

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

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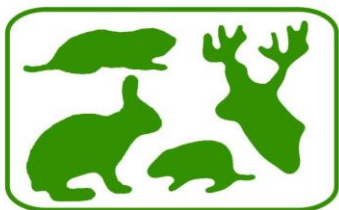
Resource Practices Branch

Ministry of Forests, Lands, Natural Resource Operations, and Rural Development

8th Floor, 727 Fisgard Street

Victoria, B.C.

V8W 1R8



Principal Investigator:

Dr. Thomas P. Sullivan

tom@appliedmammal.com

Applied Mammal Research Institute

11010 Mitchell Avenue

Summerland, BC

V0H 1Z8

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1.0 Executive Summary

Stand thinning and fertilization are silvicultural practices designed to sustain wood and biomass production while concurrently creating a diversity of forest habitat conditions to meet the goals of biodiversity conservation. Nitrogen fertilization is a major way to improve the future timber supply, increase the size of individual trees without sacrificing stand volume, address age-class imbalances, and increase long-term harvest levels. 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 include mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), moose (*Alces alces*), and woodland caribou (*Rangifer tarandus*). Smaller herbivores include the snowshoe hare (*Lepus americanus*) and several species of voles. All of these mammals rely on a wide range of herbaceous (summer range) and shrub-tree (winter range) plant species as their major forage resources.

Impacts of fertilization on forest vascular plant species may have important consequences for the nutrition, cover, and consequent survival of these herbivores, particularly in winter. 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. However, a detailed examination of the biomass response of individual species of forage plants to consecutive nutrient additions in forests of British Columbia (BC) has not been done. Thus, this project was designed to assess the influence of large-scale repeated fertilization, up to 20 years after the onset of treatments, on biomass production of

forage plants, particularly total grasses, total forbs, shrubs (19 species), and trees (6 species) for native mammalian herbivores. A secondary objective was to assess the responses of total mosses and total terrestrial lichens, as part of the ground-layer vegetation, to forest fertilization.

Project areas were located in lodgepole pine (*Pinus contorta* var. *latifolia*) stands near Summerland, Kelowna, and Williams Lake in south-central BC, Canada. Each study area had eight replicate stands: four unfertilized, and four fertilized five times at 2-year intervals. Optimum nutrition treatments were initiated in 1994 at which time stands were 12-14 years old. Sampling of understory vegetation was designed to measure the effects of fertilization on biomass of groups and individual plant species within herb, shrub, and tree layers.

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 recorded in this project serve as summer forage for mule deer, moose, elk, and woodland caribou. Fireweed (*Epilobium angustifolium*), a preferred forage for mule deer, increased dramatically 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, but in the second 5-year fertilization period the treatment did start to enhance shrub growth. Saskatoon berry (*Amelanchier alnifolia*), prickly rose (*Rosa acicularis*), red raspberry (*Rubus idaeus*), and willow (*Salix* spp.) appeared to have escaped the herb layer suppression

and increased in biomass. 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. Understory Douglas-fir (*Pseudotsuga menziesii*) responded positively to fertilization, but subalpine fir (*Abies lasiocarpa*) and the three deciduous tree species did not. Deciduous tree species such as paper birch (*Betula papyrifera*), poplars (*Populus* spp.), and some coniferous tree species (*A. lasiocarpa* and *P. menziesii*) may be readily eaten by ungulates in winter.

Dwarf shrubs such as kinnikinnick (*Arctostaphylos uva-ursi*), twinflower *Linnaea borealis*, and dwarf blueberry (*Vaccinium caespitosum*) declined in fertilized stands. Mean biomass of black huckleberry (*V. membranaceum*) appeared lower in fertilized than unfertilized stands, but this difference was not statistically significant. Increasing cover of grasses and nitrophilous herbs, as well as canopy cover from rapidly growing crop trees, in fertilized stands may have contributed to the decline of some dwarf shrubs. Mean biomasses of falsebox (*Pachistima myrsinites*), trailing raspberry (*Rubus pubescens*), and grouseberry (*V. scoparium*) were similar in unfertilized and fertilized stands. *Vaccinium* and *A. uva-ursi* are major sources of berry crops for red-backed voles (*Myodes* spp.) and other small mammal species.

Mean crown volume index of total mosses and terrestrial lichens declined significantly in fertilized stands. Mean crown volume index of mosses returned to comparable levels in unfertilized and fertilized stands in the post-treatment years 2008 and 2013. However, terrestrial lichens in post-fertilized stands did not return to levels found in unfertilized stands.

Forage plants growing in at least partial understory conditions with a degree of overhead canopy cover may 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 30 to 40 years old, and hence most forage plants would have some degree of canopy cover. Snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*) and black bears (*Ursus americanus*) may preferentially feed on fertilized trees. There may sometimes 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.

We investigated the responses in mean biomass of forage plants in all of our groups and individual species of vascular plants, and mean crown volume index of mosses and terrestrial lichens, to the 1 to 5 applications of fertilizer in this study. For 1 application: total grasses and *R. acicularis* increased; *V. caespitosum* declined. For 2 applications: total herbs and total understory increased; *A. uva-ursi*, mosses, and lichens declined. For 3 applications: total forbs and *R. idaeus* increased; *L. borealis* declined. For 4 applications: *A. alnifolia* and *P. menziesii* increased. The other individual shrub and tree species and total shrubs were not affected by any of the fertilizer applications. Operational fertilization with one application of nitrogen in these forests seemed positive, or relatively benign, in terms of changes in biomass of understory forage plants. 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.

2.0 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 canadensis*), moose (*Alces alces*), and woodland caribou (*Rangifer tarandus*) which are often associated

with 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, 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 shrub-tree (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 (Table 1). 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 lichens, 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*). 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*) and black cottonwood (*Populus trichocarpa*), as well as the shrubs alder

Table 1. Important forage plants for native mammalian herbivores in interior forests of British Columbia^a that may be relevant to those areas with application of urea fertilizer. Lists of herb, shrub, tree, and lichen species are given.

Herbs		Shrubs		Trees & Lichens	
<i>Anaphalis margaritacea</i>	Pearly everlasting	<i>Acer glabrum</i>	Douglas maple	<i>Abies lasiocarpa</i>	Subalpine fir
<i>Arnica cordifolia</i>	Heart-leaved arnica	<i>Alnus sinuata</i>	Sitka alder	<i>Betula papyrifera</i>	Paper birch
<i>Aster</i> spp.	Asters	<i>Amelanchier alnifolia</i>	Saskatoon berry	<i>Picea glauca engelmannii</i>	Interior spruce
<i>Calamagrostis rubescens</i>	Pinegrass	<i>Arctostaphylos uva-ursi</i>	Kinnickinnick	<i>Populus tremuloides</i>	Trembling aspen
<i>Carex</i> spp.	Sedges	<i>Ceanothus velutinus</i>	Snowbrush	<i>Populus trichocarpa</i>	Black cottonwood
<i>Cornus canadensis</i>	Bunchberry	<i>Cornus stolonifera</i>	Red-osier dogwood	<i>Pseudotsuga menziesii</i>	Douglas-fir
<i>Epilobium angustifolium</i>	Fireweed	<i>Corylus cornuta</i>	Beaked hazel	Terrestrial lichens	
<i>Equisetum</i> spp.	Horsetail	<i>Linnaea borealis</i>	Twinflower	<i>Cladina</i> spp.	
<i>Galium boreale</i>	Northern bedstraw	<i>Lonicera involucrata</i>	Black twinberry	<i>Cladonia</i> spp.	
Grasses		<i>Lonicera utahensis</i>	Red twinberry	<i>Stereocaulon</i> spp.	
<i>Lupinus</i> spp.	Lupine	<i>Mahonia aquifolium</i>	Oregon-grape		
<i>Taraxacum officinale</i>	Dandelion	<i>Pachistima myrsinites</i>	Falsebox		
<i>Trifolium</i> spp.	Clover	<i>Rosa acicularis</i>	Prickly rose		
		<i>Rubus ideaus</i>	Red raspberry	Arboreal lichens	
		<i>Salix</i> spp.	Willows	<i>Alectoria</i> spp.	
		<i>Shepherdia canadensis</i>	Soapberry	<i>Bryoria</i> spp.	
		<i>Spiraea betulifolia</i>	Birch-leaved spiraea	<i>Cetraria</i> spp.	
		<i>Symphoricarpos albus</i>	Snowberry		
		<i>Vaccinium caespitosum</i>	Dwarf blueberry		
		<i>Vaccinium membranaceum</i>	Black huckleberry		
		<i>Vaccinium scoparium</i>	Grouse berry		
		<i>Viburnum edule</i>	Highbush cranberry		

^aReferences:

Mule Deer: Kufeld et al., 1973; Deschamp et al., 1979; Willms et al., 1980; Wallmo and Regelin, 1981; Bunnell, 1990; Waterhouse et al., 1994; Serrouya and D'Eon, 2008.

Elk: Cook, 2002; Hodder et al. 2013.

Moose: Franzmann, 1981; Pierce, 1984; Renecker and Hudson, 1988; Lautenschlager et al., 1997; Newbury et al., 2007; Hodder et al., 2013.

Woodland Caribou: Thomas et al., 1994; Cichowski et al., 2004.

Snowshoe hares: Kohler and Brittell, 1990; Nagorsen, 2005.

Voies: Merritt, 1981; Reich, 1981; Smolen and Keller, 1987; McAllister and Hoffman, 1988.

(*Alnus* spp.), prickly rose (*Rosa acicularis*), and red-osier dogwood (*Cornus stolonifera*) (Table 1). 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 (Table 1).

Snowshoe hares occupy dense stands of conifers, or deciduous tree species, with understory shrubs, 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 Brittell, 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 in forest ecosystems. 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 may also occupy 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). 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+b; Mansson 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, at an operational scale, has

not been done. Thus, this project was designed to assess the influence of large-scale repeated fertilization, up to 20 years after the onset of treatments, on biomass production of forage plants, particularly grass, forb, shrub, and tree species for native mammalian herbivores. A secondary objective was to assess the responses of mosses and terrestrial lichens, as part of the ground-layer vegetation, to forest fertilization. This report follows the earlier publication reviewing the influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests (Sullivan and Sullivan, 2017a). The current report focuses specifically on biomass production (quantity) of forage plant species, on an annual basis, and its relationship to native mammalian herbivores, in repeatedly fertilized stands of young lodgepole pine (*Pinus contorta* var. *latifolia*) in the southern and central interior of British Columbia (BC).

3.0 Methods

3.1. Study areas

Three study areas were located in southern BC where candidate stands of young (12 to 14 year old) lodgepole pine 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 interspersation of experimental units (Hurlbert, 1984) and the logistics and access for conducting the operational-scale treatments of 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_{dm}) 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* x *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 some single and group seed-tree reserves of Douglas-fir began in this area in 1978 in response to an outbreak of mountain pine beetle (MPB) (*Dendroctonus ponderosae*). Depending on the original composition of the harvested stands and the degree of windthrow after harvesting, the number of residual Douglas-fir ranged from none to 1 or 2 trees per ha in our candidate stands. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species made up of three harvested units with pre-thinning stand densities ranging from 9,980 to 11,150 stems/ha. In 1993 at the start of the study, mean ($\pm$ SE) stand diameter (DBH, diameter at breast height, 1.3 m above the soil surface) ranged from 2.2 ± 0.1 cm to 4.1 ± 0.1 cm and mean stand height ranged from 2.3 ± 0.1 m to 3.4 ± 0.1 m, with a mean age of 13 years. In 2013, at 20 years after the start of treatments, mean ($\pm$ SE) stand diameter ranged from 9.1 ± 0.2 cm to 19.4 ± 0.3 cm and mean stand height ranged from 7.8 ± 0.1 m to 10.4 ± 0.1 m, with a mean age of 33 years. Area of stands ranged from 4.4 to 11.3 ha.

The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04'N; 119°34'W) in the MS_{dm} 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. One large unit (84.8 ha) with a pre-thinning density of 8,686 stems/ha was shaped in a horseshoe with an unharvested riparian buffer zone separating the two arms. This riparian zone had a steep ravine and varied in width from 75 to 300 m. The overall unit was separated into eight treatment stands as per the experimental design. In 1993, the mean ($\pm$ SE) stand diameter (DBH) and height ranged from 3.1 ± 0.1 cm to 4.7 ± 0.1 cm and 3.0 ± 0.1 m to 4.1 ± 0.1 m, respectively, with a mean stand age of 13 years. In 2013, the mean ($\pm$ SE) stand diameter ranged from 13.4 ± 0.5 cm to 20.4 ± 0.7 cm and mean stand height ranged from 10.8 ± 0.2 m to 12.6 ± 0.2 m, with a mean stand age of 33 years. Area of stands ranged from 9.5 to 11.9 ha.

The Cariboo study area was located in the Alex Fraser Research Forest (University of BC), 75 km northeast of Williams Lake, BC (52°29'N; 121°45'W) in the Sub-Boreal Spruce (SBS_{dm}) 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. The SBS has a continental climate and seasonal extremes of temperature. Mean annual temperature is 1.7-5.0 °C, and precipitation ranges from 440 to 900 mm. In mature stands, interior

hybrid spruce, subalpine fir and some Douglas-fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. This unit covered 80 ha and was clearcut harvested in 1976 followed by some natural regeneration and some planting of lodgepole pine in 1983. Pre-thinning stand density was 3,333 stems/ha. Eight treatment stands were located on this unit. Paired stands were contiguous on one side only. In 1993, the mean stand diameter (DBH) and height ranged from 4.4 ± 0.2 cm (mean $\pm$ SE) to 7.2 ± 0.3 cm and 3.4 ± 0.1 m to 5.4 ± 0.2 m, respectively, with a mean stand age of 13 years. In 2003, DBH ranged from 10.9 ± 0.3 cm to 16.8 ± 0.4 cm and stand height ranged from 8.2 ± 0.1 m to 10.2 ± 0.2 m. Area of stands ranged from 1.5 to 4.5 ha.

