post-eruption management practices (e.g., salvage logging, tree planting, grass seeding) and the physiographic characteristics of the area (Dale et al. 2005). For example, vegetation cover remains limited on unmanaged areas of the pyroclastic flow, mudflow, and tree removal area (Titus and Householder 2007), whereas red alder (*Alnus rubra*) and graminoids/moss now extensively cover the debris avalanche (Adams et al. 1987, Dale 1989, Dale and Adams 2003, Dale et al. 2005), and small saplings that survived under snowpack on the blowdown and scorched areas have since grown into young forests (Crisafulli et al. 2005).

On industrial forest lands inside the blast zone, down and standing timber was salvaged logged and the area replanted with conifer seedlings shortly after the eruption. As a result of these activities, succession to dense, closed-canopied areas of trees has occurred, particularly at low elevations (Crisafulli et al. 2005). In contrast, on industrial lands adjacent to the blast zone timber harvest has continued on 40 to 60-year rotations. Across the region there has been a 43% reduction in timber cutting since 1985 related to the conservation of old-growth forests and a diminished demand for a continuous supply of timber (Miller and McCorquodale 2006, Washington Department of Natural Resources 2007). As a result, the increasing closed-canopy forests within the blast zone combined with reduced timber cutting by the United States Forest Services (USFS), and recent use of herbicides on industrial lands have raised concerns for the loss of early seral vegetation in a portion of the range of the Mount St. Helens elk (*Cervus elaphus*) population in southwestern Washington, USA (Miller and McCorquodale 2006).

The Mount St. Helens elk herd in the recent past was one of the most important herds in Washington providing significant recreational, aesthetic, and economic benefits (Miller and McCorquodale 2006). At the time of the eruption Washington Department of Fish and Wildlife estimated about 1500 elk were killed within the blast zone (Merrill 1987). After the Mount St. Helens eruption, the recovery of the elk population in the blast zone was rapid due to immigration into the area, which was attributed to initial restrictions on human access, rapid recovery of forage in low ash/tephra areas, and seeding of grass-legume mixes (Raedeke et al. 1986, Merrill et al. 1995). By the late 1990s periodic elk winter mortality became apparent along the north fork of the Toutle River (McCorquodale et al. 2014). More recently Cook et al. (*in press*) reported low body fat levels and pregnancy rates for elk in western Oregon and Washington. Poor nutritional condition has been presumed to be related to the combined effects of the closed canopy within the blast zone and the routine use of herbicides on industrial lands outside the Monument (Miller and McCorquodale 2006). As a result, management by the Washington Department of Fish and Wildlife recently has been directed at increasing animal harvests to reduce the Mount St. Helens elk population (McCorquodale et al. 2014). However, because no large-scale assessment of changes in forage conditions for elk has been quantified, it is unclear how the carrying capacity has changed since the eruption, particularly on the elk summer range, which is known to have an influence on the productivity of an elk population (Cook et al. 2001, Cook et al. *in press*).

In this study, we evaluated the summer Nutritional Carrying Capacity (NCC) since 1980 for a portion of the Mount St Helens elk herd in and adjacent to the Mount St. Helens blast zone since 1980 to assess changes in habitat quality due to forest succession based on successional trends in the area. Early successional forest stands in the Pacific Northwest have the highest abundance and quality of forages for elk, but by ~15-20 years the forest canopy closes resulting in understory loss until forest thinning or canopy gaps develop after about 60-120 years and shade-tolerant forages typically low in digestible energy (DE) increase (Alaback 1982, Witmer et al. 1985, Jenkins and Starkey 1996, Hanley 1984). Intensive trials with tame elk have shown elk foraging in mid to late seral communities have lower DE intake and calf growth compared to those foraging in early seral stands (Cook et al. *in press*).

We modified the Forage Resource Evaluation System (FRESH, Hanley et al. 2012) originally developed for black-tailed deer (*Odocoileus hemionus sitkensis*) to estimate nutritional carrying capacity for elk in the Mount St. Helens blast zone and adjacent areas at 5-year intervals from 1980 to 2010. We derived inputs for the model by developing vegetation maps, simulating temporal changes in digestible energy (DE) across the landscape from long-term permanent plots or from forage-stand age relationships for the region and DE of plant species, and assuming a range of energy requirements for lactating elk in summer from the literature. We focused on energy requirements of lactating elk for the period of late-summer (August) because females with low body fat at the onset of breeding season can result in reduced probability of ovulation and pregnancy (Cook et al. 2001), and because Cook et al. (1996, 2004, *in press*) reported a relationship between late-summer nutrition and elk calf growth and survival over the next winter. We did not include digestible protein constraints in the model because within the Pacific

Northwest of Oregon and Washington protein deficiencies were less pronounced than DE deficiencies, with some areas supporting protein intake levels in excess of maintenance requirements (Merrill 1994, Jenkins and Starkey 1996, Cook et al. *in press*).

We used the NCC model to assess hypotheses about spatio-temporal patterns of nutritional carrying capacity since the eruption. First, because forest stands across portions of the Mount St. Helens blast zone are now showing canopy closure, there is the general perception that the carrying capacity for the elk population in this area has been declining (Miller and McCorquodale 2006). However, we hypothesized that the advancing forest succession in highly disturbed areas of the blast zone, particularly in the Monument, may be offsetting the decline in nutritional carrying capacity of elk summer range outside the Monument. We also assessed the effect of using herbicides on these patterns because herbicide application in areas surrounding the Monument have been common since about 1995. Finally, we assessed the effect of other factors such as human disturbance, physiographical characteristics, and the interspersion of forage and cover in altering the spatial pattern in predicted nutritional carrying capacity of elk summer range inside and outside the Monument because elk are less likely to select certain types of areas and avoid others (Rowland et al. 2013). By incorporating elk habitat selection we provided a more realistic spatial overview of changes in elk summer nutritional carrying capacity. This study is one of few to assess long-term impacts of volcanic eruptions on a large mammal, and illustrates an approach to anticipate the consequences of current forest successional trends from forest disturbances from either natural recovery or alternative forest management scenarios.

2. Methods

2.1 Study Area

The 132,410-ha study area is located in Southwest Washington in the USA (Fig. 2.1). Administrative units within the study area include three Washington Department of Fish and Wildlife game management units (GMU, Loo-wit (522), Margaret (524), Toutle (556)), the Monument, USFS lands, and the Washington Department of Fish and Wildlife's Wildlife Management Area in the Toutle river drainage. Industrial lands primarily to the west of Mount St. Helens are under the jurisdiction of Washington Department of Natural Resources (18% of study area) and Weyerhaeuser Company (51%). Private lands comprise <1% of the area. Forty-seven percent of the study area is designated by the U.S. Geological Survey as part of the 1980 blast zone, and forty-five percent of the blast zone currently falls within the Monument. For this study we refer to areas inside and east of the Monument as 'inside the Monument' due to similarities in the initial disturbance of the eruption and the delayed natural recovery of plant community types; all areas to the west of the Monument are considered 'outside the Monument'.

The area is mountainous with elevation ranging from 127 m to 2550 m. The climate is Pacific maritime with wet, mild winters and dry, cool summers (Franklin and Dryness 1973). The lands outside the blast zone fall within 4 potential vegetation series (Franklin and Dryness 1973) including the western hemlock series (35% of study area), Pacific silver fir series (26%), mountain hemlock series (8%), and a combination of Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and Subalpine fir (*Abies lasiocarpa)* (<1%). Hereafter we refer to only the 3 main vegetation series. Within the blast zone, we used six disturbance zones designated by the

United States Geological Survey based on the ecological and geophysical disturbances (Table 2.1). Private industrial and Department of Natural Resources forest lands in and adjacent to the blast zone are on 40 to 60-year timber harvesting cycles (Miller and McCorquodale 2006). Routine use of herbicides within the first two years after harvest began in about 1995 (Wagner et al. 2004, Geary 2013).

The elk population inhabiting the entire Mount St. Helens herd unit was estimated to be 13,300 in 2005 (Miller and McCorquodale 2006), 4,290 in 2009, and 5,132 in 2011 (McCorquodale et al. 2014). Within the 5 GMUs in the study area, declines were reported only in GMU 556 (~20-25%) and GMU 524 (40-60%) by 2013 (McCorquodale et al. 2014). Following the eruption, hunting began in 1982 during November (bull and cow elk) and December (cow elk) which influenced elk movement during the winter months with a tendency to be inside the Monument (Merrill 1987). Currently elk are subject to an archery season in early September and permit-based rifle season from September to mid-January, with primary hunts for cow elk in November. The role that natural predators play in elk mortality at Mount St. Helens is unknown (Miller and McCorquodale 2006), but potential predators include black bears (*Ursus americanus*), cougars (*Puma concolor*), and coyotes (*Canis latrans*). The study area is popular among locals and tourists for hunting and recreation, contributing to multibillion-dollar revenue each year (Miller and McCorquodale 2006).

2.2 Land Cover Maps

Areas inside and outside the Monument were subject to different forest management treatments. Because areas inside the Monument for the most part recovered naturally with little management intervention, we classified the area according to disturbance zones and plant communities within disturbance zones. Because areas outside the Monument were subjected to timber management, we classified the area according to forest stand age. We classified the mountain hemlock as Pacific silver fir because Cook et al. (*in press*) did not distinguish between these types due to similarities in forage in this region. All other forest types (Douglas fir, grand fir, Parkland, and subalpine fir) comprised < 1% of the area and were classified as Pacific silver fir forest because they occurred at high elevations (> 600 m).

2.2.1 Outside the Monument

Western hemlock and Pacific silver fir areas were classified as one of eight stand ages (0-2, 3-5, 6-9, 10-13, 14-20, 21-40, 41-150, 150+ years) based on 2012 stand initiation maps provided by Weyerhaeuser Company and the Washington Department of Natural Resources and modified by Geary (2013). To adjust for changes in stand age between 1980 and 2010 to predict changes in forage resources, we retrospectively constrained the stand age from 2012 in time back to 1980. For stands that were cut between 1980 and 2010, we assumed the stands were 60-years old prior to harvest (Weyerhaeuser Company 2016, Washington Department of Natural Resources 2007). For the blast zone area outside the Monument we assumed the area was devoid of vegetation in 1980. The majority of down trees in this area were salvaged within 2-3 years after eruption and Douglas fir trees were replanted (Crisafulli et al. 2005); therefore, for each subsequent study year we advanced the stand age by 5 years (i.e., in 1980 the blast zone outside the Monument was 0 years and in 2010 the stand age was 30 years). We then used a potential natural vegetation map (Ecoshare: Interagency clearinghouse of ecological information, United

States Forest Services 2010) to classify stands of a particular age as either western hemlock or Pacific silver fir.

2.2.2 Inside the Monument

Five of the disturbance zones (pyroclastic flow, mudflow, debris avalanche deposit, blow down, and scorched) were mapped according to the US Geological Survey (1980), and the remaining disturbance zone (tree removal) was mapped according to the US Department of Agriculture (1981). Due to the high heterogeneity within disturbance zones (Crisafulli et al. 2005), we classified each disturbance zone into one of six plant community types (barren, moss, grass and forb, shrub, alder trees or conifer). We used isocluster unsupervised cluster classification in ArcGIS 10.2 (ESRI, Redlands, CA) with Landsat MSS image for 1980 and six Landsat Thematic Mapper images for 1985 to 2010 into 30 classes of plant community types (Table 2.2). To assign the 30 classes into a plant community type we used two approaches. For years 1980-1990 we used a combination of normalized difference vegetation index (NDVI) and aerial photographs (Table 2.2) to link NDVI values to plant community types. NDVI is a greenness index that scales from -1 to +1 based on the visual and near infrared where a value close to 0 corresponds to barren ground and a value close to +1 means high density of green vegetation (Colwell 1974, Kollenkark et al. 1982, Huete et al. 1985, Lawrence and Ripple 1998, Lawrence 2005). We first calculated the NDVI values for each of the years, then using aerial photographs we binned the NDVI values into six bins to represent the plant community types. When possible we used the aerial photographs to assign plant community types, and for areas that were difficult to differentiate between plant community types we relied on the NDVI values and collapsed classes into a plant community type based on the associated NDVI bin. For years 1995-

2010 we used high resolution spectral imagery to collapse classes into plant community types. We then iteratively created the confusion matrix and based on the Cohen's Kappa Statistic (k) we collapsed classes into the five plant community types (Table 2.2).

2.3 Forage Biomass and DE

2.3.1 Outside the Monument

2.3.1.1 Herbaceous and Shrub Sampling in Stand Ages

We used estimates of species-specific biomass of herbaceous species in eight Pacific silver fir stand-age classes (0-2, 3-5, 6-9, 10-13, 14-20, 21-40, 41-150, 151+ years) and four western hemlock stand-age classes (14-20 to 40-150+) from Cook et al. (*in press*) and from Geary (2013) for four stand-age classes (0-2 to 10-13 years) within western hemlock stands (Table 2.1). Geary (2013) followed the same herbaceous and shrub sampling methods as Cook et al. (*in press*). We used forage biomass data from Geary (2013) for stands 0-13 years in western hemlock because he presented data for both herbicide-treated and untreated early seral stands. We estimated the percent change from herbicide and no treatment for each stand-age class, and used the percent change of each class to calculate the effect of herbicides for Pacific silver fir. For forest stands that were initiated prior to 1995, we assumed no stands were treated with herbicides whereas in 1995 and thereafter we assumed herbicides were routinely used within the first two years after harvest and used Geary's (2013) data for herbicide-treated sites (Table 2.1). We did not have site-specific data on other management practices, such as tree thinning that is used on 5% of the area outside the Monument (Washington Department of Fish and Wildlife 2016) so these effects are not reflected in our estimates.

2.3.1.2 Herbaceous and Shrub Sampling on Wildlife Management Area

On the Washington Department of Fish and Wildlife's wildlife management area, we used biomass estimates provided by Merrill (1987) for 1985 and Geary (2013) for 2010; for 1990-2010 we used a linear extrapolation of biomass between 1985 and 2010. For 1980 we made the assumption that the area was devoid of vegetation due to the close proximity to the blast. For 1985-1990 we used the species composition provided by Merrill (1987) and for 1995-2010 we used the species composition provided by Geary (2013).

2.3.2 Inside the Monument

We estimated biomass of herbaceous plants and shrub CAG within the Monument based on long-term data on changes in species cover and forage-cover relationships we developed across the disturbance zones in 2014-2015.

2.3.2.1 Herbaceous Biomass

Protocols to estimate herbaceous plant cover on permanent plots differed among disturbance types. For areas on the pyroclastic flow (n =19 macroplots), mudflow (n =10), and in the tree removal zone (n =20) we used data from the permanent plots established by del Moral et al. (2012) in 1985 and repeatedly sampled to 2010. For 1980 we assumed areas were devoid of vegetation and we used data from the first year of sampling (1986) for 1985. Species-specific estimates of cover were recorded visually on an area basis (m^2) within 20, 10x10-m macroplots placed at 50-m intervals along transects at each of 3 disturbance zones. For areas on the debris avalanche, we used cover data from 63 permanent plots along two 1.9-km transects established in

1981 by Dale et al. (2005) and repeatedly sampled through 2010. We used data from 1981 for the year 1980, and the closest previous year for 1985-2005, (e.g. 1989 for 1990) and data collected in 2010. Dale et al. (2005) recorded cover visually by species as the percent horizontal cover (%) within a 250-m^2 circular macroplot placed at 50-m intervals along each transect. We converted percent cover to a 1-m^2 basis, i.e. plant species of 10% cover this was equivalent to 25 m^2 in area. In scorched (n =2) and blow down (n =17) we used cover data from USFS's permanent plots established in 1984 and periodically sampled until 2005. We assumed areas were devoid of vegetation in 1980 because of their proximity to Mount St. Helens, and used data collected in 1984 for 1985, 1994 for 1995, and data from 2000 and 2005. For 2010 we linearly extrapolated the percent change in biomass of forage classes from 2000 to 2005, assuming species specific biomass within a forage class increased at similar rates. The USFS recorded percent cover in m^2 by species within a 250-m^2 plot.

We estimated species-specific biomass of herbaceous species (B_i) on permanent plots as:

$$B_i = \frac{C_i}{\Sigma C_i} B_j \qquad \text{(eqn. 1)}$$

where C_i is the cover (m^2) of species i in forage class j, and B_j is total biomass in forage class j.

2.3.2.2 Shrub Biomass

Shrubs and saplings were defined as individual rooted stems < 2 m. We estimated current annual growth (current annual growth, g/m^2), defined as new growth within the year, for the 26 major species comprising >1% of any permanent macroplot between 1980-2010 (Appendix C). For each of the shrub species we estimated cover (m^2) by recording two cross-perpendicular sections of the canopy cover. For a representative branch on the shrub, we then recorded two-cross-perpendicular sections of the canopy cover. We then estimated cover (m^2) of the branch by multiplying the two cross-perpendicular measures to obtain an estimate of area for the branch. We estimated the area of the shrub by multiplying the two cross-perpendicular measures of the shrub. We clipped the current annual growth from the branch, dried the biomass at 100^{o} C for 48 hours, and weighed to the nearest 0.01g. We then extrapolated the cover and biomass estimates for the branch to the entire shrub by multiplying both by a factor of x (ratio of branch to entire shrub), so that the cover of the branch is equivalent to the cover of the entire shrub.

2.3.2.3 Spatial Extrapolation of Forage Biomass from 1980 to 2010

To spatially extrapolate the biomass inside the Monument at 5-year intervals, we assigned each permanent plot a plant community type based on the plant community map (Section 2.2.2). We averaged the biomass of each species across all permanent plots within similar plant community types, and extrapolated the average biomass to all areas of the same community type within a disturbance zone of a given year. When there were no permanent plot data for a specific plant community type within a disturbance type in a particular year (35% of the time across plant community types and years), we obtained biomass estimates in two ways. First, we used an average of the previous 5-year and the following 5-year interval (i.e., if biomass in 2000 was 1000 kg/ha and in 2010 500 kg/ha, we used 750 kg/ha of biomass 2005). Second, we used biomass estimates from the same year within the same plant community type in a similar disturbance zone, where we defined a similar disturbance zone based on successional timing in the recovery of the blast zone based on a preliminary analysis. For example, the scorched disturbance zone began to develop shrub plant communities in 1990 and the blowdown began to develop shrub plant communities in 1995; for the missing biomass estimates of the blowdown shrub plant community type in 2000, we used the scorched plant community type biomass in 1995.

2.4 Standing Digestible Energy

We estimated standing DE based on estimated biomass (kg/ha), species-specific estimates of digestibility (%), and gross energy content (kcal/g). Species specific estimates of digestibility were based on data from Cook et al. (*in press*), Geary (2013), and Merrill (1987) and can be found in Appendix D. We used average gross energy (kcal/g) values from Cook et al. (*in press)* for a forage class as: 4.505 $\pm$ 0.348 kcal/g (mean $\pm$ SD) for graminoids, 4.497 $\pm$ 0.166 kcal/g for forbs, 4.603 $\pm$ 0.192 kcal/g for deciduous shrubs, 4.803 $\pm$ 0.419 kcal/g for evergreen shrubs and ferns. The digestible dry matter (%) values were obtained from either in vitro analysis using inoculum from a rumen-fistulated elk maintained on an alfalfa diet (Tilley and Terry 1963) or by chemical detergent analysis (Hanley et al. 1992). For species that DE (kcal/g) estimates were not provided for (15% of the species), a DE estimate was assigned based on average DE of the forage class (Appendix D).

2.5 Forage selectivity

We included biomass only of species considered 'accepted' by elk to calculate nutritional carrying capacity. Forage selectivity was quantified based on foraging trials with tame elk in enclosure pens in western hemlock communities in Washington and Oregon (Cook et al. *in press*). Cook et al. (*in press*) defined forage preference classes as selected, neutral, and avoided for each species using the Ivlev index derived as $(D_i-B_i)/(D_i+B_i)$ (Ivlev 1961), where D refers to the proportions of biomass of species *i* in the diet and B is the proportion of biomass of species *i* in the pen at the beginning of the foraging trial. Diet of foraging elk was determined based on bite count and bite size of plant species that elk fed on in the pen. The Ivlev index values range from -1 to +1 (Ivlev 1961), with selected species being those whose 95% confidence limits across trials were greater than 0, avoided species < 0 and neutral species confidence limits included 0. In this work we defined accepted species to include neutral and selected species. For species not provided by Cook et al. (*in press*), we used data provided by Geary (2013), Merrill (1987), and published literature (Jenkins and Starkey 1996) to classify species as accepted or avoided.

2.6 Nutritional carrying capacity

We used the FRESH model of Hanley et al. (2012) to estimate NCC. The model addresses the interaction of forage availability and nutritional quality in terms of available DE quantified within a 30x30-m cell and incorporates realistic constraints related to elk foraging behavior. We derived estimates of nutritional carrying capacity based only on the accepted species (Cook et al. *in press*). We calculated nutritional resources in the 900-m^2 cell by averaging nutritional resources available to an animal that has access to forage within a unit the size of an elk home range surrounding the cell. In addition, we constrained the estimates of nutritional carrying capacity by the relative use of the 30x30-m cell where use was derived from a habitat selection model of elk.

