Elk nutritional resources: Herbicides, herbivory and forest succession at Mount St. Helens

A.B. Geary [a], E.H. Merrill [a,*], J.G. Cook [b], R.C. Cook [b], L.L. Irwin [c]

[a] Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada
[b] National Council for Air and Stream Improvement, 1401 Gekeler Lane, La Grande, OR 97850, USA
[c] National Council for Air and Stream Improvement, 3816 Salish Trail, P.O. Box 68, Stevensville, MT 59870, USA

ABSTRACT

Concern exists about the effects that silvicultural herbicides, past herbivory, and forest succession may have on the carrying capacity for ungulates in the vicinity of Mount St. Helens in southwest Washington. We independently evaluated the effects of both operational herbicides and ungulate herbivory on biomass and available digestible energy of forages in a chronosequence of early-succession (ES) forest stands using a retrospective, paired-site design. We distinguished between trends in biomass by classifying species as avoided (used less than available) or accepted (used equal or more than available) forages for elk based on recent research involving foraging trials of hand-raised, tractable elk in western Oregon and Washington. Herbicide application reduced biomass of accepted forages (kg/ha) for only two years, whereas the initial reduction in avoided biomass persisted throughout the 13-year ES period that we evaluated. The reduction in avoided species was not associated with an increase in accepted species, which may be related to herbivory. We observed that forest canopy closure even at 10–13 years was similar in stands treated and untreated with herbicides, suggesting herbicides did not shorten the seral window when palatable forages were abundant. Because dry matter digestibility of accepted species was generally higher than avoided species, digestible energy (DE, kcal/ha) available to elk was similar to trends in accepted and avoided biomass. An initial 2-year increase in modelled estimates of dietary DE in herbicide-treated stands in years 1–2 resulted from a rapid recovery of plants with high digestibility. In contrast to herbicide treatments, effects of ungulate herbivory on ES communities increased with stand age with a reduction of deciduous shrub height but not densities, reduced biomass of accepted but not avoided species, and reduced standing DE of accepted species outside exclosures. Despite the influence of herbicide applications, herbivory, or their interactions, nutritional resources for elk were equal or more available in ES stands than in mid- and late-succession stands, highlighting the importance of maintaining ES stands for elk in this region.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Early-succession (ES) forests are essential habitats for ungulate species in many parts of North America because available forage declines as the forest canopy closes (Witmer et al., 1985). This is particularly true in forests of the Pacific Northwest where understory biomass can exceed 4000 kg/ha during the first 10 years of stand establishment, but then decline to <100 kg/ha as the canopy closes (Alaback, 1982; Hanley, 1984; Harper, 1987; Jenkins and Starkey, 1996; Witmer et al., 1985; Cook et al., 2016). Wildfires and wind storms historically created the majority of ES forests in the Pacific Northwest (Agee, 1993), but since the early 1950s, timber harvest has been the major disturbance creating ES stands in this region (Weisberg and Swanson, 2003). Over the last several decades, the increased use of wood aggregate products, competition with foreign markets, and protection of old growth forests for spotted owls (Strix occidentalis Xantus de Vesey) has led to declines in timber harvest and the loss of ES stands in western Washington and Oregon, particularly on federal lands (Franklin and Spies, 1991; Perez-Garcia and Barr, 2005; Washington Department of Natural Resources, 2012). Thus, the majority of ES stands in western Washington now exist primarily on private industrial timberlands (Washington Department of Natural Resources, 2012) where silvicultural herbicides are routinely used to enhance fiber production (Wagner et al., 2004). A suite of silvicultural herbicides is used operationally 1–2 times during the

* Corresponding author.
  E-mail address: emerrill@ualberta.ca (E.H. Merrill).

early-successional window to reduce competing grass and broad-leaf woody plants (Blake et al., 1987; Brodie and Walstad, 1987; Freedman et al., 1993). Although the understory recovers post application (Blake et al., 1987; Brodie and Walstad, 1987; Stein, 1999), herbicide application may alter plant community composition and the long-term forage value of the understory community to ungulates (Strong and Gates, 2006).

Information on the effects of herbicides on understory plant communities in the Pacific Northwest is accumulating (Clark et al., 2009). For example, sword fern (*Polystichum munitum* C. Presl), a highly competitive evergreen species that is unpalatable to most ungulates, may be reduced for more than 5 years following herbicide application (Stein, 1995), whereas high-value forage species for elk (*Cervus elaphus* Erxleben), such as wooly catsear (*Hypocharis radicata* L.) and *Crepis* spp., may increase with the frequency of herbicide application because their short life cycle permits them to establish between treatments (Peter and Harrington, 2009). On the other hand, 50–70% reductions in cover of palatable woody plant species with herbicide application have been documented, which may directly reduce browse availability (Freedman et al., 1993; Stein, 1999), but also may indirectly alter the abundance of forbs and grasses due to reduced shading.

Concerns have risen regarding the combined effects of declining ES stands and routine herbicide application on elk and black-tailed deer (*Odocoileus hemionus columbianus* Richardson) populations in the Pacific Northwest (Washington Department of Fish and Wildlife, 2006; Oregon Department of Fish and Wildlife, 2008). Black-tailed deer populations have been regionally declining (Oregon Department of Fish and Wildlife, 2008), and low pregnancy rates and body fat levels have been reported for elk in western Oregon and Washington (Cook et al., 2013). However, only Ulappa (2015) has directly assessed the effects of operational herbicide treatments on nutritional resources available to ungulates in detail, and their study was directed at black-tailed deer. Because black-tailed deer and elk have different requirements and may select for different plant species (Leslie et al., 1984; Kirchhoff and Larsen, 1998), we focused on evaluating effects of operational herbicide application on nutritional resources for elk in ES stands ranging in age from 1 to 13 years and of ungulate herbivory on stands ranging in age from 1 to 6 years on commercial timberlands around Mount St. Helens, Washington. We used a nutritional approach modified from Cook et al. (2016), who classified plant species as accepted (used equal or more than available) or avoided (used less than available) by elk based on foraging trials with hand-raised, tractable elk (henceforth, tractable elk) in western hemlock forests of western Oregon and Washington. We focused on differences in understory biomass (kg/ha), standing digestible energy (DE, kg/ha), and modelled dietary DE (kcal/g) of these plant classes in summer because elk reproduction and survival has been related to summer and autumn nutrition (Cook et al., 2004, 2013). Because of the high productivity of vegetation in the Pacific Northwest, we predicted that (1) herbicide applications would initially reduce forage availability but a reduction in residual forest dominants, such as swordfern, salal (*Gaultheria shallon* Persh) and Oregon grape (*Mahonia nervosa* Nutt.), would promote rapid growth of shade-intolerant herbs and shrubs to improve nutritional resources for elk, and (2) that the early-successional window of abundant forage would decline more quickly in areas treated with herbicides than in untreated sites because of the increased growth rates of crop trees and associated forest canopy closure. Because elk populations have been high in this area since the Mount St. Helens eruption in 1980 (Washington Department of Fish and Wildlife, 2006), and ungulates may themselves alter the plant community via selective foraging, we also evaluated the influence of ungulate herbivory on the forage resource where herbicides were applied. We predicted that herbivory might substantially reduce abundance of accepted forage due to focused foraging on these species. Although our sampling design did not permit direct comparison of the impacts of herbivory to herbicides, we present results of both treatments to qualitatively compare their relative influences on nutritional resources for elk in this area.

2. Methods

2.1. Study area

The study was conducted near Mount St. Helens in southwest Washington in an area bordered by Swift Reservoir in the south and Rife Lake in the north (Fig. 1). The climate is Pacific maritime with wet, mild winters and dry, cool summers (Franklin and Dyrness, 1988). Topography of the area is rolling to mountainous with elevations ranging from 240 m to 1200 m. The area supports 3 major forest zones (Franklin and Dyrness, 1988) including the western hemlock series (75% of study area), Pacific silver fir (*Abies amabilis* Parl.) series (20%), and mountain hemlock (*Tsuga mertensiana* (Bong.) Sarg.) series (<1%), but we limited stand selection to the western hemlock-swordfern series because of the difficulty of finding untreated sites in these other forest zones.

The area includes private industrial timberlands of the St. Helens Tree Farm operated by Weyerhaeuser Company (70%) and public lands under the jurisdiction of the Department of Natural Resources (10%), Mount St. Helens National Monument managed by the United States Forest Service (12%), a state wildlife area managed by Washington Department of Fish and Wildlife (WDFW), and a small percentage of non-industrial private landowners. The dominant land use in the area is forestry with the majority of the study area managed for mid-successional Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands harvested on 40-year cycles.

The area is inhabited by a portion of the Mount St. Helens elk herd, which remains one of the largest herds in Washington (McCorquodale et al., 2014). After the volcanic eruption, the elk population in the Mount St. Helens blast zone recovered quickly, which was attributed to rapid recovery of natural forage, broadcast seeding of grass-legume mixes, and restrictions on human access and elk harvest (Merrill, 1987; Merrill et al., 1995; Raedeke et al., 1986). The estimated elk population across the 5 WDFW Game Management Units (520, 524, 522, 550, 556; total 2754 km^2) in the Mount St. Helens area ranged from approximately 2700 to 5000 elk during 2009–2013 (McCorquodale et al., 2014). Additionally, the black-tailed deer population in the Mount St. Helens region was estimated at approximately 500 (Davis et al., 2010).