3.2. *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. Unfertilized and fertilized stands at 1000 stems/ha in 1999, 2008, and 2013 are illustrated in Fig. 1a-f, with an aerial view of all treatment stands at the Kelowna area in 2003 (Fig. 2). Unfortunately, the Cariboo replicate was decimated by MPB 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 (≤ 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

Figure 1. Photographs (summer) of unfertilized and fertilized (F) lodgepole pine stands at Summerland-Kelowna, 1000 trees per ha, (a) 1999 (with mule deer), (b) 1999 F, (c) 2008, (d) 2008 F, (e) 2013, (f) 2013 F. Treatment stands were thinned in 1993, fertilized five times from 1994 to 2002; and all stands pruned in 1998.

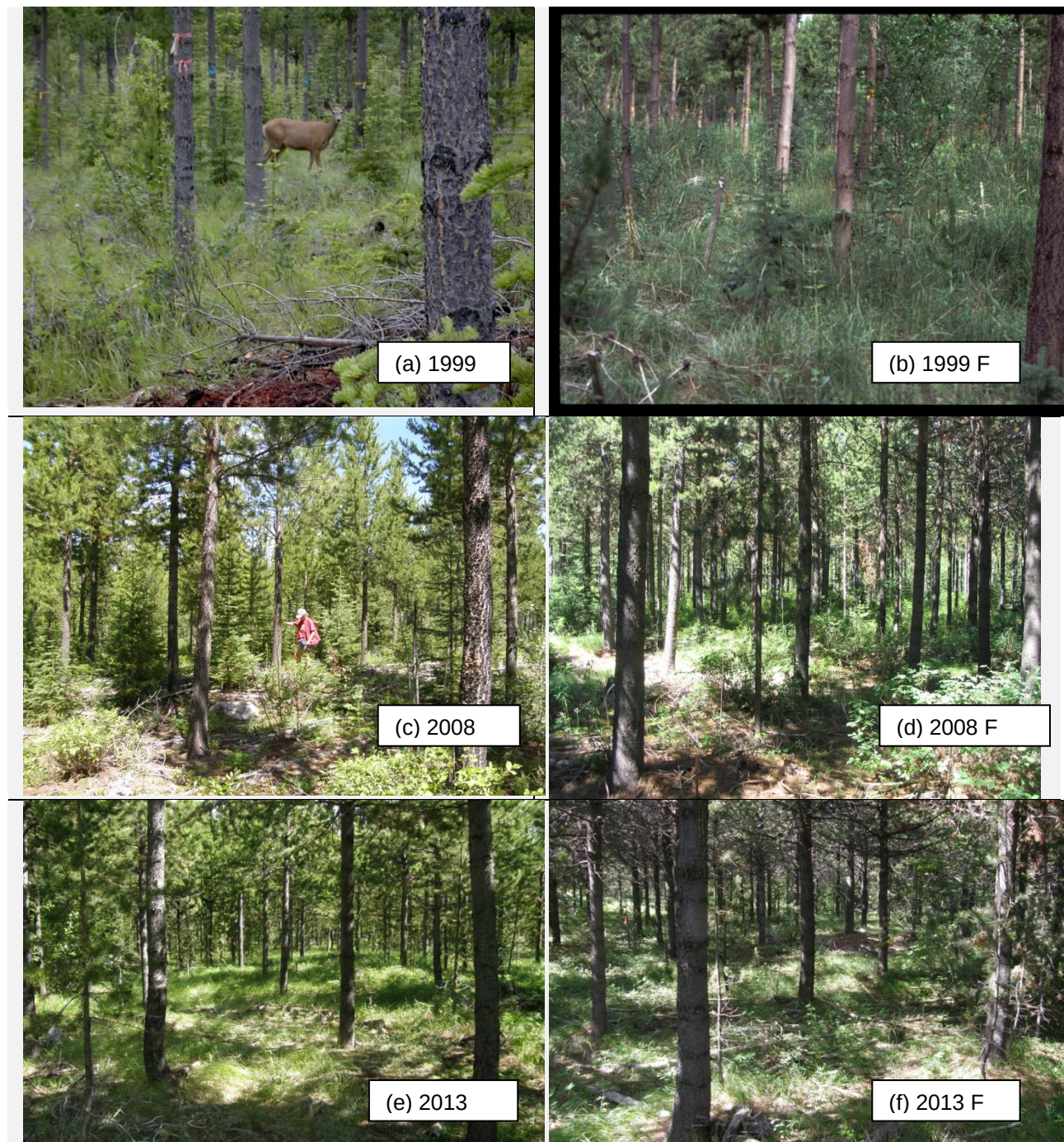
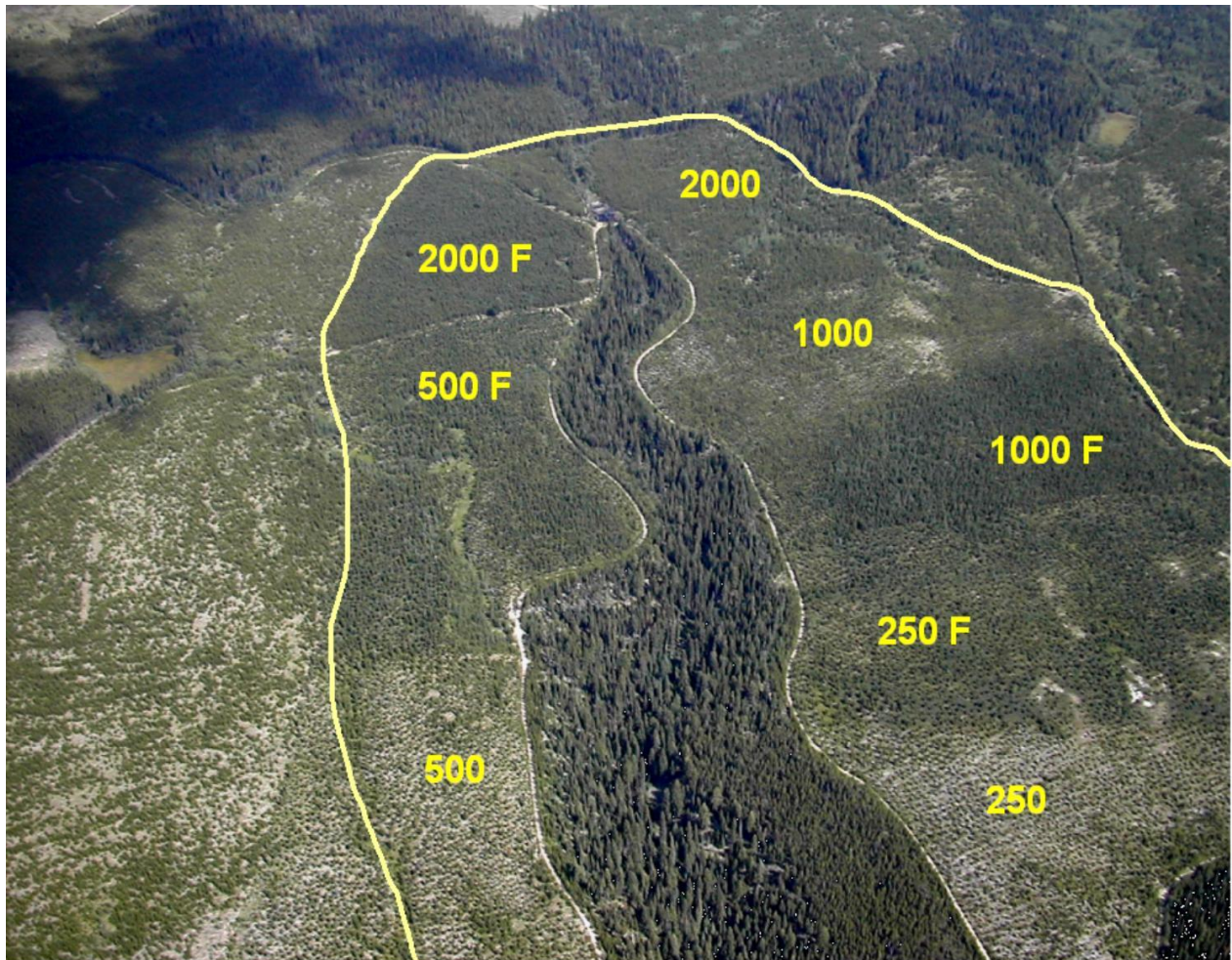


Figure 2. Photograph of the range of PCT+FERT treatments at the Kelowna replicate block with 4 stand densities (stems/ha) not fertilized and fertilized (F) 10 years after initiation of treatments in summer 2003.



Summerland area was not affected by MPB and represented an undisturbed complete replicate block over the 20-year period (1993 to 2013).

Thus, all three replicates were intact for the first 10 years of the project (1993 to 2003) which represented the “fertilization period” that is of most interest to measuring the response of forage species to nutrient additions. All three study areas had summer grazing by cattle (*Bos taurus*).

3.3. *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 (100 P), 100 kg/ha Potassium (100 K), 50 kg/ha Sulfur (50 S), 25 kg/ha Magnesium (25 Mg), and 1.5 kg/ha Boron (1.5 B). The objective was to maintain a foliar N level of 1.3% with foliar levels of all 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 pre-commercial thinning 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). A pruning (3-m lift) was done in all stands with densities < 2000 stems/ha in 1998, five years after PCT. Typical rotation times for intensively managed stands such as these would be 40-50 years.

3.4. *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 x 5-m plots. Each plot contained three sizes of nested sub-plots: a 5-m x 5-m subplot for sampling trees, a 3-m x 3-m sub-plot for sampling shrubs, and a 1-m x 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 ($\text{m}^3/0.01 \text{ ha}$) 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. 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.

3.5. 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 determined the correlation between crown volume index and biomass and developed regression equations to determine biomass from the estimates of crown volume index for individual species of herbs and shrubs. There were strong and significant correlations between crown volume index and 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). Shrubs were categorized into three height classes: dwarf (< 0.25 m), low-middle (0.25 to 2.0 m), and tall (> 2.0 m). 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 to 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 more than 95% of the total crown volume index of the shrub layer (Appendix 1). Sample sizes for *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 (Appendix 1). 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 and direct measures of plant biomass. 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.

3.6. 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, total herbs, (b) total shrubs, (c) total understory vegetation, (d) individual shrub and tree species known as 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 the repeated fertilization treatments in 2008 and 2013, respectively. Stand density had no effect on abundance of total understory herbs and shrubs, nor was there any density x 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 x 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 for 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 x 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 (Appendix 2). Where significant treatment effects were detected that also had significant treatment x 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).

4.0 Results

4.1. *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 2). Mean biomass of grasses was significantly ($P \leq 0.05$) higher in fertilized than unfertilized stands during the two 5-year fertilization periods (Table 3; Fig. 3a). The significant ($P = 0.02$) treatment x time interaction in the first period indicated that in each of the four fertilized years (1995 to 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

Table 2. Results of a one-way ANOVA for biomass production of grasses, forbs, total herbs, total shrubs, total understory vegetation (herbs+shrubs), mosses, and terrestrial lichens in replicate stands during the pre-treatment year 1993 ($n=12$) and post-treatment years of 2008 ($n=8$) and 2013 ($n=8$).

Plant group	Year					
	1993		2008		2013	
	$F_{1,22}$	P	$F_{1,14}$	P	$F_{1,14}$	P
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						
herbs+shrubs	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	0.05	7.88	0.01

stands in the second period (Table 3; Fig. 3b). On average, mean biomass of forbs (kg/ha) ranged from 126 to 133 in the 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

Table 3. Results of RM-ANOVA for biomass production (kg/ha) of grasses, forbs, total herbs, total shrubs, total understory vegetation, mosses, and 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					
	<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>		<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>	
	<i>F</i> _{1,22}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{1,22}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>
Grasses	4.47	0.05	6.52*	<0.01	4.58*	0.02	5.02	0.04	5.51*	<0.01	1.61*	0.21
Forbs	2.68	0.12	4.02*	0.05	3.68*	0.06	5.27	0.03	4.23*	0.02	1.75*	0.18
Total herbs	3.92	0.06	4.25*	0.04	4.11*	0.05	5.78	0.03	6.57*	<0.01	2.00*	0.13
Total shrubs	0.05	0.83	14.16*	<0.01	0.71*	0.53	1.99	0.17	8.46*	<0.01	3.28*	0.06
Total herbs+shrubs	4.64	0.04	5.24*	0.02	4.13*	0.04	8.25	<0.01	5.48*	<0.01	1.30*	0.28
Total mosses	4.51	0.05	2.43*	0.06	5.25*	<0.01	12.38	<0.01	12.52*	<0.01	6.42*	<0.01
Total terrestrial lichens	7.15	0.01	6.92*	<0.01	0.25*	0.85	38.40	<0.01	2.77*	0.07	2.18*	0.12

Figure 3. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) grasses, (b) forbs, and (c) total herbs 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.

