

## Influence of repeated fertilization on forage production for native mammalian herbivores in young lodgepole pine forests

Pontus M.F. Lindgren<sup>a</sup>, Thomas P. Sullivan<sup>b,\*</sup>

<sup>a</sup> Applied Mammal Research Institute, 11010 Mitchell Ave., Summerland, British Columbia V0H 1Z8, Canada

<sup>b</sup> Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada



### ARTICLE INFO

#### Keywords:

Fertilization  
Forage plants  
Herbs and shrubs  
Lodgepole pine forest  
Mammalian herbivores  
Native ungulates

### ABSTRACT

Stand thinning and fertilization are silvicultural practices designed to enhance wood and biomass production. Applications of nitrogen-based fertilizers make nutrients potentially available to all trees, plants, and wildlife in a given forest ecosystem, and therefore may affect productivity of forage plants for native mammalian herbivores. Species associated with areas of forest fertilization in temperate and boreal zones of North America include mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and woodland caribou (*Rangifer tarandus*), snowshoe hare (*Lepus americanus*), and several species of voles. Impacts of fertilization on forest plant species may have important consequences for the nutrition, cover, and consequent survival of these herbivores, particularly in winter. This study tested the hypothesis ( $H_1$ ) that large-scale repeated fertilization, up to 20 years after the onset of treatments, would enhance the biomass production of forage plants, particularly grass, forb, shrub and tree species for native mammalian herbivores. A secondary hypothesis ( $H_2$ ) predicted that mosses and terrestrial lichens would decline as part of the ground vegetation in fertilized stands. Study areas were located in lodgepole pine (*Pinus contorta* var. *latifolia*) stands near Summerland, Kelowna, and Williams Lake in south-central British Columbia, Canada. Each study area had eight replicate stands: four unfertilized, and four fertilized five times at 2-year intervals.

Mean biomass of total grasses responded dramatically starting in the first year after fertilization. Total forbs and herbs also followed this pattern, although not to a significant degree until after the second and third applications of fertilizer. All of the dominant grasses and forbs serve as summer forage for mule deer, moose, elk, and woodland caribou. Fireweed (*Epilobium angustifolium*), a preferred forage for mule deer, increased in fertilized stands. Grasses and dominant herbs in fertilized stands provide excellent forage and cover habitat for snowshoe hares and *Microtus* voles.

Mean biomass of total shrubs was not affected by fertilization. However, saskatoon berry (*Amelanchier alnifolia*), prickly rose (*Rosa acicularis*), and red raspberry (*Rubus idaeus*) increased significantly in biomass in fertilized stands. Willow (*Salix* spp.) also increased in biomass, but was variable across treatment stands. Snowshoe hares respond favourably to enhanced shrub growth for food and cover in fertilized stands. All of these shrubs are readily eaten by deer, moose, and elk, and their structural attributes provide security and thermal cover. Mean biomass of understory Douglas-fir (*Pseudotsuga menziesii*) responded positively to fertilization, but sub-alpine fir (*Abies lasiocarpa*) and the three deciduous tree species did not. Dwarf shrubs such as kinnikinnick (*Arctostaphylos uva-ursi*), twinflower (*Linnaea borealis*), and dwarf blueberry (*Vaccinium caespitosum*) declined in fertilized stands. Thus,  $H_1$  was partially supported for some species. Increasing cover of grasses and nitrophilous herbs, and canopy cover from rapidly growing crop trees, in fertilized stands may have contributed to the decline of some dwarf shrubs. Mean crown volume index of total mosses and terrestrial lichens declined significantly in fertilized stands, thereby supporting  $H_2$ .

Mean biomass of total grasses (increase), *R. acicularis* (increase), and *V. caespitosum* (decline) were significantly affected after one application of fertilizer. Repeated applications of fertilizer may enhance biomass of some additional forage forbs and shrubs, but reduce biomass of some dwarf shrubs, mosses, and lichens.

\* Corresponding author.

E-mail address: [tom.sullivan@ubc.ca](mailto:tom.sullivan@ubc.ca) (T.P. Sullivan).

## 1. Introduction

Stand thinning and fertilization are silvicultural practices designed to sustain wood and biomass production on a shrinking forest landbase while concurrently creating a diversity of forest habitat conditions to meet the goals of biodiversity conservation (Moore and Allen, 1999; Hartley, 2002; Monkkonen et al., 2014). In particular, nitrogen fertilization is a major way to improve the future timber supply and potentially mitigate impacts on other values from the loss of forests (Fox et al., 2007; Sullivan et al., 2013). Addition of nutrients reduces the time required for target stands to reach a harvestable size, and thus increase supplies of wood fibre (Albaugh et al., 2004; Jokela et al., 2004). In addition, fertilization increases the size of individual trees without sacrificing stand volume, and hence may be particularly useful for addressing age-class imbalances and for increasing long-term harvest levels (Brockley, 2005; Lindgren and Sullivan, 2013a). Fertilization and thinning have increased biomass production in second-growth forests across northern Europe (Nabuurs et al., 2007; Bergh et al., 2008), the southeastern United States (USA) (Albaugh et al., 2004; Fox et al., 2007), and coastal and interior forests of British Columbia (BC) (Weetman et al., 1992; Brockley, 2007a; Lindgren and Sullivan, 2013a), and other parts of North America (Demarais et al., 2017).

Aerial and land-based applications of nitrogen-based fertilizers to enhance forest growth makes nutrients potentially available to all trees, plants, and wildlife in a given ecosystem, and therefore may have direct and indirect effects on wildlife and biodiversity (see review by Sullivan and Sullivan, 2017a). Native species of mammalian herbivores include mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and woodland caribou (*Rangifer tarandus*) which are often located in, or near, areas of forest fertilization. Another major mammalian herbivore, the snowshoe hare (*Lepus americanus*), is widespread in boreal, sub-boreal, and western montane forests of North America. This leporid is a major prey species for a wide variety of carnivores and birds of prey and is a keystone species in these forest ecosystems (Boutin et al., 1995; Boutin et al., 2003). Similarly, another group of forest mammals that are ubiquitous and also forage on various vascular and non-vascular plants include the meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*M. longicaudus*), heather vole (*Phenacomys intermedius*), and southern red-backed vole (*Myodes gapperi*). All of these mammals rely on a wide range of herbaceous (summer range) and tree-shrub (winter range) plant species as their major forage and cover resources.

Mule deer and elk forage on a wide variety of grasses and forbs during summer months (Kufeld et al., 1973; Cook, 2002). In areas of relatively high snowpacks, mule deer seem to require mature and old-growth forest stands with high levels of canopy closure for snow interception during winter months (Armleder et al., 1994). These old forests have characteristics that intercept snow and supply forage via herbs, shrubs, arboreal lichen, and Douglas fir (*Pseudotsuga menziesii*) litterfall (Dawson et al., 1990; Nyberg, 1990). Shrub forage species include trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), willows (*Salix* spp.), saskatoon berry (*Amelanchier alnifolia*), and high-bush cranberry (*Viburnum edule*) (Hodder et al., 2013). Moose follow a similar forage selection pattern in summer with the addition of sedges from riparian areas. In winter, moose may also utilize mature and old-growth forests for snow interception cover (Balsom et al., 1996), and they prefer similar trees and shrubs as mule deer, including subalpine fir (*Abies lasiocarpa*), black cottonwood (*Populus trichocarpa*), alder (*Alnus* spp.), and rose (*Rosa* spp.) (Pierce, 1984; Hodder et al., 2013). Woodland caribou forage on a variety of herbs similar to the other ungulates, as well as terrestrial and arboreal lichens in summer, and shrubs and arboreal lichens in winter (Thomas et al., 1994).

Snowshoe hares occupy dense stands of conifers, or deciduous tree species, which provide the necessary food and cover (Koehler, 1990; Mowat and Slough, 2003). Hares also need early seral vegetation to feed on a variety of grasses, sedges, and forbs in summer (Koehler and

Brittill, 1990; Hodges, 2000). Trembling aspen, paper birch, willows, alders, maples, and *Vaccinium* spp., as well as conifers such as Douglas-fir, pines, and spruces are eaten in winter (Nagorsen, 2005).

*Microtus* voles occupy early successional (herb and shrub stages) forest habitats after disturbance and also naturally occurring meadows and riparian areas. They readily consume most available species of grasses, sedges, and herbaceous plants, as well as the bark and cambium of shrubs and trees in winter (Reich, 1981; Smolen and Keller, 1987). The heather vole occupies these same habitats, as well as upland coniferous and mixed forests. Food habits of heather voles include foliage and fruits of willow, kinnikinnick (*Arctostaphylos uva-ursi*), *Vaccinium* spp., soapberry (*Shepherdia canadensis*), and *Rosa* spp. (McAllister and Hoffman, 1988). The red-backed vole commonly inhabits late successional coniferous and deciduous forests across temperate and boreal North America. This vole feeds on vegetative parts of plants, nuts, seeds, berries, mosses, lichens, ferns, and fungi as well as roots and bark of deciduous trees (Merritt, 1981).

Impacts of fertilization on forest vascular plant species may have important consequences for the nutrition and survival of herbivores, particularly in winter. As reviewed by Sullivan and Sullivan (2017a), the majority of responses of understory herbs to nitrogen fertilization showed an increase in abundance, whereas some shrubs in repeatedly fertilized stands eventually increased in abundance in long-term studies. However, abundance of dwarf shrubs declined (Turkington et al., 1998; Lindgren and Sullivan, 2013b), as did the non-vascular bryophytes and terrestrial lichens in fertilized stands. In the few studies that have been conducted with mammalian herbivores, relative abundance of mule deer, moose, hares, voles and the quantity and quality of vascular plant forage were usually increased by forest fertilization (Edenius, 1993; Nams et al., 1996; Ball et al., 2000; Sinclair et al., 2001; Sullivan et al., 2006a; Sullivan et al., 2006b; Månsson et al., 2009; Sullivan and Sullivan, 2014).

Although these results suggest that fertilized vegetation may be beneficial for mammalian herbivores, a detailed examination of the biomass response of individual species of forage plants to consecutive nutrient additions, designed to enhance timber growth and yield, has not been done. Thus, this study tested the hypothesis (H<sub>1</sub>) that large-scale repeated fertilization, up to 20 years after the onset of treatments, would enhance the biomass production of forage plants, particularly grass, forb, shrub, and tree species for native mammalian herbivores. A secondary hypothesis (H<sub>2</sub>) predicted that the non-vascular mosses and terrestrial lichens, as part of the ground-layer vegetation, would decline in fertilized stands in response to enhanced biomass of herb and shrub layers. This paper is one of several periodic publications reporting on long-term responses of tree and stand growth (Lindgren et al., 2007; Lindgren and Sullivan, 2013a, Sullivan and Sullivan, 2017b), mammals (Sullivan et al., 2012), cattle and range management (Lindgren and Sullivan, 2014a,b; Lindgren et al., 2017), and biodiversity (Sullivan et al., 2009) to fertilization. The current paper reports specifically on biomass production (quantity) of forage plant species, on an annual basis, and its relationship to native mammalian herbivores in these experimental stands.

## 2. Methods

### 2.1. Study areas

Three study areas (Summerland, Kelowna, and Cariboo) were located in southern British Columbia (BC), Canada, where candidate stands of young (12–14 year old) lodgepole pine (*Pinus contorta* var. *latifolia*) had relatively uniform tree cover, comparable diameter, height, and density of trees prior to stand treatments. Location, proximity (boundaries), and size of candidate stands were determined by a balance between adequate interspersions of experimental units (Hurlbert, 1984) and the logistics and access for conducting the operational-scale treatments of pre-commercial thinning (PCT) and

fertilization. The Summerland study area was located in the Bald Range 25 km west of Summerland in south-central BC (49°40'N; 119°53'W) within the Montane Spruce (MS<sub>dm</sub>) biogeoclimatic zone (Meidinger and Pojar, 1991) at an elevation range of 1450–1520 m with gently rolling topography and sandy loam soil. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7 °C and precipitation ranges from 380 to 900 mm. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea engelmannii* × *Picea glauca*) and subalpine fir are the dominant shade-tolerant trees. Douglas-fir is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen is a common seral species with paper birch and black cottonwood occurring on some moist sites. Clearcut harvesting of lodgepole pine with natural regeneration of pine began in this area in 1978.

The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04'N; 119°34'W) in the MS<sub>dm</sub> biogeoclimatic subzone (Meidinger and Pojar, 1991). Topography of this area is also gently rolling to flat with sandy loam soil at 1220–1240 m elevation. This area was also clearcut harvested in 1979–1980 and regenerated naturally to lodgepole pine with the other coniferous species, including western larch (*Larix occidentalis*), as minor components.

The Cariboo study area was located in the Alex Fraser Research Forest (University of British Columbia), 75 km northeast of Williams Lake, BC (52°29'N; 121°45'W) in the Sub-Boreal Spruce (SBS<sub>dm</sub>) biogeoclimatic zone (Meidinger and Pojar, 1991). While this study area was located in a different zone than the two areas to the south, the MS and SBS zones have many similarities, including comparable mean winter and snow conditions. The general topography is gently rolling to flat at 850–870 m elevation. In mature stands, interior hybrid spruce, subalpine fir and some Douglas-fir are mixed with extensive stands of lodgepole pine. Area (ha) of stands ranged from 4.4 to 11.3 (Summerland), 9.5 to 12.6 (Kelowna), and 1.5 to 4.5 (Cariboo). All study areas had summer grazing by cattle (*Bos taurus*). Further details of study stands are given in Lindgren et al. (2007).

## 2.2. Experimental design

Initially, the three study areas acted as regional replicates. Each study area had four densities: 250 (very low), 500 (low), 1000 (medium), and 2000 (high) stems/ha with and without a repeated fertilization treatment. Treatments were assigned to stands in a randomized complete block design. Unfortunately, the Cariboo replicate was decimated by mountain pine beetle (MPB) (*Dendroctonus ponderosae*) in 2005, and hence was a part of this study for the first 10-year period (1993 to 2003) only. An outbreak of MPB in 2008, and a ground fire in 2009, resulted in partial disturbance of the Kelowna replicate, leaving small ( $\leq 0.50$  ha) “islands” of relatively undisturbed forest. These stands provided supplemental data for those datasets collected from the Summerland area in 2008 and 2013. The Summerland area was not affected by MPB and represented an undisturbed complete replicate block over the 20-year period (1993–2013). Thus, all three replicates were intact for the first 10 years of the project (1993–2003) which represented the “fertilization period” that is of most interest to measuring the response of forage species to nutrient additions.