2.6.1 Nutritional Resource Availability

We used the biomass estimates and DE content of accepted species described above as inputs to the FRESH model. We calculated the number of elk (days/ha) that can be supported based on resources within an elk home range sized unit around a 30x30-m cell because elk are exposed to forage in areas of more than one 30x30-m cell on the landscape (Hanley et al. 2012). We used the average home range size as 1063±869 ha using data from 23 GPS-collared elk in 2009-2011. Using this home range size assumed that home ranges of elk have not changed significantly since 1980, which is only moderately supported because Merrill (1987) found minimum convex polygon

home range size of 24 cow elk between 1981-1985 was highly variable averaging 2800±2300 ha.

To estimate the forage for a 30x30-m cell using average resources available within a home range-sized area, we calculated the dietary DE (kcal/ha) subject to the following constraint:

$$\frac{P_1 B_1\, DE_1 + P_2 B_2\, DE_2 + \cdots + P_n B_n\, DE_n}{P_1 B_1 + P_2 B_2 + \cdots + P_n B_n} \geq DE_{constant} \qquad \text{(eqn. 2)}$$

where $DE_{constraint}$ is the digestible energy (kcal/g) level for the inclusion of the species in the nutritional carrying capacity estimate, B_n is the biomass of each species (n), P_n is the percent of each species that can be consumed, which was set to 100% as the baseline. Although we used 100%, because no species could comprise more than 40% of the diet, we found consumption generally plateaued at 40% of the forage biomass (see Results). The model also imposed two foraging constraints on forage access: (1) a cell was not considered to contribute nutritional resources to the NCC if accepted biomass was < 150 kg/h because Cook et al. (*in press*) reported elk could not forage profitably within an area accepted species biomass lower than this threshold; (2) we set the maximum percentage of a species within a diet to 40% (Cook et al. *in press*). We used this constraint because elk are largely generalists with their diets rarely dominated by one species (Cook 2002). Lastly, we assessed the effects of a range of values of each of these constraints, from baseline, on estimates of nutritional carrying capacity in a sensitivity analysis.

We estimated the nutritional carrying capacity (elk days/ha) for a pixel in 3 steps. First, we estimated the average selected biomass with a moving window the size of a home range (1063 ha) and assigned the value to each 30x30-m cell within the home range; we then moved the window over 20 cells (determined during a-priori testing of 10, 20 and 30 to optimize computing time and estimating the forage at a local level) to another area of overlapping home range and iterated the process. Second, we then estimated the mean selected biomass for all iterations for a 30x30-m cell. Third, we used this value to estimate digestible energy available subject to the above constraints to estimate number of elk days/ha (nutritional carrying capacity) for each cell with the following formula:

$$\frac{((P_1B_1 + P_2B_2 + \cdots + P_nB_n) - B_{\min\ constant})}{DI} x\ 1000 = Elk\ days/ha \qquad \text{(eqn. 3)}$$

where *DI* is the daily dry matter intake of an elk set at 7997 g/day for high, 7272 g/day for maintenance, and 6903 g/day for low quality diets. Also, $B_{min\ constant}$ is the minimum amount of accepted biomass available for an elk for forage profitably, 150 kg/ha (*Cook et al. in press*). Lastly, *Elk days/ha* is the response variable in our nutritional carrying capacity model, used to calculate the number of days an elk can be supported in hectare based on the nutritional availability and the elk's nutritional requirements.

2.6.2 Elk Energy Requirements

We used daily estimates of required dry matter (g/day) for a lactating elk in late summer (August) taken from Cook et al. (2004: Fig. 6). The dry matter intake requirements were based on a captive heard of 57 lactating Rocky Mountain elk within Northeastern Oregon from years 1995 to 1998 (Cook et al. 2004). We present nutritional carrying capacity based on three levels of dietary DE and associated dry matter intake formulated as: high (2.9 kcal/g, 7997 g, 227 kg elk), medium (2.7 kcal/g, 7272 g, 213 kg elk) and low (2.5 kcal/g, 6903 kcal/g, 205 kg elk) nutritional diets (Cook et al. 2004: Fig. 6). The high levels represented no restrictions on reproductive performance, the medium level was to maintain requirements of an elk so that fat reserves were held constant, and the low nutritional level diet reduced probability of pregnancy by 80% (Cook et al. 2004: Fig. 4). We used the high level of nutrition for our baseline assessment because diet quality was known to be high after the eruption of Mount St. Helens (Merrill et al. 1995), and our focus was on assessing trends over time.

2.6.3 Resource Selection Function and Relative Landscape Use

Following Beck et al. (2006), we derived the expected relative use of each 30x30-m cell (900 m^2) within the study for each year as a weight for constraining the contribution of a cell to the NCC due to the effects of landscape features on its probability of use. We created the relative use map by first developing a resource selection function (RSF, Johnson et al. 2006) and then using the RSF to predict to relative use across the landscape for a given potential NCC (Boyce and McDonald 1999).

2.6.3.1 Resource Selection Function

We used telemetry locations of 23 GPS-collared female elk using the study area in summer (June - October) in 2009-2011 to develop a single RSF. Because we used data only from 2009-2011 and applied the RSF across the 30-year period, we included 4 covariates that Rowland et al. (2013) showed were consistently important in predicting habitat use across 21 elk populations in western Washington and Oregon. We did not use the Rowland et al. (2013) resource utilization function because of the unique habitats in the Monument.

Elk were immobilized in February from a helicopter with a carfentanil citrate/xylazine hydrochloride mixture that was reversed by injecting naltrexone hydrochloride and yohimbine hydrochloride (McCorquodale et al. 2014, Geary 2013). A vestigial canine was extracted to determine age (Matson's Lab, Milltown, MT, USA) and elk were fitted with either Telonics TGW-4700-3 or Lotek 3300 store-on-board GPS collars that were programmed to relocate elk every 2 or 3 hours. All handling followed procedures in compliance with Washington Department of Fish and Wildlife's Animal Restraint and Chemical Immobilization Policy (POL-M6003). Our analysis used locations only between 0500-1900 when elk were most likely to be feeding (Appendix B). We used the same number of locations (n = 1140/elk) for each individual with 10% of the points withheld from the final model (2,622 points) for model assessment. Random locations (available) were generated in 1:1 use:available points within the individual's home range where the home range was estimated using a 95% kernel density (Seaman et al. 1999).

In the selection model we used dietary DE (kcal/g) as calculated by FRESH using accepted species to control for nutritional resources and to assess the impact of slope, distance to forest-cover edge, and distance to public roads. Dietary DE was created using the methods outlined above. Slope was derived from a digital elevation map provided by the United States Geological Survey (2013). For these two variables we used the average value within a 250-m buffer around GPS and random locations. A 250-m buffer was used because it is currently used as the buffer size in the Westside Elk Habitat Model (Rowland et al. 2013). Public roads were defined as accessible to the public without a gate, for years 1990-1995 public road data was obtained from the United States Census Bureau, and for 2010 from the Washington Department of Transportation. For study years 1980-1985, we used the public road data from 1990. For distance to the nearest forest edge, we assumed cover to be areas > 14 years on managed lands, and shrub plant community types inside the Monument. Distance to forage-cover edges were digitized using the plant community type maps in ArcGIS 10.2 (ESRI, Redlands, CA). Public roads and forage-cover edges were measured as distance (m) from an elk location or random point. Covariates were standardized for each of the study years by subtracting the mean and dividing by the standard deviation of a variable using the available values across the composite home range of the 23 elk. Prior to modeling we assessed multi-colinearity between all covariates with a variability index factor ($|r| > 0.6$, Sawyer et al. 2006).

We used a mixed-effects model with individual animal intercepts (Gilles et al. 2006, Aarts et al. 2008, Matthiopoulos et al. 2011, Mabille et al. 2012). We used logistic regression to estimate the coefficients of an exponential resource selection function:

$$w_j(x_{ij}) = \exp(\beta' x_{ij} + \gamma'_j z_{ij}) \qquad \text{(eqn. 4)}$$

where β is the vector of selection coefficients, $\gamma'_j z_{ij}$ is associated with the random intercept of elk j, and i refers to location of the *j* animal. We assessed the RSF model in predicting use following methods outlined in Boyce et al. (2002). We first predicted the RSF value of every 30x30-m^2 cell and grouped values into equal-area bins. We then correlated the midpoint RSF value of the RSF bin to the frequency of the withheld telemetry locations adjusted by area within each resource selection bin (Boyce et al. 2002).

2.6.3.2 Relative Use

We calculated relative use *U* of each 30x30 m cell following Boyce and McDonald (1999):

$$U_{(xi)} = w_{(xi)} A_{(xi)} / \sum w_{(xj)} A_{(xj)} \qquad \text{(eqn. 5)}$$

where $w(x_i)$ is our resource selection value of the cell *x* for year *i*, $A(x_i)$ is the area of each cell (Appendix E).

2.6.3.3 Use-constrained nutritional carrying capacity

We estimated the use-constrained NCC (NCC$_{constrained}$) based on the FRESH-derived NCC within a 900-m^2 cell for each 5-year period (i) and the relative use of the cell by elk as:

$$NCC_{constrained(xi)} = NCC_{(x)} \times U_{(xi)} \qquad \text{(eqn. 6)}$$

To determine the nutritional carrying capacity constrained of a cell, we compared the NCC to the $NCC_{constrained}$, and when the NCC exceeded the $NCC_{constrained}$ we used value of $NCC_{constrained}$ for the cell.

3. Results

3.1 Landcover Maps

The four disturbance zones most altered by the eruption, the pyroclastic flow, mudflow, debris avalanche and tree removal, comprised 32% of the Monument and showed similar patterns of recovery (Fig. 2.2). These areas transitioned from being mostly barren ground in the first 10 years after the eruption to being moss-dominated communities in 1990. From 1995-2010 succession resulted in grass/forb and shrubs/tree saplings averaging 27% and 18% of these disturbance types, respectively. Only on the debris avalanche deposit did red alder trees become a major plant community type comprising 61% of this disturbance zone by 2010. The blowdown and scorched disturbance zone comprised 68% of the Monument. Succession progressed more quickly in these areas and by 2010 the zones were 23-34% grass/forb, 15-21% shrub/sapling, and 47-53% conifer (Fig. 2.2).

Outside the Monument, GMUs 522 and 524 had a higher proportion of 0-2 stand ages in 1980 than GMU 556 because 22% and 75%, respectively, of the areas affected by the eruption vs. 3% in GMU 556. By 1995 extensive areas (67-90%) in these 2 GMUs were at 15 years of age when canopy closure occurs, and by 2010 77-92% of the area was comprised of stands of 20-40 years, where canopy closure was complete. In contrast, GMU 556 had a higher diversity of stand ages across the study years with early seral stands (1-13 years) averaging 32% across study years.

Old-growth forests (150+ years) comprised < 3% in any of the GMUs.

3.2 Forage dynamics

3.2.1 Accepted biomass

Inside the Monument the rate of understory recovery was slowest in the 3 most devastated disturbance zones, and this trend was consistent through 2010. Although total biomass increased faster on the pyroclastic flow than on the mudflow (Appendix F: Fig. F.1), increases in accepted forages did not occur increase because the pyroclastic flow was heavily dominated by a moss community (Fig. 2.2), and moss is not an accepted forage. The most rapid recovery of total biomass and accepted species in the Monument occurred in the low-impact, scorched zone (Fig. 2.4, Appendix F: Fig.F.1), which peaked in 2000 and thereafter declined due to canopy closure associated with increased dominance of conifer trees (Fig. 2.2). A similar decline in both total and accepted biomass occurred in the blast zone area outside the Monument, but the decline occurred 5 years earlier (i.e. 1995) compared to inside the Monument (Appendix F: Fig.F.1). This was due to the rapid replanting of crop trees on industrial forests outside the Monument after salvage logging soon after the eruption. There was a continual increase in total understory biomass in the blowdown and on the debris avalanche that did not peak until 2005 when total and accepted biomass either leveled off or started to decline (Fig. 2.4, Appendix F: Fig.F.1). On the debris avalanche the decline likely resulted from an increasing closure of overstory of alder trees whereas the decline in the blow down was associated with canopy closure of conifers (Fig. 2.2).

Outside the Monument, the blast zone area within the GMUs had little to no biomass in 1980 but provided high total and accepted biomass until 1995 (Fig. 2.4, Appendix F: Fig.F.1) when biomass began to decline. This decline was consistent with succession of early seral forests up to ~15 years when the effects of canopy closure on understory occurs. As a result, the total and accepted biomass in GMUs 522 and 524 declined substantially by 1995. A similar pattern associated with eruption did not occur in GMU 556; nevertheless, there was a steady decline in seral stands <15 years resulting in a decline in accepted biomass (Fig. 2.3, 2.4)

3.2.2 Standing Digestible Energy

Standing digestible energy inside and outside the Monument, closely followed the general trends of the accepted biomass because accepted species tended to be highest in dry matter digestibility (Fig. 2.5, Appendix D: Table D.1).

3.3 Resource Selection Function and Relative Use

Elk selection increased for areas with high digestible energy, steeper slopes, near forest edge but farther from public roads according to the following model:

$$w_j(x_{ij}) = \exp((0.09)DE + (0.01)Slope - (0.03)DistEdge + (0.03)DistPR) \qquad \text{(eqn. 9)}$$

where dietary *DE* represents digestible energy of accepted biomass (kcal/g), slope is the average within 250-m buffer (%), *DistEdge* represents the distance to forage-cover edge (m), and *DistPR* is distance to public roads (m). All covariates were found to be significant ($p<0.05$). We found that the midpoint of the 10 RSF classes was related to the frequency of use of elk within the classes (r =0.78, df=8, p=0.01) in 2009-2010 based on elk locations withheld from model development (Fig. 2.6).

Median RSF values for the different portions of the study area reflect the overall quality of the habitat that influenced predicted use in these areas. The average elk selection for areas inside the Monument increased over time due to improving dietary DE with increasing accepted biomass and recovery of forest patches that lead to areas being closer to forest edge (Table 2.3). Although GMU 556 maintained a relatively high dietary DE in accepted biomass due the extent of early seral stands and moderate distance to edge due to the diversity of forest stand ages over time (Fig. 2.4), overall elk selection was low as a result of relatively high road densities reflected in areas on average being closer to roads. In contrast, overall selection for areas in GMU 524 was relatively high over time despite low dietary DE in accepted biomass because of relatively few roads. GMU 522 had the lowest median selection values over time despite relatively high dietary DE in accepted biomass because overall areas were relatively far from edge and close to roads (Table 2.3).

Relative use values for the different areas were strongly related to the RSF values ($r=0.97, p<0.0001, n=33$) as expected, and therefore followed the same spatio-temporal trends as the RSF values, with relative use being highest inside the Monument and GMU 524, followed by GMU 556 and 522 (Table 2.3).

3.4 Elk Carrying Capacity

3.4.1 Nutritional Carrying Capacity

For the first 10 years after the eruption, the average elk NCC (elk/ha) outside the Monument was 178 – 739% higher than inside the Monument (Fig. 2.7). NCC within the GMUs peaked in 1985, declined in 1990, and then remained stable or somewhat increased. This trend occurred for two reasons. First, 52% of the area outside the Monument consisted of seral forest < 15 years in 1985, including the recovering blast zone (31% of the area outside the Monument) and early seral stands after timber harvest (21% across GMUs). Second, we assumed areas outside the Monument, herbicides were broadly applied in 1995 and thereafter. Reduction in biomass due to herbicides in the first 1-2 years after stand initiation, the average elk NCC was reduced on average by 4±1% in GMU 522, 27±17% in GMU 556, and 19±12% in GMU 524 between 1995 and 2010 (Fig. 2.9). Outside the Monument in 1995, there also was a drop in total NCC because canopy closure begins at 15 years, and new timber cuts did not offset these declines because they comprised only 2±0.8% across the GMUs (Fig. 2.3). After 1995, the patterns in elk NCC in GMUs 522 and 524 diverged due to the increase in total timber harvest from 1995-2010 in GMU 524, 365 ha, compared to 21 ha of timber harvest in GMU 522 (Fig. 2.3).

Inside the Monument initially recovery was more gradual with the number of elk capable of being supported peaking over most of the area 20 years after the eruption in 2000 (Fig. 2.7), There was a decline in 1995 prior to the peak in carrying capacity related to the decline in accepted biomass and dietary DE because of a 161% increase in conifer communities on the scorched zone from 1990 to 1995 (Fig. 2.3-2.5). The increase in the carrying capacity inside the Monument in 2000 (Fig. 2.7) was due to a peak in accepted biomass on the scorched disturbance zone (Fig. 2.4). The decline in carrying capacity by 28% reflected the decline in accepted biomass in the scorched area from 2000-2010 (Fig. 2.7) related to the increase in conifer communities. As a result, the decline in elk days/ha outside the Monument from 2000-2010 was partially compensated for by the increase in carrying capacity inside the Monument (Fig. 2.9) due to the increase in accepted biomass on the blowdown and debris avalanche deposit (Fig. 2.4).

3.4.2 Constrained Nutritional Carrying Capacity

The constrained NCC ($NCC_{constrained}$) was 2 - 49% lower than the original NCC aross years, with trends across years being similar among areas with three exceptions (Fig. 2.7). First, although forage-based NCC in GMU 556 was high in 1980, use in this area was diminished by 38% due to an abundance of roads (Table 2.3). Although roads increased after 1980 in GMU 556 (Table 2.3), the difference between the NCCand $NCC_{constrained}$ decreased because NCC became the limiting factor due to the decline in accepted biomass (Fig. 2.4). Second, although NCC peaked in the Monument in 2000 and began to decline thereafter, this pattern was not evident in the $NCC_{constrained}$. Inside the Monument from 1980-1995 the limiting factor was the forage-based NCC because accepted biomass was low (Fig. 2.4); however, from 2000-2010 the accepted biomass increased and the limiting factor then became relative use. The upward trend in $NCC_{constrained}$ from 2000-2010 occurred because of a 17% increase in the relative use between 2000 - 2010 due to increasing dietary DE associated with a decreased in average distance to forest cover edges (Table 2.3). Third, the $NCC_{constrained}$ of GMU 524 increased from 2005-2010, but a similar increase was not evident in NCC (Fig. 2.7). In 2010, GMU 524 had its lowest accepted biomass across years resulting in a low NCC (Fig. 2.7), and a decline in relative use that was related to a 56% decrease in the distance to roads (Table 2.3). Overall, the $NCC_{constrained}$ still showed that the inside of the Monument is compensating for the decline in carrying capacity outside the Monument after 1995 until 2010 (Fig. 2.9), where 2010 has the highest carrying capacity, 63% greater than in 1985 when outside the Monument was at its peak in carrying capacity (Fig. 2.8, Fig. 2.10).

3.5 Sensitivity Analysis

Setting the level of dietary DE threshold necessary for an elk to meet a standard of maintenence or reproductive requirements has the greatest influence on the estimate of elk days/ha. Above 2.9 kcal/g there was little change in the number of elk days/ha because the abundance of forage greater then this threshold became limiting. However, with a 8% and 14% decrease in the dietary DE constraint from the 2.9 kcal/g baseline threshold to the 2.68 kcal/g and 2.48 kcals/g, elk on a maintenance and low quality diet, resulted in an 895% and 4495% increase in the number of elk days/ha with variability increasing as baseline dietary DE declinced (Fig. 2.5, 2.11). The increase in elk supported occurred because elk were able to form diets of lower quality, but with the implication that elk would not as readily meet reproductive requirements. Dry matter intake had less of an effect on elk day/ha than dietary DE threshold with elk days/ha decreasing by 14% when dry matter intake increased from 6903 g/day to 7997 g/day, holding DE constant at baseline levels. Elk days/ha increased more rapidly (3%) as maximum percent of a species comprised of the diet increased from only 30 to 35% but the rate of increase was not as great thereafter (Fig. 2.12). We assumed the maximum that an elk could eat of the selected biomass was 100%, maximum consumption had little effect on elk days until elk ate less than 40% because the 40% constraint on the diet, resulting in consumption greater then this threshold not having affected our elk days/ha. The elk days/ha was least influenced by the constraint of the minimum amount of biomass available for an elk for forage profitabily, with only a 0.03% decrease in elk days/ha as the biomass constraint changed from 150 kg/ha to 187 kg/ha (Fig. 2.12). Biomass of accepted species <150 kcal/ha represented only 0.6% of the study area in 2010, and with the highest percentage of 62% occuring in 1980.

4. Discussion

The current concern for a decline in the habitat quality for the Mount St. Helens elk herd is supported by our analysis for low elevation, industrial lands, due to the dynamics of early seral communities that were either clearcut or impacted by the eruption in 1980. Forest succession in the blast zone outside the Monument has been similar to that following timber harvest in the Pacific Northwest due to low ash and tephra depth, and the salvage logging and replanting of crop trees shortly after the eruption (Collins and Dunne 1988, Halpern et al. 1990, Merrill et al. 1995, Titus and Householder 2007). By 1995 canopy closure of these stands likely increased by 40 to 70% comparable to stands of 15 years after timber harvest (Alaback 1982, Witmer et al. 1985, Jenkins and Starkey 1996, Hanley 1984). Canopy cover has been reported to be the best predictor of accepted biomass for both elk (Geary 2013, Cook et al. in *press*) and deer (Ulappa 2015). In stands of 15 years of age, accepted species was less than 400 – 500 kg/ha, which Cook et al. (*in press*) reported resulted in reduced dietary DE intake because elk began to include more low quality, avoided species in their diet (Cook et al. *in press*). Because new clearcuts did not offset the loss of early seral stands created by the eruption, average accepted biomass dropped and remained lower than this threshold after 1995 in all three management units outside the Monument. In the one management unit that was marginally affected by the eruption, accepted biomass also declined because previous cutting patterns resulted in a 67% decrease in early seral stands over time.