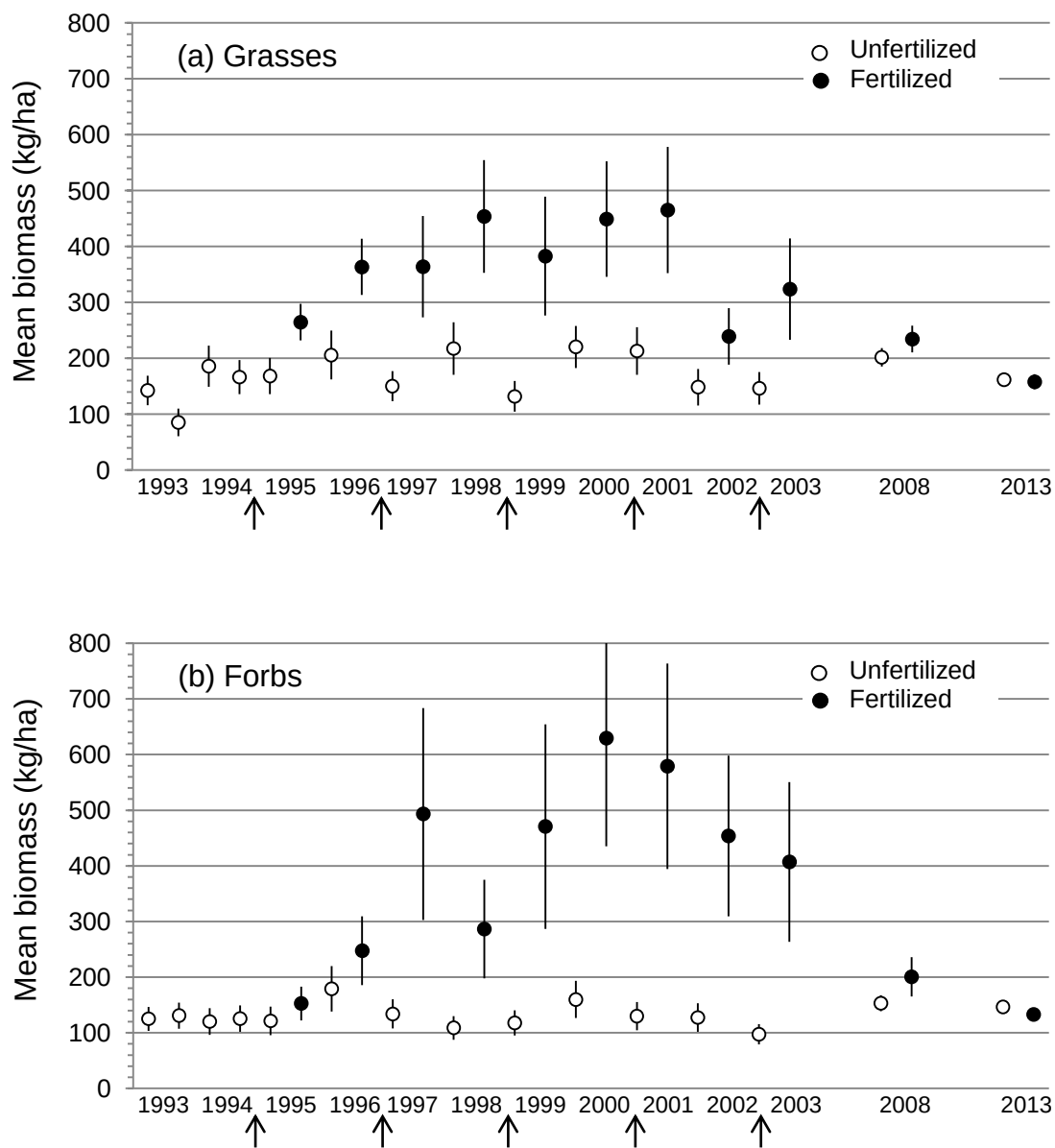
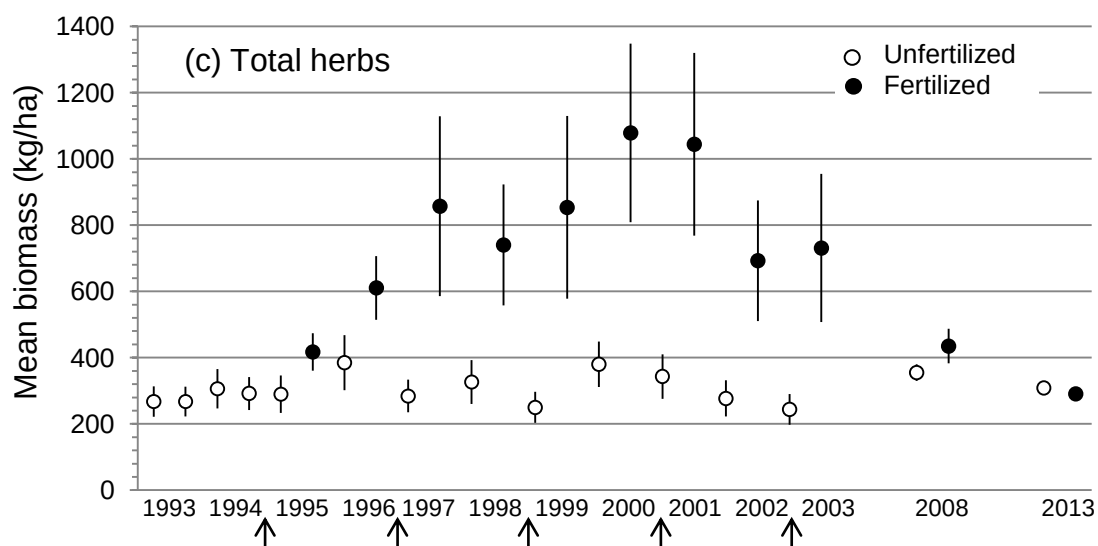


Figure 3. (continued)

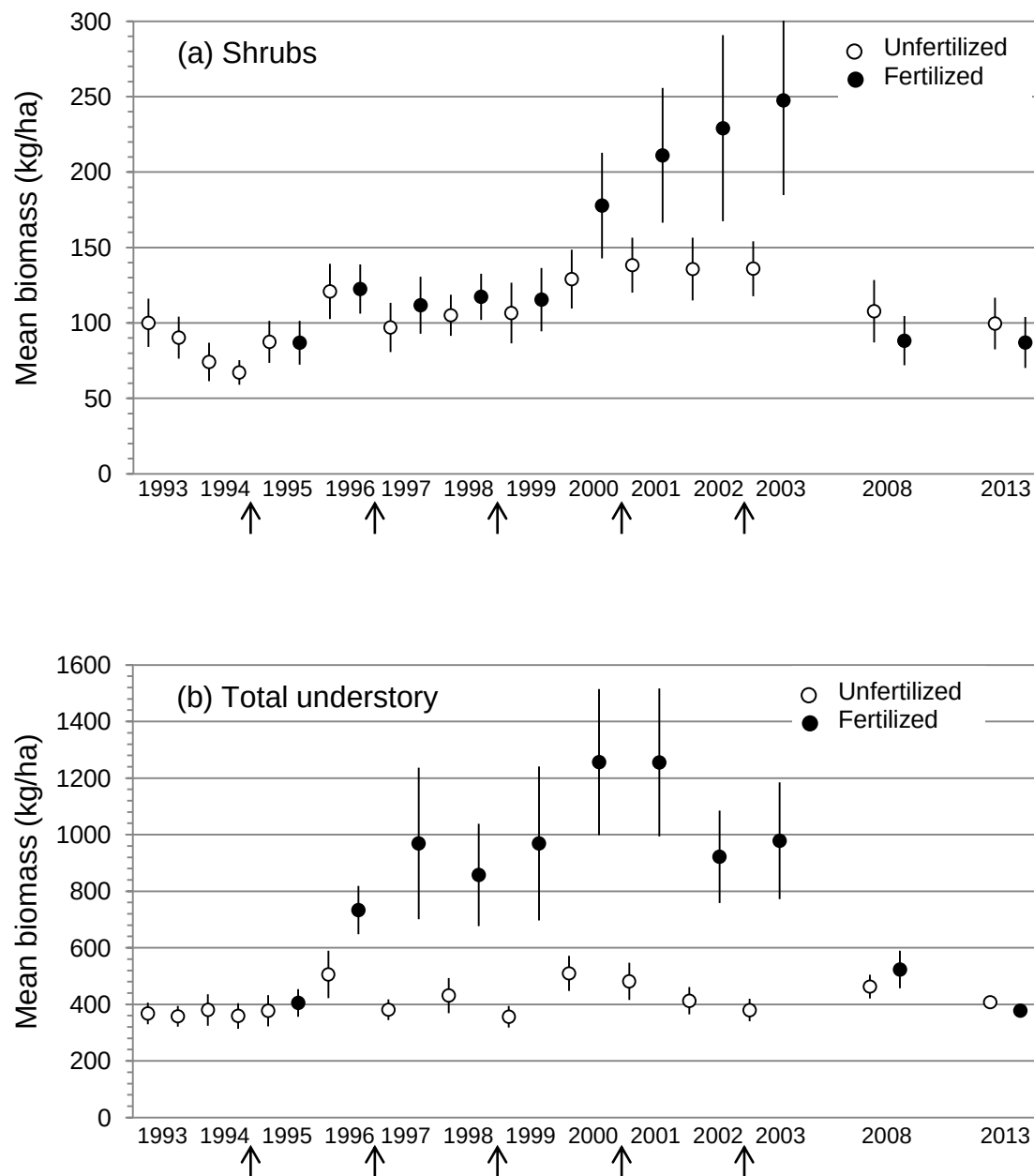
= 0.06) in the first period (Table 3; Fig. 3c). On average, mean biomass (kg/ha) of total herbs ranged from 299 to 318 kg/ha in the unfertilized stands and 583 to 880 kg/ha in the fertilized stands in the 10-year fertilization period. There was a significant ($P < 0.01$) effect of time in each period 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 2), 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*), and American vetch (*Vicia americana*).

4.2. 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 2). Mean biomass of shrubs was not affected by fertilization; however, mean biomass did increase significantly ($P < 0.01$) over time in both periods (Table 3; Fig. 4a). In addition, a treatment x 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. 4a). 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 3; Fig. 4b). The significant ($P = 0.04$) treatment x time interaction in the first period indicated that in the first three years (1994 to 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 for biomass of total understory vegetation as abundance of herbs and shrubs generally increased in the fertilized stands.

Figure 4. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) shrubs, and (b) total herbs and shrubs (understory) 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.



4.3. 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 the fertilized stands in the second period (Table 4; Fig. 5a). This decline began in 1997 after the second application of fertilizer (Fig. 5a). The overall mean ($\pm$ SE) biomass (kg/ha) in the second period was 18.1 ± 1.4 in the unfertilized stands and 6.5 ± 1.0 in the fertilized stands. Mean biomass of twinflower (*Linnaea 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 ± 0.6 in the unfertilized stands and 2.3 ± 0.3 in the fertilized stands in the second period (Table 4; Fig. 5b). 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 4; Fig. 5c). Overall mean ($\pm$ SE) biomasses ranged from 18.0 ± 1.7 to 25.4 ± 2.9 in the unfertilized stands and 6.6 ± 0.9 to 4.0 ± 0.6 in the fertilized stands in the first and second 5-year periods, respectively. The significant ($P < 0.01$) treatment x 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. 5c). There was a significant difference in biomass of *V. caespitosum* between

Table 4. 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					
	<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>		<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>	
Dwarf (< 0.25 m)	<i>F</i> _{1,21}	<i>P</i>	<i>F</i> _{4,84}	<i>P</i>	<i>F</i> _{4,84}	<i>P</i>	<i>F</i> _{1,21}	<i>P</i>	<i>F</i> _{4,84}	<i>P</i>	<i>F</i> _{4,84}	<i>P</i>
<i>Arctostaphylos uva-ursi</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>F</i> _{1,22}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{1,22}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>	<i>F</i> _{4,88}	<i>P</i>
<i>Linnaea borealis</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>F</i> _{1,20}	<i>P</i>	<i>F</i> _{4,80}	<i>P</i>	<i>F</i> _{4,80}	<i>P</i>	<i>F</i> _{1,20}	<i>P</i>	<i>F</i> _{4,80}	<i>P</i>	<i>F</i> _{4,80}	<i>P</i>
<i>Pachistima myrsinites</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>F</i> _{1,5}	<i>P</i>	<i>F</i> _{4,20}	<i>P</i>	<i>F</i> _{4,20}	<i>P</i>	<i>F</i> _{1,5}	<i>P</i>	<i>F</i> _{4,20}	<i>P</i>	<i>F</i> _{4,20}	<i>P</i>
<i>Rubus pubescens</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>F</i> _{1,7}	<i>P</i>	<i>F</i> _{4,28}	<i>P</i>	<i>F</i> _{4,28}	<i>P</i>	<i>F</i> _{1,7}	<i>P</i>	<i>F</i> _{4,28}	<i>P</i>	<i>F</i> _{4,28}	<i>P</i>

<i>Vaccinium caespitosum</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
	$F_{1,12}$	P	$F_{4,48}$	P	$F_{4,48}$	P	$F_{1,12}$	P	$F_{4,48}$	P	$F_{4,48}$	P
<i>Vaccinium scoparium</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
Low - middle (0.25 – 2.0 m)												
	$F_{1,13}$	P	$F_{4,52}$	P	$F_{4,52}$	P	$F_{1,13}$	P	$F_{4,52}$	P	$F_{4,52}$	P
<i>Lonicera involucrata</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
	$F_{1,12}$	P	$F_{4,48}$	P	$F_{4,48}$	P	$F_{1,12}$	P	$F_{4,48}$	P	$F_{4,48}$	P
<i>Lonicera utahensis</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
	$F_{1,7}$	P	$F_{4,28}$	P	$F_{4,28}$	P	$F_{1,7}$	P	$F_{4,28}$	P	$F_{4,28}$	P
<i>Mahonia aquifolium</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
	$F_{1,15}$	P	$F_{4,60}$	P	$F_{4,60}$	P	$F_{1,15}$	P	$F_{4,60}$	P	$F_{4,60}$	P
<i>Ribes lacustre</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
	$F_{1,6}$	P	$F_{4,24}$	P	$F_{4,24}$	P	$F_{1,6}$	P	$F_{4,24}$	P	$F_{4,24}$	P
<i>Rosa acicularis</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
	$F_{1,16}$	P	$F_{4,64}$	P	$F_{4,64}$	P	$F_{1,16}$	P	$F_{4,64}$	P	$F_{4,64}$	P
<i>Rubus idaeus</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
	$F_{1,6}$	P	$F_{4,24}$	P	$F_{4,24}$	P	$F_{1,6}$	P	$F_{4,24}$	P	$F_{4,24}$	P
<i>Shepherdia canadensis</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
	$F_{1,22}$	P	$F_{4,88}$	P	$F_{4,88}$	P	$F_{1,22}$	P	$F_{4,88}$	P	$F_{4,88}$	P

<i>Spiraea betulifolia</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
	$F_{1,3}$	P	$F_{4,12}$	P	$F_{4,12}$	P	$F_{1,3}$	P	$F_{4,12}$	P	$F_{4,12}$	P
<i>Symphoricarpus albus</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
	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P
<i>Vacc. membranaceum</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
Tall (> 2.0 m)												
	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P
<i>Alnus sinuata</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
	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P	$F_{1,9}$	P	$F_{4,36}$	P	$F_{4,36}$	P
<i>Amelanchier alnifolia</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
	$F_{1,19}$	P	$F_{4,76}$	P	$F_{4,76}$	P	$F_{1,19}$	P	$F_{4,76}$	P	$F_{4,76}$	P
<i>Salix spp.</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

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 4; Appendix 3a, b, c). 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 periods (Table 4; Appendix 4a, b, c). Mean biomass of *R. lacustre* was significantly different in unfertilized and fertilized stands in the first but not second 5-year period (Table 4; Fig. 6a). 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 ($P < 0.01$) different in unfertilized and fertilized stands in both periods (Table 4; Fig. 6b). Overall mean ($\pm$ SE) biomasses (kg/ha) ranged from 38.9 ± 3.8 to 54.0 ± 6.2 in the unfertilized stands and 74.2 ± 8.1 to 286.7 ± 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

Figure 5. 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 to 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.