2.2. Silvicultural management and herbicide treatments

Silvicultural management by the Weyerhaeuser Company in this area typically consists of high-density planting of rapidly growing conifer seedlings within one year after harvesting. The company also typically applies herbicides aerially prior to conifer planting as a chemical site preparation treatment and sprays a second application during the second growing season to release conifer seedlings from competing graminoids and woody shrubs. Herbicide mixtures across the sites varied, but site preparation mixtures typically included combinations of glyphosate (1.12–2.80 kg/ha), sufometuron methyl (0.06–0.16 kg/ha), metsulfuron methyl (0.04–0.84 kg/ha) and imazapyr (0.14–0.63 kg/ha), whereas release treatments included combinations of clopyralid (0.16–0.47 kg/ha), atrazine (2.24–4.48 kg/ha), hexazinone (0.28–1.68 kg/ha), 2-4D (1.57–2.35 kg/ha), glyphosate (1.12–2.80 kg/ha), and sufometuron methyl (0.06–0.16 kg/ha).
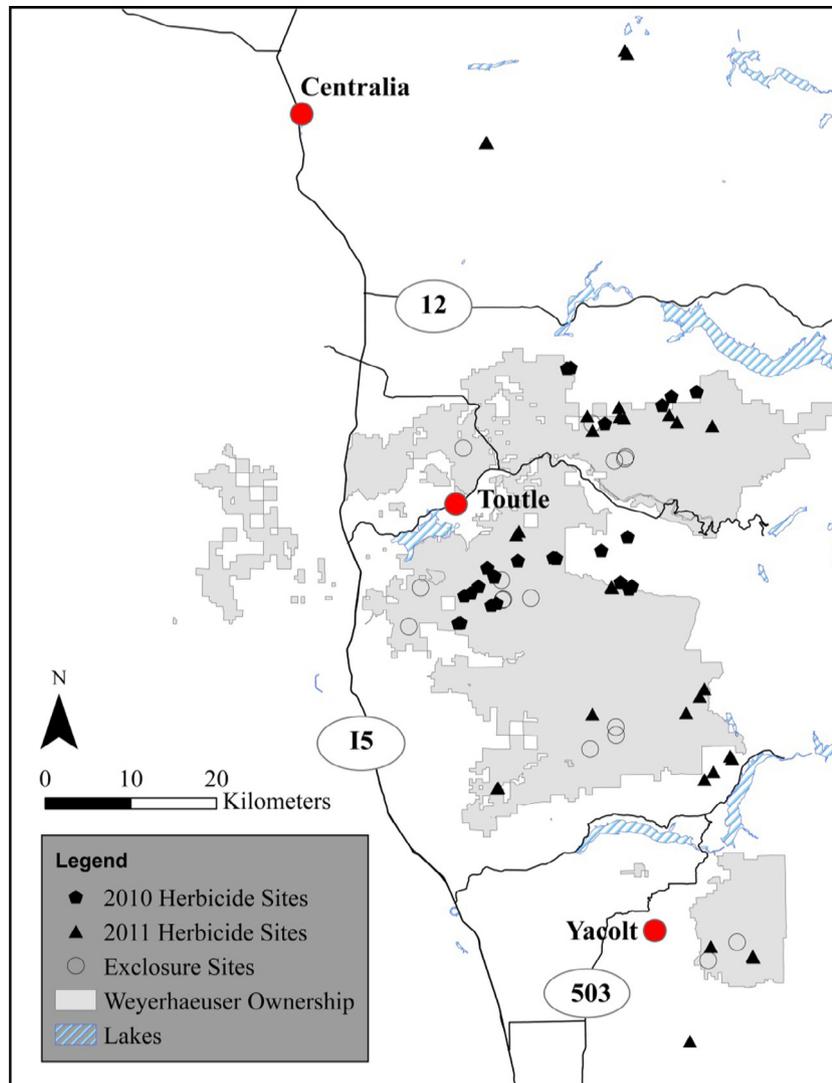
Fig. 1. Location of study sites sampled in 2010–2011 near Mount St. Helens in southwestern Washington, USA. Symbols represent paired macroplots with and without herbicide application or paired macroplots within or adjacent to an exclosure.

2.3. Field design and sampling

To assess the influence of herbicide applications and ungulate herbivory on elk nutritional resources we sampled sites in the western hemlock-swordfern series at elevations ranging from 113 to 833 m using a retrospective approach. We used a case-controlled design by selecting 27 stands untreated with herbicides based on operational records and local guidance of forest managers. We selected the closest herbicide-treated stands (50–6012 m apart) with the same stand age and similar elevation, aspect, slope, slope position, and soil type. As a result, our design prioritized controlling for specific environmental factors rather than closeness of paired sites. At the time of sampling, paired sites were 1–2 yr (n = 5), 3–5 yrs (n = 11), 6–9 yrs (n = 6), 10–13 yrs (n = 5). Sampling of sites occurred between 30 July and 30 August in 2010 (n = 12 pairs) and 1 July to 30 September in 2011 (n = 15). To assess effects of herbivory on vegetation, we sampled 16 established ungulate exclosures and paired adjacent plots (within 50 m) using the same selection criteria as described above. Exclosures ranged in size from 0.121–2.83 ha and were constructed of 4 × 4 wood fence posts and a heavy gauge steel fence 2 m high. Sampling of plots inside and outside exclosures occurred from 1 August to 30 September in 2011; at the time of sampling these sites were 1–2

(n = 3), 3–4 (n = 7), and 5–6 (n = 6) years of age since planting. Sites where exclosures occurred were subject to the same site preparation, release mixtures, and rates of herbicide treatments as described above. We note that because all exclosure sites were located in stands that had been treated with herbicides, this design limited direct comparison of the effects of herbicides vs. herbivory on vegetation. Grouping of stand ages into age classes in both analyses was chosen to balance sample sizes within classes while allowing the data to show specific trends within stand ages.

We followed the vegetation sampling protocols of Cook et al. (2016) within a sample plot. We established a 0.4-ha macroplot with 5 parallel transects systematically placed across the macroplot. We clipped current annual growth of forbs, graminoids, and shrubs, and standing biomass of ferns from 2 cm to a height of 2 m (reach of an elk) within two 2-m² circular plots along each transect for a total of 10 clipped plots per macroplot (site). However, we also clipped the previous year's growth (out to the second growth node) for conifers and evergreen shrubs, because elk will sometimes also consume this older growth (Cook et al., 2016). Harvested vegetation was sorted and bagged by plant species, oven dried at 60 °C to constant weight, and weighed to the nearest 0.1 g. Along each transect, overstory canopy cover of trees >2 m was estimated at 10 points using an ocular sighting tube (i.e.,

moosehorn) and averaged for the macroplot (Bunnell and Vales, 1990; Cook et al., 1995).

At exclosure sites, we used a different approach to estimate shrub biomass inside and outside exclosures because clipping shrub biomass within the small plots was believed to produce less precise estimates due to their patchiness. We counted the number of shrub or deciduous tree stems (rooted stems) by species in 6 belted transects (2×15 m) and recorded average crown height (cm) and 2 perpendicular cross-sectional diameters (cm) on up to 10 representative rooted stems for each species per shrub plot. Individual stem volume (height $\times$ mean diameter, n $\sim$ 60) was used to estimate mean current annual growth (g/stem) for a shrub species based on allometric relationships (Merrill, 1987) and multiplied by shrub density to estimate shrub current annual growth (kg/ha) by species in each macroplot. To compare biomass estimates from clipped versus allometric predictions, we estimated shrub biomass from each method using data from 16 of the sites not fenced (1–6 yrs). We found biomass of shrubs estimated using allometric predictions was not significantly different ($P = 0.58$) between methods, with the exception of salal and Oregon grape, which were overestimated by 1.9 ± 4.5 times ($P = 0.05$) across plots. As a result, we report adjusted estimates of biomass of these two shrubs in the tables and in the text to compare the magnitude of the differences between herbicides and herbivory, but we statistically compared unadjusted values inside and outside exclosures.

2.4. Forage selection classes

We classified plant species found in sites that were untreated or herbicide-treated and exclosed or unexclosed into two forage selection classes (avoided and accepted) that were derived from the three classes (avoided, neutral, and selected) used by Cook et al. (2016). The three classes were developed for understory plants in the western hemlock series from 89, week-long foraging trials with tractable elk (n = 25) in ES and closed canopy forests in the Coastal and Cascade ranges of Oregon and Washington during summer and early autumn from 2000–2002. Tractable elk have been shown to have similar diet selection to wild elk (Olsen-Rutz and Urness, 1987; Spalinger et al., 1997; Yarrow, 1979). Cook et al. (2016) determined diet composition using standard bite count methodology (Collins and Urness, 1983; Wickstrom et al., 1984) and measured forage availability as described above. Selection values of each plant species were based on the Ivlev index (I) derived as $(D_i - B_i)/(D_i \pm B_i)$ (Ivlev, 1961) where D and B are the proportions that the biomass of species i comprised either of the diet (D_i) or of the available biomass (B_i) in a pen at the beginning of the foraging trial. Values ranged from -1 to $+1$; "avoided" species had average $I < 0$ with a 90% confidence interval, and "accepted" species were those whose 90% confidence interval either included zero or was greater than zero. For 23 (0.3% of total biomass across all sites) species found at Mount St. Helens that were not encountered by Cook et al. (2016), we used results of elk fecal analyses from Mt. St. Helens (Merrill, 1987), published literature (Jenkins and Starkey, 1996), and our expert opinion to assign a forage selection class.

2.5. Standing and dietary digestible energy

Standing digestible energy (DE, kcal/ha) available in the understory at treatment sites was estimated from sampled biomass (kg/ha), gross energy values (kcal/g) obtained from Cook et al. (2016), and digestible dry matter (%) of species. Of the 217 plant species sampled, we assigned individual species digestibility values to 83% ± 16 of the species based on three sources: digestibility of samples collected in the study area in August 2011 and analyzed using detergent fiber analysis at Washington State Habitat

Nutrition Lab following methods of Robbins et al. (1987a, 1987b); digestibility values of samples collected in August at Mount St. Helens by Merrill et al. (1995) and analyzed at Washington State Habitat Nutrition Lab following methods of Tilley and Terry (1963) using inoculum from a rumen-fistulated elk maintained on an alfalfa diet; and digestibility values from the PNW reported in the literature for August to October (Canon et al., 1987; Damiran et al., 2002; Hanley and McKendrick, 1983; Jenkins and Starkey, 1996; Kirchhoff and Larsen, 1998; Leslie et al., 1984; Rhodes and Sharrow, 1990). To assign digestibility values to those species for which no estimates were available, we used the mean digestibility of forage classes (forbs: 63.08% ± 9.31; deciduous shrub leaves and twigs: 55.84 ± 11.21; graminoids: 54.04 ± 8.40; ferns: 39.63 ± 5.83; evergreen trees/shrubs: 35.85 ± 7.24) because they differed in digestibility (ANOVA, $df = 4$, $P > 0.01$, Bonferroni adjustment, $P < 0.05$). For gross energy (kcal/g), we used those of plant classes: 4.80 ± 0.42, mean ± SD for evergreens plants (shrubs, trees, and ferns), 4.60 ± 0.19 for deciduous shrubs, 4.51 ± 0.35 for graminoids, and 4.50 ± 0.17 kcal/g for forbs (Cook et al., 2016).

We estimated total available DE (kcal/ha) for accepted and avoided species in each macroplot as the sum of the product of biomass, B_i, and DE_i, where DE_i is the product of the proportional dry matter digestibility and gross energy (kcal/g) of the respective plant species or forage class. We estimated dietary DE_j (kcal/g) at site j of a foraging elk as:

$$DietaryDE_j = \sum U_{ij}DE_i = \sum \frac{w_i A_{ij}}{\sum_i^n w_i A_{ij}} DE_i$$

where U_i is the proportional use of plant species i at site j assuming encounter proportional to species biomass availability (A_i) and species selection (w_i) given an encounter (Lele et al., 2013). Selection by elk was based on the mean selection ratio (w_i) for species i from tractable elk foraging trials in 49 Western Hemlock/Swordfern/ *Oxalis* (WHPO) sites across western Oregon and Washington (Cook et al., 2016) as percent of the diet consumed of species i by an elk during a foraging trial divided by percent of species i of the total biomass available to the elk during a foraging trial (Geary, 2014). Species information is provided in Supplemental materials: Table 1.