A second concern for habitat declines in the Mount St. Helens area, and more broadly in the Pacific Northwest, has been the broad-scale application of herbicides for silvicultural treatments in clearcuts. Application of operational herbicides in the Pacific

Northwest have been shown to reduce both accepted and avoided species by 54-84% in the first 1-3 years following stand initiation (Harrington et al. 1995, Stein 1995, Dinger 2007, Maguire et al. 2009, Geary 2013, Ulappa 2015). In our study, we assumed herbicide application at stand initiation reduced accepted biomass by 77% during the first 2 years based on research in our study area (Geary 2013). We estimated this resulted in an average 23±7% decline in elk days/ha from 1995-2010 across the three management units we studied. Ulappa (2015) also reported a 26% decline in the deer day/ha of black-tailed deer compared to when herbicides were not used in study area in western Washington.

Whereas application of herbicides as a forest regeneration tool may have reduced the forage availability, we did not consider other management practices in estimating the trends in accepted biomass, such as commercial forest thinning, that can stimulate understory growth. Early commercial thinning typically occurs as early as 20 years (Thomas et al. 1999) and can increase the production of understory species by allowing more sunlight to reach the understory and increase understory abundance (Raedeke and Lemkuhl 1984, Peter and Harrington 2009) including forage eaten by elk (Strong and Gates 2006). Cook et al. (*in press*) reported a 5-10% decrease in canopy cover on 20-60 year stands; however, they found little evidence for thinning altering abundance of accepted biomass in Pacific silver fir stands, but in western hemlock stands there was on average 67% increase in total species biomass across three sites in western Oregon and Washington. If commercial thinning were considered in this study, we would see an increase in the elk days/ha within the blast zone from 2000-2010, because 25 - 40% of the area outside the Monument from 1995-2010 are western hemlock stands greater than 20 years.

In contrast, inside Monument where vegetation has been left to recover naturally after the eruption, patterns of forage succession were highly variable, and did not conform to the same rapid forest succession as on industrial timber lands. On the pyroclastic flow, vegetation recovery was slow and plant cover was low and initially comprised of pioneering herbs such as *Agrostis dietoensis*, *Luzula parviflora*, *Anaphalis margaritaces*, and in particular a lupine (*Lupinus* spp.) species, which is a nitrogen fixing species that formed dense patches in portions of this area (del Moral and Clampitt 1985, Nuhn 1987, Wood and del Moral 1988, del Moral et al. 1995, del Moral et al. 2010). As a result, lupine facilitated the growth of other species after it died (~5 years) by increasing the soil fertility (del Moral et al. 1995, del Moral and Lacher 2005, del Moral et al. 2010). Despite these small-scale dynamics, barren ground dominated about a third of this area through 2010. Moss communities, which contained little acceptable biomass, became well established and covered about a third of the pyroclastic flow by 1995, whereas forb/grass-dominated communities were not abundant until 2005 when they covered ~35% of this area. Although our results indicate the extent of barren ground has decreased and forb/grass community has increased over time, acceptable biomass within forb/grass-dominated communities on the pyroclastic flow fell below the 400-500 kg/ha, which may constrain elk intake rates limiting the value of these communities to elk. Distinguishing between barren ground and moss communities were least accurate with remote sensing and better accuracy would require more fine-resolution images and ground truthing than was possible within this study. Even considering this limitation, it was clear that the abundance of accepted biomass remained relatively low on the pyroclastic flow through 2010.

In contrast, understory vegetation capable of supporting elk consistently improved in four disturbance types that comprised over 90% of the Monument we studied. On the debris avalanche during the first few years post eruption the dominant species were lupine, fireweed (*Chamerion angustifolium*), and Canada thistle (*Cirsium arvense*), which became less abundant by 1990 (Dale et al. 2005). By 1995 red alder (*Alnus rubra*), a fast growing, woody pioneer species and another nitrogen fixer (Russell 1986, Adams et al. 1986) became well established on the debris avalanche (Dale et al. 2005). Alders flourished on the debris avalanche deposit because of its moisture promoted high germination rate (Adams et al. 1987). Although red alder is not a selected browse species, elk will browse young saplings (Schopmeyer 1974). Because it grows more rapidly and is more tolerant to browsing than conifers, over time the community has seen an increase in red alder comprising over 25% of the debris avalanche by 2005. As the trees have grown, canopy cover has closed shading the understory by 2010, resulting in a decline of accepted biomass. Patterns of understory recovery in the scorch and blowdown areas within the Monument were most similar to those on industrial lands (Witmer et al. 1985, Jenkins and Starkey 1996, Hanley 1984, Alaback 1982); however, comparable peak levels of accepted biomass (i.e., 840±403 kg/ha, Geary 2013, Cook et al. *in press*) were delayed 10 years and 15 years, respectively. Although understory recovery in the tree removal area was also compositionally similar to these communities (Crisafulli et al. 2005), understory vegetation showed a definitive increase reaching levels of only 25-33% of peak biomass of other communities by 2010. As a result of the successional lag in the understory recover in these 4 disturbance types, elk nutritional carrying capacity across the Monument increased, while decreasing on industrial lands to the west of the Monument. These large-scale dynamics of summer forage may have partially compensated for the reduced NCC given that elk migrate to high elevations in summer (Miller and McCorquodale 2006, McCorquodale et al. 2014).

Our description of carrying capacity dynamics were derived using several assumptions. First, we used accepted biomass as the basis for evaluating potential NCC. Cook et al. (*in press*) found that availability of accepted biomass closely corresponded to levels of dietary DE of tame elk in these communities, which influenced elk foraging behavior, DE intake, and calf growth. If we had used total biomass, as in early models of NCC (Wallmo et al. 1977, Hobbs and Swift 1985, Irby et al. 2002, Coughenour et al. 1996), it is likely both the number of elk that could be supported and NCC trends would have differed because total biomass outside the Monument from 1980-1995 was higher than inside the Monument from 2000-2010, resulting in the Monument not offsetting the decline in elk carrying capacity on managed land. Further, by basing our estimates on accepted biomass we have incorporated other nutritional constraints implicitly because high levels of secondary plant compounds and fiber can also influence forage selection and quality (Robbins 1987, Minson and Wilson 1994, Robbins et al. 1995, Hobbs 2003, Cook et al. 2004).

We based NCC estimates on elk being able to obtain a high quality diet (2.91 kcal/g), which is a level that was sufficient to meet total reproductive demands (Cook et al. 2004). By lowering the threshold level of DE concentration and associated increase in intake in the model, our sensitivity analysis showed elk carrying capacity for lactating cow elk across the entire landscape increased by 8-14 times; nevertheless overall trends were similar, except variability in elk use days/ha among years increased as the baseline dietary DE threshold and intake levels declined. We also assumed that a single species could not comprise more than 40% of the diet because elk are generalists (Moran 1973, Hobbs et al. 1981, Cook 2002) and a mixed diet can minimize the effects of high secondary compounds in some species (Hanley 1987, Van Horne et al. 1988, Happe et al. 1990). With this assumption, our sensitivity analysis showed that only about ~ 40% of the accepted biomass could be consumed despite us assuming otherwise. Therefore, our results are consistent with the 40-50% utilization of plant species to sustain understory vegetation used in other studies deriving ungulate carrying capacities (Beck et al. 2006, Davis et al. 2010, Wagoner et al. 2013, Ulappa 2015, Steenweg et al. 2016). In any event, our goal was to compare broad-scale trends in NCC over time rather than establish definitive population numbers of elk on the landscape because model assumptions, particularly the DE threshold and the dry matter intake levels, influence actual elk days/ha. By keeping assumptions constant across our study years it allowed us to document changes in habitat quality as it related to succession changes.

Although the patterns of nutritional resources on the landscape we describe may indicate spatio-temporal changes in the landscape to support elk, the ability of elk to take advantage of changing nutritional resources can be constrained by other factors. The selection model we used to constrain the potential habitat quality for elk focused on factors that broadly influence elk use in the Pacific Northwest and used in the Westside Elk Habitat Model (Rowland et al. 2013), which is now used in managing elk habitat in this region. Similar to their models, we found forage quality most influenced by elk selection followed by distance to forage-cover edges, distance to public roads, and slope. As a result, successional patterns in vegetative communities around Mount St. Helens had a strong effect by altering not only the nutritional resources available to elk, but also influencing elk use due to edge effects of recovering forests because it has been demonstrated that elk use is highest where there are forage-cover ratios of 40:60 (Rodrick and Milner 1991).

Our approach to constraining NCC may not reflect patterns in actual elk use over time for several reasons. First, we assumed elk habitat selection did not change over the period 1980-2010. Selection can change as a function of both habitat availability and elk density (Anderson et al. 2012, van Beest et al. 2016), but we did not include these effects in our model. However, Merrill (1994) reported that within the first five years after the eruption, elk strongly selected for open areas in the blast zone associated with an abundance of high quality forbs during early summer and shifted to areas with an abundance of total herbaceous biomass when forb biomass declined. Further, because road data were unavailable between 1980 and 1985, we used road data from 1990 to assess elk habitat selection during these years, which was not consistent with the observed increase in road density from 1990-2010. Early studies of elk use in the blast zone found elk would tolerate logging roads and timber operations if close to cover edges, but avoided the public use roads that existed (Czech 1991). If there were lower road densities prior to 1990, estimates of NCC would have been somewhat higher in these years. However, most accessible roads were logging roads during the initial years after the eruption with the major public road network being open after the first five years post eruption.

In incorporating the resource selection function into our carrying capacity model we found there to be a 2-49% decline in elk days/ha across years and inside/outside the Monument, compared to when only nutritional resources were considered. Beck et al. (2006) reported a more conservative decline of 18 to 35% for elk in northeastern Nevada, USA during autumn 1999 and 2000, when constraining their carrying capacity model by elk selection for plant community types. In contrast, Davis et al. (2010) reported a 70 to 81% decline in deer nutritional carrying capacity from 1984-2002 when weighting estimates by selection of roads and forage-cover, within a portion GMU 524 that included the blast zone. However, approaches to constraining carrying capacity differed. Davis et al. (2010) reduced NCC from 50% when areas were within 100 m of a road to 10% when neither cover or forage existed in an area, whereas we followed the approach of Beck et al. (2006) and reduced elk based on their relative use of the area only when the expected NCC was higher than the $\mathrm{NCC}_{\mathrm{constrained}}$. In either case, even though the absolute values of elk supported were lower, we found that NCC and $\mathrm{NCC}_{\mathrm{constrained}}$ tracked each other over time with one exception. Although $\mathrm{NCC}_{\mathrm{constrained}}$ was lower, the proportional decline in elk use days was relatively less indicating that the number of elk that can be supported inside Monument may not yet be declining compare to past years (Fig. 2.8). The spatial maps of $\mathrm{NCC}_{\mathrm{constrained}}$ clearly show the shift in elk carrying capacity from outside the MSHVNM in the first 15 years to an increasing but spatially variable $\mathrm{NCC}_{\mathrm{constrained}}$ inside the Monument from 2000-2010.

In conclusion, this study is one of the few to assess the long-term impact of a volcanic eruption on a large mammal, and illustrates an approach that is capable of anticipating the potential consequences of current forest successional trends from forest disturbances over large areas from either natural recovery or alternative forest management scenarios. We found there to be a decline in the elk nutritional carrying capacity outside the Monument after 1985 due to forest succession even if there were small scale difference dues to herbicides (Geary 2013) or the effects of early salvage logging (Titus and Householder 2007). We found evidence for the hypothesis that advancing forest succession inside the Monument may be partially offsetting the effects of canopy closure either in areas that were clearcut at the time of the eruption or were in the blast zone and were replanted shortly after the eruption. However, in large portions of the Monument, nutritional resources in early seral communities may have peaked except in dramatically disturbed areas like the mudflow and pyroclastic flow. Although other factors like human disturbance associated with roads may create local effects on the potential carrying capacity of elk in this region, forest succession as it related to providing nutritional resources and maintaining forage-cover ratios, is key to maintain high quality habitat for elk.

Table 2.1. Disturbance zones and stand age descriptions inside and outside the Mount St. Helens National Volcanic Monument (Monument), the plant community type (PCT) within each disturbance zone, the sources for the permanent plot data, and the number of microplots sampled within each plant community type during 2014 and 2015. The descriptions of the disturbance zones inside the Monument were provided by the United States Geological Survey (1981).

	Disturbance Zone	Area (ha)	PCT	No. Plots	Source	Description
Inside Monument	Pyroclastic Flow	1470	Barren	34	del Moral et al. (2012)	This zone was affected by direct blast and pyroclastic deposits and has been altered by the development of small wetlands. It is located around 1122-m in elevation. Nearly all vegetation was removed by the blast or buried in deep pumice deposits.
			Moss	26		
			Grass and Forb	23		
			Shrub	17		
	Mudflow	775	Barren	16		In 1980 the mudflow destroyed a large portion of the vegetation of the Muddy River basin and disturbed more than 20-km of river corridor between the volcano crater and Swift River. The most destructive mudflow emerged from the debris avalanche deposit and flowed down the North and South Fork Toutle River valley.
			Grass and Forb	34		
	Tree Removal	3633	Barren	18		This zone is approximately 8-miles (13-km) in radius, an area where everything was blown away with the blast, hence the name "tree removal zone".
			Moss	10		
			Grass and Forb	40		
			Shrub	7		
	Debris Avalanche Deposit	3293	Barren	27	Dale et al. (2005)	The debris avalanche deposit is located on the north side of the mountain. The DAD has a heterogeneous topography. There are flat areas where the mudflow moved across the debris deposit. These areas retained the air-fall tephra that was emitted by the volcano.
			Moss	15		
			Grass and Forb	9		
			Shrub	30		
	Blowdown	18816	Grass and Forb	52	USFS (unpublished data)	This area is an intermediate area between the scorched and the tree removal zone, it extends out to distanced as far as 19-miles from the volcano in this zone there was a large amount
			Shrub	80		

			Conifer	15		of broken off trees at the base of the trunk where they were later removed.
	Scorched	2483	Grass and Forb	23		This area is also referred to the "seared zone" or the "standing dead" zone where the area is comprised on trees remaining standing but singed brown by the hot gases of the blast. This is the outermost edge of the impact area.
			Shrub	31		
			Conifer	30		
Outside Monument	Western Hemlock Forest	53485	1-2 yr		Geary (2013)	Occur at low elevations, ranging from 150-640 m. Western Hemlock (*Tsuga heterophylla*) and Douglas fir (*Pseudotsuga menziesia*) most often dominate this forest type, with the ocassional occurnace of western red cedars (*Thuja plicata*), red alder (*Alnus rubra*), and maple (*Acer spp*., Cook et al. *in press*). The understory composition is dependent on site conditions but is most often dominated by salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), swordfern (*Polystichum munitum*), and salmonberry (*Rubus spectabilis*, Cook et al. *in press*).
			3-9 yr			
			10-13 yr			
			14-20 yr		Cook et al. (*in press*)	
			21-40 yr			
			41-150 yr			
			150+ yr			
	Pacific Silver Fir Forest	28272	1-2 yr		Cook et al. (*in press*)	Generally, occur at mid elevations (641-1280 m). Understory sites are dominated by a mix of lady fern (*Athyrium filix-femina*), huckleberry (Vaccinium spp.), salmonberry, twinflower (*Linnaea borealis*), and trailing blackberry (*Rubus ursinus*, Cook et al. *in press*). In early seral stages, these taxa, along with shade intolerant and semi-intolerant taxa (Franklin and Dryness 1988, Henderson et al. 1992, Cook et al. *in press*). The mountain hemlock series co-occurred at high elevation (>1280 m) in wet cool areas.
			3-9 yr			
			10-13 yr			
			14-20 yr			
			21-40 yr			
			41-150 yr			
			150+ yr			
	Wildlife Management Unit	334	Seeded Mudflow		WDFW (2006)	Area is located 6 km west of the MSH blast zone along the North Fork Toutle river. The area is characterized by grassland and many non-native forbs which were periodically seeded with grasses and legumes in the area since the early 1980's because of the value as an important wintering location for elk around MSH.

Table 2.2. Remote sensing imagery used in unsupervised classifications of the plant community types for 1980-2010 at Mount St. Helens. We used a series of aerial photographs to verify our plant community type classification, using the verification sources we completed the confusion matrix for each of the study years.

	1980	1985	1990	1995	2000	2005	2010
Source	USGS	USGS	USGS	USGS	USGS	USGS	USGS
Sensor	MSS	TM	TM	TM	TM	TM	TM
Date	5 September	20 June	20 July	3 August	16 August	14 August	9 July
Time (GMT)	18:14:23	18:25:54	18:15:53	17:59:46	18:33:29	18:43:52	18:26:32
Path, Row	49, 28	46, 28	46, 28	46, 28	46, 28	46,28	46,28
Cloud Cover (%)	0	6	0	10	0	0	0
Cell Size (m)	60 x 60	30 x 30	30 x 30	30 x 30	30 x 30	30 x 30	30 x 30
Verification Source	USGS	USGS	USGS	Google Earth	Google Earth	Google Earth	USDA
Confusion Matrix Points	106	100	100	105	107	100	597
Cohen's Kappa Statistic	0.89	0.84	0.85	0.86	0.84	0.83	0.85

Table 2.3. Mean values of environmental covariates, predicted resource selection values, and relative elk use inside the Mount St. Helens National Volcanic Monument (Monument), and outside the Monument in game management units (GMU) 522, 524, and 556. The mean and standard deviation columns refer to the average and standard deviation across time within each of the areas.

Variable	Units	Area	1980	1985	1990	1995	2000	2005	2010	Mean	SD
Digestible Energy of Accepted Species	kcal/g	Monument	1.68	2.13	2.20	2.29	2.53	2.50	2.59	2.27	0.32
		GMU 522	2.56	2.58	2.64	2.59	2.61	2.60	2.61	2.60	0.03
		GMU 524	2.56	2.29	2.31	2.33	2.34	2.35	2.66	2.41	0.14
		GMU 556	2.61	2.61	2.61	2.62	2.62	2.62	2.65	2.62	0.01
Slope	%	Monument	39	--	--	--	--	--	--	--	--
		GMU 522	39	--	--	--	--	--	--	--	--
		GMU 524	30	--	--	--	--	--	--	--	--
		GMU 556	31	--	--	--	--	--	--	--	--
Distance Edge	meters	Monument	467	489	348	211	237	177	62	284	157
		GMU 522	336	222	243	159	464	943	680	435	285
		GMU 524	187	186	153	154	128	119	113	149	30
		GMU 556	223	291	449	575	618	575	294	432	162
Distance to Roads	meters	Monument	1601	1601	1601	1504	1493	1201	851	1407	283
		GMU 522	136	136	136	125	121	118	114	127	9
		GMU 524	487	487	487	450	444	372	239	424	91
		GMU 556	178	178	178	172	173	158	88	161	33
Median Resource Selection		Monument	0.61	0.71	0.70	0.67	0.83	0.77	0.98	0.75	0.12
		GMU 522	0.34	0.40	0.44	0.46	0.56	0.54	0.27	0.43	0.11
		GMU 524	0.50	0.55	0.61	0.59	0.73	0.65	0.35	0.57	0.12
		GMU 556	0.38	0.44	0.49	0.49	0.63	0.56	0.33	0.47	0.10
Median Relative Use (xe^{-1000})		Monument	0.43	0.51	0.50	0.48	0.59	0.55	0.69	0.44	0.19
		GMU 522	0.24	0.29	0.31	0.32	0.40	0.38	0.12	0.28	0.13
		GMU 524	0.35	0.39	0.43	0.42	0.52	0.46	0.25	0.37	0.17
		GMU 556	0.27	0.31	0.35	0.35	0.45	0.40	0.21	0.31	0.14