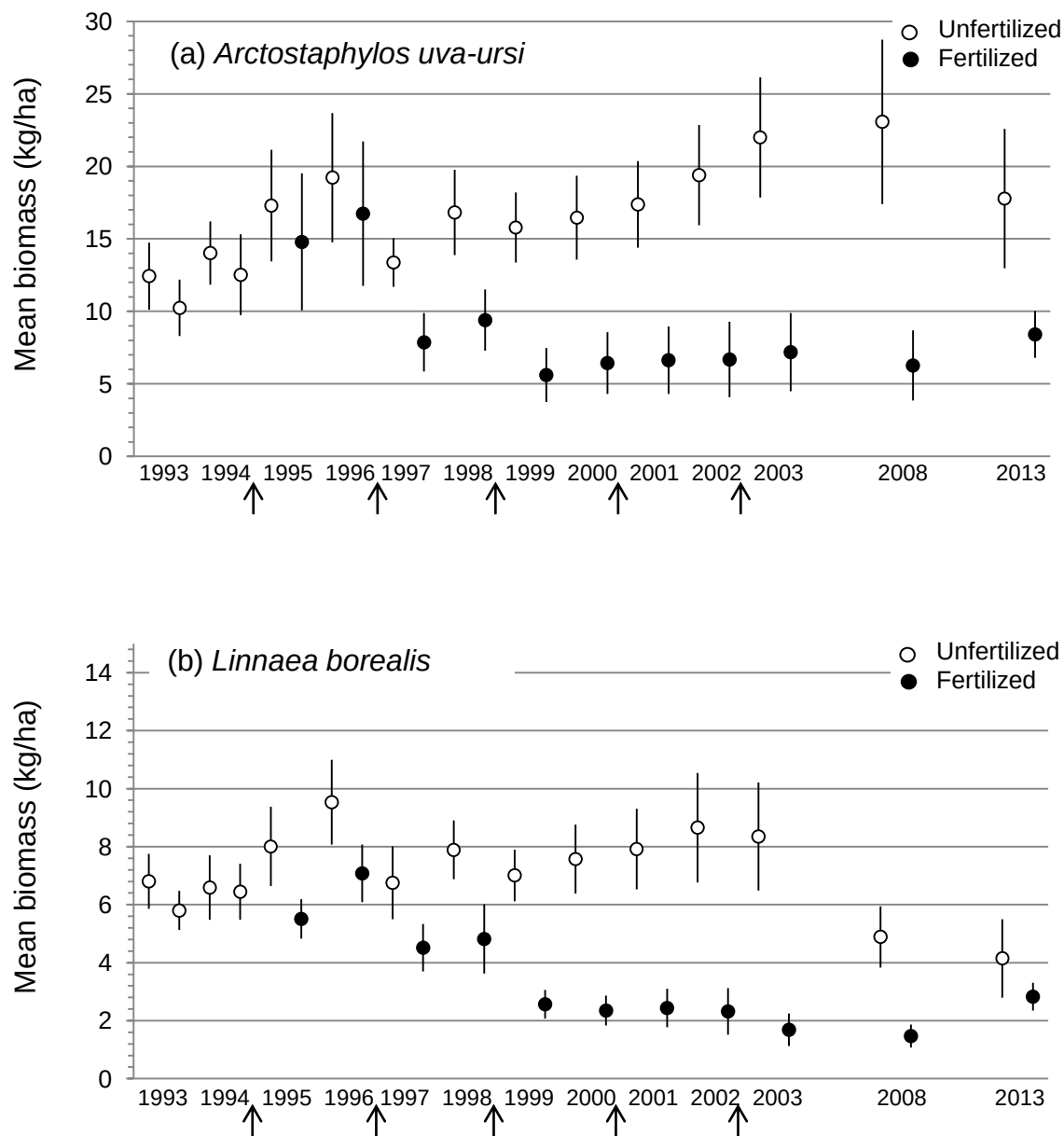
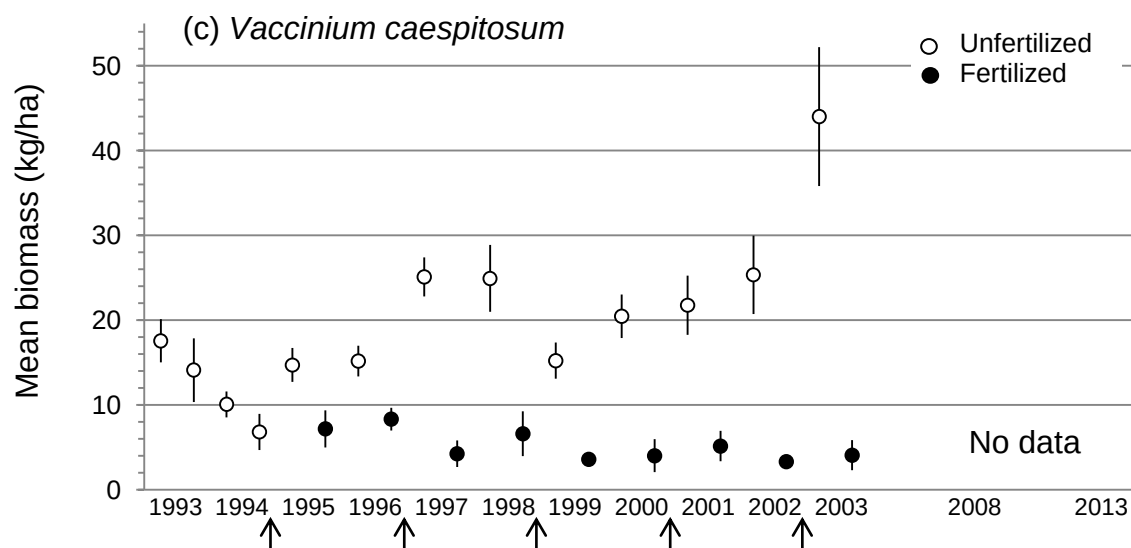


Figure 5. (continued)



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 4; Fig. 6c), with an overall mean (SE) biomass of 0.8 ± 0.2 in the unfertilized and 3.8 ± 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 were statistically similar ($P > 0.05$) between treatment stands in both periods (Table 4). However, overall mean biomass was 5.3 times higher in the unfertilized than fertilized stands in the second period for *S. canadensis* (Appendix 5a), with the converse true for *S. albus* where overall mean biomass was 3.2 times higher in the fertilized than unfertilized stands in the second period (Fig. 7a). 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

Figure 6. 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 to 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.

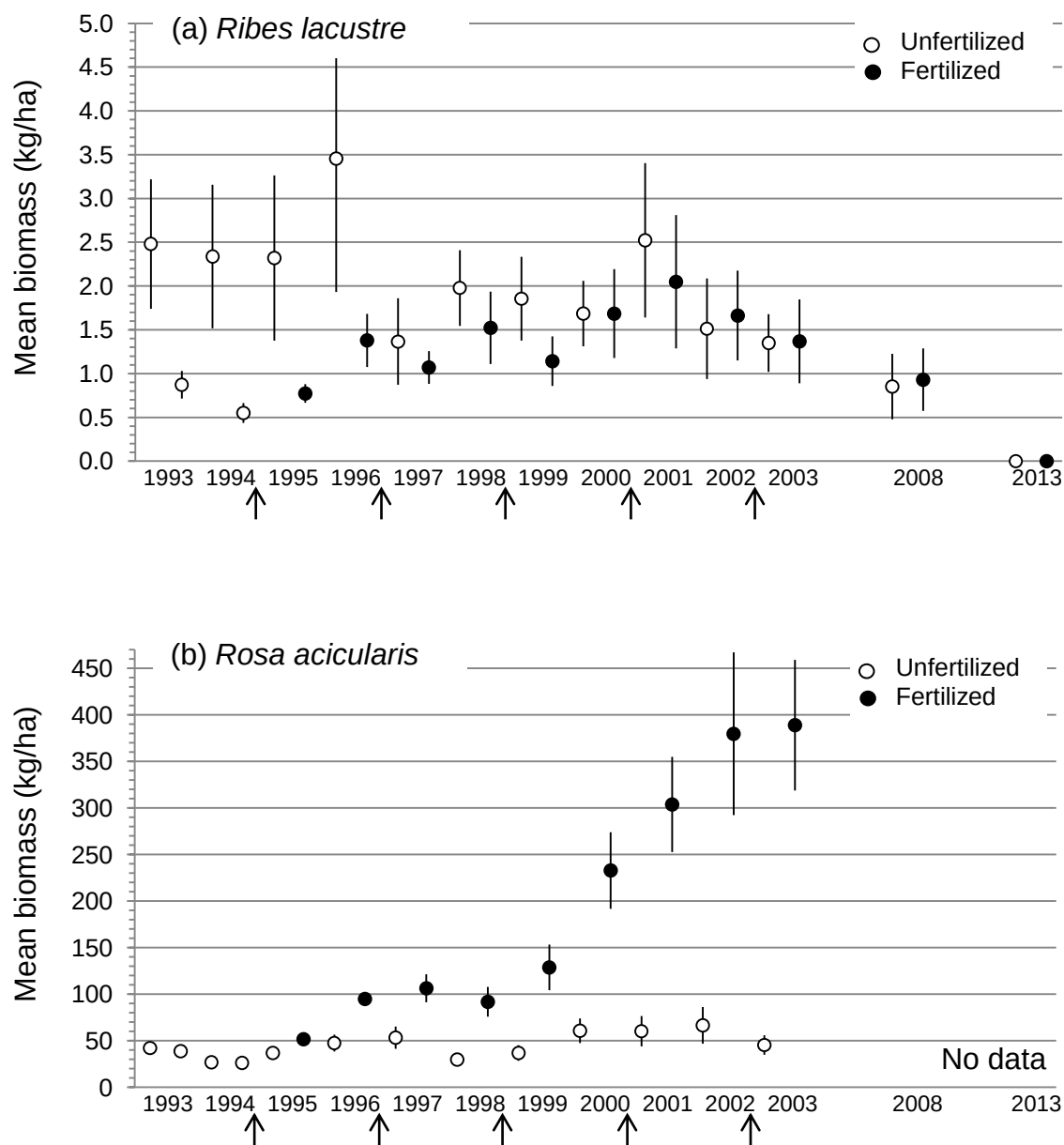
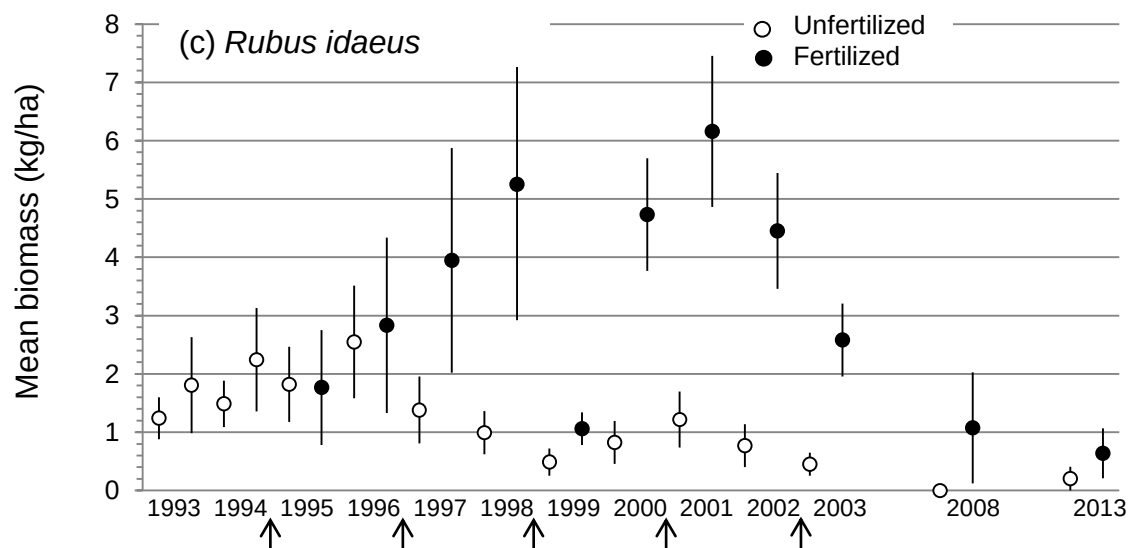