2.6. Statistical analysis

We used Pearson's product moment correlations to evaluate whether there were relationships between total, accepted, or avoided biomasses, and tree canopy cover. We tested for significant ($\alpha = 0.05$) main effects (age, treatment) of herbicide application or herbivory and for a treatment $\times$ age interaction for biomass and standing DE (total, accepted, avoided), and dietary DE components of the understory vegetation using ANOVA based on a split-plot design because plots were paired within sites. All references to age and years refer to time since crop trees were planted, and crop trees were always planted within 1 year of harvest. Post-hoc tests of treatment differences were based on paired t-tests within stand ages. Square root or log transformations were used when data violated assumptions of normality or equality of variance. All statistical analyses were performed in STATA 12 (StataCorp, College Station, Texas).

3. Results

3.1. Herbicides

3.1.1. Biomass

Total biomass ranged from 98 kg/ha to 5148 kg/ha across sites and ages in ES stands. Biomass of avoided species comprised the

greatest proportion (65 ± 22%, mean ± SD) of total biomass (2482 kg/ha ± 1249). As a result, biomass of avoided species was positively correlated with total biomass in herbicide-treated and untreated sites (Fig. 2a). In contrast, accepted biomass was positively correlated with total biomass only in herbicide-treated sites (Fig. 2b), whereas accepted and avoided biomass were inversely related only in stands with no herbicide application (Fig. 2c). Accepted biomass was negatively correlated to overstory canopy cover in both treated ($r = -0.39$, $P = 0.05$, n = 27) and untreated sites ($r = -0.37$, $P = 0.06$, n = 27) in stands between 1 and 13 years, whereas avoided biomass was positively correlated to overstory canopy cover only in untreated sites ($r = 0.50$, $P < 0.01$, n = 27).

We found no year effect on biomass (total, avoided, or accepted) at sites within the same age class sampled in 2010 and 2011 ($P > 0.15$), so data were combined across years for further analysis. Avoided and accepted biomasses were reduced by 64% and 85% in herbicide-treated sites, respectively, in the first two years after stand establishment (Table 1, Fig. 3a). The initial decline in biomass at treated sites was primarily related to a decline in biomass of ferns ($P < 0.01$, paired t-test), graminoids ($P < 0.01$), *Rubus* spp. ($P < 0.01$), and salmonberry (*Rubus spectabilis,* Pursh). In contrast, forb biomass was not significantly different, but was higher at 3 of 5 herbicide-treated sites where the avoided forb, woodland groundsel *(Senecio sylvaticus* Nestl.), dominated (Table 2).

After two years, biomass (total, avoided, and accepted) was similar between treatments until 10–13 years, but compositional differences were still evident (Table 2, Fig. 3a). There was an increase in grasses ($P < 0.05$), such as velvet grass (*Holcus lanatus,* L.) and *Agrostis* spp., in stands of 3–9 years in treated sites; but the abundance of residual forest species, such as swordfern and evergreen shrubs including Oregon grape and salal, was lower ($P < 0.05$) in treated sites. Biomass of forbs and deciduous shrubs did not differ between treatments, but accepted species like thistle (*Cirsium* spp.) and trailing blackberry (*Rubus ursinus* Cham. & Schltdl.) were found consistently more often, and red alder (*Alnus rubra* Bong.) less often in treated sites (Table 2). At 10–13 years, biomass of accepted forage comprised a smaller amount of the total biomass than in previous years, but was similar between treatments (Table 1, Fig. 3a). In contrast, biomass of avoided species was 52% lower ($P < 0.05$) on treated sites, which was associated with a reduction in swordfern (Table 2, Fig. 3a).

3.1.2. Digestible energy

Accepted species were more frequently of high dry matter digestibility than avoided species ($X^2 = 10.8$, $df = 3$, $P = 0.02$, Fig. 4) with the mean percent digestibility of accepted species (57.5 ± 1.04, n = 164) being almost 20% higher than that of avoided species (48.1 ± 1.48, n = 53). Standing DE (kcal/ha) afforded by accepted species was lower in herbicide-treated stands than in untreated stands in the first 1–2 years after herbicide treatment ($P = 0.01$) but not in years 3–9, which reflected the trend in biomass of accepted species (Fig. 5a). Standing DE of total biomass was lower in herbicide-treated sites between 10 and 13 years ($P < 0.05$) because of lower biomass of avoided species (Fig. 5a), whereas standing DE of accepted species in stands of years 10–13 was similar between treated and untreated sites.

Modelled dietary DE was highest in stands 1–2 years of age after herbicide treatment ($P = 0.02$) because highly digestible, accepted species, including red huckleberry (*Vaccinium parvifolium* Sm.) and wooly catsear, were proportionally more abundant. However, the initial increase did not persist because after 2 years, treatment sites frequently were dominated by grasses such as *Agrostis* spp. and velvet grass (Table 2), which were relatively low in digestibility (Supplemental materials: Table 1). In contrast, modelled dietary DE was higher in untreated than treated stands in years 3–5 ($P = 0.04$) due to a high proportion and diversity of digestible species including snowberry (*Symphocarpus albus* S.F. Blake), *Rosa* spp., *Viola* spp., and wood rush (*Luzula* spp.). After the first 5 years there was no treatment difference in dietary DE (Fig. 6a).

3.2. Herbivory

3.2.1. Biomass

At herbivory sites, biomass outside exclosures, which was subject to herbicide treatment and herbivory, was comparable to that
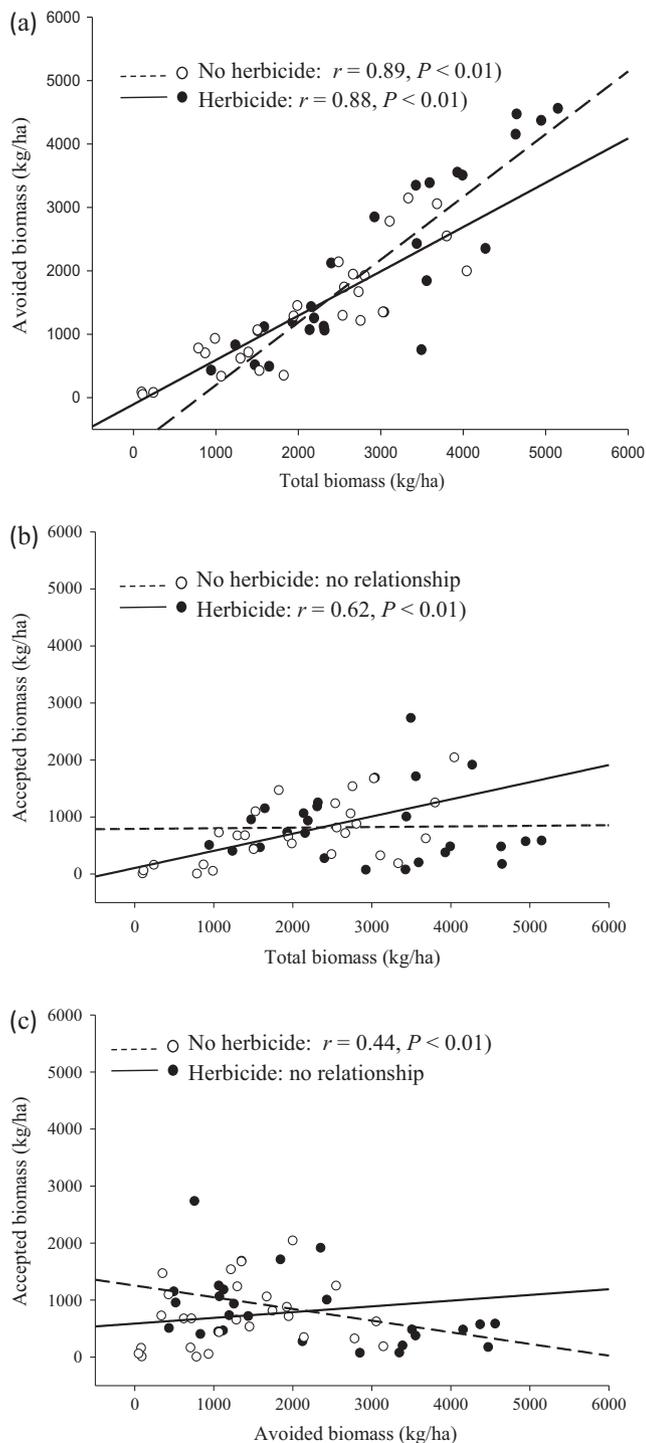

Fig. 2. Relationship between total biomass and (a) avoided biomass, (b) accepted or (c) accepted versus avoided biomass in stand ages ≤13 years near Mount St. Helens sampled in 2010–2011.

Table 1
Summary of treatment main effects (herbicide application and age or herbivory and age) and age x treatment interaction on biomass of total plant understory, avoided or accepted biomass, and biomass of vegetation classes. Note: woody plants include deciduous trees and all shrubs excluding *Rubus* spp.

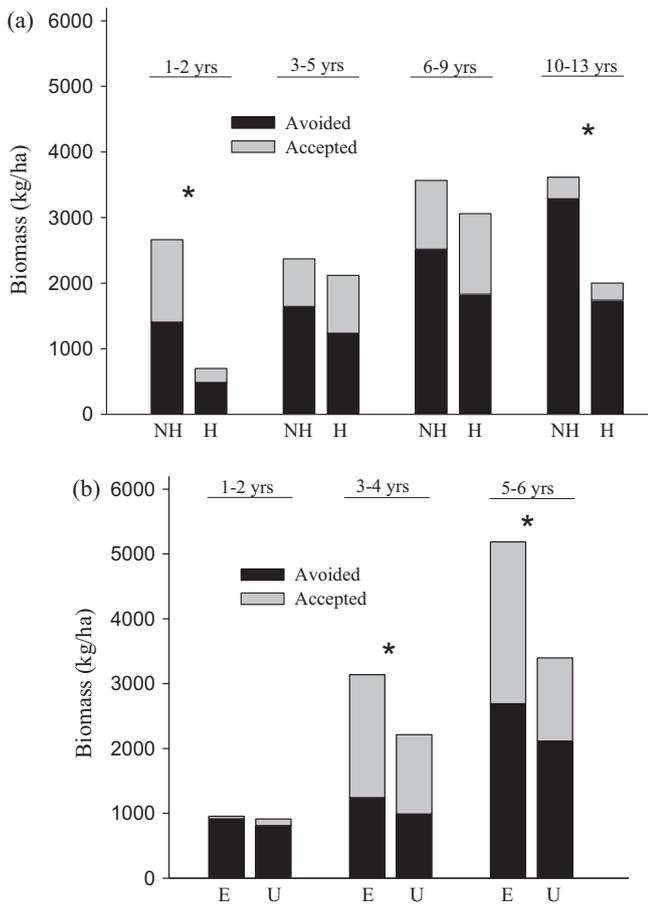|	Treatment		Age		Interaction	
	F-value	P	F-value	P	F-value	P
Herbicides						
Total	17.97	<0.01	4.27	0.02	2.95	0.05
Avoided	15.22	<0.01	3.05	0.05	1.56	0.23
Accepted	3.66	0.07	6.36	<0.01	6.95	<0.01
Conifer	0.65	0.43	5.34	<0.01	1.51	0.24
Ferns	18.84	<0.01	3.68	0.03	1.79	0.17
Forbs	0.18	0.67	6.97	<0.01	0.49	0.69
Graminoids	1.45	0.24	1.69	0.20	7.64	<0.01
Rubus spp.	3.69	0.07	2.02	0.14	3.33	0.04
Shrubs	1.98	0.15	2.54	0.12	0.23	0.87
Herbivory						
Total	20.10	<0.01	21.62	<0.01	3.40	0.07
Avoided	2.73	0.13	7.50	<0.01	0.25	0.79
Accepted	14.66	<0.01	14.15	<0.01	4.99	0.03
Conifer	0.25	0.63	30.41	<0.01	0.17	0.86
Ferns	0.05	0.82	3.07	0.08	0.30	0.75
Forbs	2.31	0.15	0.94	0.42	0.14	0.87
Graminoids	3.83	0.07	11.69	<0.01	0.62	0.56
Rubus spp.	3.98	0.07	8.29	<0.01	2.43	0.13
Shrubs	29.75	<0.01	6.34	<0.01	1.35	0.29

