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**Long-term influence of stand thinning and repeated
fertilization on forage production in young lodgepole pine
forests**

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Abstract: Integration of trees with forage and livestock production as silvopastoralism is another potential component of intensive forest management. Stand thinning and fertilization may enhance growth of crop trees and understory forage for livestock. We tested the hypothesis that large-scale pre-commercial thinning (PCT) (particularly heavy thinning to ≤ 1000 stems/ha) and repeated fertilization, up to 20 years after the onset of treatments, would enhance production of graminoids, forbs, and shrubs as cattle (*Bos taurus* L.) forage. Results are from two long-term studies: (1) PCT (1988-2013) and (2) PCT with fertilization (PCT-FERT) (1993-2013) of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands in south-central British Columbia, Canada. Mean biomass estimates of graminoids, forbs, total herbs, and shrubs were not affected by stand density. However, fertilization enhanced mean biomass estimates of graminoids, forbs, and total herbs, but not shrubs. Thus, the density part of our hypothesis was not supported, but the nutrient addition part was supported at least for the herbaceous components. Biomass of the herbaceous understory was maintained as a silvopasture component for up to 20 years (stand age 13 to 33 years) in fertilized heavily thinned stands, prior to canopy closure.

Keywords: cattle grazing; fertilization; herbaceous forage; lodgepole pine forest; stand thinning.

Introduction

The silvicultural practices of stand thinning and fertilization have been used successfully to increase biomass production in temperate zone forests (Moore and Allen 1999; Fox et al. 2007). Another potential component of intensive forest management is silvopastoralism which is an agroforestry practice that intentionally integrates trees with forage and livestock production (Sharrow 1999; Clason and Sharrow 2000). Depending on how and where it is applied, this form of agroforestry has the potential to be more integrated and profitable than single resource management (McDonald and Fiddler 1993; Husak and Grado 2002). Forage productivity peaks soon after any disturbance that removes tree cover or foliage (e.g., insect outbreaks, wildfire, harvesting). Cattle readily forage on graminoids, forbs, and some shrub species during summer grazing in these upland forest habitats (Willms et al. 1980; Holechek et al. 1982; Quinton 1984). There is then a predictable decline over successional time as the tree layer regains dominance and shades out the understory forage. Natural succession limits the post-disturbance period when the forage resource is capable of sustaining grazing cattle (*Bos taurus* L.) to a range of 10 to 15 years in most temperate and boreal coniferous forests (Wikeem et al. 1993).

Stand thinning reduces shade and delays canopy closure, and hence may increase forage yields and prolong the silvopasture potential relative to unthinned stands (Moore and Deiter 1992; Peitz et al. 2001). In addition, the quality and quantity of forage produced within forest rangeland may be enhanced by fertilization (Wikeem et al. 1993; Sullivan et al. 2012; Lindgren and Sullivan 2014a). From a forest ecosystem perspective, positive biomass responses of understory vegetation have been reported

for stand thinning (Sullivan et al. 2001; Lindgren et al. 2006) and fertilization (Thomas et al. 1999; VanderSchaaf et al. 2002; Lindgren and Sullivan 2013a). Enhanced biomass production of trees and understory vegetation in intensively managed forests may also help to mitigate climate change by providing a steadily increasing carbon sink (Hedwall et al. 2014).

However, as discussed by Sullivan et al. (2013), we have yet to document (other than some retrospective studies) long-term decadal changes in stand structure and understory vegetation in intensively managed forests. Thus, to date, there is a very narrow window of time to make extended extrapolations about the development and longevity of changes in forage production for cattle from various forest stand treatments. In addition, the range of pre-commercial thinning (PCT) levels in young forests is quite narrow with a major focus on wood production from an economic perspective. For example, in British Columbia (BC), young lodgepole pine stands have historically been thinned to within a very narrow range of stand densities, typically 1600-2000 stems/ha, with very few stands < 1000 stems/ha (Sullivan et al. 2013). Similarly, in lodgepole pine forests of the Pacific Northwest of the United States, stocking targets range generally from 1650 to 2250 stems/ha, but with variable densities depending on site index (Koch 1996). If creation of “openings” for development and persistence of forage production is desired, then substantially lower densities of PCT are required. Again, as noted by Sullivan et al. (2013), there is a dearth of actual silvicultural treatments designed to grow timber rapidly while simultaneously enhancing other forest values such as silvopasture.