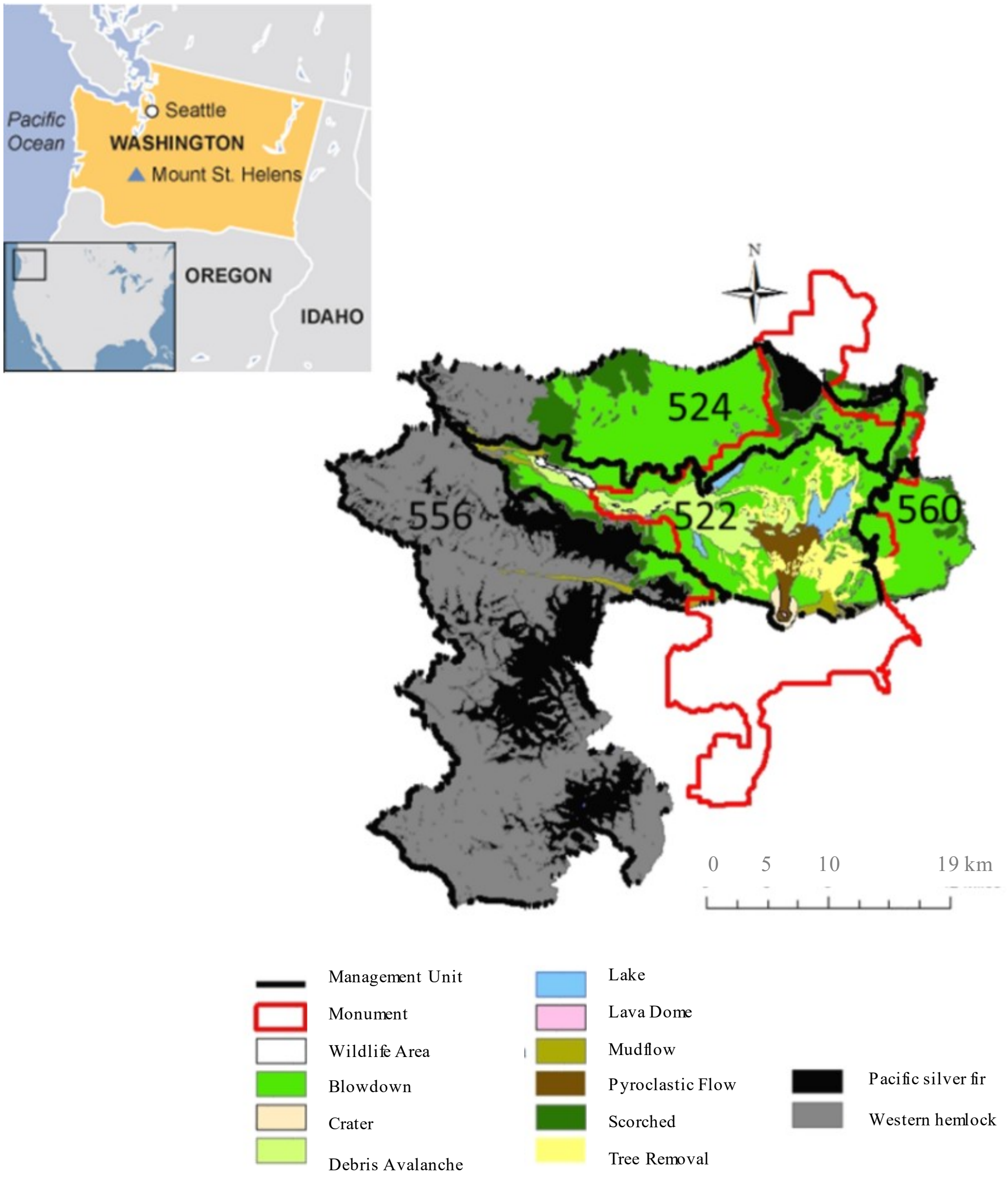


Figure 2.1. The 132,410-ha Mount St. Helens study area located in the southwest Washington. Shown are the boundaries of the disturbance zones and Pacific silver fir and western hemlock forests. Washington Department of Fish and Wildlife (WDFW) game management units are shown by black outline (Loo-wit; 522, Margaret; 524, Lewis River; 560, and Toutle; 556) and the Mount St. Helens National Volcanic Monument boundary is shown in red outline. The blastzone is comprised of the areas labelled pyroclastic flow, tree removal, mudflow, debris avalanche deposit, blowdown, and scorched.

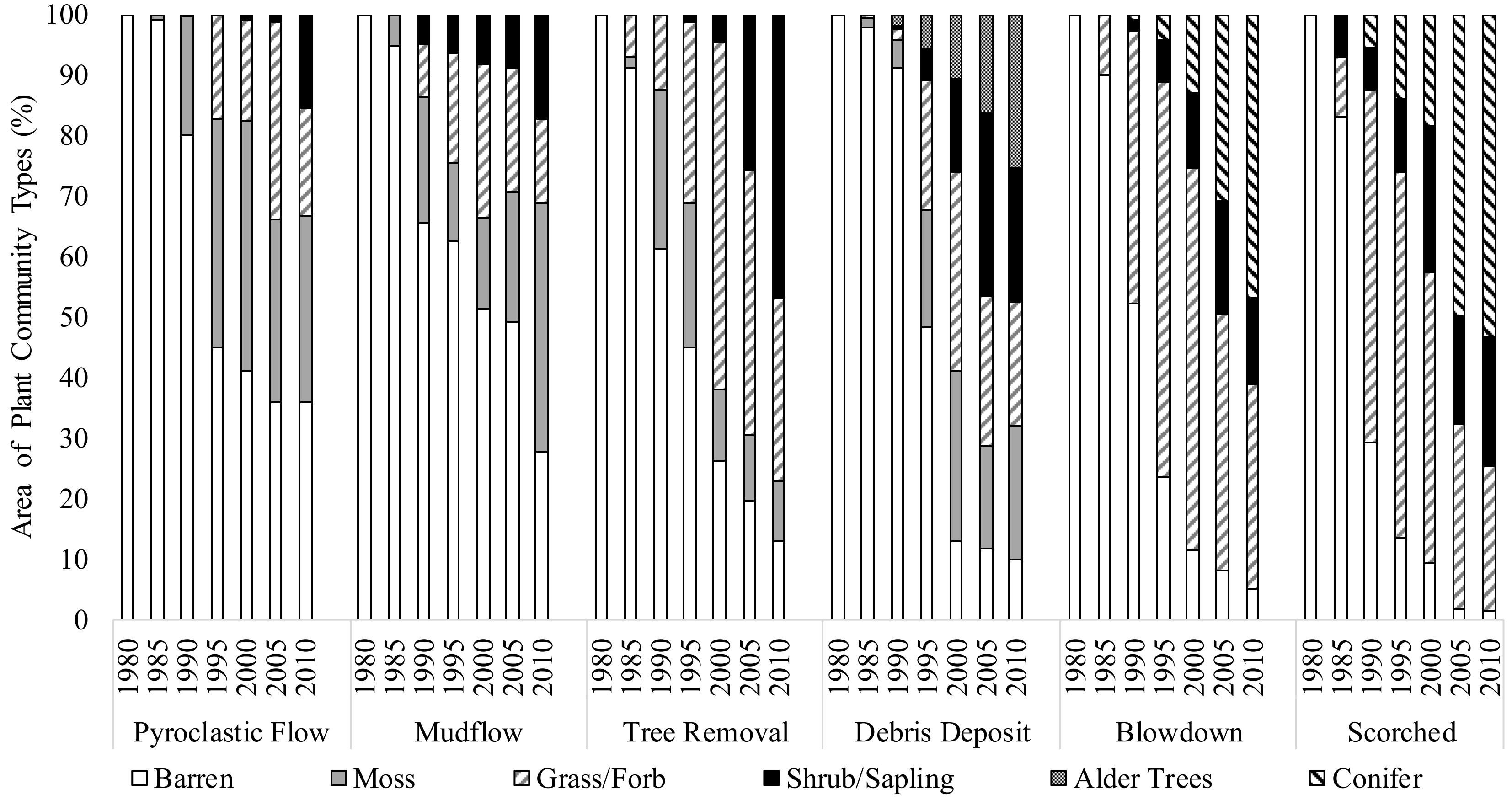


Fig. 2.2. The percent area of each plant community type within each disturbance zone from 1980-2010 within and east of the Mount St. Helens National Volcanic Monument determined using Landsat and unsupervised remote sensing.

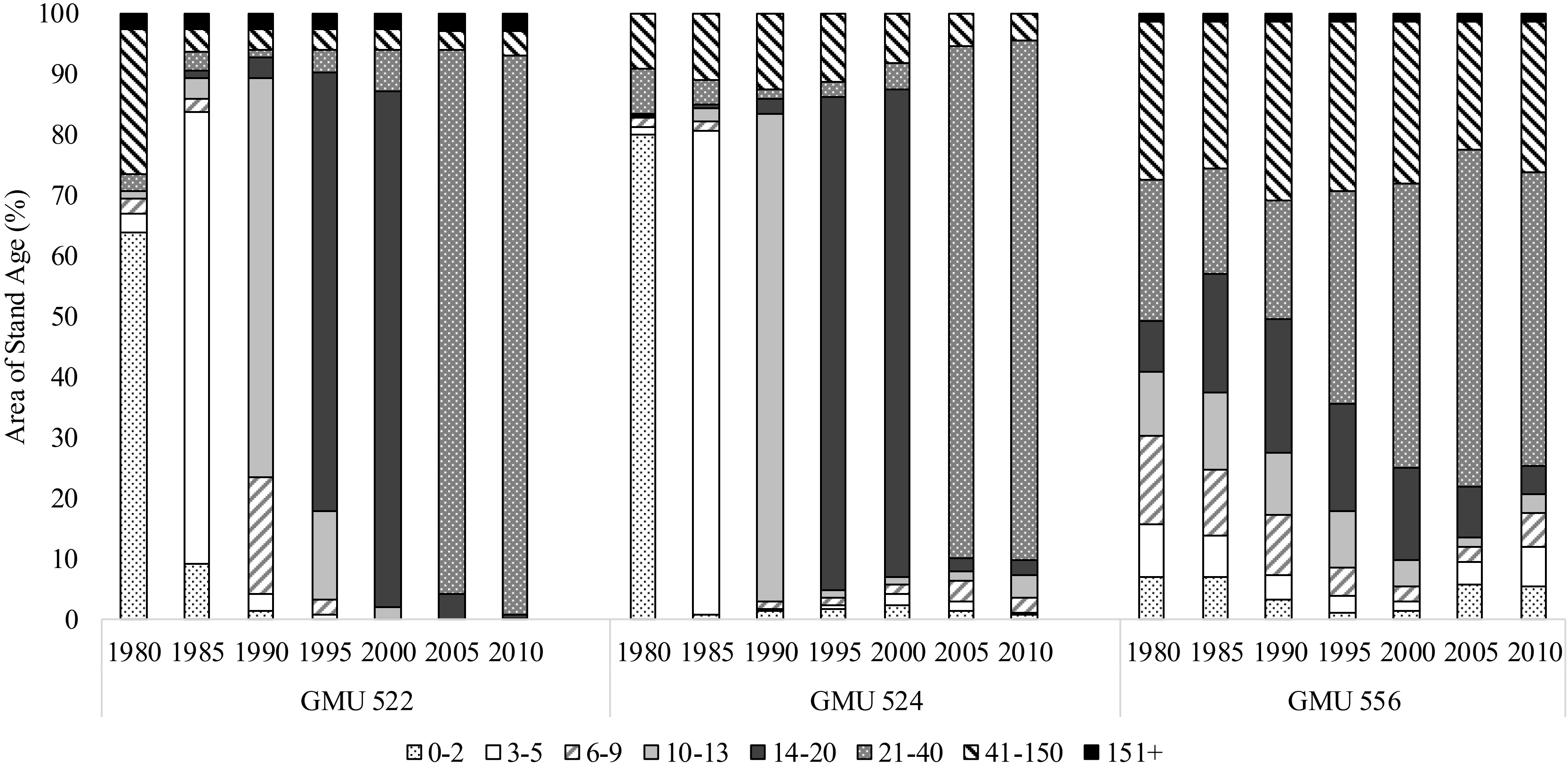


Fig. 2.3. The percent area of each stand age from 1980-2010 within the Game Management Units and blast zone outside the Mount St. Helens National Volcanic Monument. The wildlife management area is not included due to homogeneity within study years, and only containing a single plant community type of seeded mudflow.

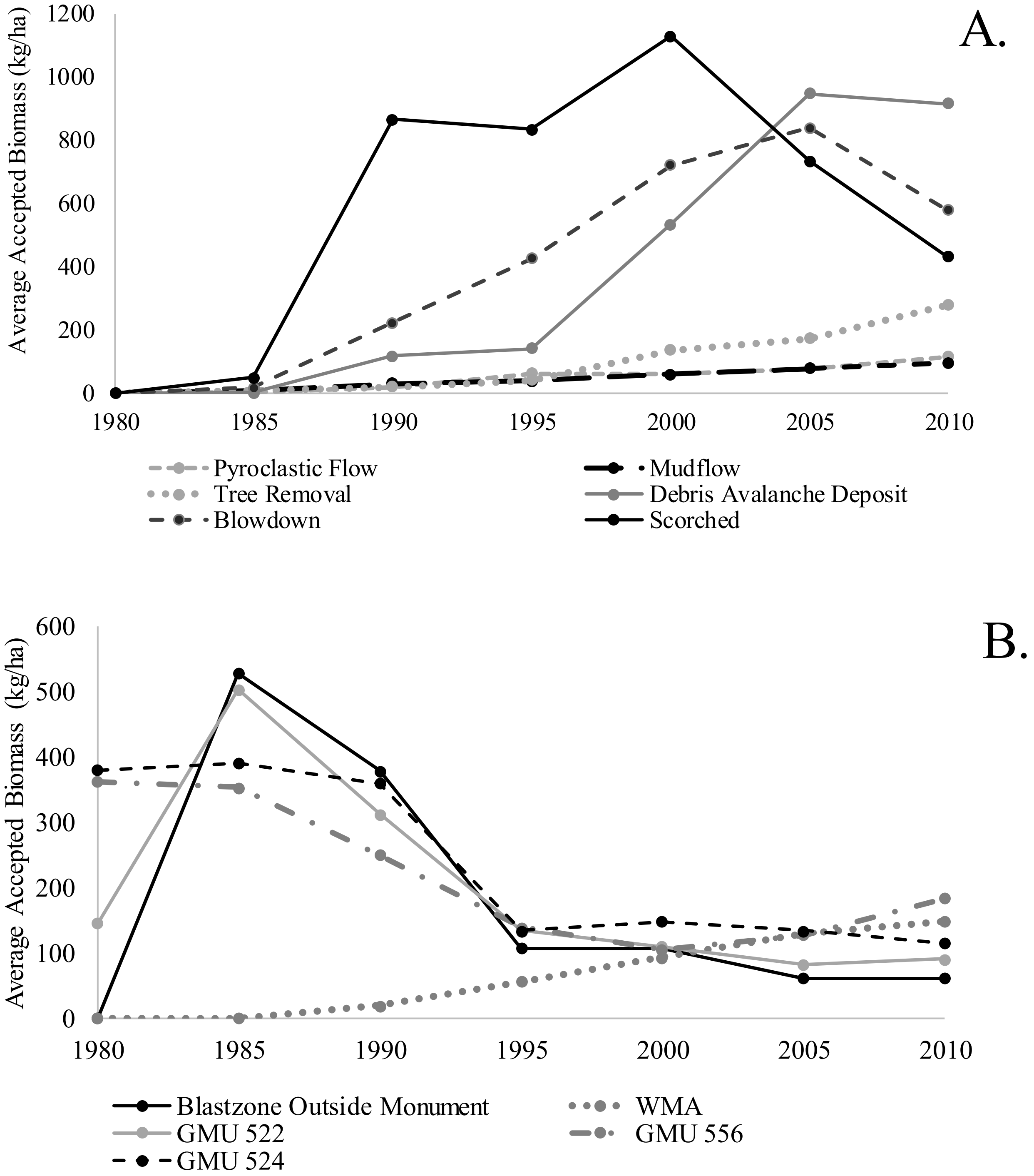


Fig. 2.4. The average accepted biomass (kg/ha) for disturbance zones within the Mount St. Helens National Volcanic Monument (A.) and outside the Mount St. Helens National Volcanic Monument (B.) for each of the study years.

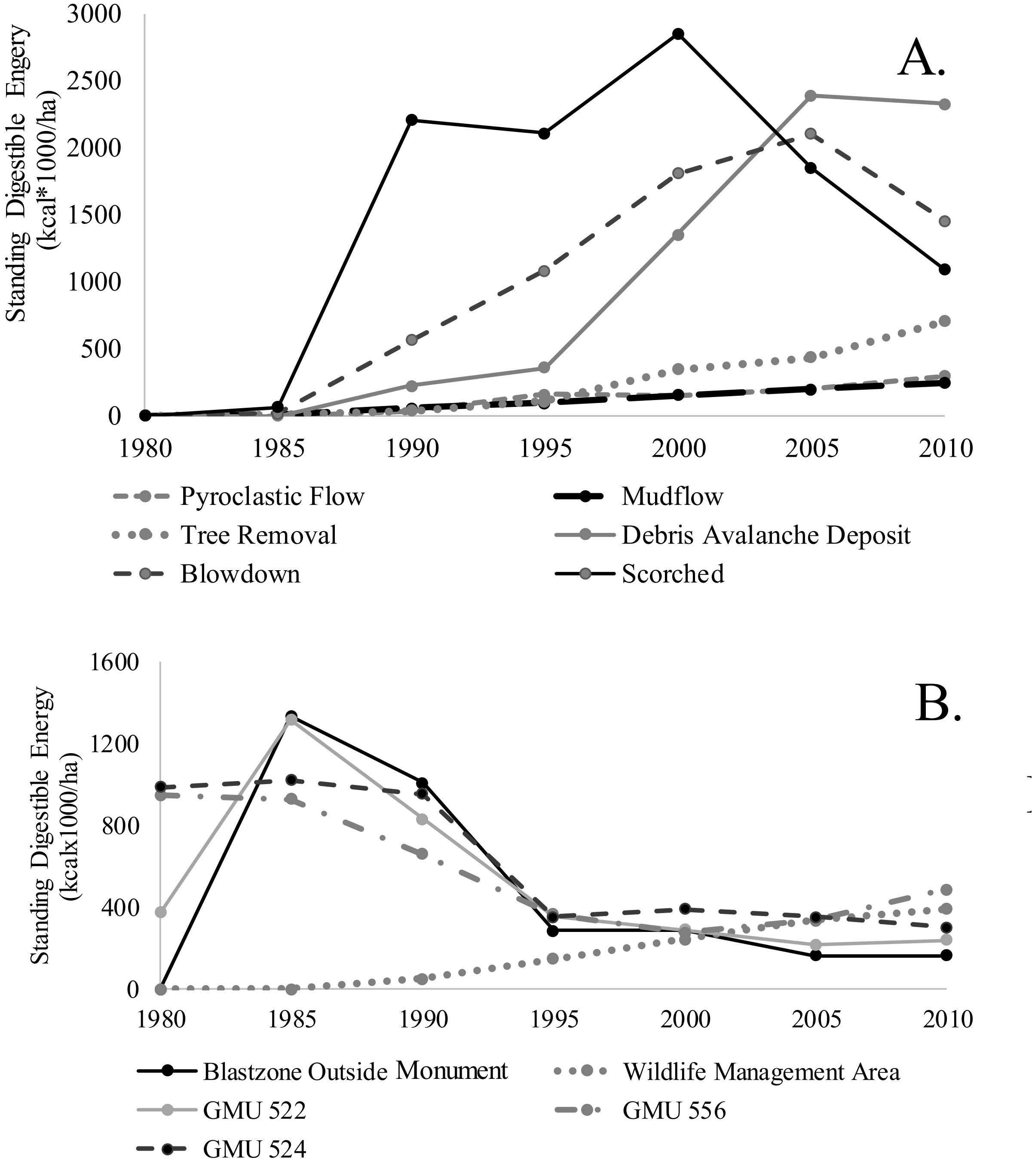


Fig. 2.5. The average accepted digestible energy (kcal x 1000/ha) for disturbance zones within the Mount St. Helens National Volcanic Monument (A.) and outside the Mount St. Helens National Volcanic Monument (B.) for each of the study years. These estimates were based on the weighted average, weighted by the area of the plant community type or stand age within each disturbance zone inside the Mount St. Helens National Volcanic Monument or area outside the Mount St. Helens National Volcanic Monument.

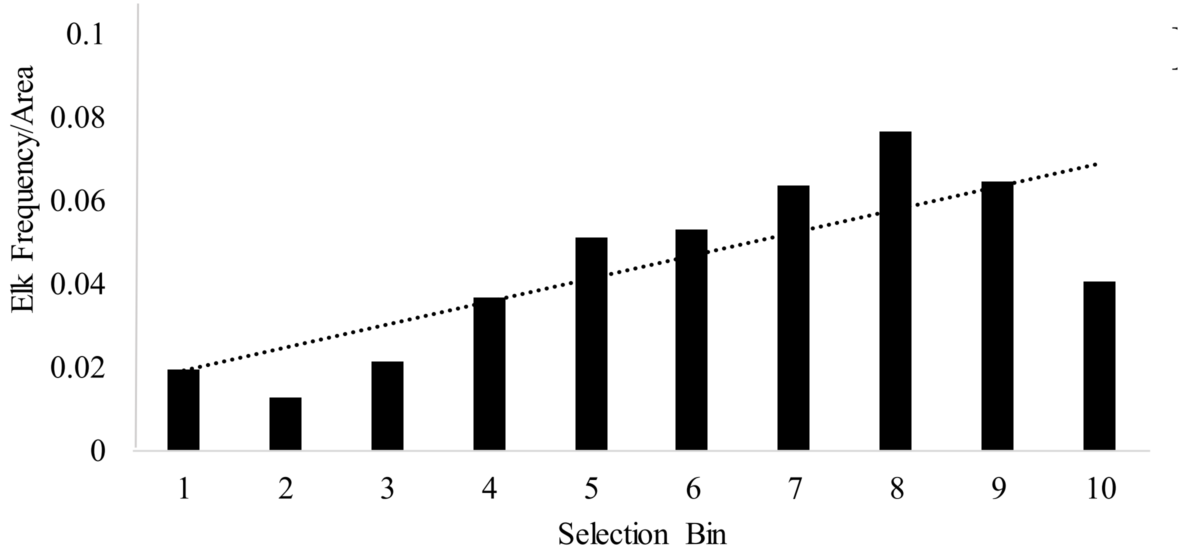


Fig. 2.6. Elk resource selection function validation, the frequency of elk within each selection bin is constrained for area of each bin, using an independent sample of 23 female elk at Mount St. Helens during the summer months of 2009-2010. The ten selection bins were created using quantiles and are as follows: 1 (0.30-0.94); 2 (0.94-0.97); 3 (0.97-0.98); 4 (0.98-0.99); 5 (0.99-1.01); 6 (1.01-1.02); 7 (1.02-1.03); 8 (1.03-1.04); 9 (1.04-1.07); 10 (1.07-1.27).