Fig. 3. Mean forage biomass of total, avoided, and accepted forages sampled in 2010–2011 in stands (a) treated with operational herbicides (H) or no application (NH) within stand ages 1–2 (n = 5), 3–5 (n = 11), 6–9 (n = 6); 10–13 (n = 5) and (b) inside (E) or outside (U) exclosures (both treated with herbicides) in stands 1–2 (n = 3), 3–6 (n = 7), and 5–6 (n = 6) years of age. A star indicates a significant difference ($\alpha \leq 0.05$) in accepted or avoided biomass between treatments within age classes.

of herbicide-treated sites of the same age (Fig. 3a and b). Total biomass increased with time since harvest inside and outside exclosures (Table 1). Biomass of avoided species was similar inside and outside exclosures, whereas after 2 years, accepted species biomass averaged 35 and 43% lower (P < 0.01) outside the exclosure in years 3–4 and 5–6 after harvest (Fig. 3b). Lower accepted biomass outside the exclosures was largely due to a reduction in shrubs species frequently selected by elk (Supplemental materials: Table 1), such as *Rubus* spp. (P < 0.01), bitter cherry (*Prunus* spp.), red alder, Cascara buckthorn (*Rhamnus purshiana* DC.), *Ribes* spp. and red huckleberry (Tables 3 and 4). The higher shrub biomass inside exclosures was the result of increased shrub height rather than increased densities (Supplemental materials: Table 2). Douglas-fir biomass was also consistently higher inside the exclosures up to 4 years (P = 0.05), but not thereafter. We found a negative relationship between leader height of Douglas fir and increasing shrub biomass (P < 0.01, r = −0.95) in years 5–6 inside but not outside exclosures. In contrast to woody species, biomass of grass species, including velvet grass, *Agrostis* spp. and blue wild rye (*Elymus glaucus* Buckley), was higher outside exclosures in years 3–4 (P = 0.05), with this trend remaining at 4 of 6 sites in years 5–6 (Table 3).

3.2.2. Digestible energy

Standing and dietary DE outside the exclosures followed a trend similar to other herbicide-treated sites open to herbivory (Figs. 5 and 6). Inside exclosures, standing DE increased more rapidly with stand age than outside exclosures after the first two years. Herbivory resulted in a 25% and 40% reduction in total DE and a 33% and 49% reduction in accepted DE in years 3–4 and 5–6 outside the exclosures, respectively (Fig. 5b, Table 5). We found no significant effects of exclosure treatment or age on dietary DE (Fig. 6b). The lack of an effect was related to high variability of palatable shrub species and forbs, such as fireweed (*Chamerion angustifolium* (L.) Holub), pearly everlasting (*Anaphalis margaritacea* (L.) Benth. & Hook.), wooly catsear, and lower abundance of graminoids outside the exclosures. High variability in unpalatable swordfern also existed inside exclosures (Table 3).

Table 2
Species consistently higher or lower at herbicide treated or untreated sites within stand age class. Species characteristics are presented with mean biomass (kg/ha) difference between treatments, percent (%) of sites where species abundance was higher or lower, and number of sites (n) where a biomass difference was calculated. Positive mean values indicate higher biomass in sites untreated with herbicides and negative mean values indicate a lower biomass at sites untreated with herbicides. Sample sizes were 1–2 yr (n = 5), 3–5 yrs (n = 11), 6–9 yrs (n = 6), 10–13 yrs (n = 5).

Higher biomass in untreated sites								Lower biomass in untreated sites						
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	Species	Class	Pref	Type	Mean	SD	%	n
1–2 Years								**1–2 Years**						
Polystichum munitum	FE	A	RE	797	460	100	5	*Senecio sylvaticus*	F	A	RU	−258	265	100	5
Holcus lanatus	G	N	RU	395	382	100	5	*Galium triflorum*	F	N	RE	−2	3	80	5
Rubus spectabilis	MS	N	RE	300	260	100	3								
Rubus discolor	MS	A	RU	221	207	100	3	**3–5 Years**						
Hypochaeris radicata	F	S	RU	217	331	80	5	*Pseudotsuga menziesii*	CT	A	RE	−364	411	70	10
3–5 Years								*Holcus lanatus*	G	N	RU	−230	215	90	10
Pteridium aquilinum	FE	A	RU	781	848	88	8	*Rubus ursinus*	MS	A	RE	−194	150	82	11
Gaultheria shallon	S	A	RE	444	547	83	6	*Agrostis* spp.	G	N	RU	−129	98	91	11
Alnus rubra	DT	S		178	385	83	6	*Cirsium* spp.	F	N	RU	−107	94	64	11
Mahonia nervosa	S	A	RE	167	212	71	7	**6–9 Years**						
6–9 years								*Holcus lanatus*	G	N	RU	−777	633	67	6
Polystichum munitum	FE	A	RE	526	596	67	6	*Rubus ursinus*	MS	A	RE	−299	247	67	6
Rubus spectabilis	MS	N	RE	169	89	100	5	*Cirsium* spp.	F	N	RU	−120	70	67	6
Rubus parviflorus	MS	S	RE	38	59	100	5	*Acer circinatum*	S	S	RE	−74	77	80	5
Oxalis oregana	F	S	RE	17	6	100	4	*Digitalis purpurea*	F	A	RU	−69	66	83	6
Stellaria borealis	F	N	RU	16	18	100	3	**10–13 years**						
10–13 years								*Pteridium aquilinum*	FE	A	RU	−77	70	60	5
Polystichum munitum	FE	A	RE	1364	1481	80	5	*Holcus lanatus*	G	N	RU	−56	50	75	4
								Vaccinium parvifolium	S	S	RE	−45	50	80	5
								Sambucus racemosa	S	N	RE	−41	67	100	3
								Acer circinatum	S	S	RE	−30	24	100	3

[a] Classes: *Carex* (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), *Rubus* spp. (MS), and Shrubs (S).
[b] Forage preference: Avoided (A), Neutral (N), and Selected (S) from Cook et al. (2016); we combined neutral and selected forage into accepted forage.
[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE).
[d] Mean for positive values was calculated from all sites where species 'x' was more abundant at an untreated site, and mean for negative values was calculated from all sites where species 'x' was less abundant at an untreated site.
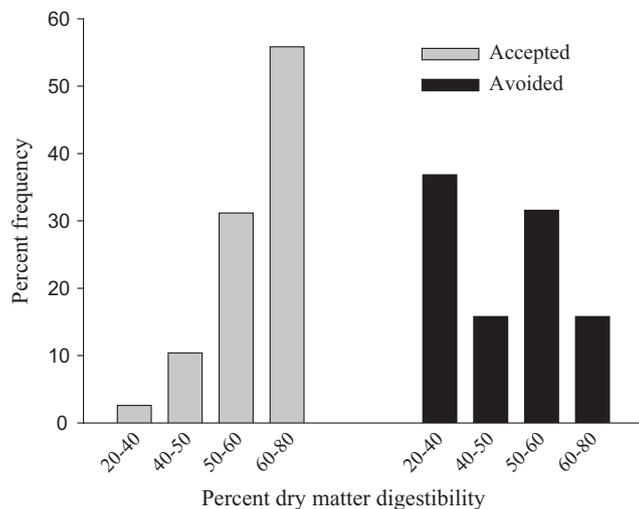

Fig. 4. Percent frequency of accepted and avoided forages within four dry matter digestibility (DMD%) classes.

4. Discussion

4.1. Nutritional resources for ungulates in western Washington hemlock communities

Total biomass in the ES stands of western hemlock where we assessed herbicide application and herbivory in the vicinity of Mount St. Helens was high (2482 kg/ha ± 1249) and comparable to levels reported previously for similarly managed stands in western hemlock sites in western Oregon and Washington (Alaback, 1982; Cook et al., 2016; Hanley, 1984; Harper, 1987; Jenkins and Starkey, 1996; Ulappa, 2015; Witmer et al., 1985), but lower than the 3853–7640 kg/ha range of biomass that is reached within 10–15 years after timber harvest in other forest types of the Pacific Northwest (Boldor, 2007; Karakatsoulis and Kimmins, 1993; Messier and Kimmins, 1990; Schoonmaker and McKee, 1988). Although total biomass is high, species avoided by elk, which we showed were typically low in digestibility, comprised the majority (65 ± 22%) of the available biomass in these ES stands. Ulappa (2015) reported a comparably high proportion (67%) of total biomass was avoided by black-tailed deer in herbicide-treated and untreated stands over a broader region in western Washington. Past assessments of forest succession and forestry practices based on changes in total species biomass (e.g., Witmer et al., 1985) may poorly indicate changes in availability of nutritional resources and the consequences to elk in the Pacific Northwest because avoided plants comprise the majority of the biomass. Recent results of foraging trials with tractable elk in western Washington and Oregon confirmed that biomass of accepted species was more correlated with nutrition and was a better predictor of animal performance than total biomass (Cook et al., 2016). For this reason, we distinguished between accepted and avoided species in our assessment of the effects of herbicides and herbivory on the understory to make a more direct link to animal performance.