Thus, this study was designed to test the hypothesis that large-scale PCT (particularly heavy thinning to ≤ 1000 stems/ha), and repeated fertilization, up to 20 years after the onset of treatments, would enhance production of understory vegetation, particularly graminoids, forbs, and shrubs as cattle (*Bos taurus* L.) forage. 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 2013b), mammals (Sullivan et al. 2010, 2012), and biodiversity (Sullivan et al. 2009) to these treatments. The current paper reports specifically on forage production for cattle in these experimental stands and how this relates to silvopasture management.

Study areas and methods

Experimental designs and study areas

Data from two separate long-term studies with 25- and 20-year datasets were used to test our study hypothesis: (1) PCT (1988-2013) and (2) PCT with fertilization (PCT-FERT) (1993-2013). The PCT study was located at each of three regional replicate areas in south-central BC, Canada: Penticton Creek, Kamloops, and Prince George. In 1988, stands were PCT to target densities of 500 (low), 1000 (medium), and 2000 stems/ha (high), and unthinned stands had densities >3000 stems/ha (unthinned). Treatments were assigned to stands in a randomized complete block design. Unfortunately, overstory trees at the Kamloops and Prince George areas were devastated by the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopk.) in 2005. The Penticton area was unaffected, and hence represents an undisturbed replicate block over the 25-year period. The disturbed Kamloops area also continued

after 2005 with measurements of abundance of herb, shrub, and understory tree layers and some surviving overstory tree layers. For the purposes of this paper, data from both Penticton and Kamloops were utilized.

The PCT-FERT study had four densities: 250 (very low), 500 (low), 1000 (medium), and 2000 stems/ha (high) with and without a repeated fertilization treatment, and an unthinned-unfertilized stand, replicated initially at each of three areas: Summerland, Kelowna, and Cariboo. Treatments were assigned to stands in a randomized complete block design. Unfortunately, the Cariboo replicate was decimated by MPB in 2005, and hence was not part of this study. The Summerland area was essentially unaffected by MPB and represented an undisturbed complete replicate block over the 20-year period. An outbreak of MPB in 2008, and a ground fire in 2009, resulted in partial disturbance of the Kelowna area, leaving small (≤ 0.50 ha) “islands” of relatively undisturbed forest. These stands provided supplemental data for those datasets collected from the Summerland area where there was little disturbance from MPB. Typical rotation times for intensively managed stands such as these would be 40-50 years. For the purposes of this paper, data from both Summerland and Kelowna were utilized.

Characteristics of the stands at each area in 2013 are listed in Table 1. Further details of study stands are given in Sullivan et al. (2001) and Lindgren et al. (2007).

PCT and fertilization treatments

At the PCT study areas, thinning was conducted in fall 1988 at Penticton and fall 1989 at Kamloops, and in fall 1993 at each of Summerland, Kelowna, and Cariboo study areas. Slash from the PCT was left on-site, which is currently standard practice in

BC. However, removal of this biomass for energy production may occur in the foreseeable future.

At the PCT-FERT study areas, fertilizer treatments were designed as large-scale “optimum nutrition” (Brockley 2005) 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 with foliar N concentration. The blended product was applied by helicopter at a rate of 906 kg/ha to each of the four fertilized stands at the two study areas. 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).

Vegetation sampling

Vegetation sampling (herbs and shrubs) was designed to measure the effects of PCT, and PCT with repeated fertilization, on individual plant species as well as community-level attributes (Lindgren and Sullivan 2013b). 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 two sizes of nested sub-plots: a 3 m x 3-m sub-plot for sampling shrubs and a 1 m x 1-m sub-plot for sampling herbs. 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). In this way, crown volume index 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 for the PCT study in 1990, 1993, 1998, 2000-2002, 2008, and 2014 (Penticton) or 2015 (Kamloops). Sampling for the PCT-FERT study 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 were not identified to species.