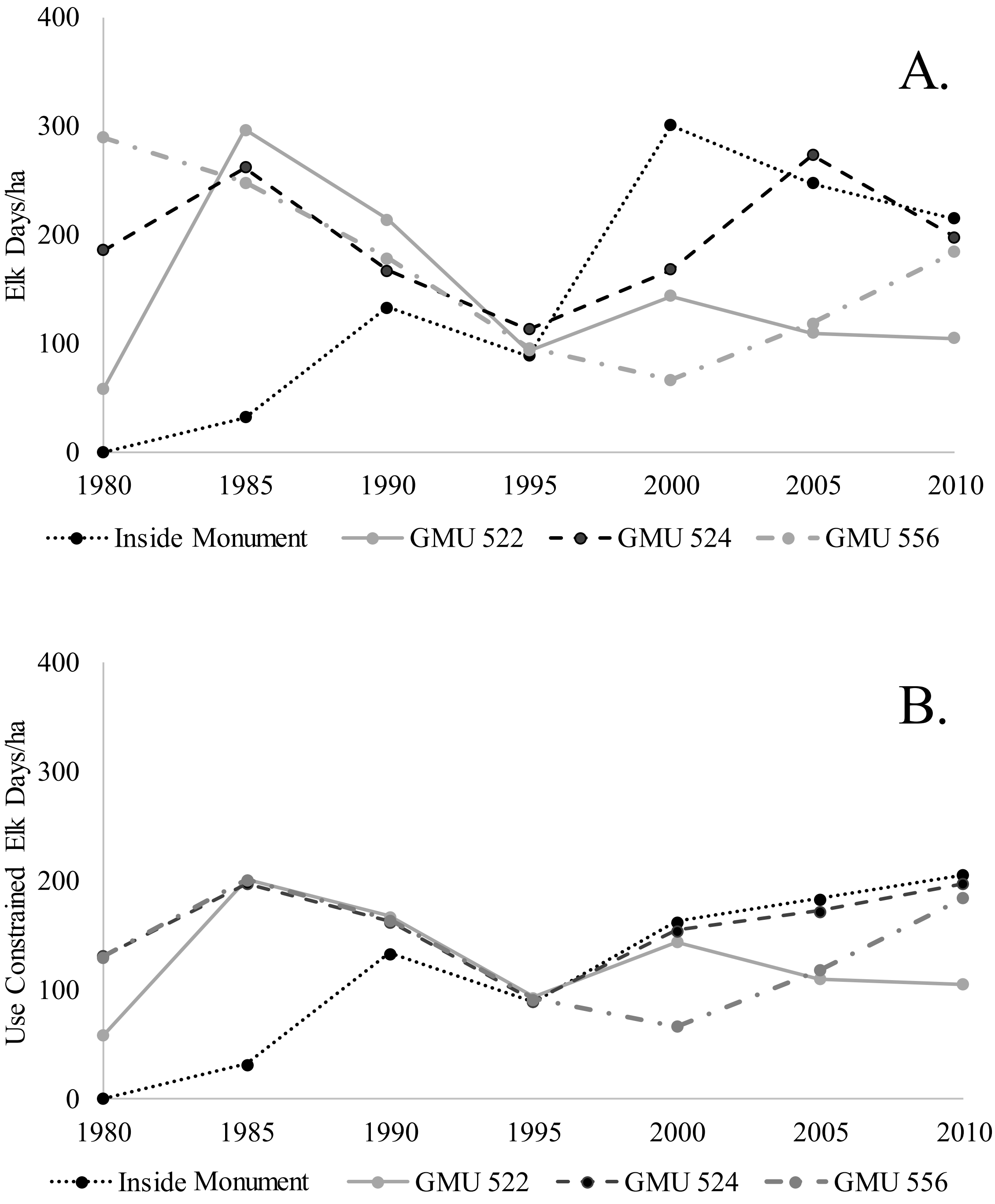


Fig. 2.7. Elk carrying capacity in the study area during the summer months (June-October) inside and outside the Mount St. Helens National Volcanic Monument (Monument), number of elk days/ha (A) and number of elk days constrained for potential elk use (B).

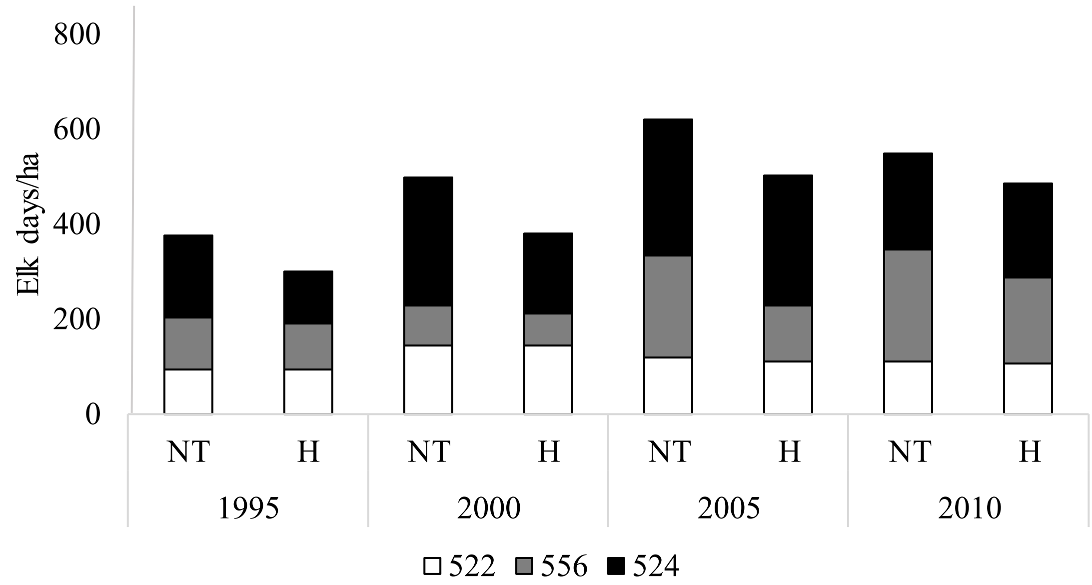


Fig. 2.8. The number of elk days/ha on game management units 522, 556, 524 during the summer months if herbicides were used (H) and if there were no treatment (NT) at Mount St. Helens beginning in the year 1995. The nutritional carrying capacity estimates are based on the requirements of a high nutritional diet (dry matter intake: 7997 g/day; digestible energy: 2.9 kcal/g).

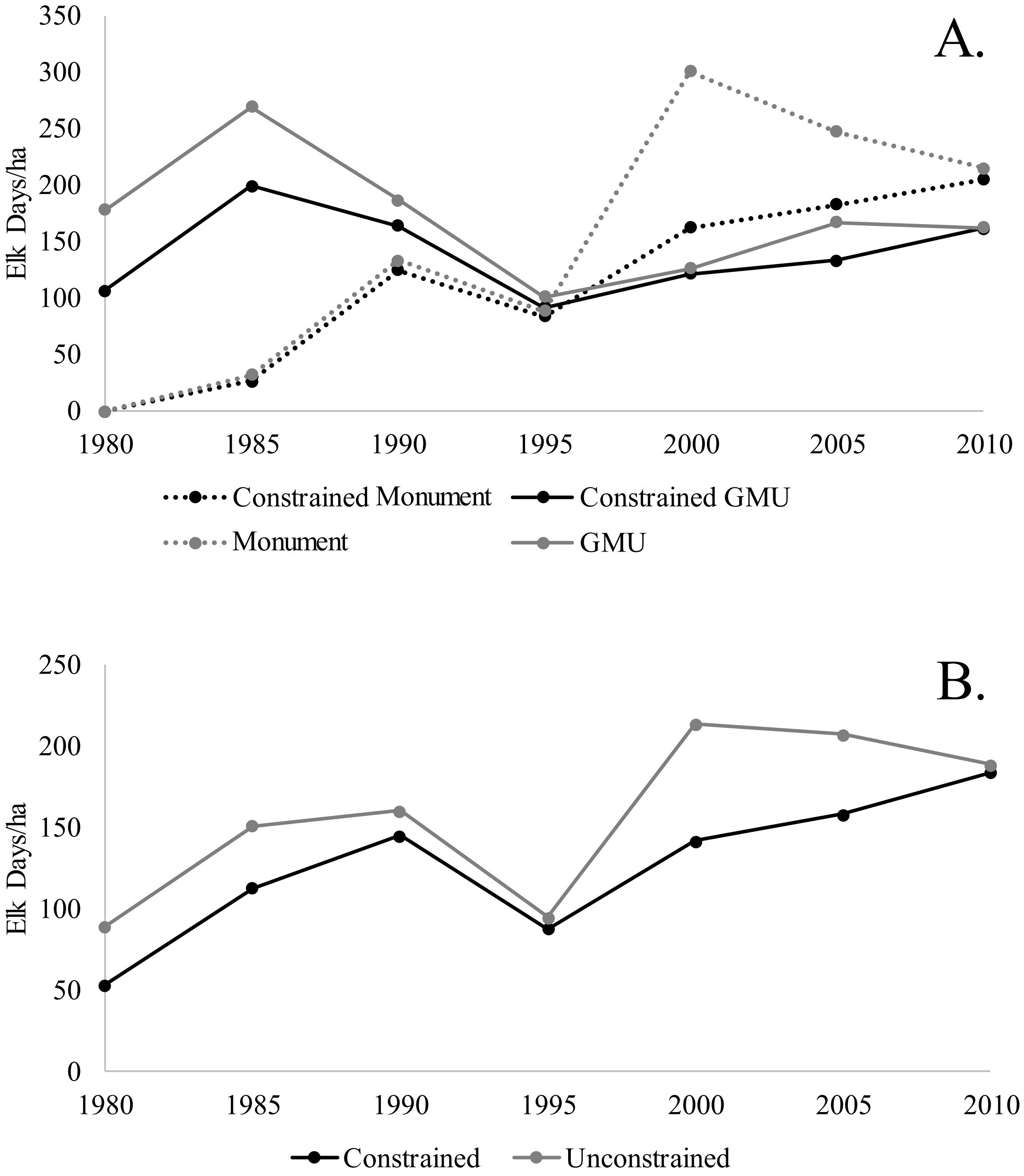
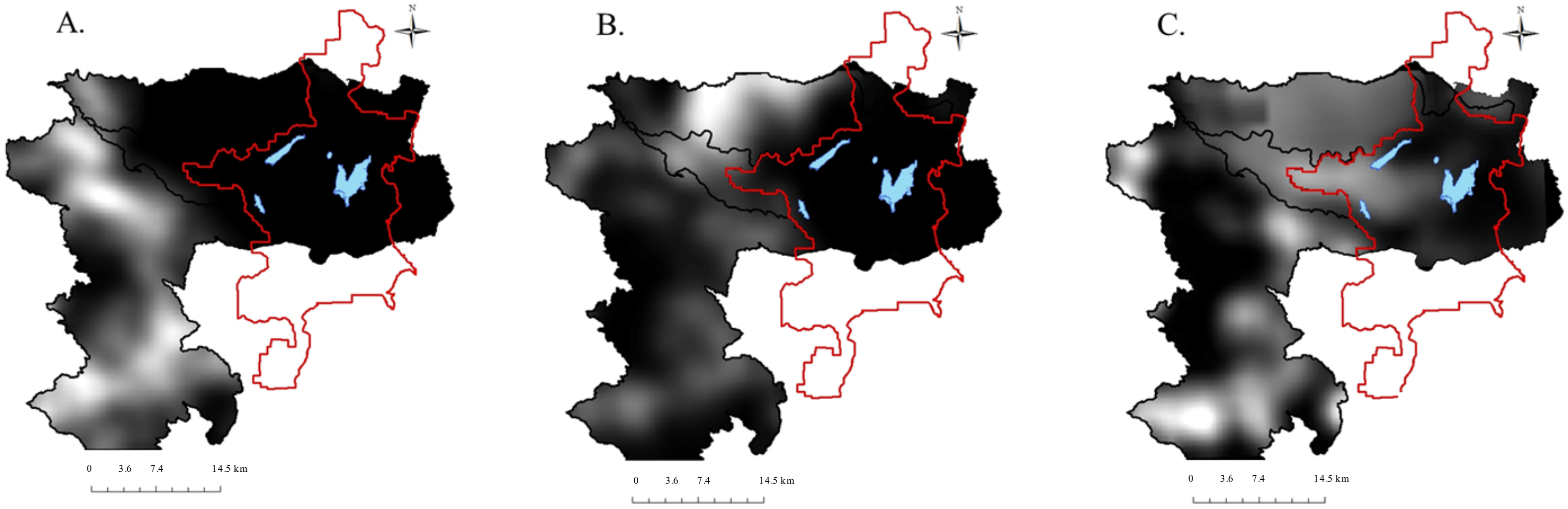


Fig. 2.9. The average elk days/ha relative use constrained (*black line*) and unconstrained (*grey line*) for inside the Mount St. Helens National Volcanic Monument (Monument, *dotted line*) and outside the Monument in the game management units (GMU, *solid line*, A). Also included are the average elk days/ha from inside and outside the Monument for unconstrained and relative use constrained (B).


A.
B.
C.
N
0 3.6 7.4 14.5 km

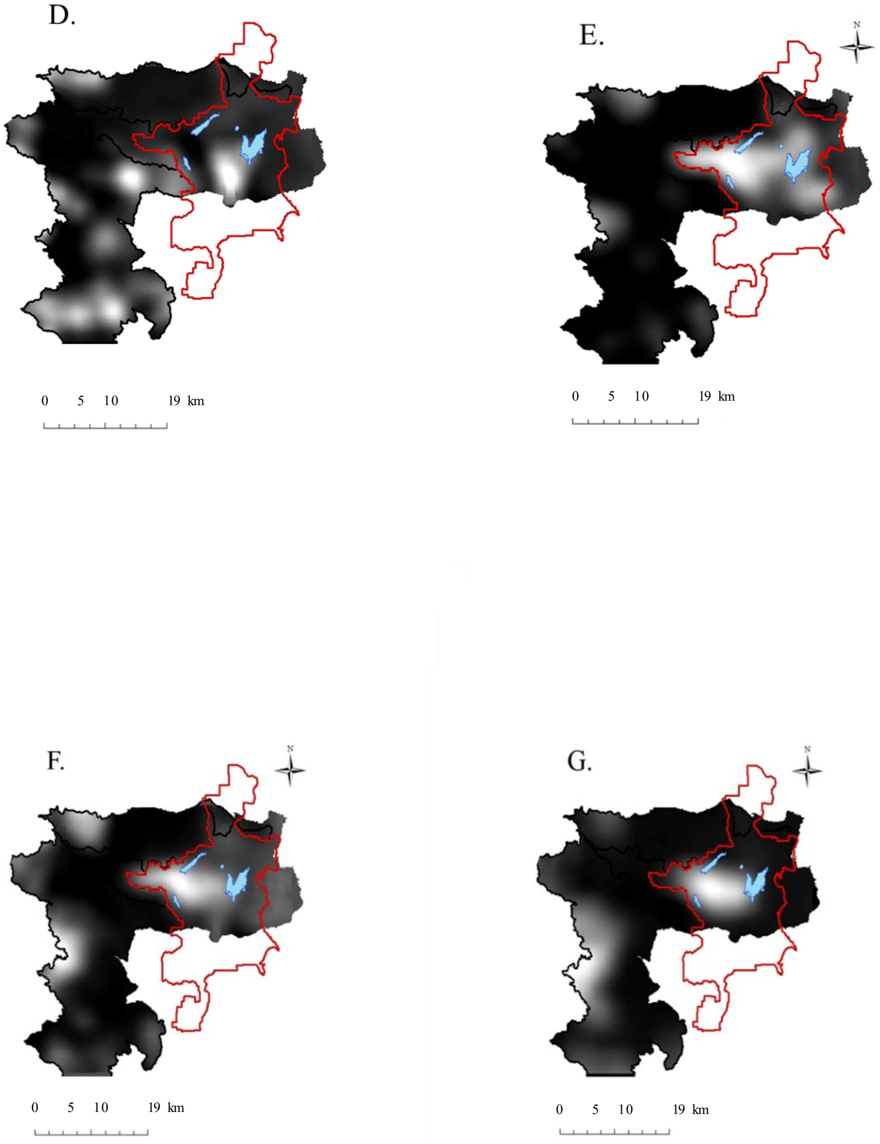


Fig. 2.10. Relative elk use constrained nutritional carrying capacity maps for elk at Mount St. Helens for 1980 (A), 1985 (B), 1990 (C), 1995 (D), 2000 (E), 2005 (F), and 2010 (G) during the summer months (June-October). Elk use was estimates using Mount St. Helens elk summer

relocations from 2009-2011. The gradient in color represents high (*white*) to low (*black*) elk nutritional carrying capacity constrained by use. Also included are the lakes (*blue polygon*), the Mount St. Helens National Volcanic Monument (*red outline*), and the game management units (*black outline*).

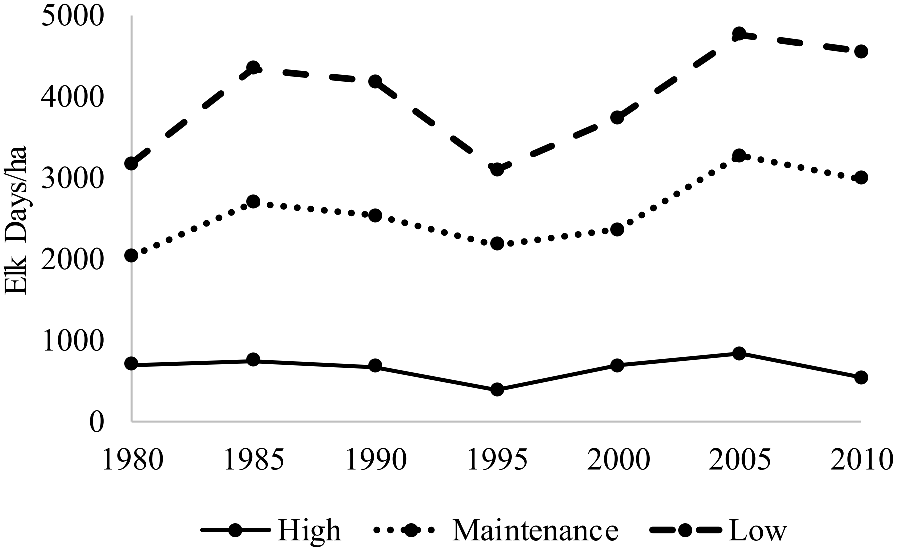


Fig. 2.11. Elk days/ha within the study area during the summer months at Mount St. Helens based on our elk nutritional carrying capacity model on a high (dry matter intake: 7997 g/day; digestible energy: 2.9 kcal/g), maintenance (dry matter intake: 7272 g/day; digestible energy: 2.68 kcal/g), and low (dry matter intake: 6903 g/day; digestible energy: 2.48 kcal/g) nutritional diet.