## 2.3. Density and fertilization treatments

The initial treatment was PCT of pine in autumn of 1993. Fertilization treatments were designed as large-scale “optimum nutrition” applications initiated in November 1994 using a blended fertilizer formulated to provide 100 kg/ha N (100 N) (urea), 100 kg/ha Phosphorus (100P), 100 kg/ha Potassium (100 K), 50 kg/ha Sulfur (50 S), 25 kg/ha Magnesium (25 Mg), and 1.5 kg/ha Boron (1.5B). The objective was to maintain a foliar N level of 1.3% with foliar levels of all

**Table 1**

Results of a one-way ANOVA for biomass production of grasses, forbs, total herbs, total shrubs, total understory vegetation, total mosses, and total terrestrial lichens in replicate stands during the pre-treatment year 1993 ( $n = 12$ ) and post-treatment years of 2008 ( $n = 8$ ) and 2013 ( $n = 8$ ). Significant values are given in bold.

Plant group	Year					
	1993		2008		2013	
	$F_{1,22}$	<i>P</i>	$F_{1,14}$	<i>P</i>	$F_{1,14}$	<i>P</i>
Grasses	0.03	0.87	1.24	0.29	0.04	0.84
Forbs	0.03	0.86	1.53	0.24	1.59	0.23
Total herbs	0.00	1.00	1.90	0.19	0.60	0.45
Total shrubs	0.21	0.65	0.55	0.47	0.27	0.61
Total understory	0.04	0.85	0.59	0.46	0.96	0.34
Total mosses	0.98	0.33	0.55	0.47	0.61	0.45
Total terrestrial lichens	0.20	0.66	4.50	<b>0.05</b>	7.88	<b>0.01</b>

other nutrients in proportional balance. The blended product was applied by helicopter at a rate of 906 kg/ha to each of the four fertilized stands at Summerland and Kelowna. Fertilizer was applied manually to stands at the Cariboo area. Foliar sampling was conducted in the year after fertilization to monitor the nutrient status of the crop trees and develop appropriate multi-nutrient formulations for subsequent fertilizer applications. Treatments were repeated at two-year intervals for a total of five applications: fall 1994, spring 1997, fall 1998, fall 2000, and spring 2003. One hundred, 200, 150, 150, and 150 for a total of 750 kg N/ha were applied. Other nutrients (Phosphorus, Potassium, Sulfur, Magnesium, and Boron) were applied with Nitrogen as prescribed from the foliar analyses. Complete descriptions of fertilization treatments are provided in Lindgren et al. (2007). In commercial forests, a typical stand density after PCT would be 2000 stems/ha, followed by one fertilization treatment. Our experiment expanded the range of stand densities considerably (Sullivan et al., 2013), followed by an “optimum nutrition” regime of fertilization treatments (Brockley, 2005). Typical rotation times for intensively managed stands such as these would be 40–50 years.

## 2.4. Forage species in understory vegetation

Sampling of understory vegetation was designed to measure the effects of fertilization on individual plant species within herb, shrub, and tree layers. This was accomplished by transect sampling and provided estimates of abundance by species. A vegetation transect measured 5 m wide by 25 m long and was made up of five contiguous 5-m × 5-m plots. Each plot contained three sizes of nested sub-plots: a 5-m × 5-m subplot for sampling trees, a 3-m × 3-m sub-plot for sampling shrubs, and a 1-m × 1-m sub-plot for sampling herbs, mosses, and terrestrial lichens. All plants were subdivided into six height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and > 3.0 m. A given species (an individual plant or group of plants of that species) was described by a visual estimate of percent cover within the appropriate height class. Crown volume index ( $m^3/0.01$  ha) was then calculated for each plant species as the product of percent cover and its corresponding height (Stickney, 1985). This measure of abundance provided the volume of a cylindroid and represented the space occupied by the plant in the community. Three permanent vegetation transects were randomly established in each treatment stand. Sampling was conducted during the period of peak productivity (July–August), and was done annually in 1993 to 2003, 2008, and 2013. Plant species were identified in accordance with Hitchcock and Cronquist (1973), MacKinnon et al. (1992), and Parish et al. (1996). Grasses, mosses, and terrestrial lichens were not identified to species in the sampling procedure, but common species were noted for each group. Abundance of tree species was measured by counts of stems rather than by volume estimates in 2008 and 2013, and hence there were no tree biomass measurements in those years.

**Table 2**

Results of RM-ANOVA for biomass production (kg/ha) of grasses, forbs, total herbs, total shrubs, total understory vegetation, total mosses, and total terrestrial lichens in response to repeated fertilization during two “5-year fertilization periods”: 1994 to 1998 and 1999 to 2003. Fertilizer was applied at the end of the growing season in 1994, 1996, 1998, 2000, and 2002. *F*-values identified by \* were calculated using a Huynh-Feldt correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Significant values are given in bold.

Plant group	1994–1998						1999–2003					
	Treatment		Time		Treatment × time		Treatment		Time		Treatment × time	
	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>
Grasses	4.47	<b>0.05</b>	6.52*	< <b>0.01</b>	4.58*	<b>0.02</b>	5.02	<b>0.04</b>	5.51*	< <b>0.01</b>	1.61*	0.21
Forbs	2.68	0.12	4.02*	<b>0.05</b>	3.68*	0.06	5.27	<b>0.03</b>	4.23*	<b>0.02</b>	1.75*	0.18
Total herbs	3.92	0.06	4.25*	<b>0.04</b>	4.11*	<b>0.05</b>	5.78	<b>0.03</b>	6.57*	< <b>0.01</b>	2.00*	0.13
Total shrubs	0.05	0.83	14.16*	< <b>0.01</b>	0.71*	0.53	1.99	0.17	8.46*	< <b>0.01</b>	3.28*	0.06
Total herbs + shrubs	4.64	<b>0.04</b>	5.24*	<b>0.02</b>	4.13*	<b>0.04</b>	8.25	< <b>0.01</b>	5.48*	< <b>0.01</b>	1.30*	0.28
Total mosses	4.51	<b>0.05</b>	2.43*	0.06	5.25*	< <b>0.01</b>	12.38	< <b>0.01</b>	12.52*	< <b>0.01</b>	6.42*	< <b>0.01</b>
Total terrestrial lichens	7.15	<b>0.01</b>	6.92*	< <b>0.01</b>	0.25*	0.85	38.40	< <b>0.01</b>	2.77*	0.07	2.18*	0.12

### 2.5. Estimating biomass from crown volume index

Biomass is a more useable measurement than crown volume index for determining responses of plant forage production in fertilized versus unfertilized stands. Therefore, we developed regression equations to determine biomass from the estimates of crown volume index for the herb components and individual species of shrubs and trees. Clipping of grasses and forbs was conducted in unfertilized and fertilized stands (180 samples) at Summerland and Kelowna in mid-July 2007 and was designed to coincide with estimated peak forage productivity. There were strong and significant correlations between crown volume index and oven-dried biomass: a positive linear relationship for grasses ( $R^2 = 0.95$ ;  $F_{1,17} = 154.50$ ;  $P < 0.01$ ) and forbs ( $R^2 = 0.79$ ;  $F_{1,17} = 26.12$ ;  $P < 0.01$ ) (Lindgren and Sullivan, 2013b).

Clipping of nine shrub species was conducted in unfertilized and fertilized stands (235 samples) at Summerland in late July 2010 and was also designed to coincide with estimated peak forage productivity. For both herb and shrub samples, we focused on leaves and twigs to represent the likely important forage components for herbivores. There were strong and significant positive linear relationships for dwarf (< 0.25 m height) ( $R^2 = 0.46$ ;  $F_{1,95} = 84.16$ ;  $P < 0.01$ ), low-middle (0.25–2.0 m height) ( $R^2 = 0.77$ ;  $F_{1,98} = 331.92$ ;  $P < 0.01$ ), and tall (> 2.0 m height) shrubs ( $R^2 = 0.90$ ;  $F_{1,36} = 312.77$ ;  $P < 0.01$ ) (Lindgren and Sullivan, 2013b). Species-specific regression equations for seven of the nine dominant shrub species were calculated; these nine species represented > 95% of the total crown volume index of the shrub layer. Sample sizes for twinflower (*Linnaea borealis*) and *Salix* spp. were insufficient for regression analyses for these species. Stature-specific regression equations were used for all other shrub species depending on their dwarf, low-middle, or tall stature. Biomass estimates for understory tree species used the regression equation for tall shrubs since their growth forms were similar. Thus, there was a strong and consistent relationship between crown volume index (CVI) and direct measures of plant biomass, and hence CVI may be a good indicator of understory processes in forests. However, as noted by Suchar and Crookston (2010), reliable indicators of understory vegetation remain elusive. We did not have biomass conversion equations for mosses and terrestrial lichens, and hence used crown volume index as the parameter for these vegetative components.

### 2.6. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA) (IBM Corp., 2016) was conducted to determine the effect of fertilization on mean biomass of (a) grasses, forbs, and total herbs, (b) total shrubs, (c) total understory vegetation, (d) individual shrub and tree species known to be forage plants for mammalian herbivores, and (e) total mosses and total terrestrial lichens. A one-way ANOVA compared the

response variables in these stands prior to the start of treatments in 1993, and at 5 and 10 years after completion of these treatments in 2008 and 2013, respectively. Stand density had no effect on abundance of understory herbs and shrubs, nor was there any density × fertilization interactions (Lindgren and Sullivan, 2013b). Similar results were generated for total mosses and total terrestrial lichens, respectively (ANOVA; stand density:  $F_{4,8} = 0.37$ ;  $P = 0.83$  and  $F_{4,8} = 2.00$ ;  $P = 0.19$ ; density × fertilizer interaction:  $F_{3,8} = 0.29$ ;  $P = 0.83$  and  $F_{3,8} = 0.30$ ;  $P = 0.83$ ). Thus, all comparisons were focused on fertilized versus unfertilized stands.

Mean response variables were measured at two levels: (a) 1994–1998 (first 5-year fertilization period) and 1999–2003 (second 5-year fertilization period). Number of replicate stands for unfertilized and fertilized treatments for grasses, forbs, total herbs, total shrubs, total understory vegetation, total mosses, and total terrestrial lichens was  $n = 12$  (3 study areas × 4 replicate stands per area). Number of replicate stands for unfertilized and fertilized treatments for individual shrub and tree species was variable and depended on the presence of a given species in treatment stands. Where significant treatment effects were detected that also had significant treatment × time interactions during 5-year fertilization periods, additional one-way analyses were conducted within individual years.

Homogeneity of variances was assessed with Levene’s test of equality of error variances. Mauchly’s *W* test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh-Feldt correction was used to adjust the degrees of freedom of the within-subjects *F*-ratio (Huynh and Feldt, 1976). In all analyses, the level of significance was at least  $P = 0.05$  (Zar, 1999).

## 3. Results

### 3.1. Herbaceous species

In the initial analysis, measures of mean biomass (kg/ha) of herbaceous plant groups were similar ( $P > 0.05$ ) in the pre-treatment year (1993) (Table 1). Mean biomass of grasses was significantly ( $P \leq 0.05$ ) higher in fertilized than unfertilized stands during the two 5-year fertilization periods (Table 2; Fig. 1a). The significant ( $P = 0.02$ ) treatment × time interaction in the first period indicated that in each of the four fertilized years (1995–1998), biomasses of grasses were higher in the fertilized than unfertilized stands. On average, mean biomass (kg/ha) of grasses ranged from 172 to 186 in the unfertilized stands and 322 to 372 in the fertilized stands in the 10-year fertilization period. Mean biomass of forbs was similar between treatment stands in the first 5-year period, but significantly ( $P = 0.03$ ) higher in the fertilized than unfertilized stands in the second period (Table 2; Fig. 1b). On average, mean biomass of forbs (kg/ha) ranged from 126 to 133 in the