Estimating biomass from crown volume index

Crown volume index approximates the cylindrical space occupied by a plant rather than biomass. Therefore, the critical first step for estimating biomass of herbs and shrubs was to determine the correlation between crown volume index and biomass. Regression equations were then used to estimate biomass from the estimates of crown

volume index for herbs and shrubs in the PCT and PCT-FERT studies. In two separate investigations in the PCT-FERT study areas, we found strong and significant correlations between crown volume index and biomass (Lindgren and Sullivan 2013a). The first study was conducted in 2007 and involved clipping 180 herb plots and correlating the estimated crown volume index with the corresponding oven-dried biomass (Lindgren and Sullivan 2014a). This herb study revealed a strong and significant positive linear relationship for both graminoids ($R^2 = 0.95$; $F_{1,17} = 154.50$; $P < 0.01$) and forbs ($R^2 = 0.79$; $F_{1,17} = 26.12$; $P < 0.01$) (Lindgren and Sullivan 2013a). The second study was conducted in 2010 and investigated the correlation between crown volume index and biomass for shrubs using similar methods as described for herbs. This shrub study revealed a strong and significant positive linear relationship for dwarf, low, and tall shrubs (Table 2). Nine dominant shrub species were targeted during this investigation and provided more than 95% of the total crown volume index of the shrub layer. Inadequate sample size for *Linnaea borealis* L. and *Salix* L. spp. precluded any species-specific regression analyses for these species. As a result, data for seven of the nine dominant shrub species were used to develop species-specific regression equations.

Statistical analysis

To analyze the effect of stand density on biomass production, a repeated measures analysis of variance (RM-ANOVA) (IBM Corp. 2015) was conducted to determine the effects of stand treatment (4 levels of PCT: 500, 1000, and 2000, and unthinned) and time on mean biomass of graminoids, forbs, total herbs, total shrubs, and total

understory vegetation. Mean response variables ($n = 4$ stands for each treatment) were measured at 5-, 10, 15-, and 20-year intervals after the thinning treatments. Measurement of response variables at 0 and 2 years post-treatment were also included for graphing purposes, but the limited degree of replication ($n = 2$) at these times precluded their inclusion in the statistical analyses. This same approach was used in the PCT-FERT study with RM-ANOVA comparisons between fertilized and unfertilized stands (averaged across the 4 thinning densities). A one-way ANOVA compared the response variables in these stands prior to the start of treatments in 1988 and 1993. In the PCT-FERT study, stand density had no effect on abundance of understory herbs and shrubs (Lindgren and Sullivan 2013b), and so comparisons were focused on fertilized and unfertilized stands. Pooling data across the 4 thinning treatments was a reasonable approach as no significant density X fertilization interactions were observed for any of the 13 sample years (2-way ANOVA; $F_{3,16}$; $P > 0.10$). Again, response variables were measured at 5-, 10, 15-, and 20-year intervals after the start of PCT-FERT treatments. Based on a one-way ANOVA, no pre-treatment differences were observed for response variables in the respective comparisons in this investigation.

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). Duncan's multiple range test (DMRT), with multiple contrasts, was used to compare mean values, whenever a

significant difference was found, based on ANOVA results (Saville 1990). In all analyses, the level of significance was at least $P = 0.05$ (Zar 1999).

Results

Herb and shrub biomass

The dominant graminoid was pinegrass (*Calamagrostis rubescens* (Buckl.) and dominant forbs were fireweed (*Epilobium angustifolium* L.), arctic lupine (*Lupinus arcticus* S. Wats.), wild strawberry (*Fragaria virginiana* Duchesne), rosy pussytoes (*Antennaria microphylla* Rydb.), and white-flowered hawkweed (*Hieracium albiflorum* Hook.). Mean biomass production (kg/ha) of graminoids, forbs, and total herbs was not affected by stand density over the 20 post-thinning years of our investigation (Table 3; Fig. 1a-c). On average, mean biomass of graminoids ranged from 200 to 326 kg/ha and that of forbs from 131 to 165 kg/ha over the 20-year period. Similarly, mean biomass of shrubs and total understory vegetation also followed this pattern (Fig. 2a-b). Mean biomass of shrubs ranged from 107 to 163 kg/ha, and that of total understory vegetation from 437 to 608 kg/ha over the 20-year period. All response variables showed a significant decline with time after an initial increase, but there were no significant treatment x time interactions (Table 3).