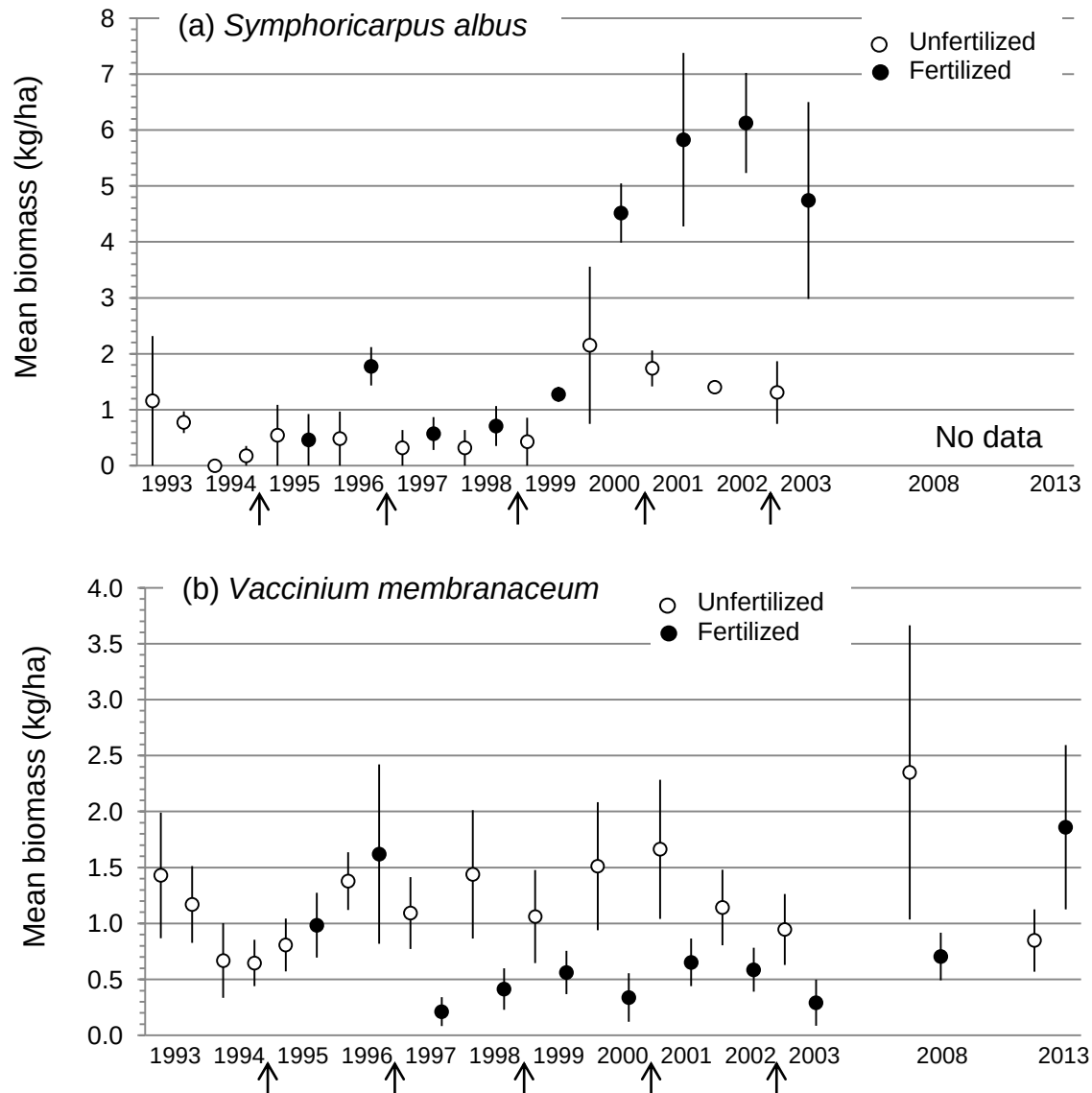
Figure 6. (continued)



biomass of *S. betulifolia* was significantly different in unfertilized and fertilized stands in the first but not second 5-year period (Table 4; Appendix 5b). 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 4; Fig. 7b).

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 *A. sinuata* was similar ($P > 0.05$) between treatment stands in both periods (Table 4; Fig. 8a). Mean biomass of *A. amelanchier* was similar between stands in the first period, but significantly ($P = 0.04$) different in the second period with the fertilized stand at 36.7 ± 5.3 kg/ha and the unfertilized stand at 13.0 ± 2.2 kg/ha (Table 4; Fig. 8b). There was a significant ($P \leq$

Figure 7. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) *Symphoricarpus 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.



0.03) effect of time as biomass generally increased after the start of fertilization. There were no data available for 2008 and 2013 for *A. amelanchier* 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

Figure 8. 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.

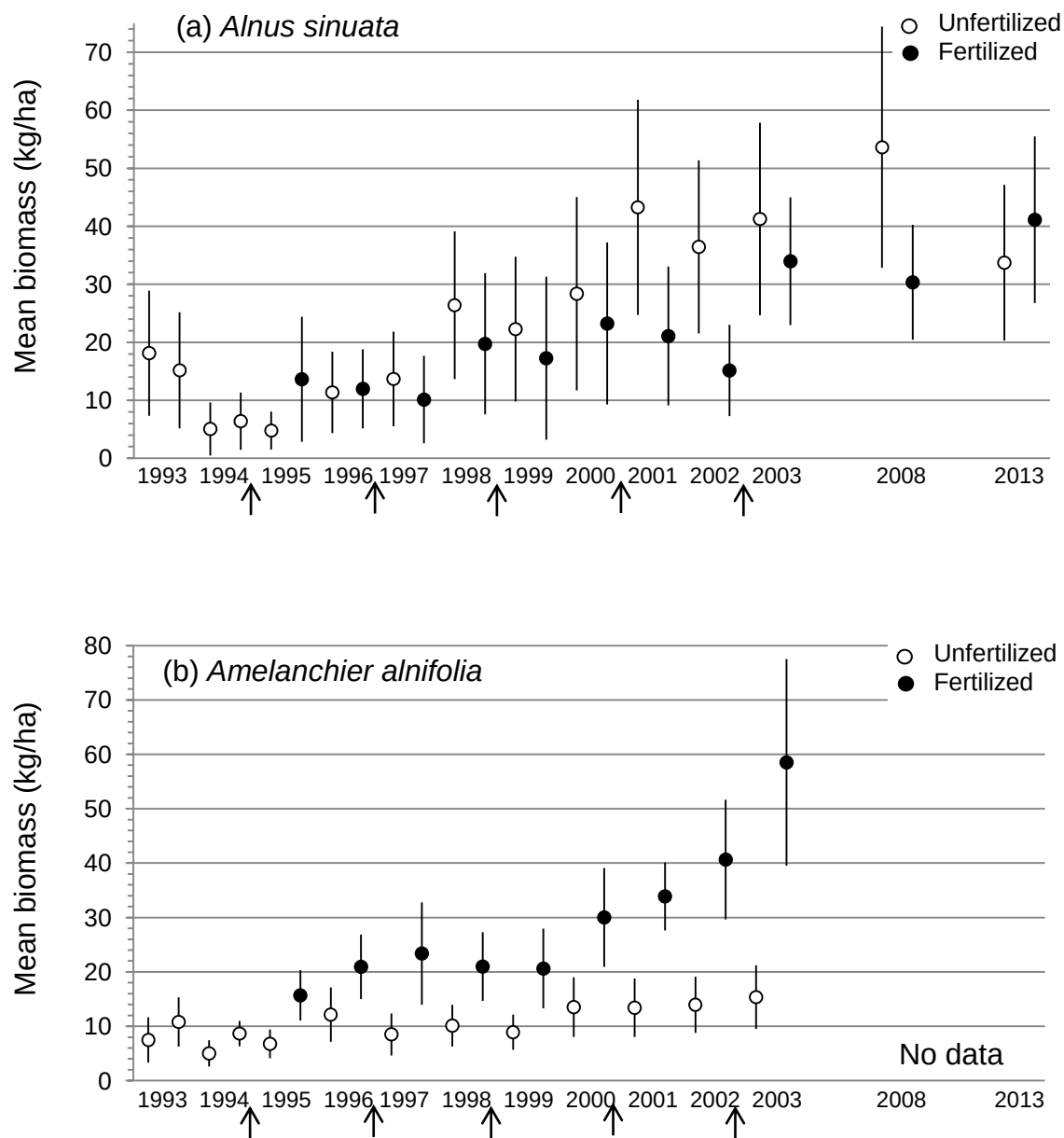
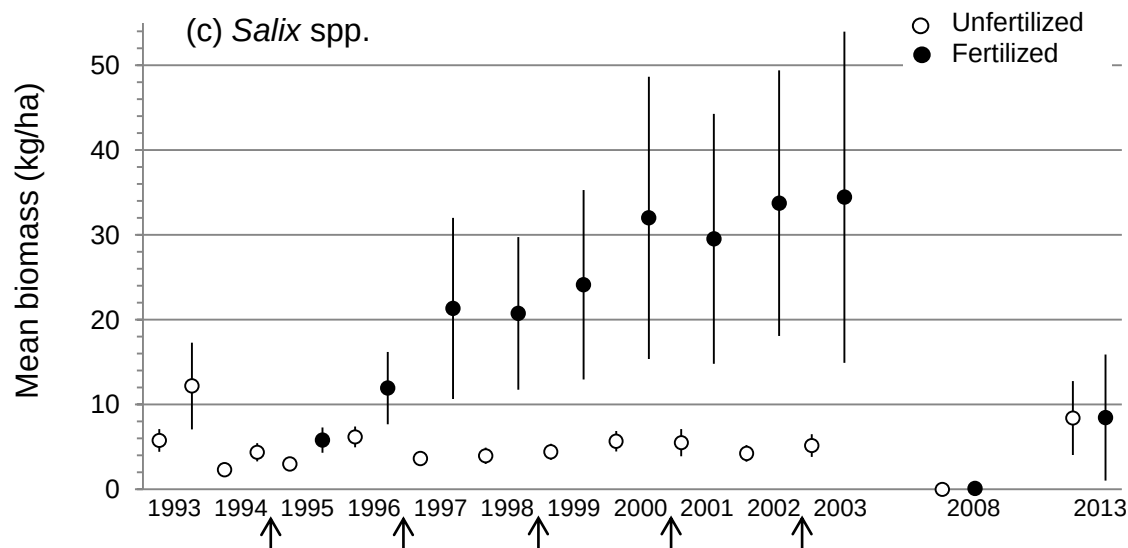


Figure 8. (continued)

in both periods (Table 4). However, overall mean biomasses for the two 5-year periods were 3.4 to 6.2 times higher in the fertilized than unfertilized stands, before declining to similar levels in the post-treatment years 2008 and 2013 (Fig. 8c). There were no treatment x time interactions for species in this tall shrub stratum.

4.4. 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 5; Fig. 9a). Mean biomass of *Picea* hybrid was highly variable in fertilized stands, and hence was not significantly different between treatment stands (Table 5). However, overall mean biomasses for the two 5-year periods were 2.5 to 3.4 times higher in the fertilized than unfertilized stands

Table 5. 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					
	<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>		<u>Treatment</u>		<u>Time</u>		<u>Treatment x time</u>	
	<i>F</i> _{1,14}	<i>P</i>	<i>F</i> _{4,56}	<i>P</i>	<i>F</i> _{4,56}	<i>P</i>	<i>F</i> _{1,14}	<i>P</i>	<i>F</i> _{4,56}	<i>P</i>	<i>F</i> _{4,56}	<i>P</i>
<i>Abies lasiocarpa</i>	0.05	0.83	3.00*	0.08	0.30*	0.71	0.16	0.69	9.03*	<0.01	0.28*	0.71
<i>Betula papyrifera</i>	<i>F</i> _{1,4}	<i>P</i>	<i>F</i> _{4,16}	<i>P</i>	<i>F</i> _{4,16}	<i>P</i>	<i>F</i> _{1,4}	<i>P</i>	<i>F</i> _{4,16}	<i>P</i>	<i>F</i> _{4,16}	<i>P</i>
	0.13	0.74	0.19*	0.86	0.27*	0.79	0.81	0.42	5.95*	0.04	2.12*	0.19
<i>Picea glauca x engelmanniana</i>	<i>F</i> _{1,16}	<i>P</i>	<i>F</i> _{4,64}	<i>P</i>	<i>F</i> _{4,64}	<i>P</i>	<i>F</i> _{1,16}	<i>P</i>	<i>F</i> _{4,64}	<i>P</i>	<i>F</i> _{4,64}	<i>P</i>
	2.48	0.14	2.79*	0.10	1.60*	0.22	2.37	0.14	6.46*	<0.01	0.82*	0.43
<i>Populus tremuloides</i>	<i>F</i> _{1,15}	<i>P</i>	<i>F</i> _{4,60}	<i>P</i>	<i>F</i> _{4,60}	<i>P</i>	<i>F</i> _{1,15}	<i>P</i>	<i>F</i> _{4,60}	<i>P</i>	<i>F</i> _{4,60}	<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> _{1,8}	<i>P</i>	<i>F</i> _{4,32}	<i>P</i>	<i>F</i> _{4,32}	<i>P</i>	<i>F</i> _{1,8}	<i>P</i>	<i>F</i> _{4,32}	<i>P</i>	<i>F</i> _{4,32}	<i>P</i>
	1.05	0.34	4.50*	0.01	1.97*	0.15	4.88	0.06	10.84	<0.01	3.42	0.02
<i>Pseudotsuga menziesii</i>	<i>F</i> _{1,18}	<i>P</i>	<i>F</i> _{4,72}	<i>P</i>	<i>F</i> _{4,72}	<i>P</i>	<i>F</i> _{1,18}	<i>P</i>	<i>F</i> _{4,72}	<i>P</i>	<i>F</i> _{4,72}	<i>P</i>
	1.22	0.28	1.09*	0.33	0.54*	0.52	4.55	0.05	5.70*	<0.01	2.14*	0.13

Figure 9. 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.