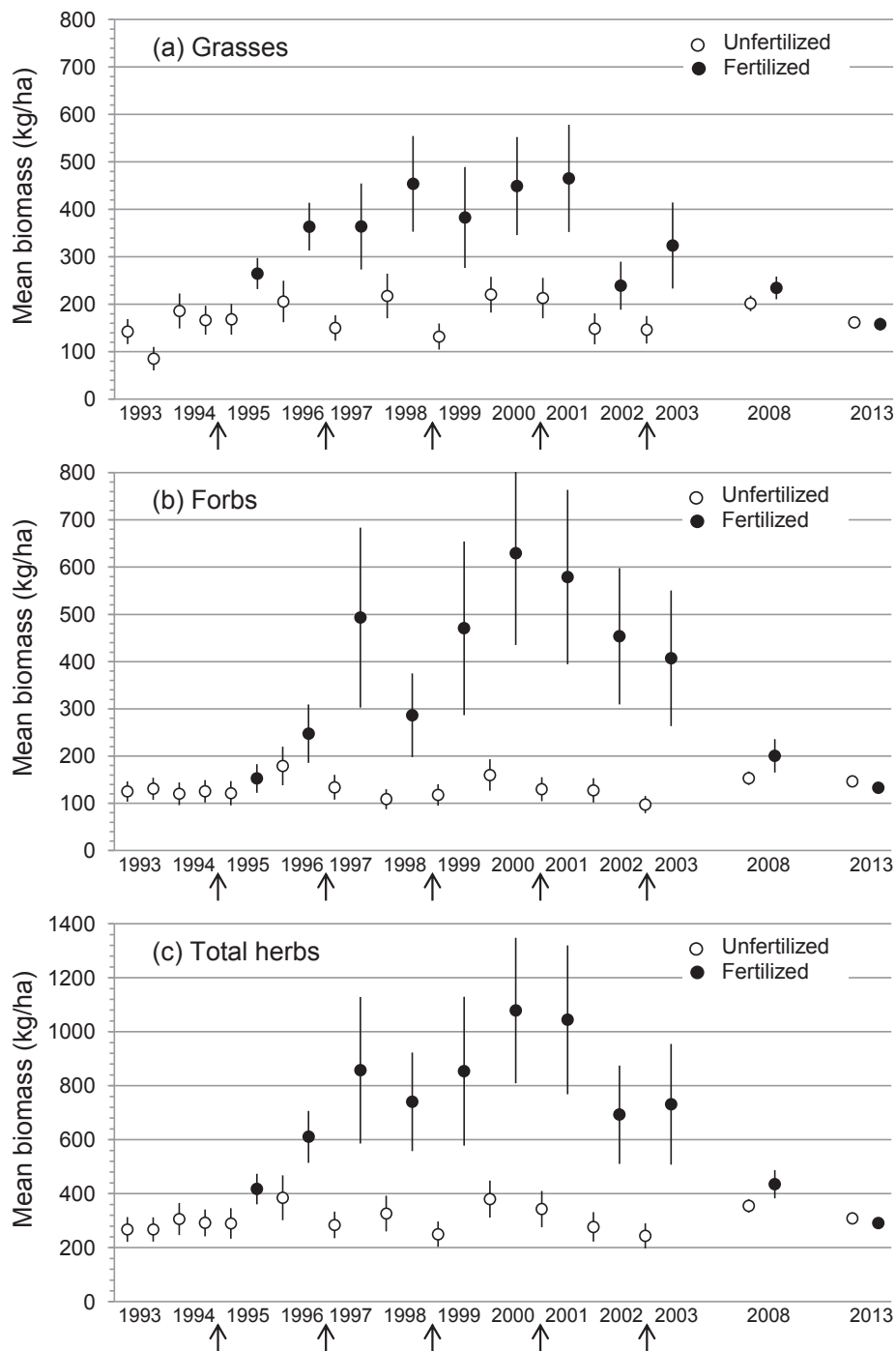


Fig. 1. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) grasses, (b) forbs, and (c) total herbs each year 1993–2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 12) and fertilized ( $n$  = 12) lodgepole pine stands. Arrow denotes application of fertilizer.

unfertilized stands and 261 to 508 in the fertilized stands in the 10-year fertilization period.

Mean biomass of total herbs was significantly ( $P = 0.03$ ) higher in the fertilized than unfertilized stands in the second period, and this difference approached significance ( $P = 0.06$ ) in the first period (Table 2; Fig. 1c). On average, mean biomass (kg/ha) of total herbs ranged from 299 to 318 kg/ha in the unfertilized stands and 583 to 880 kg/ha in the fertilized stands in the 10-year fertilization period. There was a significant ( $P < 0.01$ ) effect of time in each period for all herbaceous components as biomass generally increased in the fertilized stands. There were no significant differences in biomass of any herbaceous plant group between fertilized and unfertilized stands in either

of the post-treatment years (2008 and 2013) (Table 1), as the fertilizer effect clearly declined.

The dominant grass was pinegrass (*Calamagrostis rubescens*) at Summerland and Kelowna study areas and smooth brome (*Bromus inermis*) at the Cariboo area. Dominant forbs were fireweed, arctic lupine, wild strawberry (*Fragaria virginiana*), rosy pussytoes (*Antennaria microphylla*), white-flowered hawkweed (*Hieracium albiflorum*), heart-leaved arnica (*Arnica cordifolia*), bunchberry (*Cornus canadensis*), and common dandelion (*Taraxacum officinale*). Additional important herb species at the Cariboo study area only included fringed aster (*Aster ciliolatus*), northern bedstraw (*Galium boreale*), creamy peavine (*Lathyrus ochroleucus*), red-clover (*Trifolium pratense*), white clover (*T. repens*),

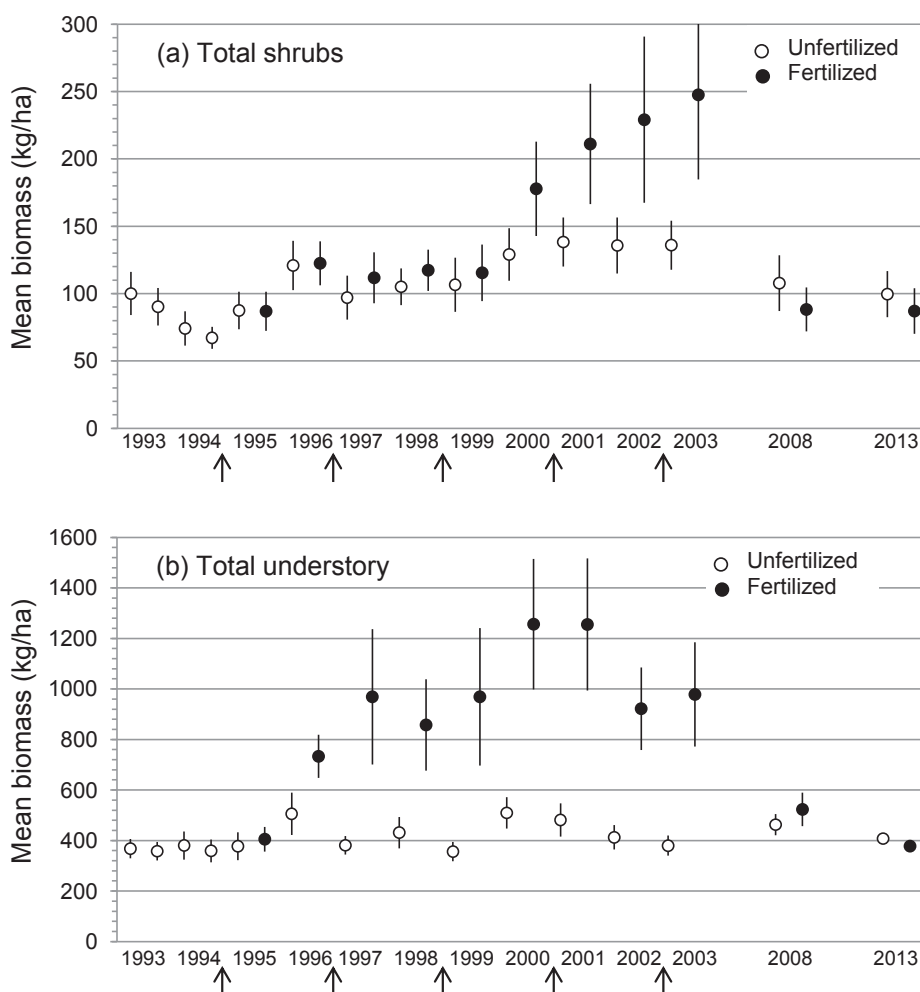


Fig. 2. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) total shrubs, and (b) total herbs and shrubs (understory) each year 1993–2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 12) and fertilized ( $n$  = 12) lodgepole pine stands. Arrow denotes application of fertilizer.

and American vetch (*Vicia americana*). Common herbaceous species in unharvested forests included pinegrass, racemose pussytoes (*Antennaria racemosa*), heart-leaved arnica, and one-sided wintergreen (*Orthilia secunda*).

### 3.2. Total shrub and understory species

Initial measurements of mean biomass of shrubs and total understory vegetation were similar ( $P > 0.05$ ) in the treatment stands in 1993, prior to the start of treatments, and at 5 and 10 years post-treatment (Table 1). Mean biomass of total shrubs was not affected by fertilization; however, mean biomass did increase significantly ( $P < 0.01$ ) over time in both periods (Table 2; Fig. 2a). In addition, a treatment  $\times$  time interaction approached significance ( $P = 0.06$ ) in the second 5-year fertilization period, and suggested that the repeated fertilizer treatment did start to enhance shrub growth. On average, mean biomass (kg/ha) of shrubs ranged from 129 to 196 in the unfertilized and fertilized stands, respectively, in the second 5-year period (Fig. 2a). Mean biomass of total herbs and shrubs (understory vegetation) was significantly ( $P \leq 0.04$ ) higher in fertilized than unfertilized stands in both periods (Table 2; Fig. 2b). The significant ( $P = 0.04$ ) treatment  $\times$  time interaction in the first period indicated that in the first three years (1994–1996), total biomasses of understory vegetation were similar, but in 1997 and 1998, these measurements were higher in the fertilized than unfertilized stands. On average, mean biomass (kg/ha) of total herbs and shrubs ranged from 415 to 428 in the unfertilized stands and 685 to 1076 in the fertilized stands in the 10-year

fertilization period. There was a significant ( $P \leq 0.02$ ) effect of time in each period for biomass of total understory vegetation as herbs and shrubs generally increased in the fertilized stands.

### 3.3. Individual shrub species

The dwarf shrub stratum was composed of six species and initial measurements of mean biomasses in the pre-treatment year (1993) were similar ( $P > 0.05$ ) between respective treatment stands for all species. Mean biomass of *A. uva-ursi* was similar in unfertilized and fertilized stands in the first 5-year period, but declined significantly ( $P < 0.01$ ) in fertilized stands in the second period (Table 3; Fig. 3a). This decline began in 1997 after the second application of fertilizer (Fig. 3a). The overall mean ( $\pm$  SE) biomass (kg/ha) in the second period was  $18.1 \pm 1.4$  in the unfertilized stands and  $6.5 \pm 1.0$  in the fertilized stands. Mean biomass of *L. borealis* followed this same pattern with no difference between treatment stands in the first 5-year period, but then a significant ( $P < 0.01$ ) difference in overall mean biomass of  $7.9 \pm 0.6$  in the unfertilized stands and  $2.3 \pm 0.3$  in the fertilized stands in the second period (Table 3; Fig. 3b). There continued to be a significant ( $P \leq 0.02$ ) difference between treatment stands in 2008, but not 2013, for these two shrub species.

Mean biomass of dwarf blueberry (*Vaccinium caespitosum*) was significantly ( $P < 0.01$ ) higher in unfertilized than fertilized stands in both periods (Table 3; Fig. 3c). Overall mean ( $\pm$  SE) biomasses ranged from  $18.0 \pm 1.7$  to  $25.4 \pm 2.9$  in the unfertilized stands and  $6.6 \pm 0.9$  to  $4.0 \pm 0.6$  in the fertilized stands in the first and second 5-

**Table 3**

Results of RM-ANOVA for biomass production (kg/ha) of individual shrub species in response to repeated fertilization during two “5-year fertilization periods”: 1994 to 1998 and 1999 to 2003. These species are known to be forage plants for various mammalian herbivores. Fertilizer was applied at the end of the growing season in 1994, 1996, 1998, 2000, and 2002. *F*-values identified by \* were calculated using a Huynh-Feldt correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Significant values are given in bold.

Group, species, and height class	1994–1998						1999–2003					
	Treatment		Time		Treatment × time		Treatment		Time		Treatment × time	
<i>Dwarf (&lt; 0.25 m)</i>												
<i>Arctostaphylos uva-ursi</i>	<i>F</i> <sub>1,21</sub>	<i>P</i>	<i>F</i> <sub>4,84</sub>	<i>P</i>	<i>F</i> <sub>4,84</sub>	<i>P</i>	<i>F</i> <sub>1,21</sub>	<i>P</i>	<i>F</i> <sub>4,84</sub>	<i>P</i>	<i>F</i> <sub>4,84</sub>	<i>P</i>
	0.81	0.38	6.35*	< 0.01	1.20*	0.31	9.11	< 0.01	4.63*	< 0.01	2.18*	0.12
<i>Linnaea borealis</i>	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>
	3.00	0.10	3.03*	0.05	0.99*	0.39	15.15	< 0.01	0.43*	0.66	1.21*	0.31
<i>Pachistima myrsinites</i>	<i>F</i> <sub>1,20</sub>	<i>P</i>	<i>F</i> <sub>4,80</sub>	<i>P</i>	<i>F</i> <sub>4,80</sub>	<i>P</i>	<i>F</i> <sub>1,20</sub>	<i>P</i>	<i>F</i> <sub>4,80</sub>	<i>P</i>	<i>F</i> <sub>4,80</sub>	<i>P</i>
	0.92	0.35	3.54*	0.05	0.20*	0.77	0.06	0.80	0.72*	0.52	1.44*	0.25
<i>Rubus pubescens</i>	<i>F</i> <sub>1,5</sub>	<i>P</i>	<i>F</i> <sub>4,20</sub>	<i>P</i>	<i>F</i> <sub>4,20</sub>	<i>P</i>	<i>F</i> <sub>1,5</sub>	<i>P</i>	<i>F</i> <sub>4,20</sub>	<i>P</i>	<i>F</i> <sub>4,20</sub>	<i>P</i>
	0.01	0.94	5.48*	< 0.01	0.41*	0.77	0.26	0.64	2.88	0.05	2.37	0.09
<i>Vaccinium caespitosum</i>	<i>F</i> <sub>1,7</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>1,7</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>
	24.36	< 0.01	5.91*	< 0.01	10.20*	< 0.01	43.18	< 0.01	10.26*	< 0.01	10.15*	< 0.01
<i>Vaccinium scoparium</i>	<i>F</i> <sub>1,12</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>1,12</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>
	0.16	0.70	4.53*	0.02	0.14*	0.87	0.22	0.64	1.92*	0.15	2.35*	0.09
<i>Low–middle (0.25–2.0 m)</i>												
<i>Lonicera involucrata</i>	<i>F</i> <sub>1,13</sub>	<i>P</i>	<i>F</i> <sub>4,52</sub>	<i>P</i>	<i>F</i> <sub>4,52</sub>	<i>P</i>	<i>F</i> <sub>1,13</sub>	<i>P</i>	<i>F</i> <sub>4,52</sub>	<i>P</i>	<i>F</i> <sub>4,52</sub>	<i>P</i>
	1.19	0.30	2.77*	0.08	0.76*	0.48	1.10	0.32	1.02*	0.38	1.21*	0.32
<i>Lonicera utahensis</i>	<i>F</i> <sub>1,12</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>1,12</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>	<i>F</i> <sub>4,48</sub>	<i>P</i>
	0.02	0.89	3.08*	0.06	1.44*	0.26	1.34	0.27	6.04*	0.02	1.08*	0.34
<i>Mahonia aquifolium</i>	<i>F</i> <sub>1,7</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>1,7</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>	<i>F</i> <sub>4,28</sub>	<i>P</i>
	0.11	0.75	0.15	0.89	3.05	0.25	0.01	0.94	1.63*	0.23	0.57*	0.60
<i>Ribes lacustre</i>	<i>F</i> <sub>1,15</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>1,15</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>
	4.82	0.04	2.77*	0.06	2.08*	0.12	0.08	0.78	2.53*	0.08	0.68*	0.55
<i>Rosa acicularis</i>	<i>F</i> <sub>1,6</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>1,6</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>
	11.76	0.01	22.17*	< 0.01	8.82*	< 0.01	20.53	< 0.01	10.10*	< 0.01	8.02*	< 0.01
<i>Rubus idaeus</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>
	1.02	0.33	0.85*	0.41	2.12*	0.15	15.76	< 0.01	7.77*	< 0.01	4.38*	< 0.01
<i>Shepherdia canadensis</i>	<i>F</i> <sub>1,6</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>1,6</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>	<i>F</i> <sub>4,24</sub>	<i>P</i>
	0.34	0.58	0.71*	0.54	0.52*	0.65	1.97	0.21	1.00*	0.37	0.83*	0.42
<i>Spiraea betulifolia</i>	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>1,22</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>	<i>F</i> <sub>4,88</sub>	<i>P</i>
	4.15	0.05	4.18*	0.02	0.44*	0.68	0.22	0.64	4.41*	< 0.01	0.53*	0.65
<i>Symphoricarpus albus</i>	<i>F</i> <sub>1,3</sub>	<i>P</i>	<i>F</i> <sub>4,12</sub>	<i>P</i>	<i>F</i> <sub>4,12</sub>	<i>P</i>	<i>F</i> <sub>1,3</sub>	<i>P</i>	<i>F</i> <sub>4,12</sub>	<i>P</i>	<i>F</i> <sub>4,12</sub>	<i>P</i>
	1.26	0.34	3.12	0.06	1.52	0.26	7.53	0.07	3.89	0.03	1.54	0.25
<i>Vacc. membranaceum</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>
	0.80	0.40	2.10*	0.11	1.61*	0.20	2.49	0.15	2.04*	0.13	1.18*	0.34
<i>Tall (&gt; 2.0 m)</i>												
<i>Alnus sinuata</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>
	0.00	0.99	5.14*	0.01	1.05*	0.38	0.43	0.53	1.73*	0.19	0.71*	0.54
<i>Amelanchier alnifolia</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>1,9</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>	<i>F</i> <sub>4,36</sub>	<i>P</i>
	1.75	0.22	8.34*	< 0.01	2.52*	0.10	5.76	0.04	5.14*	0.03	2.88*	0.11
<i>Salix</i> spp.	<i>F</i> <sub>1,19</sub>	<i>P</i>	<i>F</i> <sub>4,76</sub>	<i>P</i>	<i>F</i> <sub>4,76</sub>	<i>P</i>	<i>F</i> <sub>1,19</sub>	<i>P</i>	<i>F</i> <sub>4,76</sub>	<i>P</i>	<i>F</i> <sub>4,76</sub>	<i>P</i>
	3.49	0.08	3.56*	0.07	2.80*	0.10	3.14	0.09	1.00	0.38	0.88	0.43