Mean biomass was significantly ($P \leq 0.03$) higher in fertilized than unfertilized stands over the 20-year post-treatment period for graminoids, forbs, total herbs, and total understory vegetation (Table 3; Fig. 3a-c, 4b). These differences in mean biomass of vegetative components ranged from 2.1 to 4.4 times higher in fertilized than unfertilized stands during the fertilization period. The significant time factor showed the

increase in biomass after the start of fertilization and its decline by 15- and 20-years post-treatment. Not surprisingly, there was a significant treatment x time interaction for the three herbaceous response variables, with a lack of significant fertilizer effect during the early years followed by significantly enhanced biomass during the fertilization period, and a loss of fertilizer effect by 15 years post-treatment (Fig. 3a-c, 5a+b). Mean biomass of shrubs was not affected by fertilization, nor was there a significant time or treatment x time interaction (Table 3; Fig. 4a). Initial measurements of mean biomass in these response variables in 1993, prior to the start of treatments, were similar ($P > 0.05$).

Mean ($n = 2$) biomass of graminoids among all nine treatment stands from 1993 to 2013 for the PCT-FERT study clearly showed the positive influence of fertilization during the treatment period (1994 to 2003), and the decline to similar responses among stands in 2008 and 2013 (Fig. 5a). Mean ($n = 2$) biomass of forbs among all nine treatment stands also followed this pattern (Fig. 5b).

Discussion

Herb and shrub biomass

Stand density of lodgepole pine did not have an effect on biomass of graminoids, forbs, total herbs, or shrubs, and hence the density part of our hypothesis was not supported. This long-term result (over 20 years) was surprising given that other studies reported significant increases in herb abundance following thinning (Thomas et al. 1999; Thysell and Carey 2001; Lindgren et al. 2006; Cole et al. 2010). However, these published studies were either relatively short-term (up to 5 years post-thinning) or were

conducted in higher productivity coastal forest stands. Mean biomass of these herbaceous components in our thinned stands remained remarkably constant throughout the 20-year period; however, mean biomass in the unthinned stands did seem to decline over time. As suggested by Lindgren and Sullivan (2013a), it is possible that PCT treatments may not have had a significant impact on understory biomass because all of our young thinned stands, including the high-density stands, had relatively open canopy conditions during the early years of these two studies. In addition, all study stands were in a relatively dry environment such that soil moisture may have been limiting in some years.

The significant increase in mean biomass of graminoids, forbs, and total herbs to repeated fertilization did support the nutrient addition part of our hypothesis, at least for the herbaceous components. Fireweed, a preferred forage for cattle, was part of the forb component and abundance of this species increased dramatically in fertilized stands (Sullivan et al. 2012). These fertilization-induced increases in biomass of herbaceous components were similar to general increases in abundance of herbs recorded elsewhere, at least where overstory canopy cover was sufficiently open in fertilized stands (Riegel et al. 1991; Kellner and Redbo-Torstensson 1995; VanderSchaaf et al. 2000). A 9-year repeated fertilization experiment with annual additions of nutrients also reported overall increases in abundance of grasses and some herbs in Yukon boreal forest (Nams et al. 1993; Turkington et al. 2001). As for some fertilization effects, the influence of stand density may become significant with time as higher density stands begin to close canopy and shade out herb species, thereby limiting biomass in this understory component. This latter aspect and the end of

repeated fertilization treatments did decrease mean biomass to levels recorded in unfertilized stands at 15 and 20 years post-treatment.

Mean biomass of the shrub layer was not affected by stand density or fertilization, and hence the shrub part of our hypothesis was not supported. Reports of responses of shrub abundance to stand thinning have been variable: decreased (Wilson et al. 2009), unaffected (Lindgren et al. 2006; Lindgren and Sullivan 2013a), and enhanced relative to unthinned controls (Thomas et al. 1999). Site-specific conditions (e.g., plant community composition, level of plant competition), thinning intensity (heavy vs. light), and timing of sampling (time since thinning) may have contributed to this variability (Wilson et al. 2009). The enhanced productivity of the herb layer in fertilized stands may have contributed to the lack of shrub response during the initial years of fertilization. However, some shrubs in the fertilized stands appeared to have escaped the presumed herb layer suppression and increased in biomass, particularly the heavily thinned 250 stems/ha stands. Fertilization increased the growth rates of all shrubs by about 25-30% over control values over a 9-year period in Yukon boreal forest (Krebs et al. 2001). As with our study, there tended to be a lag time of 5 to 6 years before stable patterns of shrub response appeared (Turkington et al. 1998).