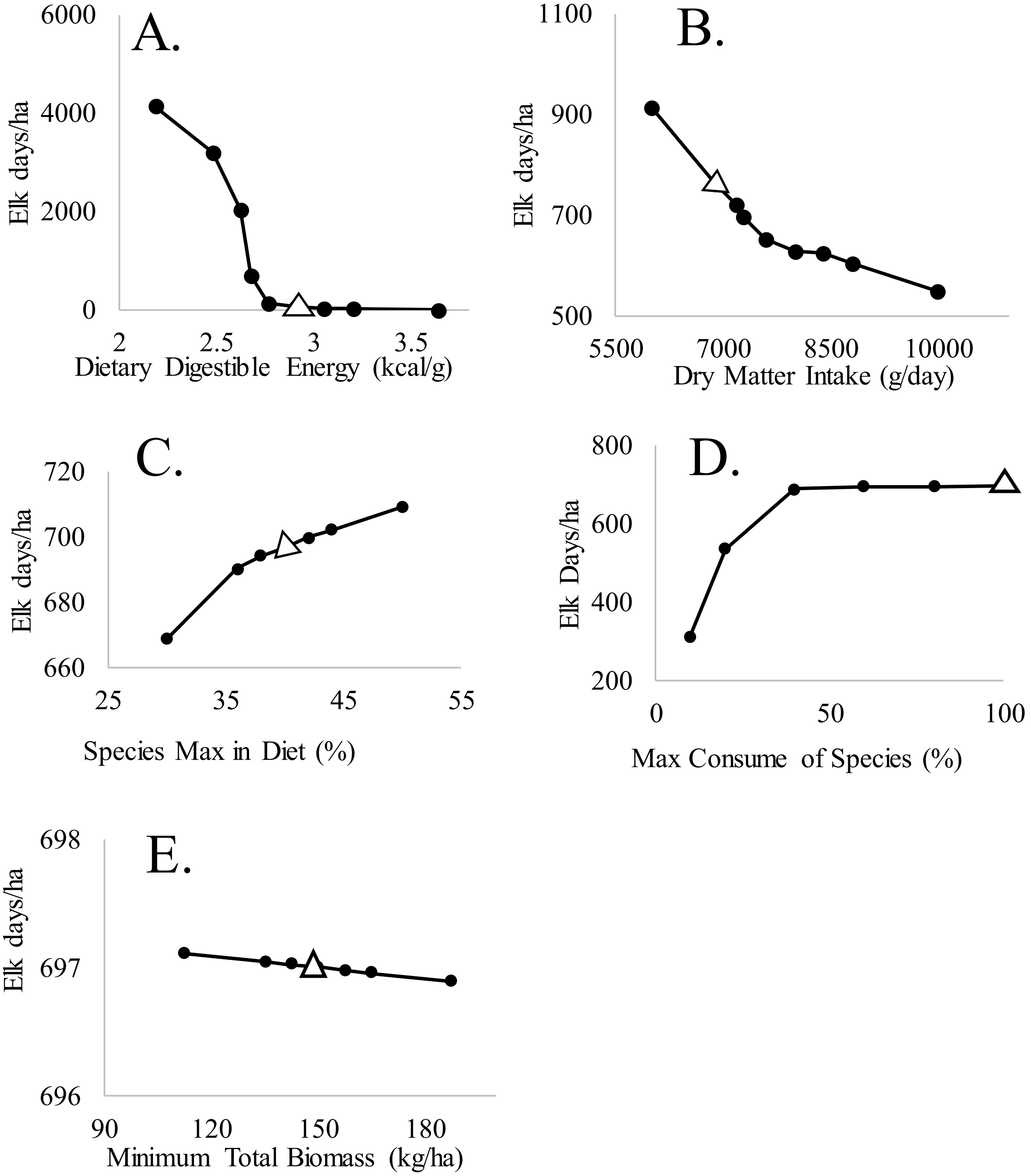


Fig. 2.12. Sensitivity analysis showing the effect of assumed model constraints on the total number of elk days/ha within the study area using biomass availability in 2010 relative to changes in the baseline values for (A) digestible energy requirement of elk (2.9 kcal/g) (B) daily dry matter intake (7997 g/day), (C) the maximum percent any one species can contribute to the diet (40%), (D) the maximum percent an elk can consume of the vegetation (100%), and (E) the minimum amount of total accepted biomass available for an area to be used by elk and included

in the estimate of elk days (150g/ha). Estimates assuming baseline values are indicated by the white triangles. Values along the x-axis for figures A-D were chosen based on increasing and decreasing baseline values by 5%, 10%, and 25% of maintenance requirements (2.68 kcal/g of digestible energy, 7272 g/day of dry matter intake).

CHAPTER 3

THESIS SUMMARY

The eruption of Mount St. Helens in 1980 devastated an area of over 60,000 ha in south west Washington. This large-scale disturbance changed the landscape and the associated nutritional carrying capacity of the area to support elk and other ungulates in the vicinity of Mount St. Helens. Merrill and Raedeke (1987) predicted that unless there was high variation in the recovery of plant communities after the 1980 eruption, managers could be faced with a long-term "boom-bust" dynamic reflecting canopy closure and loss of high quality understory typical of forest communities in this region. The advent of periodic high winter mortalities of elk starting in the late 1990s increased concerns over the loss of early seral stages in the blast zone, wide-spread herbicide use on surrounding industrial lands, and creation of late successional reserves on United States Forest Service land. The Washington State Herd Plan for the Mount St. Helens Herd recommended there was a need to better quantify elk nutrition and condition dynamics for elk as a result of changing habitat condition (Miller and McCorquodale 2005). In response to these concerns, studies were conducted from 2009-2013 assessing elk survival, body condition, pregnancy, and recruitment rates in five GMUs that represent a core area of the Mount St. Helens elk herd (McCorquodale et al. 2014). To accompany those analyses, in this thesis I compared changes in the carrying capacity in three of the core area GMUs to the Monument since the eruption as an assessment of habitat trends that may have led to the current and future elk population trends.

I found that the eruption of Mount St. Helens in 1980 set the stage for a large extent of forested area, within the core area inhabited by the Mount St. Helens elk population, to return to variable conditions of early seral habitat. Post-eruption forest succession in two of the low tephra and ash GMUs immediately west of Mount St. Helens were salvage logged and replanted, and exhibited rapid forest succession providing a flush of high quality forage for elk (Merrill et al. 1995) that peaked during the first 5-10 years after eruption (Fig. 2.5). Associated with the peak nutritional carrying capacity resources, Merrill (1987) found high pregnancy rates (0.31 for yearlings, 0.69 for 2-year-old cows, and 0.87 for 3-year-old cows), and a high average kidney fat index (45±22). Although the nonlinear relationship between the kidney fat index and ingesta-free body fat causes the kidney fat index method to be somewhat unreliable, these data are consistent with the elk population being below the potential nutritional carrying capacity, indicating density-dependent effects were unlikely to be affecting population growth in the first 5 years after the eruption. In fact, the population growth rate of herds directly west of Mount. St. Helens during this time exceeded the intrinsic growth rate' (i.e., "r max”) due to reproduction alone, and they attributed this to immigration from surrounding areas (Raedeke et al. 1986).

During the next 10-20 years, from 1990-2010, I showed that there was a decline in nutritional resources across the management units west of Mount St. Helens, commensurate with the proportion of the GMU that was impacted by the eruption. Based on my analyses, the broad-scale decline in nutritional carrying capacity was in large part related to maturing stands in the blast zone that were not being offset with the creation of new early seral stands from timber harvest elsewhere because only 4±3% were cut each year in any of the three units we studied. In the case of GMU 556, which encompasses less than 1% of blast zone and is the largest GMU in our study, timber harvest declined from 7% to 5% from 1980-2010. Further, because responses of forages are delayed 1-3 years after application of operational herbicides (Geary 2013, Ulappa

2015), broad-scale use of operational herbicides at stand initiation starting about 1995 may have exacerbated the effects of an already declining nutritional resource. Because the decline in available resources coincided with conservative elk harvests in these units (McCorquodale et al. 2014), the initial rapid population growth in elk post eruption (Raedeke et al. 1986) may have overshot the declining nutritional carrying capacity, and the coincident downward trend in forage resources likely aggravated the density-dependent effects.

Several lines of evidence support the hypothesis that elk populations west of MSH became severely food limited. First, there was increasing evidence of high herbivory (Miller and McCorquodale 2006). Geary (2013) showed herbivory from the period of 2009-2011 progressively reduced standing digestible energy with herbivory, which was attributed primarily to the reduction in the height of palatable shrubs but not shrub density. To eliminate the observed effects of herbivory substantial reductions in the elk population likely would be necessary because highly palatable shrubs are the first to be consumed and a reduction of browsing on preferred shrub species is not proportional to ungulate density (Hobbs, 1996; Nugent et al., 2001). Second, between 2009 and 2011 the ingesta-free body fat was found to be similar and low between our 3 GMUs for lactating cows (Geary 2013, McCorquodale et al. 2014). Third, beginning in 1997, periodic overwinter elk mortalities became evident along the wildlife management area in GMU 522. During the winter months, 600 elk migrate to GMU 522 from the surrounding GMUs (Miller and McCorquodale 2006). We found average dietary DE across GMUs to have been depressed by 5% and 11% in 2005 compared to 2000 and 2010. Across our study years, McCorquodale et al. (2014) also found the highest over-winter elk mortalities in 2005.

I had hypothesized that the delayed recovery of understory vegetation at the high elevations in the Monument may have offset the decline in elk carrying capacity in the management units west of Monument. This hypothesis is supported for GMUs 556 and 522, due to a decline in elk population numbers in GMU 556 and the overwinter elk mortalities on GMU 522 (McCorquodale et al. 2014). For GMU 524, we found $NCC_{constrained}$ increased and comparable to inside the Monument from 2000-2010. McCorquodale et al. (2014) also found GMU 524 to have the highest probability of pregnancy of 90% from 2009-2011 compared to GMUs 556 and 522.

Although the increase in elk carrying capacity inside the Monument may be offsetting the decline to the west of Monument, large-scale changes on the landscape caused by the eruption of Mount St. Helens still pose challenges for future ungulate management across this area. For subsequent years, we can predict a decline in elk carrying capacity inside the Monument because canopy closure begins to occur on the less disturbed areas. By 2000 the scorched disturbance zone inside the Monument peaked in accepted biomass, and by 2005 the blowdown and debris avalanche deposit peaked in accepted biomass and begun to decline in 2010 where conifer communities are becoming more dominant. In contrast, the accepted biomass in 2010 of the three highly disturbed areas, the pyroclastic flow, tree removal, and mudflow remain only 9 - 36% of the average peak in the three less disturbed sites.

Because timber cutting on the U.S. National Forest has been limited in the recent past (Washington Department of Natural Resources 2009), industrial forest lands have been providing a large part of the early seral habitats important for elk and other ungulates in this area. Because the blast zone occupies almost 20% of this core habitat for elk west of the Monument, closed-canopy forests resulting from the eruption are likely to provide relatively poor quality habitat for the next 10-20 years even with commercial thinning. In addition, new seral stands from timber harvest on industrial lands that are treated with operational herbicides reduce the accepted biomass by 77% for at least 2 years following stand initiation (Geary 2013). In response to these declining habitats, Washington Department of Fish and Wildlife has increased antlerless harvest to bring the population in line with these habitat trends (McCorquodale et al. 2014). The nutritional resources available in early seral stands within the scorched and blowdown areas of Monument may have partially offset these trends on elk summer range, but the data presented here indicate nutritional resources have peaked and may be declining. If true, the successional patterns within the more disturbed tree removal areas that exist at high elevations closest to Mount St. Helens, are likely to be important plant communities for elk summer range over the next two decades. At the same time, because forests on low elevation industrial lands are approaching the end of their 40-60-year harvest cycles, new seral stands may soon become available. Future elk management on industrial timber lands outside the Monument will remain challenging due to the spatial legacy of the eruption and the dynamics of forest succession in this region. This may be particularly true in the face of limited forest management within the Monument and conservative cutting regimes on U.S. National Forests.

Complicating elk management further in this area is the advent of the hoof rot, which was first reported in elk at Mount St. Helens in 2007- 2008 and has continued to increase in this area since that time. Hoof rot has been well described in wild and domestic ruminants and is associated with chronic hoof inflammation from various causes, including chronic laminitis (Han and Mansfield 2014). Accelerated hoof growth occurs, resulting in abnormally long hooves which cause limping and hindered movements. Scientists believe the cause is a treponeme bacteria, which likely exists in moist soil and is spread to new areas on the hooves of infected elk (Clegg et al. 2015). To help minimize the spread of the disease, Washington Department of Fish and Wildlife is requesting that hunters remove the hooves of any elk taken in affected areas and leave them on site. Studies are on-going to better understand the role that hoof rot may play in the dynamics of elk population trends across the broader Mount St. Helens elk herd.

Management Recommendations

The elk herd surrounding Mount St. Helens is one of the largest herds in Washington (Washington Department of Fish and Wildlife 2008) and have important social and economical value with a 30x30-million-dollar revenue generated annually since 1996 (Miller and McCorquodale 2006). The broad-scale successional trends created by timber harvest and the natural recovery of areas in the vicinity of Mount St. Helens present challenges for managing the elk population. I make four recommendations related to the management of elk inhabiting the Monument and surrounding GMUs of 522, 524, and 556.

1. Continue collaborative efforts among government agencies to track the future spatio-temporal trends in summer as well as winter habitat quality as a function of timber harvest and natural recovery after the eruption to provide further insight into the changes in habitat quality and its role in elk condition, reproduction and overwinter elk mortalities. The Mount St. Helens area continues to provide a unique opportunity to study the effects of changing habitat for improving our understanding of ungulate-habitat relationships in the Pacific Northwest.

2. Work with industrial forestry companies to plan for more variation in timber harvesting as the areas in the blast zone reach the end of their rotations. For example, spatially staggering areas cut by even 5-10 years could improve the mosaic of stand ages that provide more balanced forage-cover ratios, which will be key to maintaining elk habitat, especially in areas in areas like GMU 524 because of the low abundance of roads. In the short-term, this would result in a portion of the blast zone being harvested within the next 10 years, which may offset the predicted future declines in elk carrying capacity on summer range inside the Monument and provide additional wintering areas at low elevation.
3. Work with the United States Forest Services in developing silvicultural enhancements to improve elk habitat on late successional reserves, and with Weyerhaeuser in developing plans to increase operational thinning practices that may enhance elk habitat.
4. Continue habitat improvement projects on the elk winter range, in particular of the Wildlife Management Area in GMU 522 where a large number elk winter to offset summer range dynamics.

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Appendix A. Cover-biomass relationships.

To convert percent herbaceous cover (m^2) on permanent plots to biomass, in August 2014 and 2015 we sampled herbaceous plant cover (m^2) and clipped biomass in microplots across the tree removal (n microplots =13 in 2014/49 in 2015), blow down (n=112/50), and the pyroclastic flow (n=23/60), mudflow (n=33 in 2015), debris avalanche deposit (n=98 in 2015), and scorched (n=69 in) six disturbance zones in areas that were accessible by roads (but not within 250 m) and that encompassed a wide range in variation of herbaceous biomass. We located 8-12 0.25-m^2 microplots at 6-m apart and estimated cover (m^2) of each of 3 forage class (forbs, graminoids, and ferns). We then clipped total herbaceous biomass to 2 cm of ground level, separated by forage class, dried at 100° C for 48 hours and weighed to the nearest 0.01g. To derive cover-biomass relationship for each forage class, we converted horizontal cover (0.25 m^2) and biomass (g/0.25 m^2) clipped within a 0.25-m^2 microplot to m^2 basis by multiplying each metric by 4.

Shrubs were defined as rooted stems < 2 m. We estimated current annual growth (current annual growth, g/m^2), defined as new growth within the year, for the 26 major species comprising >1% of any permanent macroplot between 1980-2010 (Appendix C.). For each of the shrub species we estimated cover (m^2) by recording two cross-perpendicular sections of the canopy cover. For a representative branch on the shrub, we then recorded two-cross-perpendicular sections of the canopy cover. We then estimated cover (m^2) of the branch by multiplying the two cross-perpendicular measures to obtain an estimate of area for the branch. We estimated the area of the shrub by multiplying the two cross-perpendicular measures of the shrub. We clipped the current annual growth from the branch, dried at 100° C for 48 hours, and weighed to the nearest 0.01g. We then extrapolated the cover and biomass estimates for the branch to the entire shrub by multiplying both by a factor of x, so that the cover of the branch is equivalent to the cover of the entire shrub.

We developed predictive equations for biomass from cover (m^2) of each forage class using model selection based on AIC with regression analysis (Burnham and Anderson 2002) and tested best fit for linear and non-linear models (i.e., linear, quadratic, exponential, power, and logarithmic). We also used a mixed effects model with the year sampled as a random factor and AIC to test for year differences in the intercept. Using a similar approach, we related shrub cover (m^2) to current annual growth (g/m^2) for evergreen and deciduous shrubs separately.

We found cover (m^2) was linearly related to biomass (g/m^2) across the forage types. Controlling for sampling year did not improve the model fit for graminoids or forbs, and ferns sampled in 2015 so year was not included as a variable in the model. Slope of the relationships for graminoids did not differ significantly between the blow down, tree removal, and pyroclastic flow disturbance zones so we combined these data to produce one regression. For forbs, we found no differences in slopes between the blow down, mudflow and scorched so we also combined these data to produce one regression.

Using a mixed effects model with the year sampled as a random factor and AIC to test for best-fit we found that controlling for sampling year did not better the model fit for deciduous shrubs (AIC without year = 881.373; AIC including year = 876.347), or evergreen shrubs (AIC without year = 118.023; AIC including year = 112.366). We found cover (m^2) was linearly related to the current annual growth of deciduous shrubs (g/m^2). For evergreen shrubs we used the mean value of biomass (125 g/m^2) for all evergreen shrubs.

Appendix A.

Table A.1. Final plant cover (m^2)-biomass (g/m^2) relationships for the herbaceous forage classes within each disturbance zone; and the evergreen and deciduous shrubs across all disturbance zones. All cover-biomass regression relationships have an intercept of zero.

Disturbance Zone	Structure	Slope	R-squared	AIC
Forbs				
Mudflow	Linear	0.85	0.85	208.75
Scorched	Linear	0.60	0.57	500.48
Blowdown, Tree Removal, Debris Avalanche Deposit, Pyroclastic Flow	Linear	0.44	0.59	1937.56
Graminoids				
Tree Removal, Pyroclastic Flow	Linear	0.27	0.50	600.86
Blowdown, Mudflow, Debris Avalanche Deposit, Scorched	Linear	0.42	0.73	1433.40
Ferns				
Mudflow, Scorched, Blowdown, Tree Removal, Debris Avalanche Deposit, Pyroclastic Flow	Linear	0.49	0.73	581.26
Shrubs				
Deciduous	Linear	1.84	0.24	881.37

Appendix B. Elk feeding time at Mount St. Helens.