year periods, respectively. The significant ( $P < 0.01$ ) treatment × time interactions in the two periods for *V. caespitosum* reflected the immediate dramatic decline in biomass after the start of fertilization and relative increases in this shrub in the unfertilized stands (Fig. 3c). There was a significant difference in biomass of *V. caespitosum* between treatment stands in all years 1995 to 2003. No data were available for 2008 and 2013 for this species as the majority of data came from the Cariboo area.

Mean biomasses of falsebox (*Pachistima myrsinites*), trailing raspberry (*Rubus pubescens*), and grouseberry (*V. scoparium*) were similar ( $P > 0.05$ ) in unfertilized and fertilized stands in both periods (Table 3). There was a significant ( $P \leq 0.05$ ) effect of time for changes in biomass of all dwarf shrubs in the first 5-year period, and for *A. uva-ursi*, *R. pubescens*, and *V. caespitosum* in the second period.

Shrubs in the small-middle height stratum were composed of 10 species and initial measurements of mean biomasses in the pre-treatment year 1993 were similar ( $P > 0.05$ ) between respective treatment stands for eight species. However, mean biomasses of black gooseberry (*Ribes lacustre*) and birch-leaved spiraea (*Spiraea betulifolia*) were not similar in pre-treatment stands. Mean biomasses of black twinberry (*Lonicera involucrata*), red twinberry (*L. utahensis*), and tall Oregon-

grape (*Mahonia aquifolium*) were similar ( $P > 0.05$ ) in unfertilized and fertilized stands in both fertilization periods (Table 3). Mean biomass of *R. lacustre* was significantly higher in unfertilized than fertilized stands in the first but not second 5-year period (Table 3; Fig. 4a). This pattern may have been related to higher amounts of this shrub in the pre-treatment stands prior to fertilization.

Mean biomass of prickly rose (*Rosa acicularis*) was significantly ( $P < 0.01$ ) higher in fertilized than unfertilized stands in both periods (Table 3; Fig. 4b). Overall mean ( $\pm$  SE) biomasses (kg/ha) ranged from  $38.9 \pm 3.8$  to  $54.0 \pm 6.2$  in the unfertilized stands and  $74.2 \pm 8.1$  to  $286.7 \pm 32.4$  in the fertilized stands in the first and second 5-year periods, respectively. No data were available for 2008 and 2013 for this species as the majority of data came from the Cariboo area. Mean biomass of *R. idaeus* was similar ( $P > 0.05$ ) between treatment stands in the first 5-year period, but significantly ( $P < 0.01$ ) different in the second period (Table 3; Fig. 4c), with an overall mean (SE) biomass of  $0.8 \pm 0.2$  in the unfertilized and  $3.8 \pm 0.5$  in the fertilized stands. This difference did not persist in the post-treatment years 2008 and 2013.

Mean biomasses of soapberry (*Shepherdia canadensis*) and snowberry (*Symphoricarpus albus*) were highly variable across stands, and hence

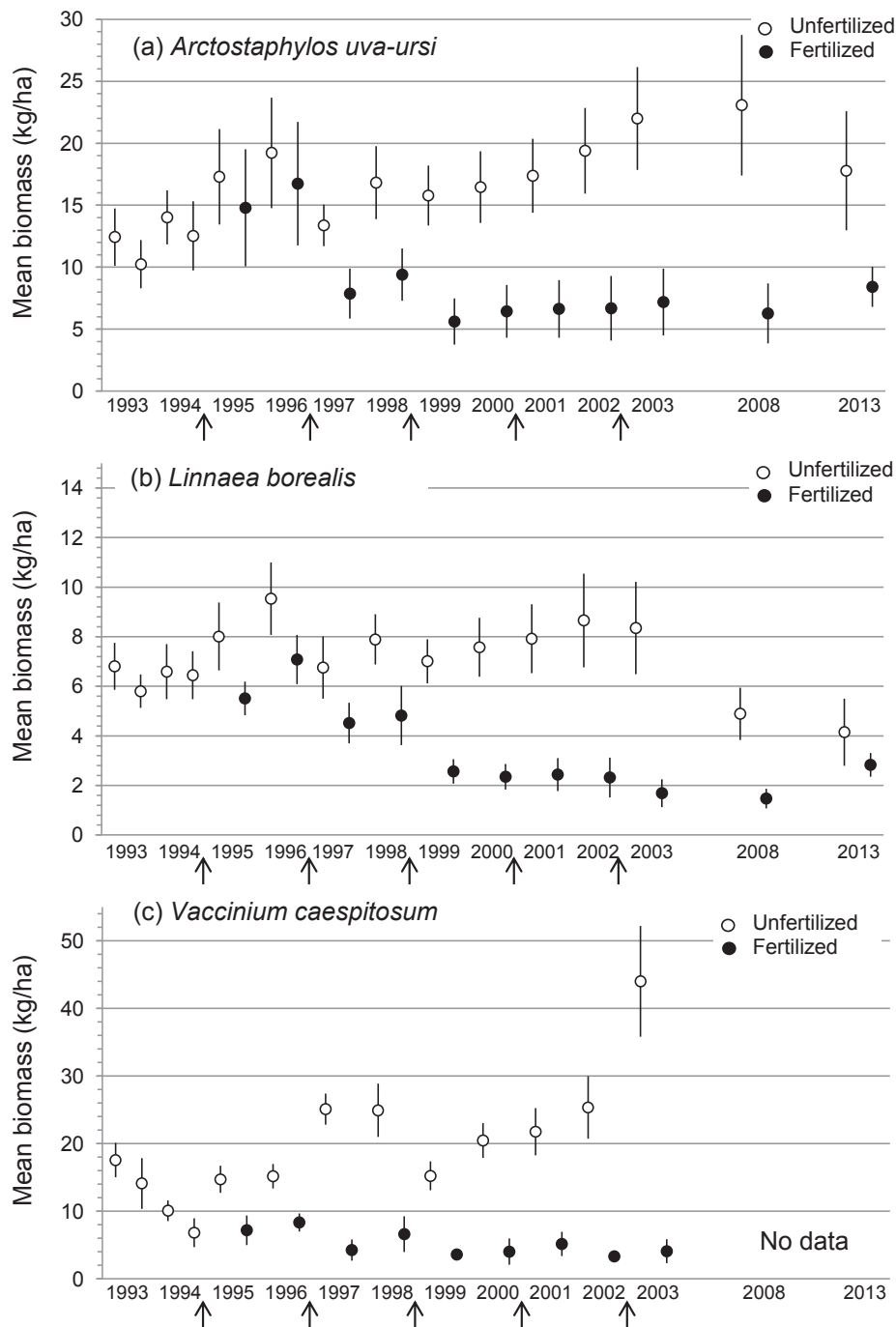


Fig. 3. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) *Arctostaphylos uva-ursi*, (b) *Linnaea borealis*, and (c) *Vaccinium caespitosum* each year 1993–2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n = 12, 12, 4$ ) and fertilized ( $n = 11, 12, 5$ ) lodgepole pine stands. Arrow denotes application of fertilizer.

were statistically similar ( $P > 0.05$ ) between treatment stands in both periods (Table 3). However, overall mean biomass was 5.3 times higher in the unfertilized than fertilized stands in the second period for *S. canadensis*, with the converse true for *S. albus* where overall mean biomass was 3.2 times higher in the fertilized than unfertilized stands (Fig. 5a). Again, no data were available for 2008 and 2013 for either of these species as the majority of data came from the Cariboo area. Mean biomass of *S. betulifolia* was significantly different in unfertilized and fertilized stands in the first but not second 5-year period (Table 3). Again, this pattern may have been related to higher amounts of this shrub in the pre-treatment stands prior to fertilization. Mean biomass of black huckleberry (*V. membranaceum*) was similar ( $P > 0.05$ ) in treatment stands in both periods, albeit with seemingly lower amounts

in the fertilized stands 1997 to 2003, but these differences were not statistically significant (Table 3; Fig. 5b).

The tall shrub stratum was composed of three species and initial measurements of mean biomasses in the pre-treatment year 1993 were similar ( $P > 0.05$ ) between respective treatment stands for all species. Mean biomass of Sitka alder (*A. sinuata*) was similar ( $P > 0.05$ ) between treatment stands in both periods (Table 3; Fig. 6a). Mean biomass of Saskatoon berry (*A. alnifolia*) was similar between stands in the first period, but significantly ( $P = 0.04$ ) different in the second period with mean biomass ( $\pm$  SE) in the fertilized stand at  $36.7 \pm 5.3$  kg/ha and the unfertilized stand at  $13.0 \pm 2.2$  kg/ha (Table 3; Fig. 6b). There was a significant ( $P \leq 0.03$ ) effect of time as biomass generally increased after the start of fertilization. There were no data available for



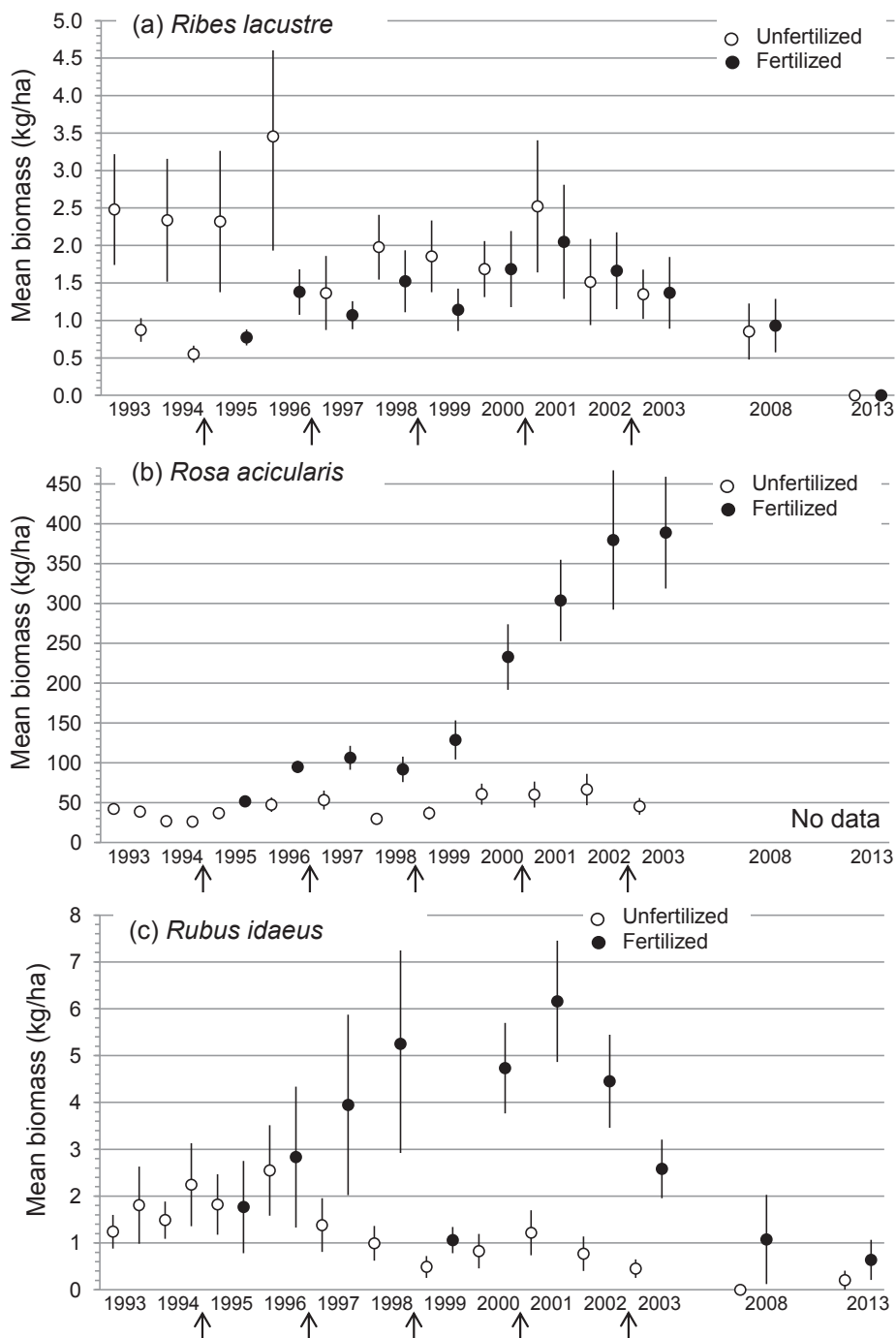


Fig. 4. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) *Ribes lacustre*, (b) *Rosa acicularis*, and (c) *Rubus idaeus* each year 1993–2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 6, 6, 8) and fertilized ( $n$  = 11, 6, 10) lodgepole pine stands. Arrow denotes application of fertilizer.