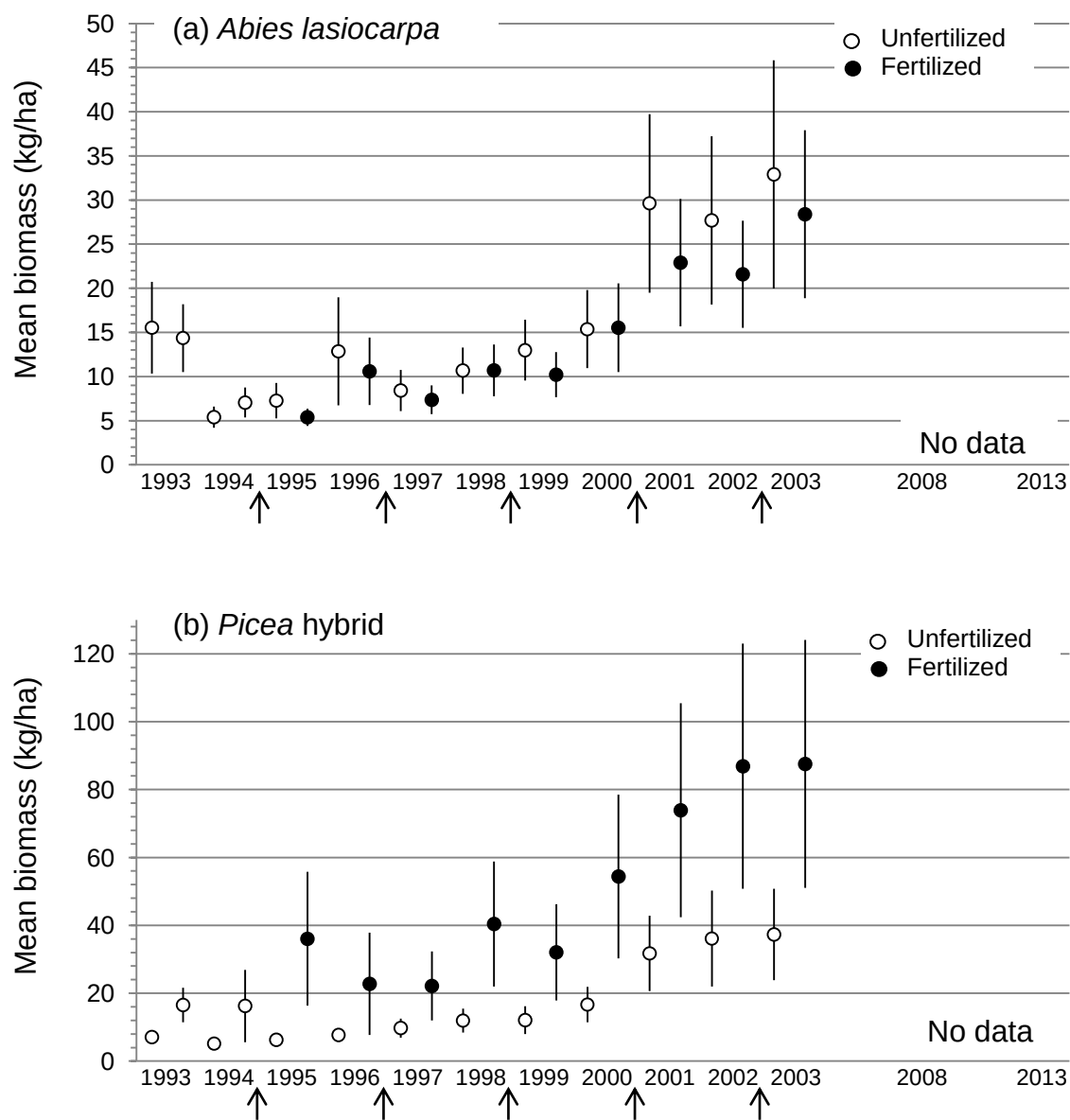
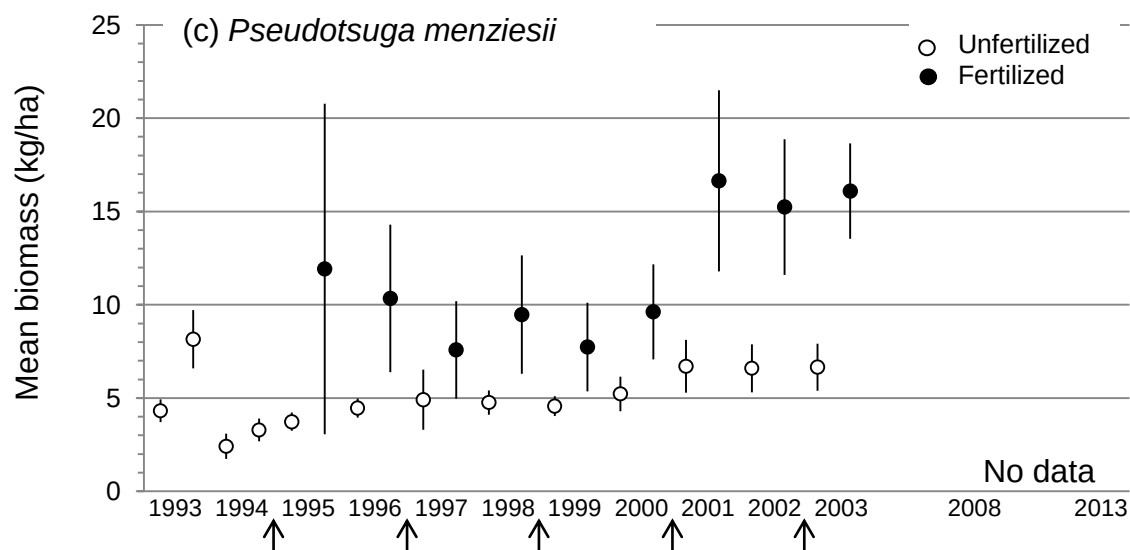


Figure 9. (continued)

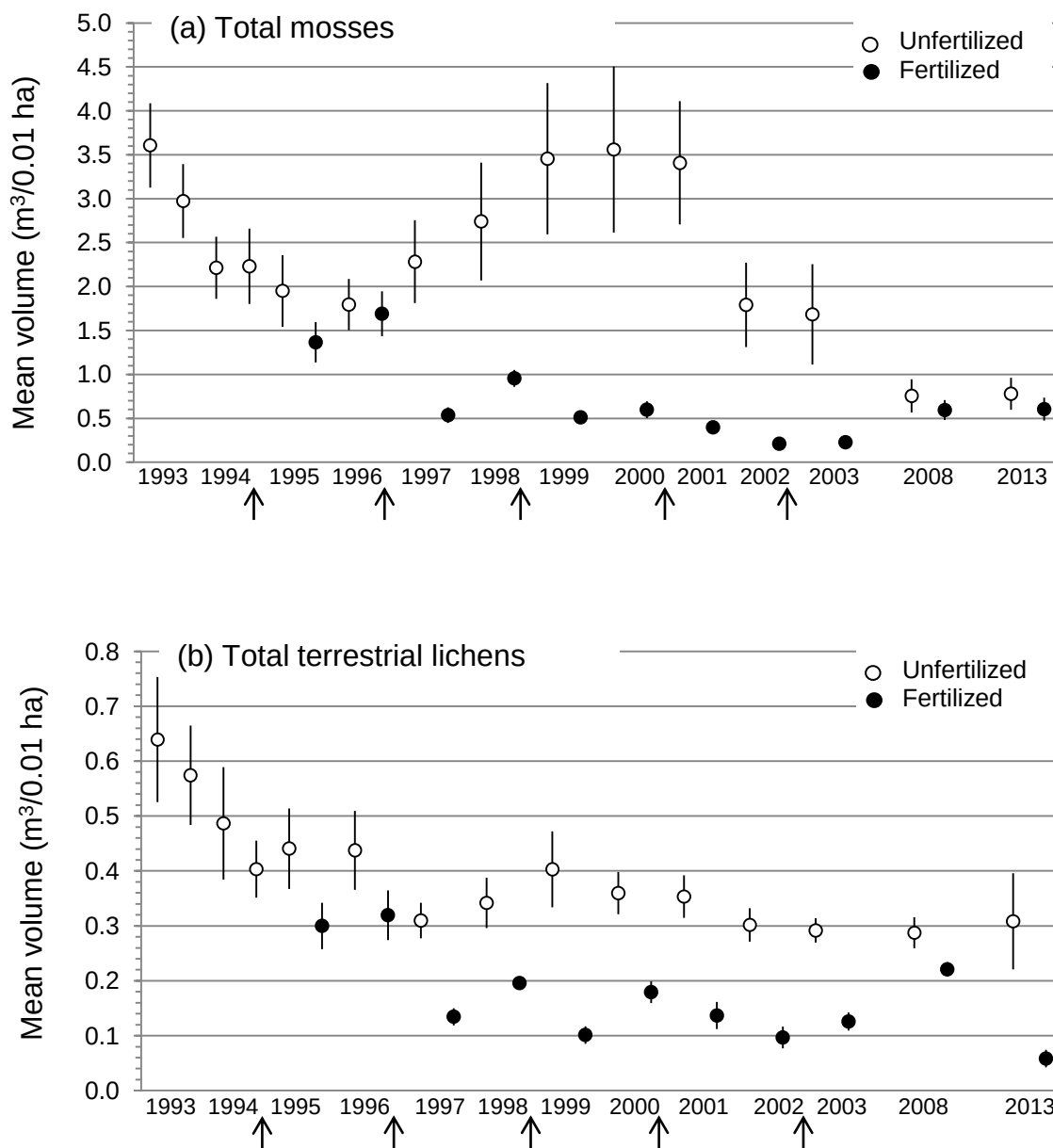
(Fig. 9b). Mean biomass of *P. menziesii* was similar ($P > 0.05$) between treatment stands in the first period, but significantly ($P < 0.01$) different in the second period (Table 5; Fig. 9c). Overall mean biomasses were 2.1 to 2.2 times higher in fertilized than unfertilized stands over the two periods. 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. 9a, b, c). There were no significant differences in mean biomass of the three deciduous tree species in unfertilized and fertilized stands (Table 5; Appendix 6a, b, c). In all cases, biomass measurements were highly variable likely owing to the clumped distribution of these species. The only significant treatment x time interaction for these understory tree species was *P. trichocarpa* in the second fertilization period (Appendix 6b).

4.5. Mosses and terrestrial lichens

Mean crown volume index of total mosses was similar ($P > 0.05$) in pre-treatment stands in 1993 (Table 2), and then significantly ($P \leq 0.05$) higher in unfertilized than fertilized stands in both 5-year fertilization periods (Table 3; Fig. 10a). Overall mean ($\pm$ SE) crown volume index ($\text{m}^3/0.01 \text{ ha}$) ranged from 2.20 ± 0.20 to 2.78 ± 0.34 in the unfertilized stands and 1.36 ± 0.13 to 0.39 ± 0.03 in the fertilized stands in the two periods, respectively. The significant ($P < 0.01$) treatment x 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. 10a). 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 2; Fig. 10a). 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 2), and then significantly ($P < 0.01$) higher in unfertilized than fertilized stands in both 5-year fertilization periods (Table 3; Fig. 10b). Overall mean ($\pm$ SE) crown volume index ($\text{m}^3/0.01 \text{ ha}$) ranged from 0.40 ± 0.03 to 0.34 ± 0.02 in the unfertilized stands and 0.27 ± 0.02 to 0.13 ± 0.01 in the fertilized stands in the two periods, respectively. The significant ($P < 0.01$) time interaction in the first 5-

Figure 10. 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.



year period and trend that way in the second period reflected a general decline in volume of lichen with time (Fig. 10b). 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 2). Common lichen species included grey reindeer lichen (*Cladina rangifera*), horn cladonia (*Cladonia cornuta*), black-foot cladonia (*Cladonia gracilis*), sulphur cladonia (*Cladonia sulphurina*), blistered paw (*Nephroma resupinatum*), devil's matchstick (*Pilophorus acicularis*), and *Peltigera* spp.

5.0 Discussion

5.1. *Herbaceous species as forage*

The substantial increase in mean biomass of grasses, forbs, and total 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, and several others as referenced in Table 1, 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 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.

5.2. 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. amelanchier*, *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 (Pierce and Peek, 1984; Nyberg, 1990). 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 gray 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 to 6 years prior to a stable pattern of 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%), 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. Clearly, 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 (Koehler 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*, or *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).

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, 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).

5.3. Mosses and terrestrial lichens

As reviewed by Sullivan and Sullivan (2017a), the significant decline in mean biomass of total mosses and total terrestrial lichens in our study followed the general pattern of responses of these non-vascular plants to fertilization. In Scandinavia, lichens such as *Cladonia* spp. and mosses *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).

5.4. 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 *Deschampia 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 (2014) reported that repeated fertilization increased crude protein content of pinegrass, a major forage source for wildlife and cattle (*Bos taurus*). Similarly, Melynychuk 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; Mansson 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 (Werner and Anderson, 2017). Operational fertilization in BC forests is normally conducted in young sapling to pole-sized stands that are usually 20 to 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 (Mansson 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; Gunderson et al., 2004).

6.0 Conclusions

As reviewed by Sullivan and Sullivan (2017a), repeated applications (2-5 and >5) of nitrogen showed a trend to either no change or declines in plant abundance. However, a single application of nitrogen is often the standard practice in BC and other parts of the Pacific Northwest, although not exclusively. Thus, we investigated the responses in mean biomass of forage plants in all of our groups and individual species of vascular plants, and mean crown volume index of mosses and terrestrial lichens, to the 1 to 5 applications in this study (Appendix 7). After a given fertilizer application, there needed to be a significant ($P < 0.05$) difference in biomass or crown volume index between unfertilized and fertilized stands that lasted for the duration of the study. For 1 application: total grasses and *R. acicularis* increased; *V. caespitosum* declined. For 2 applications: total herbs and total understory increased; *A. uva-ursi*, mosses, and lichens declined. For 3 applications: total forbs and *R. idaeus* increased; *L. borealis* declined. For 4 applications: *A. alnifolia* and *P. menziesii* increased. The other individual shrub and tree species and total shrubs were not affected by any of the fertilizer applications.

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. Operational fertilization with one application of nitrogen in these forests seemed positive, or relatively benign, in terms of changes in biomass of understory forage

plants. Repeated applications of nitrogen fertilizer may enhance biomass of some additional forage forbs and shrubs but reduce biomass of some dwarf shrubs and mosses and lichens.