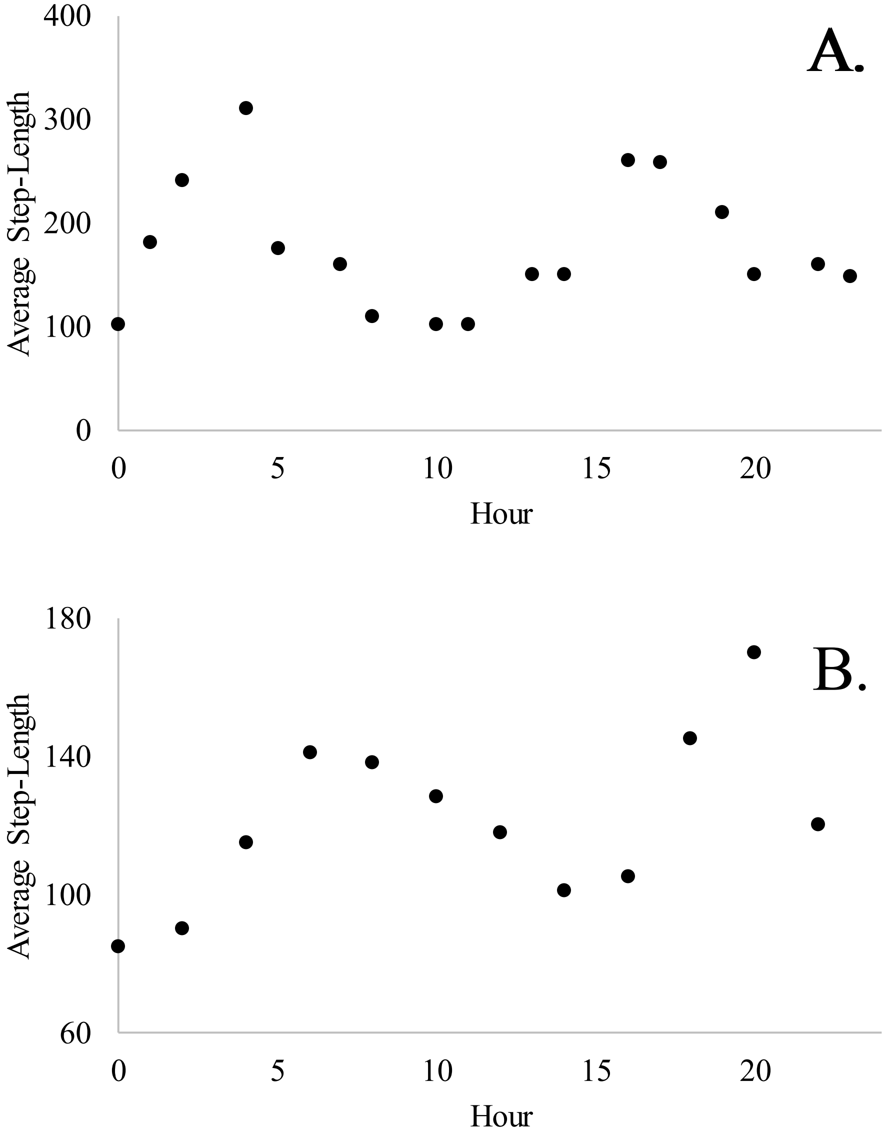
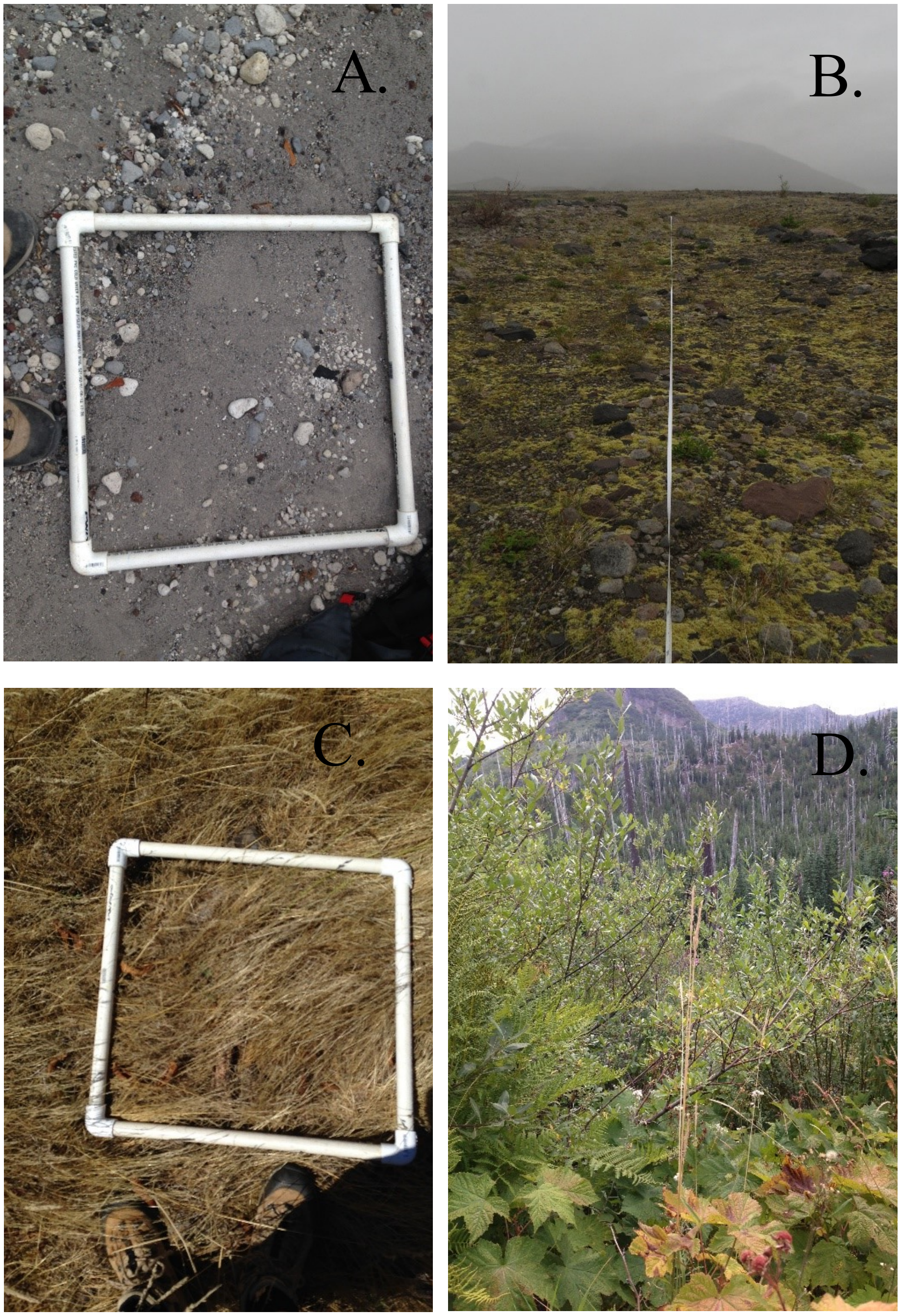


Fig. B.1. The average step-length (m) of elk on 3-hour (n=14, A) and 2-hour (n=9, B) fixed GPS-collars for years 2009-2011 provided by Geary (2013) and the Washington Department of Fish and Wildlife (2012) during the summer/late summer months (June-October) at Mount St. Helens.

Appendix C. Plant community type images at Mount St. Helens.



Appendix C.

Fig. C.1. Examples of each plant community type inside the Mount St. Helens National Volcanic Monument: barren (A), moss (B), grass and forbs (C), shrubs (D), alder (E) and conifer (F). Photographs were taken in August 2015.

Appendix D. Plant species included in carrying capacity models.

Table D.1. Accepted plant species included in the nutritional carrying capacity model, all species are either selected or neutral species. Also included are the dry matter digestibility (g, DMD) and digestible energy (kcal/g, DE) values of each species provided by Geary (2013), Cook et al. (*in press*), and Merrill (1987) sampled during the summer months (June-October). For DMD values with an '*', the DMD and DE values were calculated based on the average of a species corresponding forage class (Table D.2).

Species	**Class**	**DMD**	**DE**
Abies procera	Graminoid/Forb	32.98	3.00
Acer circinatum	Graminoid/Forb	45.92	4.88
Acer macrophyllum	Graminoid/Forb	50.10	4.62
Achillea millefolium	Graminoid/Forb	73.40	6.60
Achillea millefolium	Graminoid/Forb	73.40	3.30
Achlys triflora	Graminoid/Forb	39.63*	6.00
Actaea rubra	Graminoid/Forb	62.29*	2.81
Adenicolor bicolor	Graminoid/Forb	66.68	5.62
Adiantum pedatum	Graminoid/Forb	62.58	1.80
Agoseris aurantiaca	Graminoid/Forb	62.58	2.81
Agoseris spp.	Graminoid/Forb	62.58	2.81
Agrostis exarata	Graminoid/Forb	39.63*	4.36
Agrostis sp	Graminoid/Forb	56.76	4.36
Aira caryophyllea	Graminoid/Forb	56.76	4.14
Alnus rubra	Graminoid/Forb	56.76	4.92
Amelanchier alnifolia	Graminoid/Forb	53.37	5.24
Anaphalis margaritacea	Graminoid/Forb	78.60	3.92
Anemone deltoidea	Graminoid/Forb	56.98	5.63
Antennaria spp.	Graminoid/Forb	62.58	5.62
Apocynum androsaemifolium	Graminoid/Forb	62.29*	2.81
Aquilegia formosa	Graminoid/Forb	62.29*	2.81
Arabis spp.	Graminoid/Forb	62.58	2.81
Arenaria macrophylla	Graminoid/Forb	62.58	2.81
Arnica latifolia	Graminoid/Forb	62.29*	2.81
Arnica latifolia Bong.	Graminoid/Forb	62.29*	2.81
Aruncus dioicus	Graminoid/Forb	62.29*	2.80
Aruncus sylvester	Graminoid/Forb	62.58	2.81
Asarum caudatum	Graminoid/Forb	62.58	2.81
Asplenium viride	Graminoid/Forb	62.29*	2.81
Aster ledophyllus	Graminoid/Forb	68.00	3.06

Aster spp.	Graminoid/Forb	62.58	3.06
Astragalas spp.	Graminoid/Forb	68.00	2.37
Athyrium filix-femina	Graminoid/Forb	52.75	3.60
Berberis nervosa	Graminoid/Forb	34.40	3.30
Blechnum spicant	Graminoid/Forb	39.75	3.60
Borage spp.	Graminoid/Forb	60.36	2.71
Campanula scouleri	Graminoid/Forb	59.25	2.66
Carex spp.	Graminoid/Forb	60.68	5.46
Caryophyllaceae	Graminoid/Forb	62.29*	2.81
Castilleja miniata	Graminoid/Forb	62.58	2.81
Centaurium erythraea	Graminoid/Forb	60.36	2.71
Cerastium arvense	Graminoid/Forb	62.58	2.81
Cerastium nutans	Graminoid/Forb	62.58	2.81
Cerastium sp.	Graminoid/Forb	62.58	2.81
Cerastium viscosum	Graminoid/Forb	62.58	2.81
Cerastium vulgatum	Graminoid/Forb	62.58	2.81
Chamerion angustifolium	Graminoid/Forb	62.29*	2.81
Chamerion angustifolium	Graminoid/Forb	62.29*	2.42
Chimaphila umbellata	Graminoid/Forb	49.82	4.59
Chrysanthemum leucanthemum	Graminoid/Forb	65.51	2.95
Circaea alpina	Graminoid/Forb	60.36	5.43
Cirsium arvense	Graminoid/Forb	66.05	5.95
Cirsium arvense	Graminoid/Forb	69.58	3.14
Cirsium edule	Graminoid/Forb	66.55	5.95
Cirsium spp.	Graminoid/Forb	69.80	6.28
Cirsium vulgare	Graminoid/Forb	66.55	5.95
Cistanthe umbellata	Graminoid/Forb	62.29*	2.81
Claytonia sibirica	Graminoid/Forb	62.29*	2.81
Clintonia uniflora	Graminoid/Forb	62.58	5.63
Collomia heterophylla	Graminoid/Forb	60.36	5.42
Conyza canadensis	Graminoid/Forb	63.18	5.68
Coptis laciniata	Graminoid/Forb	62.58	5.62
Cornus stolonifera	Graminoid/Forb	63.18	2.84
Crepis capillaris	Graminoid/Forb	60.34	5.42
Crepis spp.	Graminoid/Forb	62.58	2.71
Cryptogramma cascadensis	Graminoid/Forb	62.29*	2.81
Cystopteris fragilis	Graminoid/Forb	62.29*	2.81
Cytisus scoparius	Graminoid/Forb	56.98	5.24
Dactylis glomerata	Graminoid/Forb	57.33	5.16

Deschampsia elongata	Graminoid/Forb	36.10	3.26
Dicentra formosa	Graminoid/Forb	62.58	5.62
Digitalis purpurea	Graminoid/Forb	60.36	5.42
Disporum smithii	Graminoid/Forb	62.53	2.81
Disporum spp.	Graminoid/Forb	62.58	2.81
Dryopteris austriaca	Graminoid/Forb	39.63*	1.80
Elymus glaucus	Graminoid/Forb	60.23	5.42
Elymus spp.	Graminoid/Forb	56.76	5.42
Epilobium anagallidifolium	Graminoid/Forb	56.56	5.08
Epilobium ciliatum	Graminoid/Forb	62.58	2.81
Epilobium glaberrimum	Graminoid/Forb	60.36	2.54
Epilobium minutum	Graminoid/Forb	62.33	5.35
Epilobium paniculatum	Graminoid/Forb	61.33	5.35
Epilobium spp.	Graminoid/Forb	61.36	2.28
Epilobium watsonii	Graminoid/Forb	53.73	4.84
Equisetum arvense	Graminoid/Forb	56.50	5.09
Equisetum spp.	Graminoid/Forb	50.70	4.56
Eriogonum nudum	Graminoid/Forb	62.29*	2.81
Eriogonum pyrolifolium	Graminoid/Forb	62.29*	2.81
Eriogonum umbellatum	Graminoid/Forb	62.29*	2.81
Eriophyllum lanatum	Graminoid/Forb	62.29*	2.81
Erodium circinatum	Graminoid/Forb	60.36	2.71
Erythronium spp.	Graminoid/Forb	62.29*	2.81
Eucephasis ledophyllus	Graminoid/Forb	50.00	2.81
Festuca occidentalis	Graminoid/Forb	55.97	5.04
Fragaria spp.	Graminoid/Forb	62.58	2.81
Fragaria vesca	Graminoid/Forb	62.58	5.62
Fragaria virginiana	Graminoid/Forb	60.53	5.44
Galium aparine	Graminoid/Forb	62.58	5.62
Galium oreganum	Graminoid/Forb	62.58	2.81
Galium triflorum	Graminoid/Forb	62.58	5.62
Gaultheria ovatifolia	Graminoid/Forb	32.98	3.17
Gaultheria shallon	Graminoid/Forb	27.28	2.62
Gentiana calycosa Griseb.	Graminoid/Forb	62.29*	2.81
Geranium robertianum	Graminoid/Forb	60.36	5.42
Geranium spp.	Graminoid/Forb	68.06	3.06
Geum macrophyllum	Graminoid/Forb	65.16	2.93
Gnaphalium microcephalum	Graminoid/Forb	61.33	5.52

Gnaphalium spp.	Graminoid/Forb	60.36	2.71
Goodyera oblongifolia	Graminoid/Forb	62.58	2.81
Gymnocarpium dryopteris	Graminoid/Forb	39.63*	3.60
Heracleum lanatum	Graminoid/Forb	62.29*	2.81
Heuchera glabra	Graminoid/Forb	62.29*	2.81
Heuchera micrantha	Graminoid/Forb	62.29*	2.81
Hieracium albiflorum	Graminoid/Forb	64.00	5.76
Hieracium spp.	Graminoid/Forb	62.58	5.62
Holcus lanatus	Graminoid/Forb	48.85	4.40
Holodiscus discolor	Graminoid/Forb	56.98	5.24
Hydrophyllum fendleri	Graminoid/Forb	62.29*	2.81
Hypericum perforatum	Graminoid/Forb	61.00	5.48
Hypochaeris radicata	Graminoid/Forb	63.90	5.74
Iris spp.	Graminoid/Forb	62.58	2.81
Iris tenax	Graminoid/Forb	62.58	2.81
Jacobaea vulgaris	Graminoid/Forb	62.29*	2.81
Juncus spp.	Graminoid/Forb	52.00	4.68
Lactuca muralis	Graminoid/Forb	62.58	5.36
Lactuca serriola	Graminoid/Forb	59.59	2.81
Lactuca spp.	Graminoid/Forb	62.44	5.62
Lathyrus spp.	Graminoid/Forb	62.58	2.77
Leucanthemum vulgare	Graminoid/Forb	62.29*	2.81
Logfia gallica	Graminoid/Forb	62.29*	2.81
Lomatium martindalei	Graminoid/Forb	62.29*	2.81
Lotus corniculatus	Graminoid/Forb	62.44	5.62
Lotus micranthus	Graminoid/Forb	67.30	6.06
Lotus purshianus	Graminoid/Forb	62.58	2.81
Lotus spp.	Graminoid/Forb	62.29*	2.81
Luetkea pectinata	Graminoid/Forb	62.58	2.81
Lupinus latifolius	Graminoid/Forb	62.58	5.62
Lupinus lepidus	Graminoid/Forb	77.87	3.50
Lupinus spp.	Graminoid/Forb	77.87	7.00
Luzula spp	Graminoid/Forb	62.10	5.60
Madia sativa	Graminoid/Forb	62.29*	2.81
Maianthemum canadensis	Graminoid/Forb	62.58	2.81
Maianthemum dilatatum	Graminoid/Forb	71.07	3.20
Melilotus albus	Graminoid/Forb	62.29*	2.81
Microseris spp.	Graminoid/Forb	62.29*	2.81
Mimulus moschatus	Graminoid/Forb	62.29*	2.81

Montia parvifolia	Graminoid/Forb	60.00	2.81
Montia sibirica	Graminoid/Forb	60.00	5.40
Mycelis muralis	Graminoid/Forb	62.29*	2.81
Myosotis laxa	Graminoid/Forb	62.29*	2.81
Nemophila parviflora	Graminoid/Forb	60.36	2.71
Nothochelone nemorosa	Graminoid/Forb	62.29*	2.81
Oplopanax horridum	Graminoid/Forb	68.37	5.25
Osmorhiza berteroi	Graminoid/Forb	60.36	2.71
Osmoriza chilensis	Graminoid/Forb	60.36	2.71
Oxalis oregana	Graminoid/Forb	59.00	2.65
Parentucellia viscosa	Graminoid/Forb	60.36	5.42
Pedicularis spp.	Graminoid/Forb	62.58	2.81
Penstamon spp.	Graminoid/Forb	62.58	2.81
Penstemon cardwellii	Graminoid/Forb	62.44	5.62
Penstemon serrulatus	Graminoid/Forb	64.58	2.81
Penstemon sp.	Graminoid/Forb	63.58	2.81
Petasites frigidus	Graminoid/Forb	62.29*	2.81
Phacelia hastata	Graminoid/Forb	62.58	5.62
Phacelia heterophylla	Graminoid/Forb	62.44	5.62
Phalaris arundinacea	Graminoid/Forb	56.76	5.12
Phlox spp.	Graminoid/Forb	62.29*	2.81
Pinus monticola	Graminoid/Forb	42.37*	1.50
Piperia elegans ssp. elegans	Graminoid/Forb	62.29*	2.81
Plantago lanceolata	Graminoid/Forb	62.58	5.62
Plantago major	Graminoid/Forb	62.58	2.81
Plantago spp.	Graminoid/Forb	62.58	5.62
Poa pratensis	Graminoid/Forb	56.75	5.12
Poa sp	Graminoid/Forb	54.60	4.92
Polygonum minimum	Graminoid/Forb	60.36	2.71
Polygonum sp.	Graminoid/Forb	60.36	2.71
Polypodiaceae	Graminoid/Forb	61.36	2.81
Polypogon monspeliensis	Graminoid/Forb	62.29*	2.81
Polystichum munitum	Graminoid/Forb	33.75	3.06
Populus trichocarpa	Graminoid/Forb	56.10	5.16
Potentialla spp.	Graminoid/Forb	62.29*	2.81
Potentilla drummondii	Graminoid/Forb	62.29*	2.81
Prunella Spp.	Graminoid/Forb	67.00	3.01
Prunella vulgaris	Graminoid/Forb	60.36	5.42
Prunus emarginata	Graminoid/Forb	61.82	5.70

Pseudognaphalium canescens ssp. canescens	Graminoid/Forb	60.36	2.81
Pseudotsuga menziesii	Graminoid/Forb	34.20	3.10
Pteridium aquilinum	Graminoid/Forb	45.40	4.12
Pyrola asarifolia	Graminoid/Forb	62.29*	2.81
Pyrola picta	Graminoid/Forb	62.29*	2.81
Pyrola secunda	Graminoid/Forb	62.29*	2.81
Racomitreium canescens	Graminoid/Forb	62.58	2.81
Ranunculus spp.	Graminoid/Forb	62.58	2.81
Ranunculus uncinatus var parviflorus	Graminoid/Forb	62.58	5.62
Ribes sanguineum	Graminoid/Forb	56.98	5.24
Ribes spp.	Graminoid/Forb	55.40	5.10
Rosa gymnocarpa	Graminoid/Forb	67.50	6.22
Rubus discolor	Graminoid/Forb	49.82	4.58
Rubus laciniatus	Graminoid/Forb	54.25	5.00
Rubus leucodermis	Graminoid/Forb	54.02	4.98
Rubus parviflorus	Graminoid/Forb	46.30	4.26
Rubus pedatus	Graminoid/Forb	61.07	5.25
Rubus spectabilis	Graminoid/Forb	44.78	4.12
Rubus ursinus	Graminoid/Forb	32.60	3.00
Rumex acetosella	Graminoid/Forb	60.48	5.45
Rumex acetosella L.	Graminoid/Forb	58.67	2.64
Rumex spp.	Graminoid/Forb	58.67	2.64
Rumex spp. or Rumex acetosella	Graminoid/Forb	58.67	5.28
Salix spp.	Graminoid/Forb	43.60	4.02
Sambucus spp.	Graminoid/Forb	58.00	5.34
Sanicula graveolens	Graminoid/Forb	62.29*	2.81
Saxifraga ferruginea	Graminoid/Forb	62.29*	5.62
Saxifraga ferruginea Graham	Graminoid/Forb	62.29*	2.81
Scrophularia californica	Graminoid/Forb	68.00	3.06
Scrophularia sp.	Graminoid/Forb	38.00	3.06
Sedum spathulifolium	Graminoid/Forb	62.29*	2.81
Sedum spp.	Graminoid/Forb	53.99*	2.42
Senecio jacobaea	Graminoid/Forb	62.58	2.81
Senecio sp.	Graminoid/Forb	70.01	2.81
Senecio spp.	Graminoid/Forb	70.01	3.15
Senecio sylvaticus	Graminoid/Forb	62.58	5.62
Senecio triangularis	Graminoid/Forb	62.58	5.62
Senecio vulgaris	Graminoid/Forb	70.01	2.81

Silene menziesii	Graminoid/Forb	62.29*	2.81
Silene scouleri	Graminoid/Forb	62.29*	2.81
Smilacina spp,	Graminoid/Forb	62.58	2.81
Smilacina racemosa	Graminoid/Forb	62.44	5.62
Smilacina spp.	Graminoid/Forb	62.44	5.62
Smilacina stellata	Graminoid/Forb	66.02	5.94
Solanum dulcamara	Graminoid/Forb	62.29*	2.81
Sonchus asper	Graminoid/Forb	62.58	5.62
Sorbus sitchensis	Graminoid/Forb	56.98	5.24
Spergularia rubra	Graminoid/Forb	62.29*	5.62
Spergulariasp.	Graminoid/Forb	62.29*	2.81
Spiraea douglasii	Graminoid/Forb	62.29*	2.62
Spiranthes romanzoffiana	Graminoid/Forb	62.29*	2.81
Stachys cooleyea	Graminoid/Forb	59.50	2.68
Stellaria calycantha	Graminoid/Forb	63.16	5.62
Stellaria crispa	Graminoid/Forb	62.58	5.62
Stellaria obtusa	Graminoid/Forb	63.16	5.69
Stellaria spp.	Graminoid/Forb	64.03	5.76
Streptopus amplexifolius	Graminoid/Forb	62.29*	2.81
Symphoricarpos spp,	Graminoid/Forb	72.07	6.64
Synthyris reniformis	Graminoid/Forb	62.29*	2.81
Taraxacum officinale	Graminoid/Forb	78.00	7.02
Taraxacum spp.	Graminoid/Forb	62.58	7.02
Tellima grandiflora	Graminoid/Forb	60.36	5.42
Tiarella trifoliata	Graminoid/Forb	50.93	4.58
Tiarella unifoliata	Graminoid/Forb	56.61	5.10
Tolmiea menziesii	Graminoid/Forb	28.00	2.52
Trautvetteria caroliniensis	Graminoid/Forb	62.29*	2.81
Trientalis latifolia	Graminoid/Forb	60.36	2.71
Trifolium campestre	Graminoid/Forb	58.14	5.23
Trifolium dubium	Graminoid/Forb	58.40	2.63
Trifolium repens	Graminoid/Forb	68.23	6.14
Trifolium sp.	Graminoid/Forb	61.33	5.62
Trifolium spp.	Graminoid/Forb	62.58	2.81
Trillium ovatum	Graminoid/Forb	61.33	5.52
Trillium spp.	Graminoid/Forb	60.36	2.71
Tsuga mertensiana	Graminoid/Forb	42.37*	1.50
Typha latifolia	Graminoid/Forb	62.29*	2.81