2008 and 2013 for *A. alnifolia* as the majority of data came from the Cariboo area. Mean biomass of *Salix* spp. was highly variable in the fertilized stands, and hence was statistically similar ( $P > 0.05$ ) between treatment stands in both periods (Table 3). However, overall mean biomasses for the two 5-year periods were 3.4–6.2 times higher in the fertilized than unfertilized stands, before declining to similar levels in the post-treatment years 2008 and 2013 (Fig. 6c). There were no treatment  $\times$  time interactions for species in this tall shrub stratum.

Common shrub species in unharvested forests included Sitka alder, red twinberry, falsebox, kinnikinnick, twinflower, and grouseberry.

### 3.4. Individual tree species

The understory tree stratum was composed of six species and initial measurements of mean biomasses in the pre-treatment year (1993) were similar ( $P > 0.05$ ) between respective treatment stands for five species. Mean biomass of *P. menziesii* was not similar in pre-treatment stands. Mean biomass of *A. lasiocarpa* was similar ( $P > 0.05$ ) between treatment stands in both fertilization periods (Table 4; Fig. 7a). Mean biomass of *Picea* hybrid was highly variable in fertilized stands, and hence was not significantly different between treatment stands (Table 4). However, overall mean biomasses for the two 5-year periods were 2.5–3.4 times higher in the fertilized than unfertilized stands

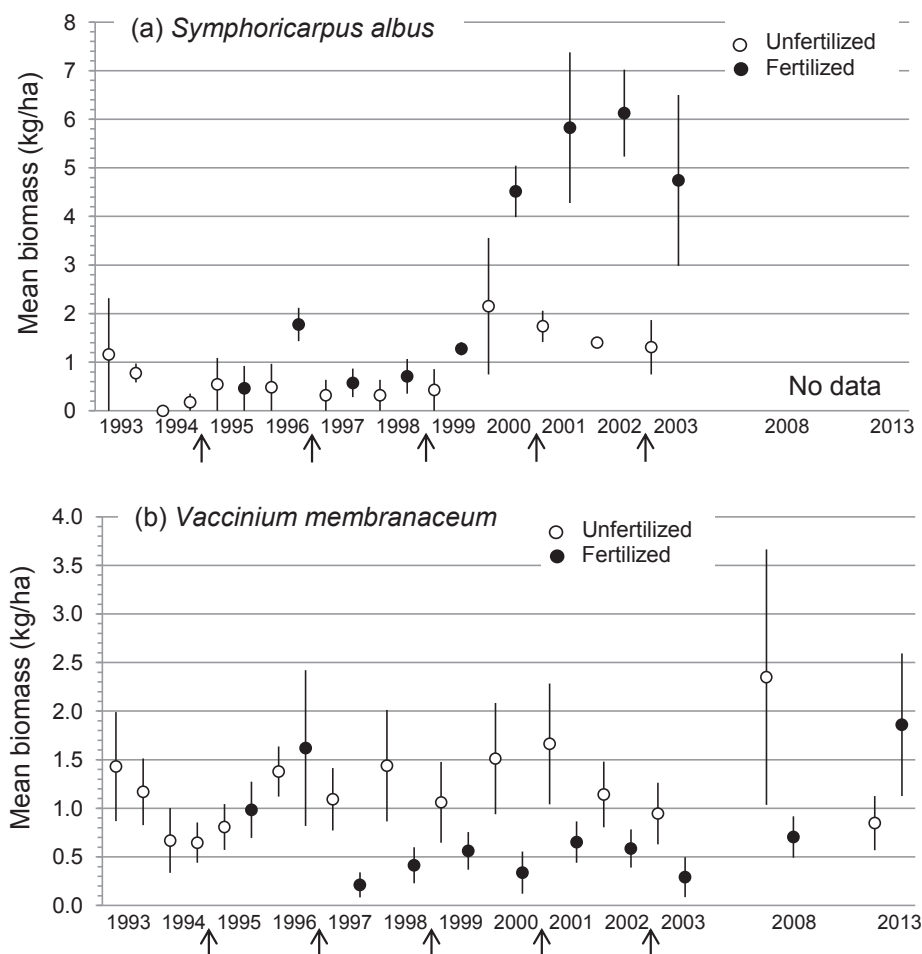


Fig. 5. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) *Symphoricarpos albus* and (b) *Vaccinium membranaceum* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 2 and 6) and fertilized ( $n$  = 3 and 5) lodgepole pine stands. Arrow denotes application of fertilizer.

(Fig. 7b). Mean biomass of *P. menziesii* was similar ( $P > 0.05$ ) between treatment stands in the first period, but significantly ( $P < 0.01$ ) different in the second period (Table 4; Fig. 7c). Overall mean biomasses were 2.1–2.2 times higher in fertilized than unfertilized stands over the two periods. A significant ( $P < 0.01$ ) time effect in the second period reflected a general increase in biomass for these three conifers from 1999 to 2003 (Fig. 7a–c). There were no significant differences in mean biomass of the three deciduous tree species in unfertilized and fertilized stands (Table 4). In all cases, biomass measurements were highly variable likely owing to the clumped distribution of these species. The only significant treatment  $\times$  time interaction for these understory tree species was *P. trichocarpa* in the second fertilization period.

### 3.5. Mosses and terrestrial lichens

Mean crown volume index of total mosses was similar ( $P > 0.05$ ) in pre-treatment stands in 1993 (Table 1), and then significantly ( $P \leq 0.05$ ) higher in unfertilized than fertilized stands in both 5-year fertilization periods (Table 2; Fig. 8a). Overall mean ( $\pm$  SE) crown volume index ( $\text{m}^3/0.01$  ha) ranged from  $2.20 \pm 0.20$  to  $2.78 \pm 0.34$  in the unfertilized stands and  $1.36 \pm 0.13$  to  $0.39 \pm 0.03$  in the fertilized stands in the two periods, respectively. The significant ( $P < 0.01$ ) treatment  $\times$  time interactions in the two periods for total mosses reflected the dramatic decline in volume after the second application of fertilizer in 1996 and relative increases of mosses in the unfertilized stands (Fig. 8a). There was a significant ( $P \leq 0.02$ ) difference in volume of mosses between treatment stands in all years 1997 to 2003. Mean crown volume index of mosses returned to comparable

levels in unfertilized and fertilized stands in the post-treatment years 2008 and 2013 (Table 1; Fig. 8a). Common moss species included silver moss (*Bryum argenteum*), common lawn moss (*Brachythecium albicans*), fire moss, (*Ceratodon purpureus*), broom moss (*Dicranum scoparium*), stair-step moss (*Hylocomium splendens*), red-stem feather moss (*Pleurozium schreberi*), and juniper haircap moss (*Polytrichum juniperinum*).

Mean crown volume index of total terrestrial lichens was similar ( $P > 0.05$ ) in pre-treatment stands in 1993 (Table 1), and then significantly ( $P < 0.01$ ) higher in unfertilized than fertilized stands in both 5-year fertilization periods (Table 2; Fig. 8b). Overall mean ( $\pm$  SE) crown volume index ( $\text{m}^3/0.01$  ha) ranged from  $0.40 \pm 0.03$  to  $0.34 \pm 0.02$  in the unfertilized stands and  $0.27 \pm 0.02$  to  $0.13 \pm 0.01$  in the fertilized stands in the two periods, respectively. The significant ( $P < 0.01$ ) time interaction in the first 5-year period, and trend that way in the second period, reflected a general decline in volume of lichen with time (Fig. 8b). Mean crown volume index of lichens remained significantly ( $P \leq 0.05$ ) lower in fertilized than unfertilized stands in the post-treatment years 2008 and 2013 (Table 1). Common lichen species included grey reindeer lichen (*Cladonia rangifer*), horn cladonia (*Cladonia cornuta*), black-foot cladonia (*Cladonia gracilis*), sulfur cladonia (*Cladonia sulphurina*), blistered paw (*Nephroma resupinatum*), devil's matchstick (*Pilophorus acicularis*), and *Peltigera* spp.

## 4. Discussion

### 4.1. Herbaceous species as forage

The substantial increase in mean biomass of grasses, forbs, and total

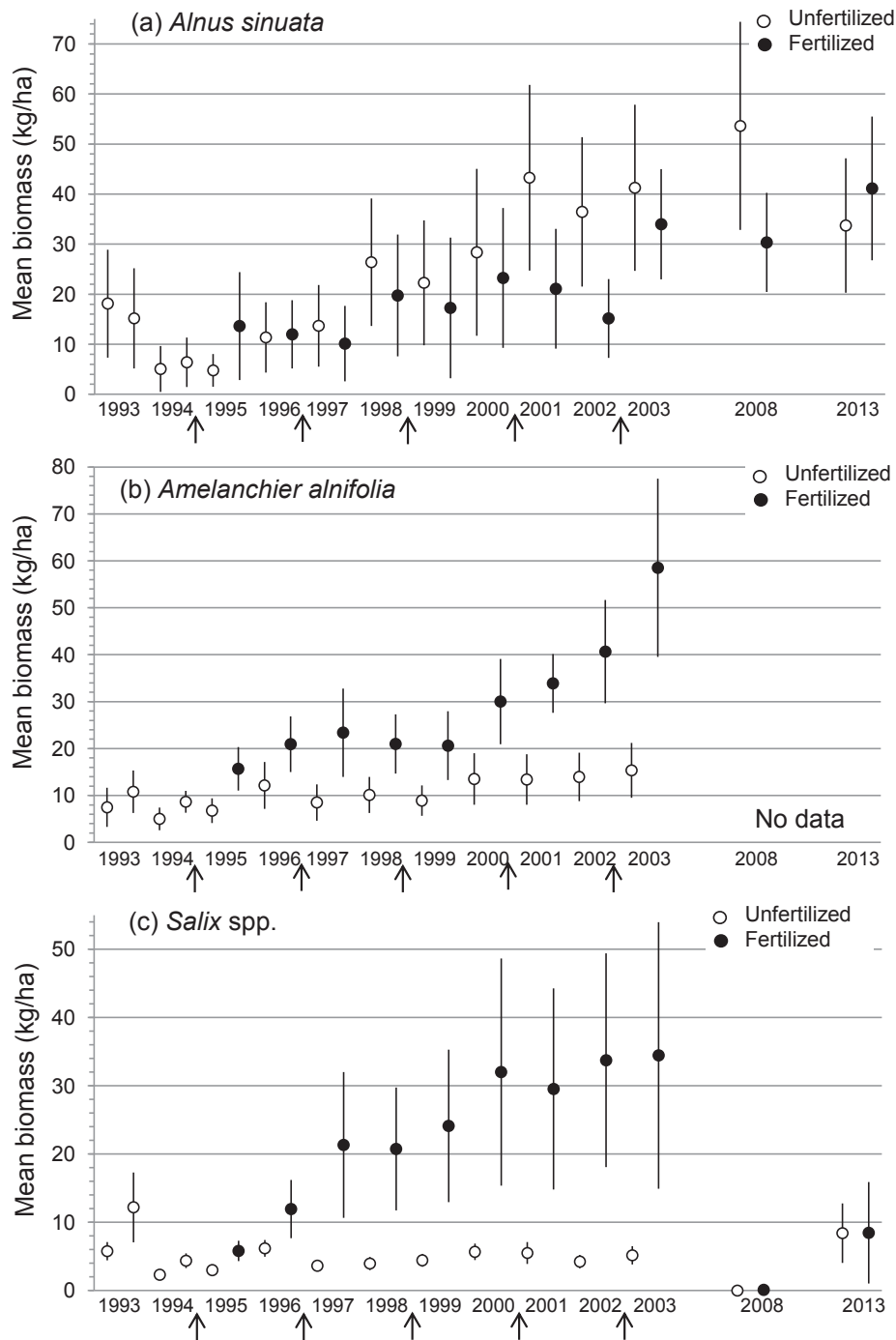


Fig. 6. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) *Alnus sinuata*, (b) *Amelanchier alnifolia*, and (c) *Salix* spp. each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 6, 6, 11) and fertilized ( $n$  = 5, 5, 10) lodgepole pine stands. Arrow denotes application of fertilizer.

herbs to repeated nitrogen fertilization was a similar result to other reports in North America and northern Europe (Sullivan and Sullivan, 2017a). Grasses, in particular, responded dramatically starting in the first year after fertilization. Forbs and total herbs also followed this pattern, although not to a significant degree until after the second and third applications of fertilizer. In another study in the interior of BC, mean abundance of total herbs, grasses, and fireweed all increased dramatically with repeated fertilization, up to 3–4 times compared with unfertilized controls (Brockley, 2007b). Grasses such as wavy hair-grass (*Deschampsia flexuosa*) and herbs such as fireweed and hairy wood rush (*Luzula pilosa*) were dominant plants in repeatedly fertilized stands in Sweden (Kellner and Redbo-Torstensson, 1995; Strengbom and Nordin,

2008). There were overall increases in grasses and some herbs (1.7–2.0 times) in response to annual fertilizer applications in a long-term experiment in the Yukon (Nams et al., 1993; Turkington et al., 1998). However, arctic lupine (*L. arcticus*) and northern anemone (*Anemone parviflora*) declined, probably owing to changes in soil nutrients and dramatic increases in abundance of grasses and fireweed (Turkington et al., 1998).