4.2. Impacts of herbicides and herbivory on nutritional resources for elk

We found two major effects of operational herbicides on understory vegetation that could impact elk nutritional resources in ES stands up to 13 years at Mount St. Helens. First, there was a short-term (2 yrs.), but substantial reduction (77 ± 13%) of
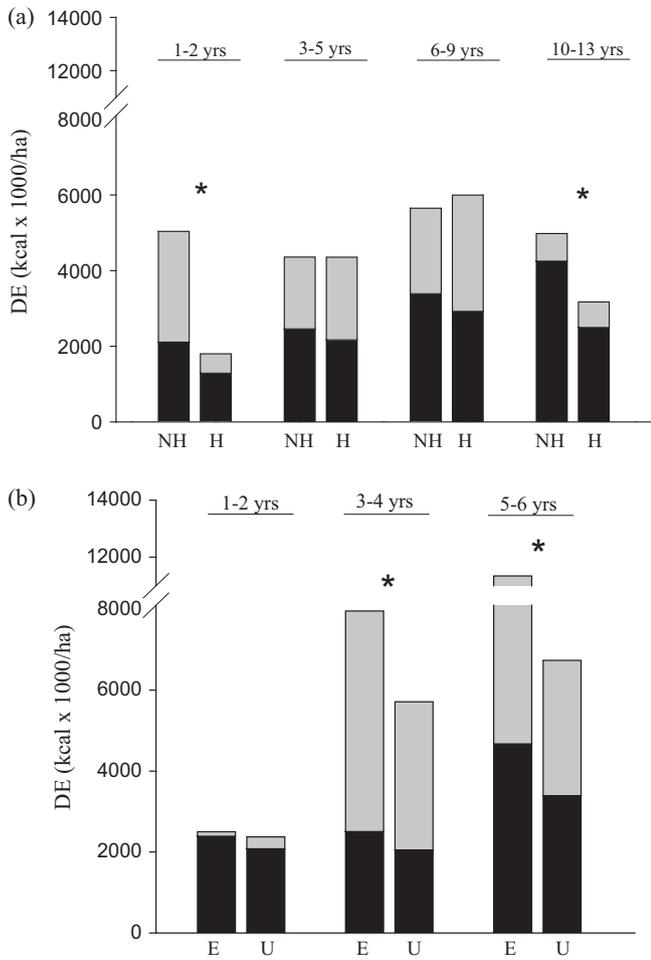
Fig. 5. Standing digestible energy (DE, kcal × 1000/ha) available in accepted and avoided elk forages sampled in 2010–2011 in southwestern Washington within sites (a) treated with operational herbicides (H) or no application (NH) or (b) inside (E) or outside (U) exclosures (both treated with herbicides). A star indicates a significant difference within an age class at α ≤ 0.05 based on a paired t-test between treatments within stand ages.

understory biomass that equally affected both accepted and avoided species. The total biomass reduction was comparable to those of 54–84% after herbicide application reported in other studies in the Pacific Northwest using a range of herbicides applications (Dinger, 2007; Harrington et al., 1995; Maguire et al., 2009; Stein, 1995). However, Cook et al. (2016) found a somewhat greater abundance in biomass of accepted species (500–800 kg/ha) in the first three years after herbicide application across sites in western Washington and Oregon than the 10–677 kg/ha we report for the first two years after herbicide application at sites near Mount St. Helens. Differences in herbicide mixes, application regimes, and environmental conditions, as well as herbivory levels, may limit direct inference from this study to other areas.

The initial reduction in biomass was associated with an elevated level of modelled dietary DE because plants that recovered quickly after herbicide application, such as wooly cat's ear and red huckleberry, were highly digestible, and low quality, avoided species were reduced. Although this suggests the potential for an increase in dietary DE by elk foraging in herbicide-treated sites during the first two years, many of these sites had accepted biomass levels below the threshold of 150 kg/ha where instantaneous intake rates decline (Cook et al., 2016). If elk avoid new clearcuts (Irwin and Peek, 1983) because of low intake rates, any short-term improvement in dietary quality related to herbicides may
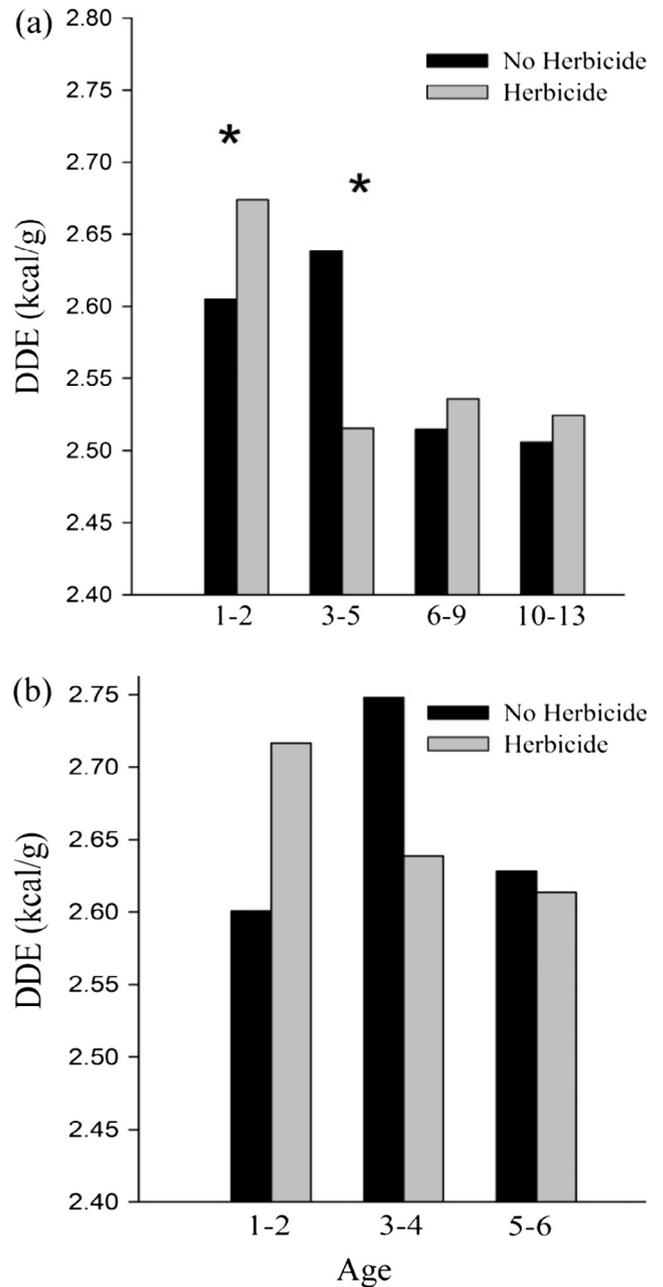

Fig. 6. Modelled dietary digestible energy (DDE, kcal/g) of an elk foraging within stands (a) treated with operational herbicides (H) or no application (NH) or (b) inside (E) or outside (U) exclosures (both treated with herbicides by stand age in southwestern Washington. See text for details. A star indicates a significant difference at α ≤ 0.05 based on a paired t-test within an age class.

not substantively benefit elk even where it exists. Nonetheless, total biomass in the 1–2 year stands where herbicide treatment occurred was at least as high when compared to biomass in later stand ages that ranged from 248 kg/ha ± 395 in mid-seral to 415 kg/ha ± 271 in late seral stages in the western hemlock series in Washington and Oregon using the same sampling protocol (Cook et al., 2016). Even more importantly, biomass of accepted species found in later stand ages was only a fraction (~6%) of the biomass of accepted species found in stands 3–13 years even where herbicides were applied (Cook et al., 2016). Thus, even with herbicide application, ES stands provide equal or better foraging opportunities than in mid- and late-succession forest stands (Cook et al., 2016).

Table 3
Species consistently higher or lower inside or outside of exclosures within stand age class: 1–2 (n = 3), 2–4 (n = 7), 5–6 (n = 6) years. Species characteristics are mean ($\bar{X}$) and standard deviation (SD) biomass (kg/ha) difference between treatments, percent (%) of sites where species abundance was higher or lower, and number of sites (n) where a biomass difference was calculated. Positive means indicate higher biomass in exclosed sites; negative means indicate a lower biomass in exclosed sites.

Higher biomass inside exclosures								Lower biomass inside exclosures							
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	Species	Class	Pref	Type	Mean	SD	%	n
1–2 years	–	–	–	–	–	–	–	1–2 years							
3–4 years								Polystichum munitum	FE	A	RE	−27	24	100	3
Sambucus racemosa	S	N	RE	752	1008	71	7	Cirsium spp.	F	N	RU	−12	13	100	3
Chamerion angustifolium	F	N	RU	436	436	71	7								
Prunus emarginata	S	N	RE	419	707	71	7	3–4 years							
Pseudotsuga menziesii	CT	A	RE	268	197	71	7	Cirsium spp.	F	N	RU	−348	461	86	7
Epilobium watsonii	F	A	RU	157	157	71	7	Elymus glaucus	G	N	RE	−173	282	75	4
Crepis capillaris	F	N	RU	148	207	80	5	Holcus lanatus	G	N	RU	−83	89	67	6
Rubus ursinus	MS	A	RE	83	87	83	6	Mahonia nervosa	S	A	RE	−57	49	83	6
Chrysanthemum sp.	F	N	RU	18	30	100	3	Agrostis spp.	G	N	RU	−45	58	83	6
Dicentra formosa	F	N	RE	14	23	75	4	Deschampsia elongata	G	A	RU	−25	22	100	7
Hypericum perforatum	F	S	RU	12	20	75	4	Poa spp.	G	A	RU	−11	8	100	3
5–6 years								5–6 years							
Pseudotsuga menziesii	CT	A	RE	711	631	67	6	Holcus lanatus	G	N	RU	−516	467	67	6
Rubus ursinus	MS	A	RE	676	769	67	6	Cirsium spp.	F	N	RU	−188	158	83	6
Prunus emarginata	S	N	RE	645	687	100	6	Hypochaeris radicata	F	S	RU	−172	282	83	6
Chamerion angustifolium	F	N	RU	445	584	100	6	Elymus glaucus	G	N	RU	−163	163	67	6
Polystichum munitum	FE	A	RE	298	213	67	6	Mahonia nervosa	S	A	RE	−85	71	67	6
Alnus rubra	DT	S	RE	289	285	100	4	Digitalis purpurea	F	A	RU	−62	73	83	6
Vaccinium parvifolium	S	S	RE	208	213	67	6	Agrostis spp.	G	N	RU	−61	68	67	6
Sambucus racemosa	S	N	RE	182	209	83	6	Senecio sylvaticus	F	A	RU	−24	46	100	4
Rhamnus purshiana	S	S	RE	153	86	75	6	Crepis capillaris	F	N	RU	−22	25	83	6
Anaphalis margaritacea	F	S	RE	104	59	100	4	Veronica officinalis	F	N	RU	−18	11	67	6
Rubus laciniatus	MS	A	RU	97	72	83	6	Carex spp.	CA	S	RE	−12	17	67	6
Hypericum perforatum	F	S	RU	39	32	75	4								
Ribes spp.	S	N	RE	26	20	75	4								
Rubus parviflorus	MS	S	RE	10	12	75	4								

[a] Classes: Carex (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), Rubus spp. (MS), and Shrubs (S).
[b] Forage preference: Avoided (A), Neutral (N), and Selected (S) from Cook et al. (2016); we combined neutral and selected forage into accepted forage.
[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE).
[d] Mean for positive values was calculated from all sites where species 'x' was more abundant at an exclosed site, and mean for negative values was calculated from all sites where species 'x' was less abundant at an exclosed site.

Table 4
Mean ($\bar{X}$) and standard deviation (SD) of predicted biomass (kg/ha) by species for accepted and avoided shrubs *sensu* Cook et al. (2016) inside (exclosed) and outside (unexclosed) 16 exclosures near Mount St. Helens, WA. A star indicates significant ($P = 0.05$, or $P = 0.01$) pairwise (S), main effect and interaction (E, E*A), or stand age effect (A).