Urtica dioica	Graminoid/Forb	60.36	2.71
Vaccinium membranaceum	Graminoid/Forb	58.40	5.38
Vaccinium parvifolium	Graminoid/Forb	58.85	2.65
Vancouveria hexandra	Graminoid/Forb	61.49	5.54
Veratreum viride Aiton	Graminoid/Forb	62.58	2.81
Veratrum viride	Graminoid/Forb	62.29*	2.81
Verbascum thapsus	Graminoid/Forb	62.29*	2.81
Veronica americana	Graminoid/Forb	60.36	5.42
Veronica officinalis	Graminoid/Forb	62.58	5.62
Veronica serpyllifolia	Graminoid/Forb	60.58	2.81
Vicia americana	Graminoid/Forb	62.58	5.62
Vicia sativa	Graminoid/Forb	62.58	2.81
Vicia spp	Graminoid/Forb	58.50	2.63
Viola adunca Sm.	Graminoid/Forb	66.17	2.98
Viola sempervirens	Graminoid/Forb	66.17	2.98
Viola spp.	Graminoid/Forb	66.17	2.98
Vulpia myuros	Graminoid/Forb	45.89	4.14
Xerophyllum tenax	Graminoid/Forb	62.58	5.63
Achnatherum occidentale	Graminoid/Forb	53.99*	2.42
Agoseris grandiflora	Graminoid/Forb	56.76	5.12
Agrostis diegoensis	Graminoid/Forb	45.34	4.31
Agrostis scabra	Graminoid/Forb	48.30	2.56
Agrostis spp.	Graminoid/Forb	55.30	4.99
Agrostis tenuis	Graminoid/Forb	51.65	4.60
Aira praecox	Graminoid/Forb	45.89	2.42
Alopecurus geniculatus L.	Graminoid/Forb	56.76	2.42
Anthoxanthum odoratum	Graminoid/Forb	53.99*	2.42
Avena spp.	Graminoid/Forb	45.89	2.07
Bromus carinatus	Graminoid/Forb	60.37	5.44
Bromus carinatus	Graminoid/Forb	56.76	2.72
Bromus sitchensis	Graminoid/Forb	65.30	5.88
Bromus Spp.	Graminoid/Forb	56.76	2.56
Bromus vulgaris	Graminoid/Forb	56.76	2.56
Calamagrostis canadensis	Graminoid/Forb	53.99*	2.42
Calamagrostis sesquiflora	Graminoid/Forb	53.99*	2.42
Carex deweyana	Graminoid/Forb	57.34	4.84
Carex laeviculmis	Graminoid/Forb	57.34	5.15
Carex mertensii	Graminoid/Forb	57.34	5.15
Carex pachystachya	Graminoid/Forb	57.34	5.15

Carex pensylvanica	Graminoid/Forb	60.68	2.73
Carex rossii	Graminoid/Forb	57.34	5.15
Carex subfusca	Graminoid/Forb	57.34	5.15
Castilleja miniata	Graminoid/Forb	57.34	4.84
Catabrosa aquatica	Graminoid/Forb	56.76	2.56
Cinna latifolia	Graminoid/Forb	53.99*	2.42
Cynosurus echinatus	Graminoid/Forb	45.89	2.07
Deschampsia atropurpurea	Graminoid/Forb	45.05	4.05
Deschampsia caespitosa	Graminoid/Forb	45.05	4.05
Eleocharis ovata	Graminoid/Forb	53.99*	2.42
Festuca arundinacea	Graminoid/Forb	53.22	4.84
Festuca myuros	Graminoid/Forb	53.72	4.78
Festuca rubra	Graminoid/Forb	55.45	2.36
Festuca spp.	Graminoid/Forb	52.45	4.72
Juncus effusus	Graminoid/Forb	56.76	2.56
Juncus ensifolius	Graminoid/Forb	52.00	2.56
Juncus mertensianus	Graminoid/Forb	53.00	4.76
Juncus parryi	Graminoid/Forb	53.00	4.76
Juncus regelii	Graminoid/Forb	52.00	2.34
Lachnagrostis filiformis	Graminoid/Forb	53.99*	2.81
Lolium perenne	Graminoid/Forb	53.99*	2.42
Luzula campestris	Graminoid/Forb	58.05	5.22
Luzula hitchcockii	Graminoid/Forb	62.10	2.80
Luzula parviflora	Graminoid/Forb	58.05	5.22
Luzula spp.	Graminoid/Forb	58.05	5.22
Melica bulbosa	Graminoid/Forb	56.76	2.56
Phleum alpinum L.	Graminoid/Forb	53.99*	2.42
Phleum pratense	Graminoid/Forb	54.60	2.42
Poa annua	Graminoid/Forb	54.60	2.46
Poa compressa	Graminoid/Forb	56.76	2.56
Poa spp.	Graminoid/Forb	53.99*	2.46
Poaceae	Graminoid/Forb	54.30	4.88
Polygonum minimum	Graminoid/Forb	53.99*	2.81
Schedonorus pratensis	Graminoid/Forb	53.99*	2.42
Schoenoplectus acutus var. acutus	Graminoid/Forb	53.99*	2.42
Scirpus microcarpus	Graminoid/Forb	53.99*	2.62
Trisetum cernuum	Graminoid/Forb	57.50	5.11
Acer glabrum	Shrub	51.30	4.93
Arctostaphylos uva-ursi	Shrub	56.67*	2.62

Ceanothus velutinus	Shrub	56.67*	2.62
Chimaphila menziesii	Shrub	49.82	2.29
Corylus cornuta	Shrub	56.98	2.62
Linnaea borealis	Shrub	32.98	2.29
Lonicera ciliosa	Shrub	56.67*	2.62
Oemleria cerasiformis	Shrub	56.98	2.62
Pachistima myrsinites	Shrub	56.67*	2.62
Physocarpus capitatus	Shrub	56.67*	2.62
Rhamnus purshiana	Shrub	58.57	2.70
Rhododendron macrophyllum	Shrub	32.98	1.58
Ribes bracteosum	Shrub	56.40	2.62
Ribes lacustre	Shrub	57.40	2.55
Rosa nutkana	Shrub	65.80	3.03
Rosa spp.	Shrub	82.60	3.80
Rubus nivalis	Shrub	56.98	2.62
Rubus spp.	Shrub	55.35	4.91
Salix lasiandra	Shrub	50.14	4.63
Salix scouleriana	Shrub	50.14	4.63
Salix sitchensis	Shrub	50.64	4.63
Sorbus scopulina	Shrub	56.83	5.24
Sorbus spp.	Shrub	56.83	5.24
Spiraea betulifolia	Shrub	56.67*	2.62
Vaccinium alaskaense	Shrub	46.90	2.16
Vaccinium ovalifolium	Shrub	53.25	4.91
Vaccinium ovatum	Shrub	49.82	2.29
Vaccinium spp.	Shrub	36.50	2.65
Whipplea modesta	Shrub	49.82	2.29
Abies amabilis	Tree	32.98	1.50
Taxus brevifolia	Tree	32.98	1.50
Thuja plicata	Tree	47.30	2.15
Tsuga heterophylla	Tree	36.05	1.63

Table D.2. Average digestible energy and dry matter digestibility values (calculated with Appendix C.) used for species that were not provided by Geary (2013), Cook et al. (*in press*), Merrill (1987).

	Graminoid	**Forb**	**Fern**	**Deciduous Shrub**	**Evergreen Shrub**	**Tree**
Digestible energy	2.42	2.81	1.80	2.62	1.54	1.50

Dry matter digestibility	53.99	62.29	39.63	56.67	32.12	42.37

Appendix E. Estimating Nutritional Carrying Capacity.

Sample calculation of elk days/900-m^2 cell when the dietary quality and the limiting factor for which a species can contribute to the total biomass within the diet constraints are met.

Table E.1. Sample nutritional inputs and constraints used for calculating the nutritional carrying capacity of elk at Mount St. Helens.

Inputs/Constraints	Value	Units
Dry Matter Intake	7997	g/day
Percent of Species Consumed	100	%
Minimum Total Biomass for Elk to Forage Profitably	150	kg/ha
Home Range Size	1045	ha
Total Accepted Biomass within a home range	4590	kg/ha

Elk days/ha within a home range:

$$\text{Equation: } \frac{((P_1B_1 + P_2B_2 + \cdots + P_nB_n) - B_{\min\ constant})}{DI}$$

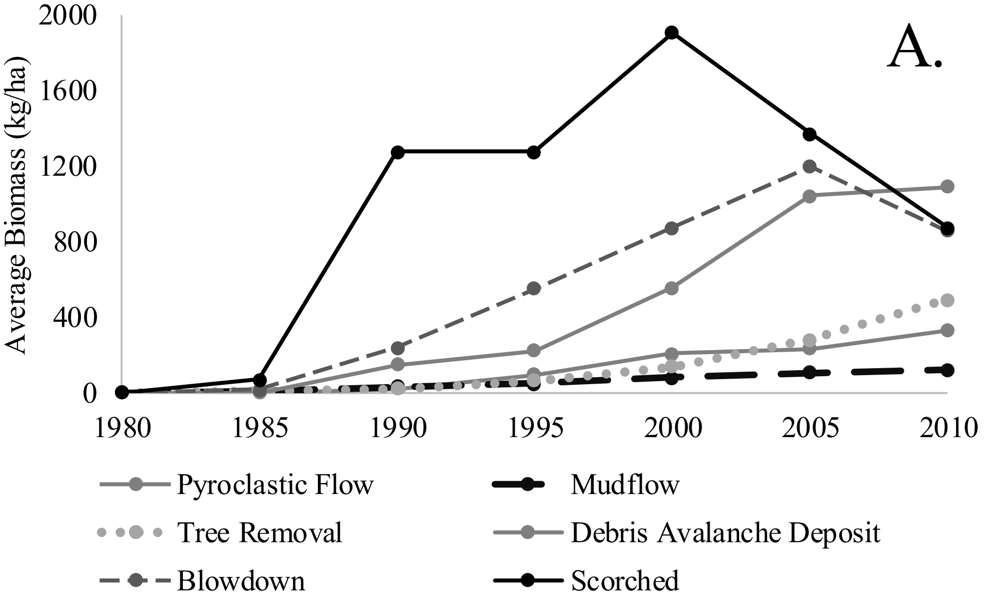
$$\frac{(1_1 16_1 (kg/ha) + 1_2 42_2 (kg/ha) + \cdots + 1_n 35_n (kg/ha)) - 150 (kg/ha)}{7997\ g/day} = \frac{4440_{kg/ha}}{7997_{g/day}}$$

$$\frac{4440_{kg/ha}}{7997_{g/day}} = 0.555_{\frac{1000}{ha}/day}\ x\ 1000 = 555_{days/ha}$$

Elk days/ha within a 900-m^2 cell:

$$555_{days/ha} x\ \frac{900}{10000} = 49.95\ days$$

Appendix F. Total biomass.



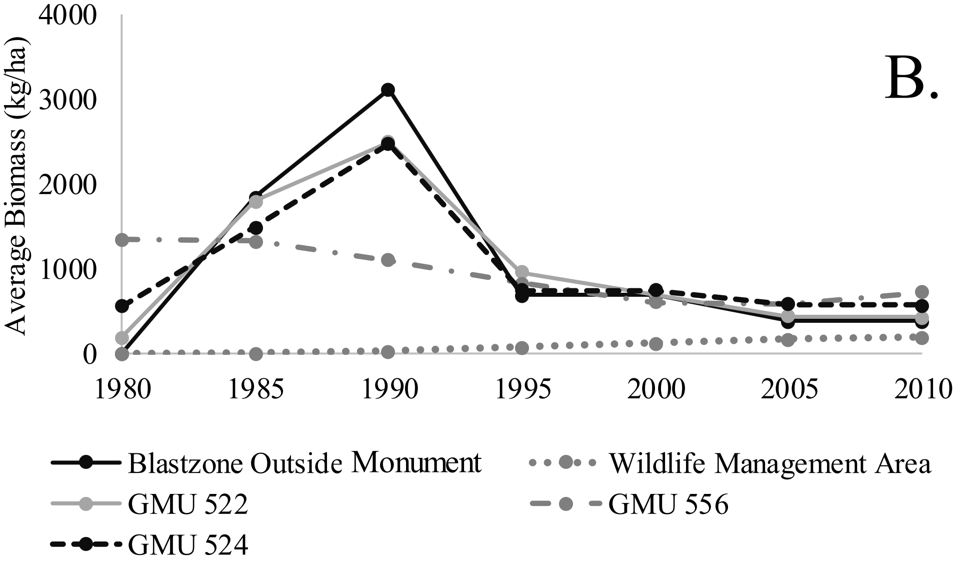


Fig. F.1. The average biomass (kg/ha) in disturbance zones within the Mount St. Helens National Volcanic Monument (A.) and outside the Mount St. Helens National Volcanic Monument (B.) for 1980-2010.

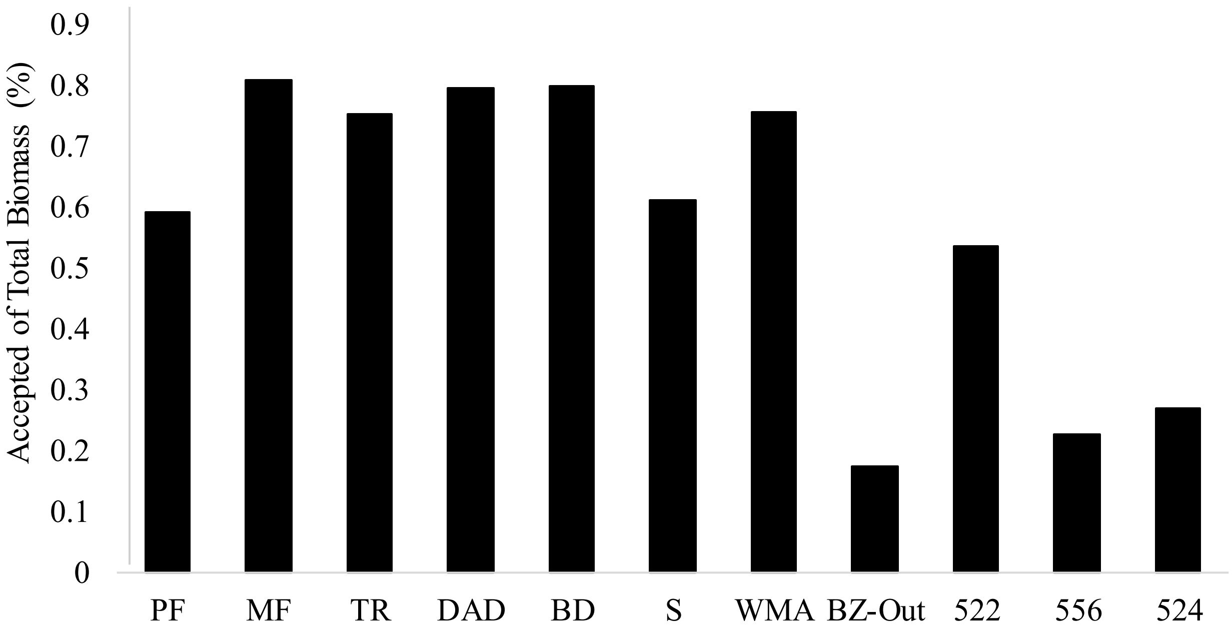


Fig. F.2. Average percent accepted biomass of the total biomass across study years for each of the disturbance zones inside the Mount St. Helens National Volcanic Monument: pyroclastic flow (PF), mudflow (MF), tree removal (TR), debris avalanche deposit (DAD), blowdown (BD), scorched (S); Wildlife Management Area (WMA); blast zone outside the Mount St. Helens National Volcanic Monument (BZ-Out); and the Game Management units (GMU): 522, 556, and 524 outside the Mount St. Helens National Volcanic Monument.

Appendix F.

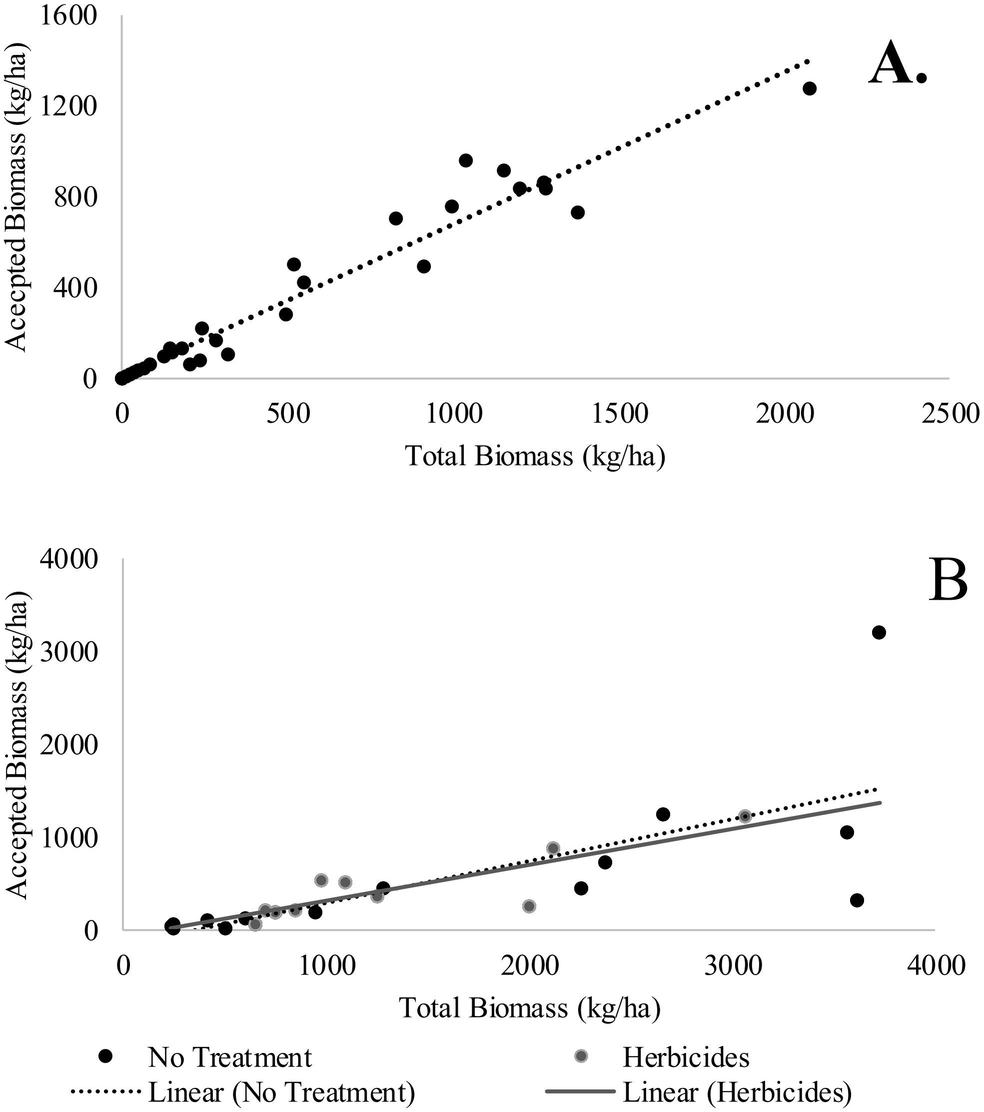


Fig. F.3. Relationship between the average total biomass (kg/ha) and the average accepted biomass (kg/ha) across all years for six disturbance zones inside the Mount St. Helens National Volcanic Monument (A) and game management units outside the Mount St. Helens National Volcanic Monument (B). The regression statistics: total and accepted biomass inside the Mount St. Helens National Volcanic Monument ($r^2 = 0.95$, df = 38, $p < 0.01$), total and accepted biomass treated with herbicides for 0-13 year stands outside the Mount St. Helens National Volcanic Monument ($r^2 = 0.72$, df = 10, $p = 0.02$), and total and accepted biomass of 0-151+ year stands not treated with herbicides (r^2=0.53, df=15, p=0.04).