All of the dominant grasses and forbs recorded in our study may serve as summer forage for mule deer, moose, elk, and woodland caribou. Fireweed, a preferred forage for mule deer, was part of the forb component and abundance of this species increased dramatically in fertilized stands (Brockley, 2007b; Sullivan et al., 2012). Positive

**Table 4**

Results of RM-ANOVA for biomass production (kg/ha) of individual tree species in response to repeated fertilization during two “5-year fertilization periods”: 1994 to 1998 and 1999 to 2003. These species are known to be forage plants for various mammalian herbivores. Fertilizer was applied at the end of the growing season in 1994, 1996, 1998, 2000, and 2002. *F*-values identified by \* were calculated using a Huynh-Feldt correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Significant values are given in bold.

Species	1994–1998						1999–2003					
	Treatment		Time		Treatment × time		Treatment		Time		Treatment × time	
<i>Abies lasiocarpa</i>	<i>F</i> <sub>1,14</sub>	<i>P</i>	<i>F</i> <sub>4,56</sub>	<i>P</i>	<i>F</i> <sub>4,56</sub>	<i>P</i>	<i>F</i> <sub>1,14</sub>	<i>P</i>	<i>F</i> <sub>4,56</sub>	<i>P</i>	<i>F</i> <sub>4,56</sub>	<i>P</i>
	0.05	0.83	3.00*	0.08	0.30*	0.71	0.16	0.69	9.03*	<b>&lt; 0.01</b>	0.28*	0.71
<i>Betula papyrifera</i>	<i>F</i> <sub>1,4</sub>	<i>P</i>	<i>F</i> <sub>4,16</sub>	<i>P</i>	<i>F</i> <sub>4,16</sub>	<i>P</i>	<i>F</i> <sub>1,4</sub>	<i>P</i>	<i>F</i> <sub>4,16</sub>	<i>P</i>	<i>F</i> <sub>4,16</sub>	<i>P</i>
	0.13	0.74	0.19*	0.86	0.27*	0.79	0.81	0.42	5.95*	<b>0.04</b>	2.12*	0.19
<i>Picea glauca</i> × <i>engelmannii</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>	<i>F</i> <sub>4,64</sub>	<i>P</i>
	2.48	0.14	2.79*	0.10	1.60*	0.22	2.37	0.14	6.46*	<b>&lt; 0.01</b>	3.82*	0.43
<i>Populus tremuloides</i>	<i>F</i> <sub>1,15</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>1,15</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>	<i>F</i> <sub>4,60</sub>	<i>P</i>
	0.52	0.48	1.06*	0.38	0.70*	0.58	0.17	0.68	1.87*	0.19	2.31*	0.14
<i>Populus trichocarpa</i>	<i>F</i> <sub>1,8</sub>	<i>P</i>	<i>F</i> <sub>4,32</sub>	<i>P</i>	<i>F</i> <sub>4,32</sub>	<i>P</i>	<i>F</i> <sub>1,8</sub>	<i>P</i>	<i>F</i> <sub>4,32</sub>	<i>P</i>	<i>F</i> <sub>4,32</sub>	<i>P</i>
	1.05	0.34	4.50*	<b>0.01</b>	1.97*	0.15	4.88	0.06	10.84	<b>&lt; 0.01</b>	3.42	<b>0.02</b>
<i>Pseudotsuga menziesii</i>	<i>F</i> <sub>1,18</sub>	<i>P</i>	<i>F</i> <sub>4,72</sub>	<i>P</i>	<i>F</i> <sub>4,72</sub>	<i>P</i>	<i>F</i> <sub>1,18</sub>	<i>P</i>	<i>F</i> <sub>4,72</sub>	<i>P</i>	<i>F</i> <sub>4,72</sub>	<i>P</i>
	1.22	0.28	1.09*	0.33	0.54*	0.52	4.55	<b>0.05</b>	5.70*	<b>&lt; 0.01</b>	2.14*	0.13

responses in relative abundance of the mountain hare (*L. timidus*) in Scandinavia (Ball et al., 2000) and the snowshoe hare in BC (Sullivan et al., 2006a) and the Yukon (Nams et al., 1996) were related to abundant growth of grasses (and herbs) in fertilized stands. Grasses and dominant herbs in fertilized stands provided excellent forage and cover habitat for *Microtus* voles in Canada (Boonstra et al., 2001; Sullivan et al., 2012; Sullivan and Sullivan, 2014) and also Scandinavia (Ball et al., 2000).

As noted by Lindgren et al. (2017) and others, although dependent on stand density of young forests, successional development towards closed canopy conditions inevitably shades out herb species, thereby limiting growth of biomass in this understory component. Mean herbaceous biomass declined to levels recorded in unfertilized stands at 15 and 20 years post-treatment in our study, presumably owing to completion of the fertilization treatments and the structural advance towards canopy closure.

#### 4.2. Shrub and tree species as forage

The increased productivity of the herb layer likely contributed to the lack of response of the overall shrub stratum. However, some shrubs in the fertilized stands, such as *A. alnifolia*, *R. acicularis*, *R. idaeus*, and *Salix* spp., appeared to have escaped the herb layer suppression and eventually increased in abundance. All of these shrubs are readily eaten by deer, moose, and elk, and their structural attributes provide security and thermal cover if needed (Pierce and Peek, 1984; Nyberg, 1990; Cook et al., 1998). Brockley (2007b) also reported substantial biomass production by *R. acicularis*, *R. idaeus*, and *Ribes* spp. in repeatedly fertilized stands in the Cariboo region of BC. *Salix* spp. and *A. alnifolia* were a large component of the shrub vegetation at one study area, but responses of these species were variable (Brockley, 2007b). Growth rates of all fertilized shrubs were increased by about 25–30% over unfertilized values, with grey willow (*S. glauca*) and bog birch (*B. glandulosa*) being dominant species in the 9-year nutrient addition project in the Yukon (Krebs et al., 2001). As observed in our study, some positive responses were noted at 1–2 years after fertilization in the Yukon study, but there was a lag time of 5–6 years prior to a stable pattern of shrub responses (Turkington et al., 1998).

Shrubs, deciduous tree species (*B. papyrifera*, *Populus* spp.), and some coniferous tree species (*A. lasiocarpa* and *P. menziesii*) may be readily eaten by ungulates in winter. A breakdown for each ungulate species in forests near Prince George, BC, was estimated by Hodder et al. (2013): mule deer (total conifers 62.7%; shrubs and deciduous trees 28.7%; lichens and other 8.6%), moose (total conifers 63.8%; shrubs and deciduous trees 35.5%; lichens and other 0.7%), and elk (total conifers 15.9%; shrubs and deciduous trees 70.4%; lichens and

other 13.7%). *Salix* spp. was a major shrub forage species for all three ungulates. Mule deer relied heavily on *P. menziesii* and moose on *A. lasiocarpa* for winter forage.

Snowshoe hares have a similar diet as ungulates in winter, but they may also forage on lodgepole pine and spruce. In addition, shrubs and trees provide both security and thermal cover for hares (Koeehler and Brittell, 1990). The mountain hare in Scandinavia (Ball et al., 2000) and the snowshoe hare in Canada (Krebs et al., 2001; Sullivan et al., 2006a) responded favourably to enhanced shrub growth in fertilized stands. Both *P. menziesii* and *Picea* hybrid responded positively to fertilization in the current study, but *A. lasiocarpa* and the three deciduous tree species did not. White spruce (*Picea glauca*) trees also responded with increased vegetative growth and seed production in the repeated fertilization study in the Yukon (Dale et al., 2001).

Dwarf shrubs such as *A. uva-ursi*, *L. borealis*, and *V. caespitosum* declined in fertilized stands in our study as did the first two species plus *V. membranaceum* in the study by Brockley (2007b). Similarly in Sweden, the increased abundance of grasses and nitrophilous herbs likely contributed to a decline in the dwarf shrubs bilberry (*V. myrtillus*), lingonberry (*V. vitis-idaea*), and heather (*Calluna vulgaris*) (Strengbom et al., 2001; Strengbom and Nordin, 2008). However, we found no difference in mean biomass of other dwarf shrubs such as *B. pubescens*, *P. myrsinites*, and *V. scoparium*. Mean biomass of *V. membranaceum* appeared lower in fertilized than unfertilized stands, but this comparison was not statistically significant. Thus, an increasing canopy cover from rapidly growing crop trees in fertilized stands may also have contributed to the decline of some dwarf shrubs (Hedwall et al., 2010; Lindgren and Sullivan, 2013b). In addition, *Arctostaphylos* spp., and perhaps other dwarf shrubs, may be constrained to function optimally within a narrow range of nitrogen levels, but are unable to deal with the higher levels encountered in operational forest fertilization regimes (Boonstra et al., 2017).

Thus, the positive response of biomass of herbaceous plants, but mixed responses of shrub and tree species, provided only partial support for  $H_1$  that biomass of forage plants would be enhanced by forest fertilization.

Reduced abundance of *M. rutilus* and *M. gapperi* in response to fertilization in the Yukon and BC, respectively, may have been related to a decline in some dwarf shrubs and their berries (Boonstra and Krebs, 2006; Sullivan et al., 2012). *Vaccinium* and *A. uva-ursi* are major sources of berry crops for red-backed voles and other small mammal species (Merritt, 1981; Nagorsen, 2005). Granath and Strengbom (2017) also reported a significant decline in wild berry production from nitrogen fertilization in Sweden. However, overall, this remains a contradictory issue primarily because of a lack of rigorous sampling and experimentation with respect to actual berry crops (Sullivan and Sullivan,

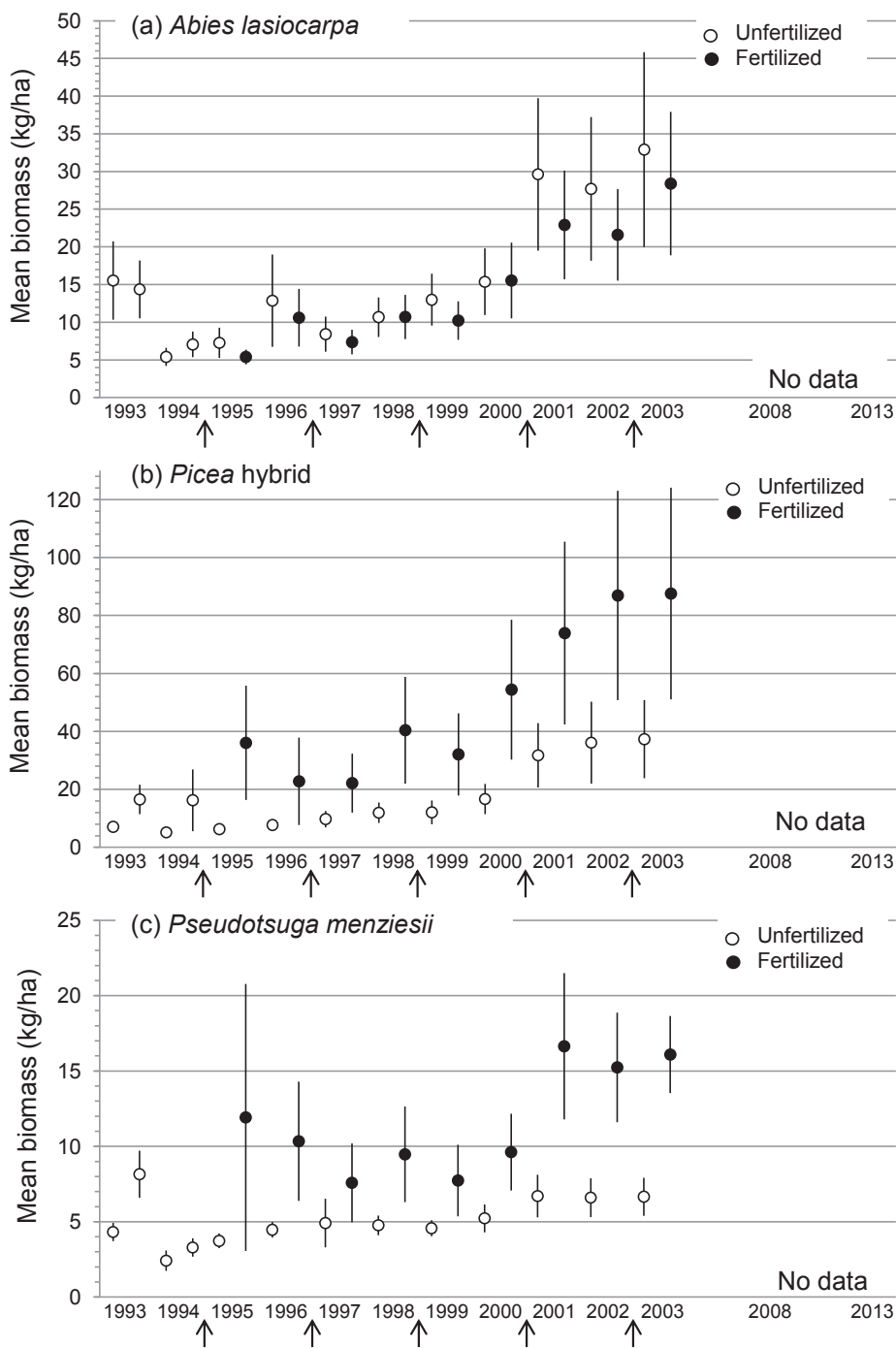


Fig. 7. Mean ( $n$  = number of replicate stands)  $\pm$  SE biomass production (kg/ha) of (a) *Abies lasiocarpa*, (b) *Picea hybrid*, and (c) *Pseudotsuga menziesii* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n$  = 8, 10, 9) and fertilized ( $n$  = 8, 8, 11) lodgepole pine stands. Arrow denotes application of fertilizer.