	1–2 years					3–4 years					5–6 years							
	Exclosed		Unexclosed			Exclosed		Unexclosed			Exclosed		Unexclosed					
Biomass	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	E	A	E*A
Accepted total	5.5	4.2	4.3	3.8		997.1	1054.3	35.9	21.7	**	867.9	618.6	68.9	71.6	**	**	**	*
Avoided total	29.4	27.6	18.6	14.2		33.2	48.2	82.4	79.0	*	279.8	370.2	139.2	104.9				
Total	34.9	30.2	23.0	16.7		1030.2	1087.6	118.3	84.2	*	1147.7	688.6	208.0	156.5	**	**	**	
ACCI	2.7	4.2	3.3	3.8		54.9	85.4	8.5	12.5		16.1	39.0	25.1	41.2				
PREM	0.7	0.9	0.2	0.4		254.0	383.9	5.5	11.2	*	473.0	441.0	5.2	5.3	*	*	*	*
RHPU	0.3	0.6	0.3	0.5		3.1	6.0	3.7	7.4		67.4	87.3	3.7	7.4				
Ribes spp.	0.0	0.0	0.0	0.0		3.5	8.2	0.3	0.6		11.2	15.7	0.1	0.3				
ROGY	0.0	0.0	0.0	0.0		2.3	6.0	1.4	2.4		27.4	43.7	2.8	6.0				
SARA	1.4	1.6	0.4	0.4		663.3	784.8	5.1	3.3	*	115.9	148.4	8.7	8.1		*	*	
VAPA	0.3	0.5	0.1	0.2		16.0	25.3	11.5	11.2		156.7	208.5	23.3	19.0			*	
MANE	28.0	27.6	15.7	12.9		32.9	48.0	76.6	81.8	*	279.8	370.2	139.2	104.9				

Species abbreviations are ACCI: *Acer circinatum*, PREM: *Prunus emarginata*, RHPU: *Rhamnus purshiana*, ROGY: *Rosa gymnocarpa*, SARA: *Sambucus racemosa*, VAPA: *Vaccinium parvifolium*, MANE: *Mahonia nervosa*, and GASH: *Gaultheria shallon*

The second effect was a reduction in the biomass of avoided plant species that persisted up to 10–13 years. We found no evidence that the decrease in biomass of avoided plants, such as swordfern and salal, resulted in a release of accepted species as we had hypothesized because we did not find an inverse relationship between biomass of accepted and avoided species where herbicides were applied (Fig. 2). Whether ungulate herbivory inhibited this response remains unknown because of the limitations of our sampling design. Nevertheless, the lower abundance of accepted species outside compared to inside exclosures,

whether treated with herbicides or not, suggests this is possible. The extent to which selective foraging can mediate vegetative response also may depend on the herbicide regimes. For example, at 3 years post-cutting Stokely (2014) reported that a single application of herbicides (autumn only) reduced native herbaceous forage and selective herbivory was greatest on deciduous shrubs, which facilitated invasive species. In contrast, after autumn plus spring application of herbicides, cervids were less selective reducing total cover including invasive species. Under a heavier herbicide regime (autumn and 2 springs), effects of cervid herbivory

Table 5
Test statistics for treatment main effects (herbicide application and age or herbivory and age) and age × treatment interaction for standing digestible energy (DE, kcal/ha) of all plant species, avoided plant species, and accepted plant species.

	Treatment		Age		Interaction	
	F value	P	F value	P	F-value	P
Herbicides						
Total DE	8.96	0.01	4.06	0.02	4.85	0.01
Avoided DE	6.42	0.02	1.85	0.17	1.22	0.32
Acceptable DE	3.33	0.08	7.31	<0.01	8.97	<0.01
Herbivory						
Total DE	26.08	<0.01	15.67	<0.01	2.36	0.12
Avoided DE	3.61	0.08	5.47	0.02	0.86	0.45
Acceptable DE	9.96	0.01	10.01	<0.01	3.87	0.05

were not observed except for a diminished effect on native-perennial herbs (Stokely, 2014).

Although we found increasing coniferous canopy influenced both accepted (negatively) and avoided (positively) biomass, we found no difference in canopy cover between 10 and 13 year stands with or without herbicides application. Thus, our study failed to support the hypothesis that herbicide application would shorten the window of time for abundant, highly palatable forage by facilitating time to canopy closure. Herbicides may have influenced tree heights or volumes, but we did not measure these. Ulappa (2015) reported that spraying with herbicides increased growth rates of conifers, but they also did not detect accelerated closure of conifer canopy in ES stands treated with herbicides. Nevertheless, accelerated canopy closure has been reported elsewhere (Edwards et al., 2004; Miller et al., 1995). Our data instead indicate that the initial reductions in biomass of avoided species after herbicide treatment, in particular shade-tolerant evergreen shrubs and swordfern, persisted up to 10–13 years, and likely never reached the biomass levels of untreated stands before canopy closure began to limit understory growth. We did find that accepted biomass declined across treatments as canopy cover increased, as was reported by Cook et al. (2016) across a broader region in the Pacific Northwest. By years 10–13 when forest canopy cover reached 58 ± 26%, biomass of accepted species at most sites approached a threshold level of 400–500 kg/ha, below which dietary DE declines because elk begin to include more avoided species in their diet (Cook et al., 2016).

In contrast to the short-term effects of applying herbicides, herbivory maintained a strong and consistent reduction in biomass and DE of accepted species, but had little effect on avoided species, as we anticipated. The diminished nutritional resources resulting from a reduction in accepted species was due to the reduction of several key shrub species, such as bitter cherry, elderberry (*Sambucus* spp.), huckleberry and rose, because deciduous shrub leaves are often nutritionally superior to forbs and grasses in late summer when herbaceous plants are mature (Baker and Hobbs, 1987; Spalinger et al., 1986). Despite the biomass reduction, overall densities of individual shrub species were not reduced in the first 6 years despite suppression of shrub height, indicating the potential for recovery if reductions in herbivore densities could lead to decreased herbivory. Similar reductions in shrub and tree sapling height due to ungulate herbivory have been reported elsewhere (Merrill et al., 2003; Horsley et al., 2003; Cote et al., 2004).

An additional effect of herbivory was the increase in biomass of grasses, which has been reported in other exclosure studies in the Pacific Northwest (Schreiner et al., 1996; Woodward et al., 1994) and where ungulate grazing is high (Harper, 1987). Grasses are tolerant to grazing because they have evolved mechanisms to successfully recoup tissue loss or stimulate above ground production under favourable conditions (Augustine and McNaughton, 1998; Strauss and Agrawal, 1999). Because an abundance of grasses may reduce tree growth (Riggs et al., 2000), an increase in grasses

under herbivory, as we observed in this study, in combination with some ungulate browsing of young tree seedlings has the potential to slow Douglas-fir stand development at least up to 5–6 years. At the same time, without some herbivory there may be rapid growth of tall shrubs that our results indicate may diminish tree growth, likely due to competition for nutrients and sunlight (Hanley and Taber, 1980; Riggs et al., 2000).

4.3. Implications for elk and forest management at Mount St. Helens

There is increasing concern about the habitat conditions for elk on managed timberlands in the vicinity of Mount St. Helens, particularly where elk habitat was affected by the 1980 eruption. Forest canopies have or are rapidly closing over much of the area and herbicides are widely used in areas where timber is harvested (Sparkes, 2016). Segments of the Mount St. Helens elk population inhabiting this broader region also have shown low body condition and pregnancy rates (Cook et al., 2013). Nutritional resources during summer play a particularly important role because demands are high for lactation, juvenile growth, gaining body fat reserves, and breeding (Cook et al., 2004, 1996; Irwin et al., 1994; Noyes et al., 2002), and summer nutrition, particularly digestible energy content of forage, is hypothesized to be most limiting in the forested systems of the Pacific Northwest (Cook et al., 2013, 2016; Harper, 1971; Merrill et al., 1995; Stussy, 1993; Trainer, 1971). The poor nutritional resources in late summer on timberlands in portions of the area surrounding Mount St. Helens, and more generally the Pacific Northwest, pose significant challenges for maintaining productive elk populations in this region (Harper, 1987; Hutchins, 2006; Cook et al., 2016).

Our modelled levels of dietary DE indicate that an elk foraging in ES western hemlock stands may not be able to achieve a dietary DE level of 2.7 kcal/g, where reproductive requirements are met, and typically their diets even in forest stands less than 10–13 years may be below 2.5 kcal/g where performance of lactating adults and their offspring are strongly reduced (Cook et al., 2004). These modelled levels of dietary DE are likely conservative because in calculating dietary use (Lele et al., 2013) we assumed the average plant selection of tractable elk across sites was constant, and that elk encountered plant species randomly, as reflected by clipped biomass sampled at the scale of the sample plot. However, plant encounters are behaviourally mediated by small-scale patch distribution and patch departure time (Jiang and Hudson, 1993; Wilmshurst et al., 2000; Searle et al., 2005, 2006). For example, in contrast to the decline in dietary DE we report after 1–2 years (Fig. 6a), Cook et al. (2016, see also Ulappa, 2015) found that during foraging trials with tractable elk in western Washington and Oregon, relatively high dietary DE could be maintained across ES stands, and foraging elk in herbicide treated stands up to 15 years were able to acquire diets that generally satisfied or modestly exceeded dietary DE requirements of 2.7 kcal/g of food; these are dietary levels roughly 0.2–0.4 kcal/g higher than we report here.

Such dietary improvements due to fine-scale selective foraging could have significant impact on animal performance (Cook et al., 2004), which points to the difficulties in indirectly assessing nutritional adequacy of plant communities based on plant availability.

At Mount St. Helens, elk populations since the 1980 eruption have been relatively high (Merrill, 1987; Washington Department of Fish and Wildlife, 2006) and herbivory, in addition to herbicides, on industrial timberlands also may have influenced the forage resources available to elk by altering the relative abundance of accepted/avoided species and changing dietary DE. Reductions in ungulate density may not translate into a proportional recovery of highly palatable shrubs (Hobbs, 1996; Nugent et al., 2001) because they are the first to be consumed. Thus, large reductions in the elk population would likely be necessary to eliminate the impact, which may not be consistent with management objectives or may lack public support. Further, reductions in herbivory to levels that effectively increase the height of shrubs may be undesirable from a forestry perspective if tall shrubs hinder growth of young conifers (Donato et al., 2012; Ristau et al., 2011). Browsing by ungulates also can alter the competitive advantages of tall shrubs for light, nutrients and moisture, which may promote understory species that are important to ungulates (Hanley and Taber, 1980; Merrill, 1994; Riggs et al., 2000). For example, we documented an increase in grasses, which are key forages for elk during winter and spring in the Pacific Northwest (Leslie et al., 1984; Merrill et al., 1995), associated either directly or indirectly to herbivory. Increased graminoids also have the potential to retard tree growth and prolong the window of high forage availability (Riggs et al., 2000), but we found no evidence for such an effect.