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9.0 Appendices

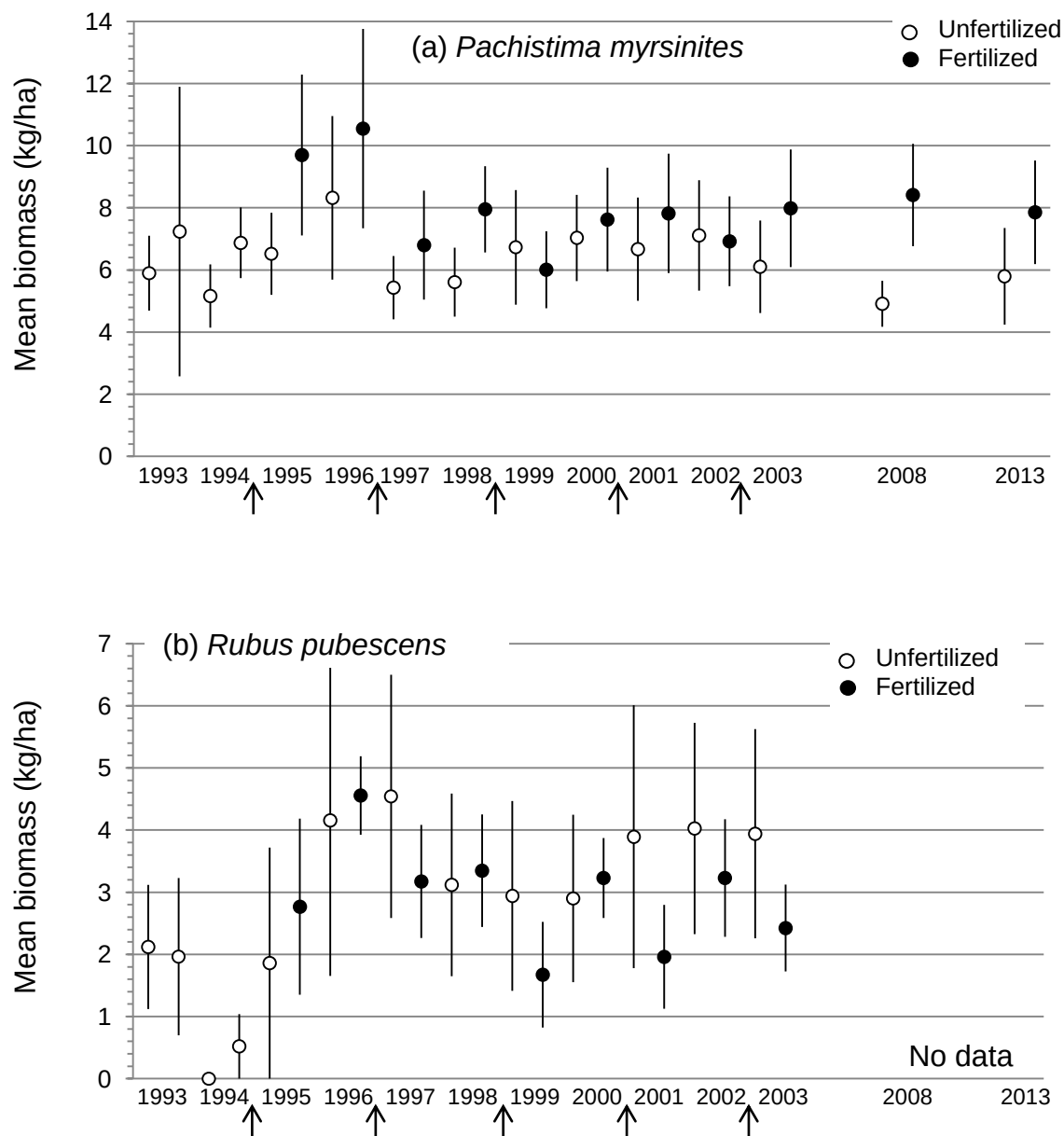
Appendix 1. Species-specific and generic regression equations correlating plant biomass and crown volume index for herb, shrub, and tree species in fertilized and unfertilized stands at the three study areas in south-central British Columbia. All regressions were significant at $P < 0.01$.

Group or species	Equation	R^2
Grasses	$y = 34.15x + 60.98$	0.90
Forbs	$y = 16.55x + 80.56$	0.62
Dwarf shrubs	$y = 103.82x + 25.97$	0.47
Low shrubs	$y = 67.35x + 9.05$	0.77
Tall shrubs	$y = 44.62x + 26.48$	0.90
<i>Alnus sinuata</i>	$y = 44.71x - 3.66$	0.92
<i>Arctostaphylos uva-ursi</i>	$y = 100.79x + 54.74$	0.66
<i>Lonicera utahensis</i>	$y = 65.19x + 27.42$	0.75
<i>Pachistima myrsinites</i>	$y = 73.37x + 24.30$	0.32
<i>Ribes lacustre</i>	$y = 60.22x + 15.78$	0.88
<i>Spiraea betulifolia</i>	$y = 32.52x + 3.79$	0.47
<i>Vaccinium scoparium</i>	$y = 89.42x + 10.00$	0.72

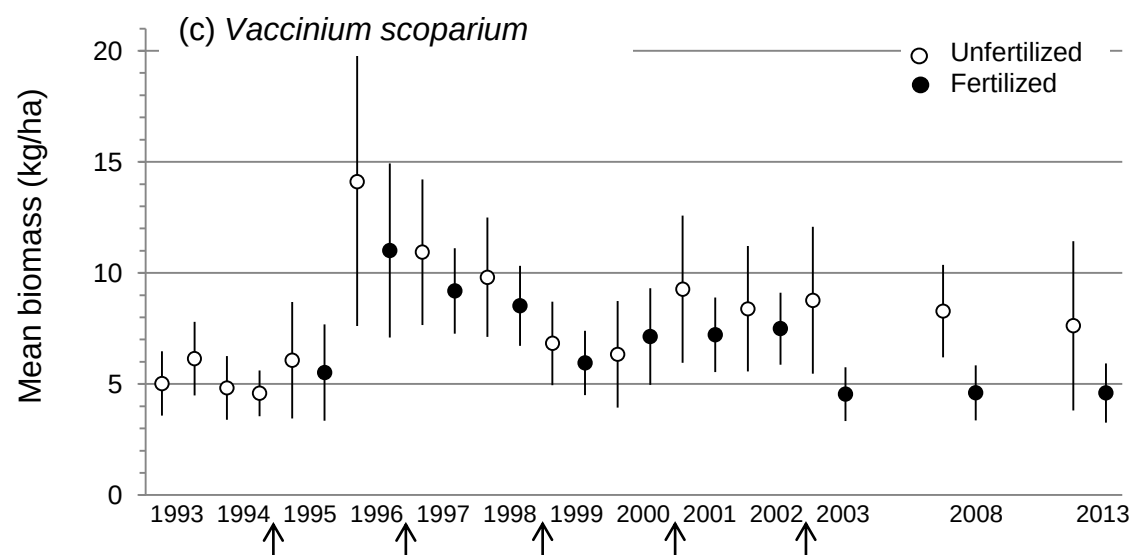
Appendix 2. Summary of replicate stands for shrub and tree species as forage plants at the three study areas. Number of replicates was dependent on presence of a given species in treatment stands.

Species	Study areas	Number of replicates	
<u>Shrubs</u>		Unfertilized	Fertilized
<i>Alnus sinuata</i>	SUM, KEL, CAR	6	5
<i>Amelanchier alnifolia</i>	KEL, CAR	6	5
<i>Arctostaphylos uva-ursi</i>	SUM, KEL, CAR	12	11
<i>Linnaea borealis</i>	SUM, KEL, CAR	12	12
<i>Lonicera involucrata</i>	SUM, KEL, CAR	7	8
<i>Lonicera utahensis</i>	SUM, KEL	8	6
<i>Mahonia aquifolium</i>	SUM, CAR	4	5
<i>Pachistima myrsinites</i>	SUM, KEL, CAR	11	11
<i>Ribes lacustre</i>	SUM, KEL, CAR	6	11
<i>Rosa acicularis</i>	SUM, KEL, CAR	6	6
<i>Rubus idaeus</i>	SUM, KEL, CAR	8	10
<i>Rubus pubescens</i>	CAR	4	3
<i>Salix spp.</i>	SUM, KEL, CAR	11	10
<i>Shepherdia canadensis</i>	CAR	4	4
<i>Spiraea betulafolia</i>	SUM, KEL, CAR	12	12
<i>Symphoricarpus albus</i>	CAR	2	3
<i>Vaccinium caespitosum</i>	KEL, CAR	4	5
<i>Vaccinium membranacium</i>	SUM, KEL	6	5
<i>Vaccinium scoparium</i>	SUM, KEL	7	7
<u>Trees</u>			
<i>Abies lasiocarpa</i>	SUM, KEL	8	8
<i>Betula papyrifera</i>	KEL, CAR	4	2
<i>Picea glauca x engelmannii</i>	SUM, KEL, CAR	10	8
<i>Populus tremuloides</i>	SUM, KEL, CAR	9	8
<i>Populus trichocarpa</i>	KEL, CAR	7	3
<i>Pseudotsuga menziesii</i>	SUM, KEL, CAR	9	11

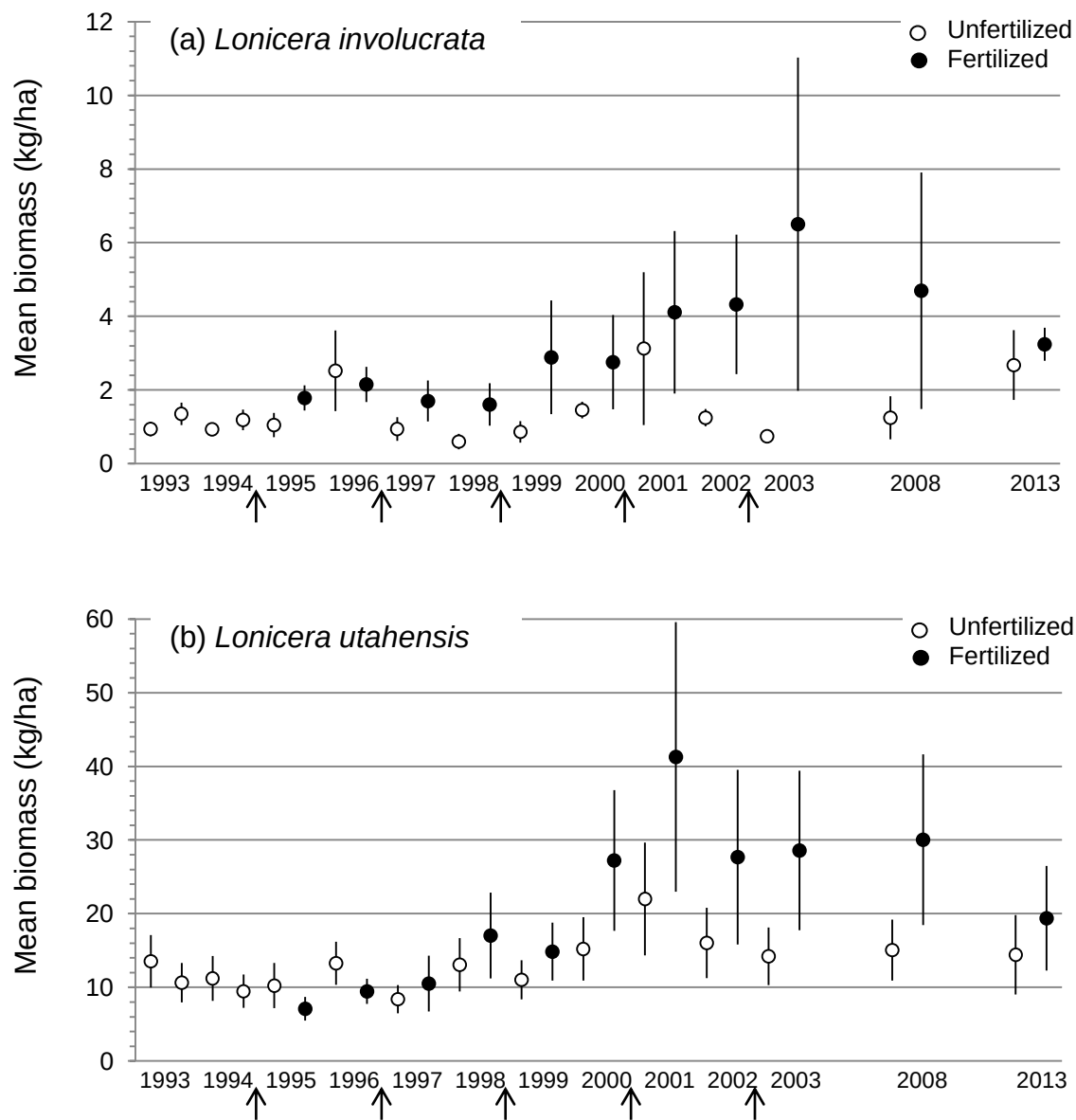
Appendix 3. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) *Pachistima myrsinites*, (b) *Rubus pubescens*, and (c) *Vaccinium scoparium* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized (n = 11, 4, 7) and fertilized (n = 11, 3, 7) lodgepole pine stands. Arrow denotes application of fertilizer.