2017a). For example, although reindeer lichens declined in response to fertilization in northern Sweden, the dwarf shrubs *C. vulgaris* and *V. vitis-idaea* apparently increased in abundance (Eriksson and Raunistola, 1993).

#### 4.3. Mosses and terrestrial lichens

The significant decline in mean biomass of total mosses and total terrestrial lichens supported our H<sub>2</sub> and followed the general pattern of responses of these non-vascular plants to fertilization. In Scandinavia, lichens such as *Cladonia* spp., *H. splendens*, and *P. schreberi* tended to disappear and may have been replaced by other moss species (Nilsen,

2001; Saarsalmi and Malkonen, 2001; Strengbom and Nordin, 2008). Increases in abundance of nitrophilous herbs such as fireweed and shrubs such as *R. idaeus* may have contributed to these declines. In BC, *H. splendens* declined in coastal fertilized stands where the study focused on control of salal (*Gaultheria shallon*) (Prescott et al., 1993). In addition, in a Quebec study of fertilized jackpine (*Pinus banksiana*) stands, *P. schreberi* and *Cladonia* spp. lichens also declined (Prescott et al., 1995). Reductions in terrestrial, and potentially arboreal lichens, in fertilized stands would have negative impacts for woodland caribou who rely on these forage sources during winter (Eriksson and Raunistola, 1993; Thomas et al., 1994).



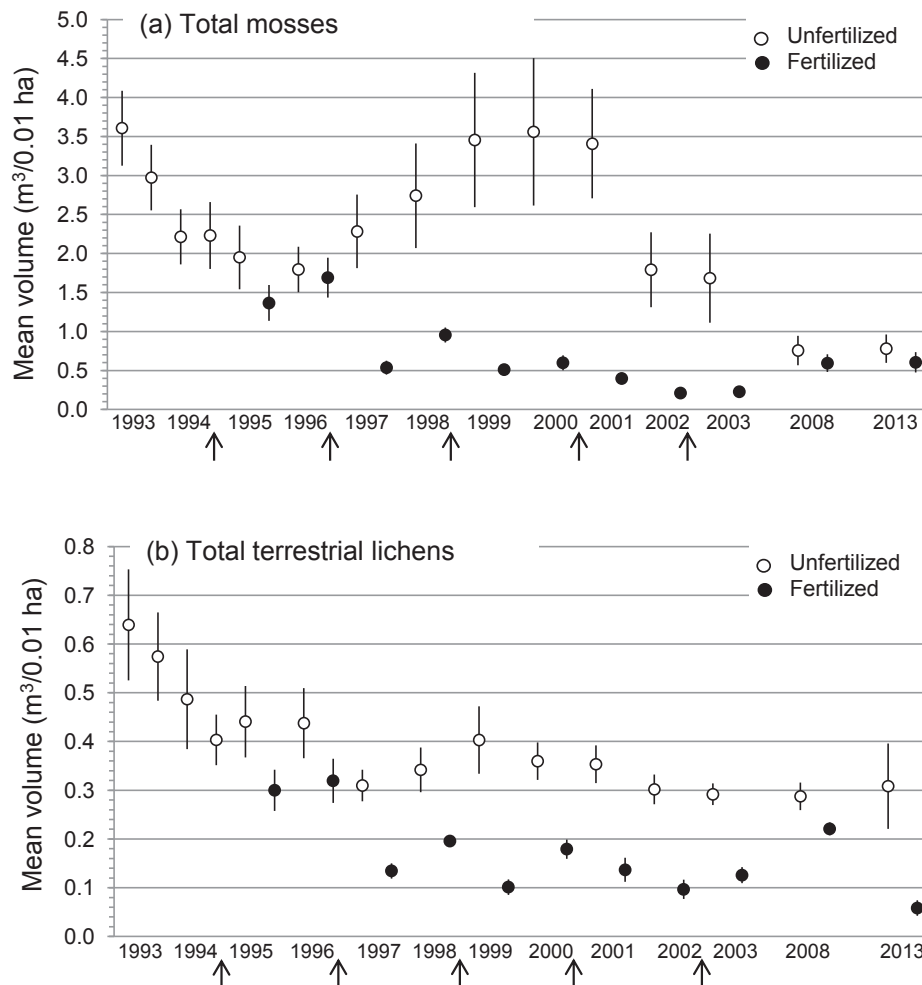


Fig. 8. Mean ( $n$  = number of replicate stands)  $\pm$  SE crown volume index ( $\text{m}^3/0.01$  ha) of (a) total mosses and (b) total terrestrial lichens each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized ( $n = 12$ ) and fertilized ( $n = 12$ ) lodgepole pine stands. Arrow denotes application of fertilizer.

#### 4.4. Forage quality and feeding damage

We did not have any data on nutritional quality of plant tissues owing to fertilization. However, nitrogen concentration of woody browse for downy birch (*B. pubescens*) and Scots pine (*Pinus sylvestris*) was significantly increased by forest fertilization in Sweden (Edenius, 1993; Ball et al., 2000). Crude protein and nitrogen concentration were increased in fertilized Scots pine stands in Norway (Solbraa and Brunvatne, 1994, as cited in Nilsen, 2001), and fertilization increased plant nitrogen concentrations in leaves of *Deschampsia flexuosa* and *Vaccinium myrtillus* in Sweden (Strengbom and Nordin, 2008; Hedwall et al., 2010). Grenier et al. (1977) reported a significant increase in crude protein in leaves and twigs of fertilized paper birch trees in moose habitat in Quebec. At five years after the most recent application in BC, Lindgren and Sullivan (2014a) reported that repeated fertilization increased crude protein content of pinegrass, a major forage source for wildlife and cattle (*Bos taurus*). Similarly, Melnychuk and Krebs (2005) found that grey willow had higher nitrogen concentration in fertilized twigs than control twigs at four years after the last fertilization application in a long-term study in the Yukon.

Addition of nutrients that enhance plant growth may also reduce the amount of secondary compounds in plant tissues that act as feeding deterrents to herbivores (Bryant et al., 1983; Månsson et al., 2009). Conversely, an improved nitrogen status of a plant may increase the availability of this element for nitrogen-containing secondary compounds (Kyto et al., 1996). However, another limiting factor to this

habitat enhancement may be the increase in secondary compounds (e.g., alkaloids, phenols, tannins) in plants growing in “open” sites such as early seral stages of succession. This process leads to dilution of nitrogen and other important nutrients, thereby disrupting digestion of forage plants (Lenart et al., 2002; Spalinger et al., 2010). Thus, forage plants growing in at least partial understory conditions with a degree of overhead canopy cover should be more digestible than those growing in the open on recently harvested sites. Operational fertilization in BC forests is normally conducted in young sapling to pole-sized stands that are usually 20–40 years old, and hence most forage plants would have some degree of canopy cover.

Another aspect of this forage improvement for wildlife is the relationship of feeding damage by mammalian herbivores to crop trees in fertilized stands. For example, increases in forage quality in Scandinavia appeared to relate directly to moose damage to Scots pine crop trees (Månsson et al., 2009). In western North America, snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*) and black bears (*Ursus americanus*) may preferentially feed on fertilized trees (Sullivan and Sullivan, 1982; Brockley and Sullivan, 1988; Nelson, 1989; Kimball et al., 1998). In at least some of these cases, there may be a trade-off between the positive effects of enhanced wildlife habitat and tree production owing to fertilization versus an increased risk of damage to crop trees. To this end, these consequences may occur not only on fertilized sites, but also within the surrounding forest (Ball et al., 2000; Gundersen et al. (2004)).

Foraging by native ungulates and cattle may have had important

influences on biomass of our herb and shrub species, particularly in fertilized stands, and contributed to variability in abundance of understory plants among different density stands (Riggs et al., 2000; Riggs et al., 2004). However, relative habitat use by mule deer, based on number of pellet-groups per ha, was not affected by stand density in either summer or winter periods, but was increased by fertilization (Lindgren and Sullivan, 2014b). Exclosures to exclude foraging by native ungulates such as mule deer and moose would have helped to further examine this potential source of variability but were not possible in this study. We did have a cattle exclosure (these structures did not preclude the presence of native ungulates) in each treatment stand to measure the influence of summer grazing on plant responses to our treatments (Lindgren and Sullivan, 2012). Herb abundance was consistently higher inside than outside exclosures in fertilized stands owing to foraging by cattle. In addition, relative habitat use by cattle was highest in the 500 and 1000 stems/ha stands, but appeared not to be positively correlated with thinning intensity (Lindgren and Sullivan, 2014b). Regardless, summer grazing by cattle was common across our three study areas and reduced the absolute biomass of grasses and forbs, but did not seem to negate the overall relative differences between fertilized and unfertilized stands.

## 5. Conclusions

Fertilized-induced changes in biomass for 19 shrub species were 4 increases, 3 declines, and 12 showed no change; 5 of 6 tree species showed no change. Only total grasses (increase), *R. acicularis* (increase), and *V. caespitosum* (decline) were significantly affected after one application of fertilizer. Repeated applications of nitrogen fertilizer may enhance biomass of some additional forage forbs and shrubs but reduce biomass of some dwarf shrubs, mosses, and lichens.

## Acknowledgements

We thank the Resources Practices Branch, BC Ministry of Forests, Lands, Natural Resource Operations, and Rural Development, Victoria, BC for funding support to prepare this manuscript. We thank Silviculture Branch, BC Ministry of Forests (MoF), Victoria, BC, the Canada-British Columbia Partnership Agreement on Forest Resource Development (FRDA II), Forest Renewal BC, Forest Innovation Investment; Gorman Bros. Lumber Ltd., Tolko Industries Ltd., Weyerhaeuser Company Limited, and the Alex Fraser Research Forest, University of BC for financial support during the field project. Operational treatments were conducted by the Silviculture sections of Penticton and Horsefly Forest Districts (MoF). We also thank the BC Ministry of Agriculture, Agriculture and Agri-Food Canada, Growing Forward: a federal-provincial-territorial initiative, and the Agricultural Greenhouse Gases Program for financial and logistical support. We also thank A. Kozak for guidance with statistical analysis and the many assistants who helped conduct the fieldwork.

## References

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource ability. *For. Ecol. Manage.* 192, 3–19.

Armleder, H.M., Waterhouse, M.J., Keisker, D.G., Dawson, R.J., 1994. Winter habitat use by mule deer in the central interior of British Columbia. *Can. J. Zool.* 72, 1721–1725.

Ball, J.P., Danell, K., Sunesson, P., 2000. Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. *J. Appl. Ecol.* 37, 247–255.

Balsom, S., Ballard, W.B., Whitlaw, H.A., 1996. Mature coniferous forest as critical moose habitat. *Alces* 32, 131–140.

Bergh, J., Nilsson, U., Grip, H., Hedwall, P.O., Lundmark, T., 2008. Effects of frequency of fertilization on production, foliar chemistry, and nutrient leaching in young Norway spruce stands in Sweden. *Silva Fenn.* 42, 721–733.

Boonstra, R., Krebs, C.J., 2006. Population limitation of the northern red-backed vole in the boreal forests of northern Canada. *J. Anim. Ecol.* 75, 1269–1284.

Boonstra, R., Krebs, C.J., Gilbert, S., Schweiger, S., 2001. Voles and mice. In: Krebs, C.J.,

Boutin, S., Boonstra, R. (Eds.), *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, Oxford UK, pp. 215–239.

Boonstra, R., Krebs, C.J., Cowcill, K., 2017. Responses of key understory plants in the boreal forests of western North America to natural versus anthropogenic nitrogen levels. *For. Ecol. Manage.* 401, 45–54.

Boutin, S., Krebs, C.J., Boonstra, R., et al., 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74, 69–80.

Boutin, S., Krebs, C.J., Boonstra, R., Sinclair, A.R.E., 2003. The role of the lynx-hare cycle in boreal forest community dynamics. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal community dynamics. Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, UK, pp. 487–509.

Brockley, R.P., 2005. Effects of post-thinning density and repeated fertilization on the growth and development of young lodgepole pine. *Can. J. For. Res.* 35, 1952–1964.

Brockley, R.P., 2007a. Effects of 12 years of repeated fertilization on the foliar nutrition and growth of young lodgepole pine in the central interior of British Columbia. *Can. J. For. Res.* 37, 2115–2129.

Brockley, R.P., 2007b. Assessing the effects of fertilization on understory vegetation in young lodgepole pine and spruce forests in central British Columbia. *Ext. Note 81*. BC Ministry of Forests and Range, Victoria, BC.

Brockley, R.P., Sullivan T.P., 1988. Relationship of feeding damage by red squirrels to cultural treatments in young stands of lodgepole pine. In: Schmidt, W.C. (Ed.), *Future Forests of the Mountain West: A Stand Culture Symposium. Proceedings*. 1986. USDA For.Serv. Gen.Tech. REP-INT243, pp. 322–329.

Bryant, J.P., Chapin III, F.S., Klein, D.R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40, 357–368.

Cook, J.G., Irwin, L.L., Bryant, L.D., Riggs, R.A., Thomas, J.W., 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. In: *Wildlife Monographs*, vol. 141.

Cook, J.G., 2002. Nutrition and food. In: Towell, D.E., Thomas, J.W. (Comp. and Eds.), *North American Elk: Ecology and Management*. A Wildlife Management Institute Book. Smithsonian Institution Press, Washington.

Dale, M.R.T., Francis, S., Krebs, C.J., Nams, V.O., 2001. Trees. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, Oxford, UK, pp. 116–137.