Private timberland managers in the PNW are mandated by law (i.e., Oregon Forest Practices Act) to successfully re-establish healthy and thriving forests soon after clearcut logging, and herbicides are a key tool to satisfy this requirement. However, where providing high quality nutritional resources for ungulates is a joint objective with intensive forestry, options may exist to diminish the initial loss of forage abundance, and increase the duration of the ES window of abundant, high quality forage without unduly reducing growth of conifer seedlings. Modest changes in herbicide mixes and application rates to lessen the initial reduction of forage or to lessen the impacts to preferred forage classes (deciduous shrubs and palatable forbs) may moderate the negative effects of herbicides that occur in the first two years after application. For example, application of the first herbicide treatment to reduce residual vegetation may, in some cases, be sufficient to achieve objectives for growth of young conifers, and the decision for a subsequent herbicide treatment could be predicated on the level of development of competing vegetation. Where herbivory does not sufficiently suppress shrub species, using herbicides to "top-kill" tall shrubs ∼ 5 years after planting conifer seedlings may sufficiently allow conifer saplings to develop without incurring strong reductions in forage growing within reach of foraging herbivores (Lautenschlager and Sullivan, 2002). Other recommendations to improve resources for ungulates include planting a lower density of conifer seedlings, pre-commercial thinning with appropriate slash management, and commercial thinning (Raedeke and Lemkuhl, 1984). However, although Cook et al. (2016) found that commercial thinning to 65% canopy closure increased abundance of accepted species, they also found that without a commensurate decline in ferns and evergreen shrubs, this translated into little change in dietary DE, and in most cases still did not achieve required levels of DE or DE intake rates. If these responses are consistent across ecotypes in the Pacific Northwest, judicious use of herbicides contingent on vegetation response combined with commercial thinning might offer better foraging options than thinning without herbicides. Additional, long-term research in quantifying vegetation response is needed to verify the value and consistency of such recommendations across sites to balance timber production and management of wildlife (Betts et al., 2013).

5. Conclusions

Early seral stands of the western hemlock ecotype appear to provide marginal but important resources in terms of dietary DE for lactating female elk to accrue body fat levels for subsequent reproduction and to support calf growth. Operational herbicides initially may exacerbate these conditions due to the 1–2-year delay in establishment and growth of forage, but do not additionally shorten the window of available nutritional resources for elk. In contrast, there exists a mandate to re-establish productive forests soon after clearcutting such that timber companies must plant high densities of conifers seedlings that, through breeding programs, have been selected for traits to enhance growth rates (Johnson et al., 1997; Silen and Wheat, 1979; Ye and Jayawickrama, 2012). This mandate has led to harvest rotations on private industrial lands as short as ∼40 yrs. Based on simulations of forage dynamics, short-rotations are expected to provide a potentially higher forage base over time that is temporally more stable over the long-term (Hett et al., 1978; Visscher and Merrill, 2009). How the temporal patterns of succession and conifer establishment on industrial forest lands compare to those after wildfires is unclear, given that time to re-establishment may not be as short as originally thought (Freund et al., 2014; Poage et al., 2009; Tepley et al., 2014). Nevertheless, we suggest that effects of herbicides on highly palatable species was short-term and did not strongly truncate ES stages, and conclude that wide-spread declines in the rate of timber harvest (Jenkins and Starkey, 1996) may exert a greater effect on the nutritional adequacy of Pacific Northwest landscapes for elk than operational use of herbicides at stand initiation. At low elevations immediately adjacent to the Mount St. Helens blast zone, large areas of even-aged, closed canopy forests are now approaching the end of their harvest rotation 37 years after the eruption. The legacy of this large-scale homogenizing disturbance poses a particularly challenging problem for wildlife managers in this area to offset the boom-bust nature of the forest succession pattern that now is inherent in this area (Merrill and Raedeke, 1987).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.06.028.

References

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.

Alaback, P.B., 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63, 1932–1948.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. 62, 1165–1183.

Baker, D.L., Hobbs, N.T., 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can. J. Zool. 65, 1978–1984.

Betts, M.G., Verschuyl, J., Giovanini, J., Stokely, T., Kroll, A.J., 2013. Initial experimental effects of intensive forest management on avian abundance. For. Ecol. Manage. 310, 1036–1044.

Blake, P.M., Hurst, G.A., Terry, T.A., 1987. Responses of vegetation and deer forage following application of hexazinone. Southern J. Appl. Forest. 11, 176–180.

Boldor, M.I., 2007. A field and simulation study of the initiation phase in Douglas-fir plantations. Thesis. University of British Columbia, Vancouver, British Columbia.

Brodie, J.D., Walstad, J.D., 1987. Douglas-fir growth and yield response to vegetation management. In: Walstad, J.D., Kuch, P.J. (Eds.), Forest Vegetation Management for Conifer Production. Wiley, New York, pp. 273–294.

Bunnell, F.L., Vales, D.J., 1990. Comparison of methods for estimating forest overstory cover – differences among techniques. Can. J. For. Res. 20, 101–107.

Canon, S.K., Urness, P.J., DeByle, N.V., 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. J. Range Manage. 40, 433–438.

Clark, L.A., Roloff, G.J., Tatum, V.L., Irwin, L.L., 2009. Forest herbicide effects on Pacific Northwest ecosystems: a literature review. National Council for Air and Stream Improvement, Technical Bulletin No. 970. Research Triangle Park, North Carolina, 63 pp. plus Appendices.

Collins, W.B., Urness, P.J., 1983. Feeding-behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47, 646–663.

Cook, J.G., Stutzman, T.W., Bowers, C.W., Brenner, K.A., Irwin, L.L., 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildllife Soc. Bull. 23, 711–717.

Cook, J.G., Quinlan, L.J., Irwin, L.L., Bryant, L.D., Riggs, R.A., Thomas, J.W., 1996. Nutrition-growth relations of elk calves during late summer and fall. J. Wildl. Manage. 60, 528–541.

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D., Irwin, L.L., 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildl. Monogr. 155, 61.

Cook, R.C., Cook, J.G., Vales, D.J., Johnson, B.K., McCorquodale, S.M., Shipley, L.A., Riggs, R.A., Irwin, L.L., Murphie, S.L., Murphie, B.L., Schoenecker, K.A., Geyer, F., Hall, P.B., Spencer, R.D., Immell, D.A., Jackson, D.H., Tiller, B.L., Miller, P.J., Schmitz, L., 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildl. Monogr. 184, 46.

Cook, J.G., Cook, R.C., Davis, R.W., Irwin, L.L., 2016. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. Wildl. Monogr. 195, 81.

Cote, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147.

Damiran, D., DelCurto, T., Bohnert, D.W., Pulsipher, G.D., Findholt, S., 2002. Comparison of techniques and grinding size to estimate digestibility of forage based ruminant diets. Proceedings, Western Section, American Society of Animal Science, vol. 53, pp. 41–344.

Davis, R.W., Bender, L.C., Mausel, P.W., Chapa-Vargas, L., Warner, R.E., 2010. Modeling post-eruption habitat changes for deer at Mount St. Helens using remote sensing and GIS. In: Patterson, M.W., Hoalst-Pullen, N. (Eds.), Geospatial Technologies in Environmental Management. Springer, Netherlands, pp. 11–28.

Dinger, E.J., 2007. Evaluating the effectiveness of commonly used herbaceous weed control regimes in a Pacific Northwest conifer plantation. Thesis. Oregon State University, Corvallis, Oregon.

Donato, D.C., Campbell, J.L., Franklin, J.F., 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? J. Veg. Sci. 23, 576–584.

Edwards, S.L., Demarais, S., Watkins, B., Strickland, B.K., 2004. White-tailed deer forage production in managed and unmanaged pine stands and summer food plots in Mississippi. Wildl. Soc. Bull. 32, 739–745.

Franklin, J.F., Dyrness, C.T., 1988. Natural Vegetation of Oregon and Washington. Oregon State Press, Corvallis, Oregon. 550 pp..

Franklin, J.F., Spies, T.A., 1991. Composition, function, and structure of old-growth Douglas-fir forests. In: Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. General Technical Report, PNW-285. U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, 110 pp.

Freedman, B., Morash, R., MacKinnon, D., 1993. Short-term changes in vegetation after the silvicultural spraying of glyphosate herbicide onto regenerating clearcuts in Nova Scotia, Canada. Can. J. For. Res. 23, 2300–2311.

Freund, J.A., Franklin, J.F., Larson, A.J., Lutz, J.A., 2014. Multi-decadal establishment for single-cohort Douglas-fir forests. Can. J. Forest Res. 44, 1068–1078.

Geary, A.B., 2014. Succession, herbicides, forage nutrition and elk body condition at Mount St. Helens, Washington. Thesis. University of Alberta, Edmonton, Alberta.

Hanley, T.A., McKendrick, J.D., 1983. Seasonal changes in chemical composition and nutritive value of native forages in a spruce-hemlock forest, southeastern Alaska. General Technical Report PNW-312. U.S. Department of Agriculture,

Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 41 pp.

Hanley, T.A., 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. J. Appl. Ecol. 21, 423–436.

Hanley, T.A., Taber, R.D., 1980. Selective plant species inhibition by elk and deer in three conifer communities in western Washington. Forest Sci. 26, 97–107.

Harper, J.A., 1971. Ecology of Roosevelt elk. Oregon State Game Commission, Portland, Oregon. 44 pp..

Harper, J.A., 1987. Ecology and management of Roosevelt elk in Oregon. Oregon Department of Fish and Wildlife, Portland, Oregon. 70 pp..

Harrington, T.B., Wagner, R.G., Radosevich, S.R., Walstad, J.D., 1995. Interspecific competition and herbicide injury influence 10-year responses of coastal Douglas-fir and associated vegetation to release treatments. For. Ecol. Manage. 76, 55–67.

Hett, J., Taber, R., Long, J., Schoen, J., 1978. Forest management policies and elk summer carrying capacity in the Abies amabilis forest, western Washington. Environ. Manage. 2, 561–566.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60, 695–713.

Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118.

Hutchins, N.R., 2006. Diet, nutrition, and reproductive success of Roosevelt elk in managed forests of the Olympic Peninsula, Washington. Thesis. Humboldt State University, Arcata, California.

Irwin, L.L., Peek, J.M., 1983. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47, 664–672.

Irwin, L.L., Cook, J.G., Riggs, R.A., Skovlin, J.M., 1994. Effects of long-term use by big game and livestock in the Blue Mountains forest ecosystems. In: Hessburg, P.F. (Eds.), Eastside Forest Ecosystem Health Assessment, Vol III, Assessment, General Technical Report PNW-325. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon,. 49 pp.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding Fishes. Yale University Press, New Haven. 302 pp..

Jenkins, K., Starkey, E., 1996. Simulating secondary succession of elk forage values in a managed forest landscape, western Washington. Environ. Manage. 20, 715–724.

Jiang, Z., Hudson, R.J., 1993. Optimal grazing of wapiti (Cervus elaphus) on grassland: patch and feeding station departure rules. Evol. Ecol. 7, 488–498.