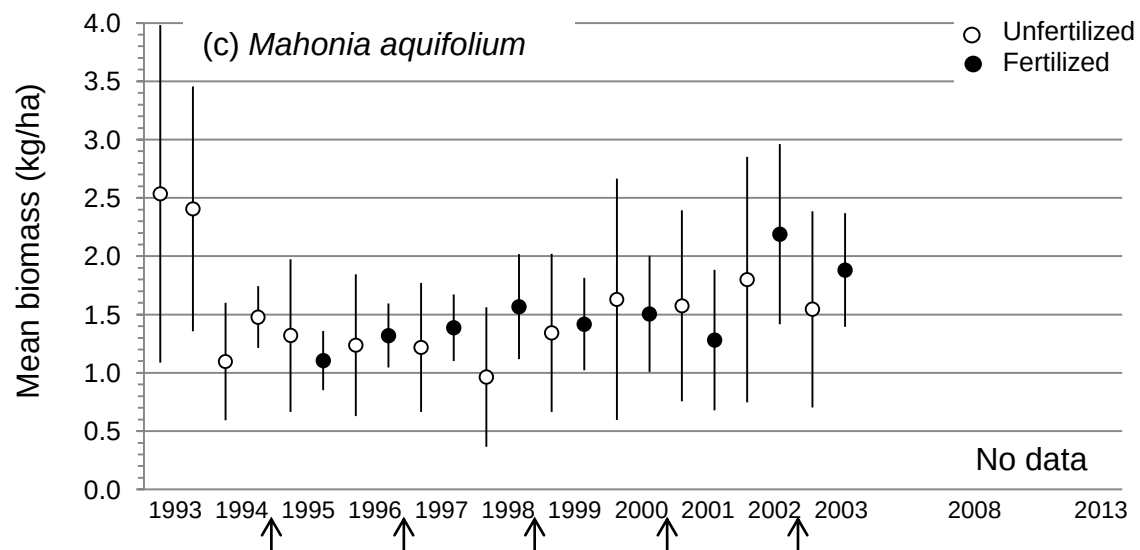
Appendix 3. (continued)



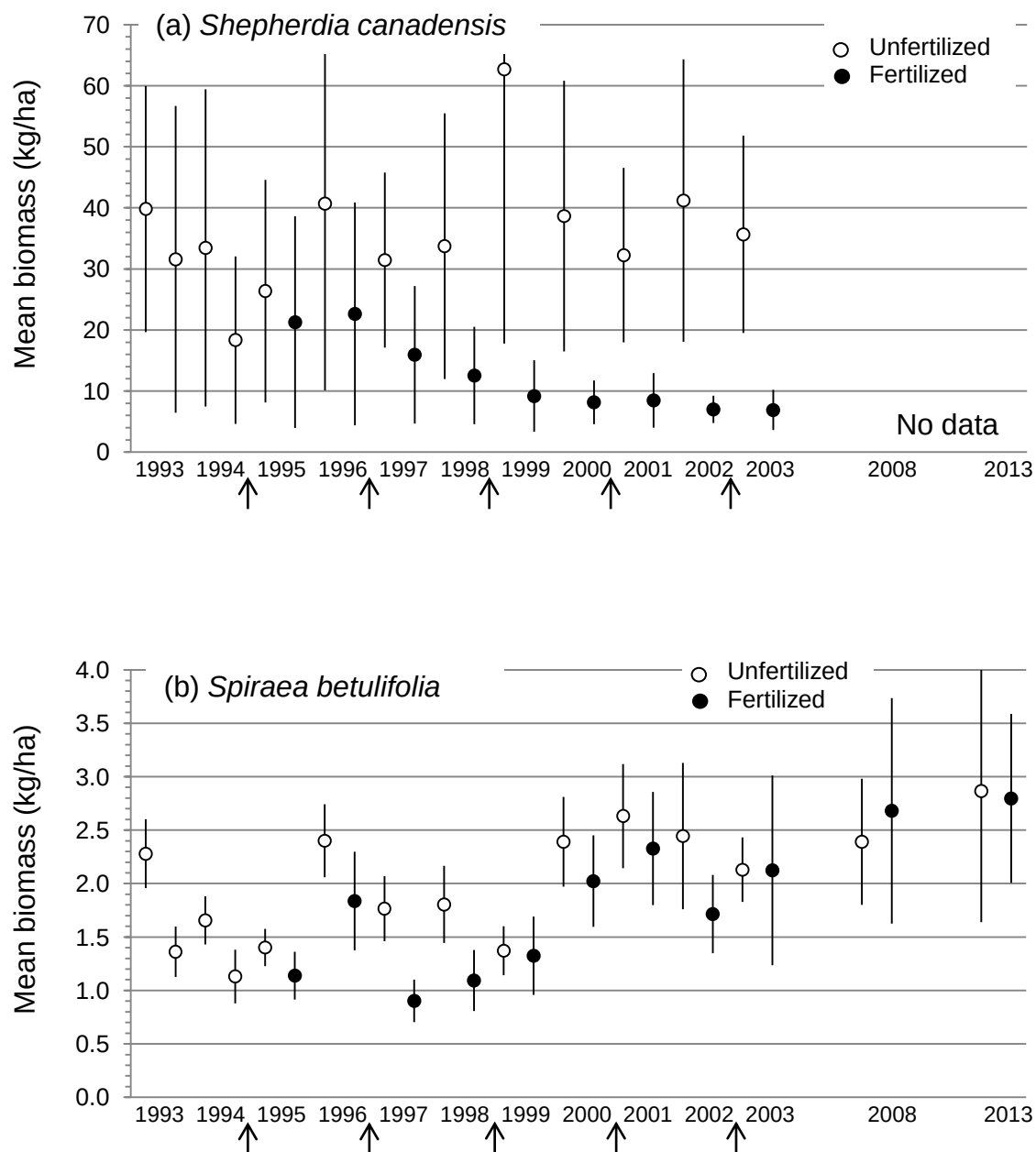
Appendix 4. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) *Lonicera involucrata*, (b) *Lonicera utahensis*, and (c) *Mahonia aquifolium* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized (n = 7, 8, 4) and fertilized (n = 8, 6, 5) lodgepole pine stands. Arrow denotes application of fertilizer.



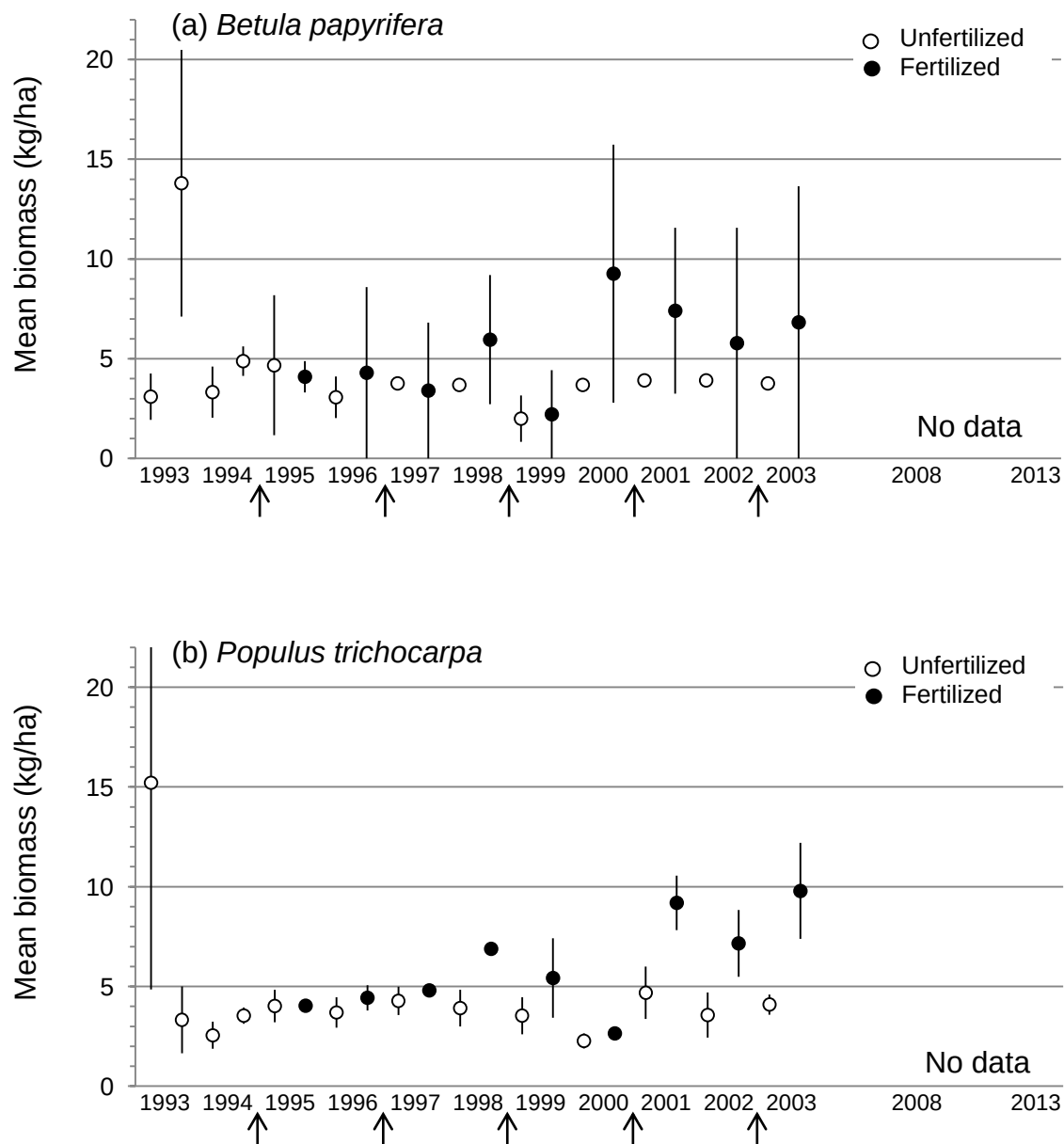
Appendix 4. (continued)



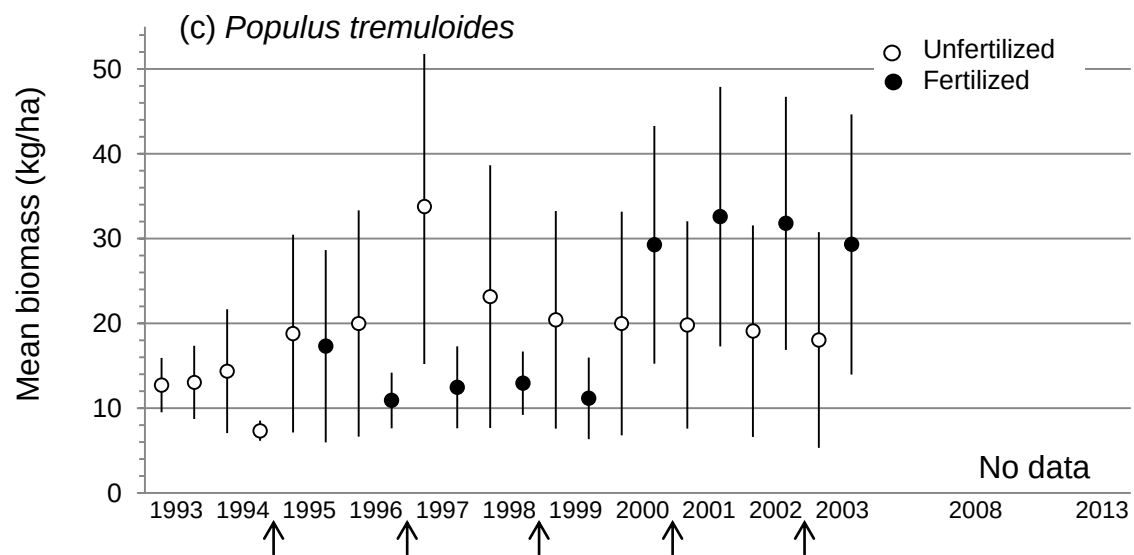
Appendix 5. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) *Shepherdia canadensis* and (b) *Spiraea betulifolia* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized (n = 4 and 12) and fertilized (n = 4 and 12) lodgepole pine stands. Arrow denotes application of fertilizer.



Appendix 6. Mean (n = number of replicate stands) $\pm$ SE biomass production (kg/ha) of (a) *Betula papyrifera*, (b) *Populus trichocarpa*, and (c) *Populus tremuloides* each year 1993 to 2003 and at 15 (2008) and 20 (2013) years post-treatment in unfertilized (n = 4, 9, 7) and fertilized (n = 2, 8, 3) lodgepole pine stands. Arrow denotes application of fertilizer.



Appendix 6. (continued)



Appendix 7. Responses in mean biomass of forage plants in all groups and individual species of vascular plants, and mean crown volume index of mosses and terrestrial lichens, to the 1 to 5 applications of nitrogen fertilizer. * denotes a significant ($P < 0.05$) difference between unfertilized and fertilized stands for that forage plant. ↑ increase; ↓ decrease; 0 no change.

Group, species, and height class	<u>Number of fertilizer applications</u>				
	1	2	3	4	5
Grasses	↑ *	↑ *	↑ *	↑ *	0
Forbs	0	0	↑ *	↑ *	↑ *
Total herbs	0	↑ *	↑ *	↑ *	↑ *
Total shrubs	0	0	0	0	0
Total herbs+shrubs	0	↑ *	↑ *	↑ *	↑ *
Total mosses	0	↓ *	↓ *	↓ *	↓ *
Terrestrial lichens	0	↓ *	↓ *	↓ *	↓ *
Dwarf shrubs					
<i>Arctostaphylos uva-ursi</i>	0	↓ *	↓ *	↓ *	↓ *
<i>Linnaea borealis</i>	0	0	↓ *	↓ *	↓ *
<i>Pachistima myrsinites</i>	0	0	0	0	0
<i>Rubus pubescens</i>	0	0	0	0	0
<i>Vaccinium caespitosum</i>	↓ *	↓ *	↓ *	↓ *	↓ *
<i>Vaccinium scoparium</i>	0	0	0	0	0

Low – middle shrubs

<i>Lonicera involucrata</i>	0	0	0	0	0
<i>Lonicera utahensis</i>	0	0	0	0	0
<i>Mahonia aquifolium</i>	0	0	0	0	0
<i>Ribes lacustre</i>	0	0	0	0	0
<i>Rosa acicularis</i>	↑ *	↑ *	↑ *	↑ *	↑ *
<i>Rubus idaeus</i>	0	0	↑ *	↑ *	↑ *
<i>Shepherdia canadensis</i>	0	0	0	0	0
<i>Spiraea betulifolia</i>	0	0	0	0	0
<i>Symphoricarpus albus</i>	0	0	0	0	0
<i>Vacc.membranaceum</i>	0	0	0	0	0
Tall shrubs					
<i>Alnus sinuata</i>	0	0	0	0	0
<i>Amelanchier alnifolia</i>	0	0	0	↑ *	↑ *
<i>Salix spp.</i>	0	0	0	0	0
Trees					
<i>Abies lasiocarpa</i>	0	0	0	0	0
<i>Betula papyrifera</i>	0	0	0	0	0
<i>Picea glauca x engelmanniana</i>	0	0	0	0	0
<i>Populus tremuloides</i>	0	0	0	0	0
<i>Populus trichocarpa</i>	0	0	0	0	0
<i>Pseudotsuga menziesii</i>	0	0	0	↑ *	↑ *