Dawson, R.J., Armleder, H.M., Waterhouse, M.J., 1990. Preferences of mule deer for Douglas-fir foliage from different sized trees. *J. Wildl. Manage.* 54, 378–382.

Demarais, S., Verschuyf, J.P., Roloff, G.J., Miller, D.A., Wigley, T.B., 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the U.S. *For. Ecol. Manage.* 385, 308–330.

Edenius, L., 1993. Browsing by moose on Scots pine in relation to plant resource availability. *Ecology* 74, 2261–2269.

Eriksson, O., Raunistola, T., 1993. Impact of forest fertilizers on winter pastures of semi-domesticated reindeer. *Rangifer* 13, 203–214.

Fox, T.R., Jokela, E.A., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. *J. For.* 105, 337–347.

Granath, G., Strebom, J., 2017. Nitrogen fertilization reduces wild berry production in boreal forests. *For. Ecol. Manage.* 390, 119–126.

Grenier, P., Bernier, B., Bedard, J., 1977. The effect of forest fertilization on crude protein content, growth, and use by moose (*Alces alces*) of paper birch (*Betula papyrifera*) in Laurentides Park, Quebec. In: *Proceedings of the 13th North American Moose Conference and Workshop*. Jasper, Alberta, pp. 258–278.

Gundersen, H., Andreassen, H.P., Storaas, T., 2004. Supplemental feeding of migratory moose: Alces alces: forest damage at to spatial scales. *Wildl. Biol.* 10, 213–223.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. *For. Ecol. Manage.* 155, 81–95.

Hedwall, P.-O., Nordin, A., Brunet, J., Bergh, J., 2010. Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilisation. *Forest Ecol. Manage.* 259, 2418–2425.

Hitchcock, C.L., Cronquist, A., 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington 730 p.

Hodder, D.P., Rea, R.V., Crowley, S.M., 2013. Diet content and overlap of sympatric mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*) during a deep snow winter in north-central British Columbia, Canada. *Can. Wildl. Biol. Manage.* 2, 43–50.

Hodges, K.E., 2000. Ecology of snowshoe hares in southern boreal and montane forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., Mckelvey, K.S., Squires, J.R. (Eds.), *Ecology and Conservation of the Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA, pp. 163–206.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.

Huynh, H., Feldt, L.S., 1976. Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split-plot designs. *J. Educ. Stat.* 1, 69–82.

IBM Corp.Inc., 2016. *IBM SPSS Statistics for Windows. Version 24.0* IBM Corp. Armonk, NY.

Jokela, E.J., Dougherty, P.M., Martin, T.A., 2004. Long-term production dynamics of loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. *For. Ecol. Manage.* 192, 117–130.

Kellner, O., Redbo-Torstenson, P., 1995. Effects of elevated nitrogen deposition on the field-layer vegetation in coniferous forests. *Ecol. Bull.* 44, 227–237.

Kimball, B.A., Turblom, E.C., Nolte, D.L., Griffen, D.L., Engeman, R.M., 1998. Effects of thinning and nitrogen fertilization on sugars and terpenes in Douglas-fir vascular tissues: implications for black bear foraging. *For. Sci.* 44, 599–602.

Koehler, G.M., 1990. Snowshoe hare, *Lepus americanus*, use of forest successional stages and population changes during 1985–1989 in North-central Washington. *Can. Field-Nat.* 105, 291–293.

Koehler, G.M., Britnell, J.D., 1990. Managing spruce-fir habitat for lynx and snowshoe

- hares. *J. For.* 88, 10–14.
- Krebs, C.J., Dale, M.R.T., Nams, V.O., Sinclair, A.R.E., O'Donoghue, M., 2001. Shrubs. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, Oxford, UK, pp. 92–115.
- Kuehl, R.O., 1994. Repeated measures designs. In: *Statistical Principles of Research Design and Analysis*. Duxbury Press, Belmont, CA, pp. 499–528.
- Kufeld, R.C., Wallmo, O.C., Feddema, C., 1973. Foods of the Rocky Mountain mule deer. U.S. Dep. Agric. For. Serv. Res. Paper RM-1, pp.1-11.
- Kyto, M., Niemela, P., Larsson, S., 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75, 148–159.
- Lenart, E.A., Bowyer, R.T., Hoef, J.V., Ruess, R.W., 2002. Climate change and caribou: effects of summer weather on forage. *Can. J. Zool.* 80, 664–678.
- Lindgren, P.M.F., Sullivan, T.P., 2012. Response of plant community abundance and diversity during 10 years of cattle exclusion within silvopasture systems. *Can. J. For. Res.* 42, 451–462.
- Lindgren, P.M.F., Sullivan, T.P., 2013a. Long-term responses of tree and stand growth of young lodgepole pine to pre-commercial thinning and repeated fertilization. *For. Ecol. Manage.* 307, 155–164.
- Lindgren, P.M.F., Sullivan, T.P., 2013b. Influence of stand thinning and repeated fertilization on plant community abundance and diversity in young lodgepole pine stands: 15-year results. *For. Ecol. Manage.* 308, 17–30.
- Lindgren, P.M.F., Sullivan, T.P., 2014a. Response of forage yield and quality to thinning and fertilization of young forests: implications for silvopasture management. *Can. J. For. Res.* 44, 281–289.
- Lindgren, P.M.F., Sullivan, T.P., 2014b. Mule deer – cattle interactions in managed coniferous forests during seasonal grazing periods in southern British Columbia, Canada. *Wildl. Res.* 41, 691–702.
- Lindgren, P.M.F., Sullivan, T.P., Sullivan, D.S., Brockley, R.P., Winter, R., 2007. Growth response of young lodgepole pine to thinning and repeated fertilization treatments: 10-year results. *Forestry* 80, 587–611.
- Lindgren, P.M.F., Sullivan, T.P., Ransome, D.B., Sullivan, D.S., Zabek, L., 2017. Long-term influence of stand thinning and repeated fertilization on forage production in young lodgepole pine forests. *Can. J. For. Res.* 47, 1123–1130.
- Littell, R.C., 1989. Statistical analysis of experiments with repeated measures. *HortScience* 24, 36–40.
- MacKinnon, A., Pojar, J., Coupé, R., 1992. *Plants of Northern British Columbia*. FRDA II B.C. Ministry of Forests and Lone Pine Publishing, Edmonton, Alberta, Canada.
- Månsson, J., Bergström, R., Danell, K., 2009. Fertilization—effects on deciduous tree growth and browsing by moose. *For. Ecol. Manage.* 258, 2450–2455.
- McAllister, J.A., Hoffman, R.S., 1988. *Phenacomys intermedius*. No. 305. American Society of Mammalogists, Provo, Utah, USA.
- Meidinger, D., Pojar, J., 1991. *Ecosystems of British Columbia*. Spec. Rep. Ser. No. 6. Res. Br., Min. For., Victoria, British Columbia.
- Melnychuk, M.C., Krebs, C.J., 2005. Residual effects of NPK fertilization on shrub growth in a Yukon boreal forest. *Can. J. Bot.* 83, 399–404.
- Merritt, J.F., 1981. *Clethrionomys gapperi*. Mammalian species. No. 146. American Society of Mammalogists, Provo, Utah, USA.
- Monkkonen, M., Juutinen, A., Mazzotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H., Tikkanen, O.-P., 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. *For. Ecol. Manage.* 134, 80–89.
- Moore, S.E., Allen, H.L., 1999. *Plantation forestry*. In: Hunter, M.L. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, New York, NY, pp. 400–433.
- Mowat, G., Slough, B., 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. *Can. J. Zool.* 81, 1736–1745.
- Nabuurs, G.J., Pussinen, A., van Brusselen, J., Schelhaas, M.J., 2007. Future harvesting pressure on European forests. *Eur. J. For. Res.* 126, 391–400.
- Nagorsen, D.W., 2005. *Rodents and Lagomorphs of British Columbia*. Volume 4. The Mammals of British Columbia. Royal BC Museum Victoria, BC.
- Nams, V.O., Folkard, N.F.G., Smith, J.N.M., 1993. Effects of nitrogen fertilization on several woody and non-woody boreal forest species. *Can. J. Bot.* 71, 93–97.
- Nams, V.O., Folkard, N.F.G., Smith, J.N.M., 1996. Nitrogen fertilization stimulates herbivory by snowshoe hares in the boreal forest. *Can. J. Zool.* 74, 196–199.
- Nelson, E.E., 1989. Black bears prefer urea-fertilized trees. *West J. Appl. Forest.* 4, 13–15.
- Nilsen, P., 2001. Fertilization experiments on forest mineral soils: a review of the Norwegian results. *Scand. J. For. Res.* 16, 541–554.
- Nyberg, J.B., 1990. Interactions of timber management with deer and elk. In: Nyberg, J.B., Janz, D.W. (Eds.), *Deer and Elk Habitats in Coastal Forests of Southern British Columbia*. Edited by British Columbia Ministry of Forests, Victoria, B.C. Special Report Series 5, pp. 99–132.
- Parish, R., Coupe, R., Lloyd, D., 1996. *Plants of Southern Interior British Columbia*. Lone Pine Publishing, Vancouver, BC Canada, pp. 464 p.
- Pierce, J.D., 1984. Shiras moose forage selection in relation to browse availability in north-central Idaho. *Can. J. Zool.* 62, 2404–2409.
- Pierce, J.D., Peek, J.M., 1984. Moose habitat use and selection patterns in north-central Idaho. *J. Wildl. Manage.* 48, 1334–1343.
- Prescott, C.E., Coward, L.P., Weetman, G.F., Gessel, S.P., 1993. Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*), in two coastal Douglas-fir forests. *For. Ecol. Manage.* 61, 45–60.
- Prescott, C.E., Kumi, J.W., Weetman, G.F., 1995. Long-term effects of repeated N fertilization and straw application in a jack pine forest. 2. Changes in the ericaceous ground vegetation. *Can. J. For. Res.* 25, 1984–1990.
- Reich, L.M., 1981. *Microtus pennsylvanicus*. No. 159. American Society of Mammalogists, Provo, Utah, USA.
- Riggs, R.A., Cook, J.G., Irwin, L.L., 2004. Management implications of ungulate herbivory in Northwest Forest Ecosystems. In: *Transactions of the North American Wildlife and Natural Resources Conference*, vol. 69, pp. 759–784.
- Riggs, R.A., Tiedemann, R.A., 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. USDA Forest Service Res. Pap PNW-RP-527. 77 p.
- Saarsalmi, A., Malkonen, E., 2001. Forest fertilization research in Finland: a literature review. *Scand. J. For. Res.* 16, 514–535.
- Sinclair, A.R.E., Krebs, C.J., Boonstra, R., Boutin, S., Turkington, R., 2001. Testing hypotheses of community organization for the Klauene Ecosystem. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, Oxford, UK, pp. 408–436.
- Smolen, M.J., Keller, B.L., 1987. *Microtus longicaudus*. No. 271. American Society of Mammalogists, Provo, Utah, USA.
- Spalinger, D.E., Collins, W.B., Hanley, T.A., Cassara, N.E., Carnahan, A.M., 2010. The impact of tannins on protein, dry matter, and energy digestion in moose (*Alces alces*). *Can. J. Zool.* 88, 977–987.
- Stickney, P.F., 1985. Data base for early post-fire succession on the sundance burn, northern Idaho. USDA For. Serv. Intermountain Res. Stat. Gen. Tech. Rep. INT-189.
- Strengbom, J., Nordin, A., 2008. Commercial forest fertilisation causes long-term residual effects in ground vegetation of boreal forests. *For. Ecol. Manage.* 256, 2175–2181.
- Strengbom, J., Nordin, A., Näsholm, T., Ericson, L., 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. *Funct. Ecol.* 15, 451–457.
- Suchar, V.A., Crookston, L., 2010. Understorey cover and biomass indices predictions for forest ecosystems of the Northwestern United States. *Ecol. Indicators* 10, 602–609.
- Sullivan, T.P., Sullivan, D.S., 1982. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. *For. Chron.* 58, 263–267.
- Sullivan, T.P., Sullivan, D.S., 2014. Fertilization, cattle grazing, and voles: Collapse of meadow vole populations in young forests? *Wildl. Res.* 41, 367–378.
- Sullivan, T.P., Sullivan, D.S., 2017a. Influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests. *Environ. Rev.* 25, 1–17.
- Sullivan, T.P., Sullivan, D.S., 2017b. Old-growth characteristics 20 years after thinning and repeated fertilization of lodgepole pine forest: tree growth, structural attributes, and red-backed voles. *For. Ecol. Manage.* 391, 207–220.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2012. Influence of repeated fertilization and cattle grazing on forest ecosystems: abundance and diversity of forest-floor small mammals. *For. Ecol. Manage.* 277, 180–195.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M., Ransome, D.B., 2006a. Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*). *Can. J. For. Res.* 36, 2080–2089.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M., Ransome, D.B., 2006b. Influence of repeated fertilization on forest ecosystems: relative habitat use by mule deer and moose. *Can. J. For. Res.* 36, 1395–1406.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *For. Ecol. Manage.* 258S, S127–S141.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2013. Stand structure and small mammals in intensively managed forests: scale, time, and testing extremes. *For. Ecol. Manage.* 310, 1071–1087.
- Thomas, D.C., Edmonds, E.J., Brown, W.K., 1994. The diet of woodland caribou populations in west-central Alberta. *Rangifer Special Issue No. 9*, pp. 337–342.
- Turkington, R., John, E., Krebs, C.J., et al., 1998. The effects of NPK fertilization for nine years on boreal forest vegetation in northwestern Canada. *J. Veg. Sci.* 9, 333–346.
- Weetman, G.F., McWilliams, E.R.G., Thompson, W.A., 1992. Nutrient management on coastal douglas-fir and Western Hemlock Stands: The Issues. In: Chappell, H.N., Weetman, G.F., Miller, R.E. (Eds.), *Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests*. Institute of Forest Resources Contrib., vol. 73. College of Forest Resources, Univ. of Washington, Seattle, pp. 17–27.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice-Hall Inc, Englewood Cliffs, N. J. 663 p.