Johnson, G.R., Sniezko, R.A., Mandel, N.L., 1997. Age trends in Douglas-fir genetic parameters and implications for optimum selection age. Silvae Genet. 46, 349–358.

Karakatsoulis, J., Kimmins, J.P., 1993. Vegetation development and Douglas-fir growth following clearcut harvesting in the CWHdm subzone: 10-year results from the Blaney chronosequence. Land Management Report, Ministry of Forests. Research Branch, Victoria, B.C., 81, vi, 23.

Kirchhoff, M.D., Larsen, D.N., 1998. Dietary overlap between native Sitka black-tailed deer and introduced elk in southeast Alaska. J. Wildl. Manage. 62, 236–242.

Lautenschlager, R.A., Sullivan, T.P., 2002. Effects of herbicide treatments on biotic components in regenerating northern forests. Forest. Chron. 78, 695–731.

Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J. Anim. Ecol. 82, 1183–1191.

Leslie, D.M., Starkey, E.E., Vavra, M., 1984. Elk and deer diets in old-growth forests in western Washington. J. Wildl. Manage. 48, 762–775.

Maguire, D.A., Mainwaring, D.B., Rose, R., Garber, S.M., Dinger, E.J., 2009. Response of coastal Douglas-fir and competing vegetation to repeated and delayed weed control treatments during early plantation development. Can. J. For. Res. 39, 1208–1219.

McCorquodale, S.M., Miller, P.J., Bergh, S.M., Holman, E.W., 2014. Mount St. Helens elk population assessment: 2009–2013. Washington Department of Fish and Wildlife, Olympia, Washington. 111 pp.

Merrill, E.H., 1987. Population dynamics and habitat ecology of elk in the Mount St. Helens blast zone. Thesis. University of Washington, Seattle, Washington.

Merrill, E.H., Raedeke, K.J., 1987. Elk harvest strategies in relation to forest succession in the Mt. St. Helens blast zone. In: Proceedings of the Western States and Provinces Elk Workshop, Wenatchee, Washington. pp 198–202.

Merrill, E.H., 1994. Summer foraging ecology of wapiti (Cervus elaphus roosevelti) in the Mount St. Helens blast zone. Can. J. Zool. 72, 303–311.

Merrill, E.H., Callahan-Olson, A., Raedeke, K.J., Taber, R.D., Anderson, R.J., 1995. Elk (Cervus-elaphus roosevelti) dietary-composition and quality in the Mount St. Helens blast zone. Northwest Sci. 69, 9–18.

Merrill, E.H., Beyer, H.L., Jones, G.P., McDaniel, G.W., 2003. Deciduous woodland conservation under heavy deer browsing on Devils Tower National Monument, USA. J. Nat. Conserv. 10, 221–232.

Messier, C., Kimmins, J., 1990. Nutritional stress in Picea sitchensis plantations in coastal British Columbia: the effects of Gaultheria shallon and declining site fertility. Water Air Soil Pollut. 54, 257–267.

Miller, J.H., Zutter, B.R., Zedaker, S.M., Edwards, M.B., Newbold, R.A., 1995. Early plant succession in loblolly pine plantations as affected by vegetation management. Southern J. Appl. Forest. 19, 109–126.

Noyes, J.H., Johnson, B.K., Dick, B.L., Kie, J.G., 2002. Effects of male age and female nutritional condition on elk reproduction. J. Wildl. Manage. 66, 1301–1307.

Nugent, G., Fraser, W., Sweetapple, P., 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial'ruminants on native forests in New Zealand. Biol. Cons. 99, 65–79.

Olsen-Rutz, K.M., Urness, P.J. 1987. Comparability of foraging behavior and diet selection of tractable and wild mule deer. Utah Department of Natural Resources, Publication No. 88-3. Salt Lake City, Utah.

Oregon Department of Fish and Wildlife, 2008. Oregon Black-Tailed Deer Management Plan. Oregon Department of Fish and Wildlife, Salem, Oregon. 61 pp..

Perez-Garcia, J., Barr, J.K., 2005. Forest products export trends update for the Pacific Northwest region. Northwest Environmental Forum, College of Forest Resources, University of Washington, Seattle, Washington, 14 pp.

Peter, D.H., Harrington, C., 2009. Six years of plant community development after clearcut harvesting in western Washington. Can. J. For. Res. 39, 308–319.

Poage, N.J., Weisberg, P.J., Impara, P.C., Tappeiner, J.C., Sensenig, T.S., 2009. Influences of climate, fire, and topography on contemporary age structure patterns of Douglas-fir at 205 old forest sites in western Oregon. Can. J. Forest Res. 39, 1518–1530.

Raedeke, K.J., Lemkuhl, J., 1984. Elk populations of Mount Rainier National Park: Status of range outside of the park. Final Report, National Park Service, Cooperative Park Studies Unit, College of Forest Resources, University of Washington, Seattle, Washington, 69 pp.

Raedeke, K.J., Merrill, E.H., McCorquodale, S.M., 1986. Estimates of intrinsic rates of increase from three Washington elk herds. In: Proceedings of the Western States and Provinces Elk Workshop. Coos Bay, Oregon, pp. 69–72.

Rhodes, B.D., Sharrow, S.H., 1990. Effect of grazing by sheep on the quantity and quality of forage available to big game in Oregon's coast range. J. Range Manag. 43, 235–237.

Riggs, R.A., Tiedemann, A.R., Cook, J.G., Ballard, T.M., Edgerton, P.J., Vavra, M., Krueger, W.C., Hall, F.C., Bryant, L.D., Irwin, L.L., Delcurto, T., 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. Research Patent PNW-RP-527. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, 77 pp.

Ristau, T.E., Stoleson, S.H., Horsley, S.B., deCalesta, D.S., 2011. Ten-year response of the herbaceous layer to an operational herbicide-shelterwood treatment in a northern hardwood forest. For. Ecol. Manage. 262, 970–979.

Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L., Schwartz, C.C., Mautz, W.W., 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68, 98–107.

Robbins, C.T., Mole, S., Hagerman, A.E., Hanley, T.A., 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion. Ecology 68, 1606–1615.

Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Sci. 34, 960–979.

Schreiner, E.G., Krueger, K.A., Happe, P.J., Houston, D.B., 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Can. J. For. Res. 26, 255–265.

Searle, K.R., Hobbs, N.T., Shipley, L.A., 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. Oikos 111, 417–424.

Searle, K.R., Vandervelde, T., Hobbs, N.T., Shipley, L.A., Wunder, B.A., 2006. Spatial context influences patch residence time in foraging hierarchies. Oecologia 148, 710–719.

Silen, R.R., Wheat, J.G., 1979. Progressive tree improvement program in coastal Douglas-fir. J. Forest. 77, 78–83.

Spalinger, D.E., Cooper, S.M., Martin, D.J., Shipley, L.A., 1997. Is social learning an important influence on foraging behavior in white-tailed deer? J. Wildl. Manage. 61, 611–621.

Spalinger, D.E., Robbins, C.T., Hanley, T.A., 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. Can. J. Zool. 64, 312–321.

Sparkes, S.N.M., 2016. Forest succession and nutritional carrying capacity of elk since the 1980 Eruption of Mount St. Helens. Thesis. University of Alberta, Edmonton, Alberta.

Stein, W.I., 1995. Ten-year development of Douglas-fir and associated vegetation after different site preparation on coast range clearcuts. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Paper PNW-RP-473. Portland, Oregon. 115 pp.

Stein, W.I., 1999. Six-year growth of Douglas-fir saplings after manual or herbicide release from coastal shrub competition. U.S. Forest Service, Pacific Northwest Research Station, PNW-RP-500. Portland, Oregon. 55 pp.

Stokely, T., 2014. Interactive effects of of silvicultural herbicides and Cervid herbivory on early seral plant communities of the northern Oregon coast range. Thesis. Oregon State Univerity, Corvallis, Oregon.

Strauss, S.Y., Agrawal, A.A., 1999. The ecology and evolution of plant tolerance to herbivory. Trends Ecol. Evol. 14, 179–185.

Strong, W., Gates, C., 2006. Herbicide-induced changes to ungulate forage habitat in western Alberta, Canada. For. Ecol. Manage. 222, 469–475.

Stussy, R.J., 1993. The effects of forage improvement practices on Roosevelt elk in the Oregon coast range. Thesis. Oregon State University, Corvallis, Oregon.

Tepley, A.J., Swanson, F.J., Spies, T.A., 2014. Post-fire tree establishment and early cohort development in conifer forests of the western Cascades of Oregon, USA. Ecosphere 5, 80.

Tilley, J., Terry, R., 1963. A two-stage technique for the in vitro digestion of forage crops. Grass Forage Sci. 18, 104–111.

Trainer, C.E., 1971. The relationship of physical condition and fertility of female Roosevelt elk (*Cervus canadensis roosevelti*) in Oregon. Thesis. Oregon State University, Corvallis, Oregon.

Ulappa, A.C., 2015. Using foraging dynamics to answer landscape management questions: the nutritional ecology of black-tailed deer. Thesis. Washtington State University, Pullman, Washington.

Visscher, D., Merrill, E.H., 2009. Temporal dynamics of forage succession for elk at two scales: implications of forest management. For. Ecol. Manage. 257, 96–106.

Wagner, R.G., Newton, M., Cole, E.C., Miller, J.H., Shiver, B.D., 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. Wildl. Soc. Bull. 32, 1028–1041.

Washington Department of Fish and Wildlife, 2006. Mount St. Helens elk herd plan. Wildlife Management Program, Washington Department of Fish and Wildlife, Olympia, Washington. 52 pp.

Washington Department of Natural Resources, 2012. Washington State Timber Harvest Summary. Washington Department of Natural Resources, Olympia, Washington. 35 pp..

Weisberg, P.J., Swanson, F.J., 2003. Regional synchroneity in fire regimes of western Oregon and Washington, USA. For. Ecol. Manage. 172, 17–28.

Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spalinger, D.E., Parish, S.M., 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48, 1285–1301.

Wilmshurst, J.F., Fryxell, J.M., Bergman, C.M., 2000. The allometry of patch selection in ruminants. Proc. R. Soc. Lond. B 267, 345–349.

Witmer, G., Wisdom, M., Harshman, E., Anderson, R., Carey, C., Kuttel, M., Luman, I., Rochelle, J., Scharpf, R., Smithey, D., 1985. Deer and elk. In: Brown, E.R. (Eds.), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington, Part 1. USDA Forest Service Publication no. R6-F&WL-192-1985, Portland, Oregon, pp. 231–258.

Woodward, A., Schreiner, E.G., Houston, D.B., Moorhead, B.B., 1994. Ungulate-forest relationships in Olympic National Park – retrospective exclosure studies. Northwest Sci. 68, 97–110.

Yarrow, K.G., 1979. Comparison of tame and wild deer food habits. Thesis. Mississippi State University, Starkville, Mississippi.

Ye, T., Jayawickrama, K., 2012. Early selection for improving volume growth in coastal Douglas-fir breeding programs. Silvae Genet. 61, 186–198.