Silvopasture management and carbon storage

The silvopastoral goal of providing forage opportunities for cattle in managed forests seemed to be met in heavily thinned fertilized stands. In terms of actual utility of forage opportunities, relative habitat use by cattle was 2.1 times higher in fertilized than unfertilized stands, and heavily (500 stems/ha) thinned stands had 4.5 and 2.8 times

more use by cattle, respectively, than unthinned stands (Lindgren and Sullivan 2014b). In addition, fertilization may result in sufficient forage production in the understory vegetation of these forest ecosystems to compensate for cattle grazing that reduces the live forage biomass available for native browsing mammals (Lindgren and Sullivan 2014b). Forest fertilization also consistently improved forage production for sheep (*Ovis aries* L.) by an increased abundance of herbs and grasses (Papanastasis et al. 1995). Lindgren and Sullivan (2014a) reported that repeated fertilization increased crude protein content of pinegrass at five years after the most recent application in our stands.

Silvopasture, as an agroforestry practice, has considerable importance as a carbon sequestration strategy with the potential for carbon storage in its multiple plant species and wide applicability in managed forests and agricultural lands (Montagnini and Nair 2004). Hedwall et al. (2014) noted that fertilization was one of the best methods of forest management to increase net CO₂ fixation. Enhanced forest productivity resulting from fertilization can increase carbon storage capacity not only by increasing biomass of trees as reported in several studies (Sathre et al. 2010; Albaugh et al. 2012), but also by increasing cattle forage in the form of graminoids and forbs as reported in our study. Although biomass of understory layers was quite low relative to the tree layers in our forests, the silvopasture component was provided for up to 20 years in heavily thinned stands, prior to canopy closure.

Stand thinning to enhance tree growth and forage production for livestock would appear to reduce the capacity for carbon sequestration because of fewer trees on the land base, and potentially reduce the risk of wildland fire. However, as noted by Jimenez et al. (2011) for maritime pine (*Pinus pinaster* Aiton) in northwestern Spain,

increased growth of residual saplings in heavily thinned stands (more than 90% reduction in density) compensated for much of the carbon storage lost by thinning, at least up to five years post-treatment. If contributions of residues and understory vegetation are taken into account, stand-level carbon storage losses resulting from pre-commercial thinning (PCT) may be further mitigated (Campbell et al. 2009; Jiménez et al. 2011). Similarly, contributions of non-crop trees (ingress) to total stand productivity appeared to be substantial within heavily thinned stands of lodgepole pine 15 years post-thinning (Lindgren and Sullivan 2013b).

A caveat was the potential influence of browsing and grazing of herbivores (both wild and domestic) on biomass in these forest ecosystems. According to a comprehensive review by Tanentzap and Coomes (2012), herbivores can reduce terrestrial above- and below-ground carbon stocks but, depending on recovery time of vegetation (i.e., little or no grazing), overall reductions may approach zero. Herbivores in our study areas included cattle, mule deer (*Odocoileus hemionus* Rafinesque), moose (*Alces alces* L.), and several species of voles (*Microtus* spp., *Phenacomys intermedius* Merriam). We did not measure the potential impact of this herbivory on biomass of understory vegetation in this investigation.

Conclusions

PCT with repeated fertilization enhanced forage biomass for cattle within upland lodgepole pine forests by increasing production and extending the period of forage availability, particularly at stand densities < 1000 stems/ha. Biomass of graminoids, forbs, and total herbs, but not shrubs, responded positively to fertilization during this 20-

year investigation. Stand thinning without fertilization had no effect on biomass of understory vegetation during this period.

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519 **Table 1.** Experimental design and characteristics of lodgepole pine stands for the PCT and PCT + FERT studies in 2013.

Study area and stand	Density (stems/ha)			Attributes of dominant tree layer				
				(mean ± SE)				
	Crop trees ¹	Non-crop ² trees	Total conifers	DBH (cm)	Height (m)	Age (yr)	Area (ha)	Canopy closure (%)
PCT								
Penticton								
Low	550	2680	3230	21.8 ± 0.3	13.9 ± 0.1	42	20.0	87.4
Medium	1190	2915	4105	18.7 ± 0.2	15.4 ± 0.1	42	20.0	89.8
High	1670	3170	4840	16.9 ± 0.2	14.7 ± 0.1	42	20.0	92.3
Unthinned	5070	3050	8120	10.1 ± 0.3	11.5 ± 0.2	42	100+	88.9
Kamloops ³								
Low	85	2525	2610	18.3 ± 4.4	14.1 ± 1.8	47	22.0	-
Medium	260	840	1100	15.8 ± 2.4	15.1 ± 1.8	47	15.0	-
High	1070	490	1560	13.6 ± 1.8	12.9 ± 0.9	47	19.0	-
Unthinned	3840	155	3995	13.1 ± 0.4	14.0 ± 0.5	47	100+	-
PCT and Fertilization								
Summerland								
Very low	264	4845	5109	19.4 ± 0.3	10.2 ± 0.1	33	11.3	70.4
Very low	226F	1365	1591	19.3 ± 0.2	9.2 ± 0.1	33	11.3	73.3
Low	496	4290	4786	16.6 ± 0.2	9.6 ± 0.1	33	7.6	76.5
Low	501F	2060	2561	18.3 ± 0.2	9.2 ± 0.1	33	7.6	86.1

Medium	923	2637	3560	15.5 ± 0.1	9.3 ± 0.1	33	4.5	85.9
Medium	911F	770	1681	18.6 ± 0.3	10.4 ± 0.1	33	4.5	86.6
High	1691	1613	3304	14.3 ± 0.2	9.4 ± 0.1	33	4.4	87.4
High	1458F	854	2312	15.5 ± 0.2	9.3 ± 0.1	33	4.4	91.0
Unthinned	8095	1125	9220	9.1 ± 0.2	7.8 ± 0.1	33	5.0	91.9
Kelowna								
Very low	281	2325	2606	19.9 ± 0.4	11.4 ± 0.2	33	10.0	69.2
Very low	242F	4967	5209	20.4 ± 0.7	11.8 ± 0.4	33	10.0	83.5
Low	576	3050	3626	16.7 ± 0.4	10.8 ± 0.2	33	11.0	78.9
Low	569F	1367	1936	18.9 ± 0.6	12.2 ± 0.4	33	11.0	93.2
Medium	982	3025	4007	17.4 ± 0.6	12.5 ± 0.3	33	9.5	90.4
Medium	841F	3025	3866	17.7 ± 0.5	12.6 ± 0.2	33	9.5	93.7
High	1722	4000	5722	13.7 ± 0.4	11.6 ± 0.2	33	11.9	89.1
High	1548F	540	2088	15.0 ± 0.4	12.2 ± 0.2	33	11.9	92.6
Unthinned	3510	1625	5135	13.5 ± 0.5	12.2 ± 0.2	33	12.6	94.2

520 ¹ Crop trees of lodgepole pine in 2013; crop trees were those trees retained during the PCT treatment.

521 ² Non-crop trees arise from ingress over time.

522 ³ 2008.

523 F = fertilized stand

Table 2. Results of the stature-specific regression analyses developed from the 9 dominant shrub species sampled. Coefficients describe the simple linear relationship between crown volume index ($\text{m}^3/0.01 \text{ ha}$) and dry biomass ($\text{g}/0.01 \text{ ha}$).

Regression attributes	Shrub stature (height range) ^a		
	Dwarf (< 0.25 m)	Low (0.25 to 2.0 m)	Tall (> 2.0 m)
Sample size (<i>n</i>)	97	100	38
Slope (<i>m</i>)	103.82	67.35	44.62
Constant (<i>b</i>)	25.97	9.05	26.48
R^2	0.46	0.77	0.90
<i>P</i> -value	<0.01	<0.01	<0.01

^aRegressions for dwarf-statured shrubs were developed by pooling the data from *Arctostaphylos uva-ursi* (L.) Sprengel, *Pachistima myrsinites* Nutt., *Vaccinium scoparium* Leib. ex Coville, and *Linnaea borealis* L.; low-statured regressions were developed by pooling data from *Ribes lacustre* (Pers.) Poir., and *Spiraea betulifolia* Pall; tall-statured regressions were developed by pooling data from *Alnus sinuata* (Regel) Rydb and *Salix* L. spp.

Table 3. Results of RM-ANOVA for biomass responses of graminoids, forbs, total herbs, shrubs, and total understory vegetation in response to lodgepole pine stand density (stems/ha): low (500), medium (1000), high (2000), and unthinned, and PCT stands fertilized and unfertilized at 5, 10, 15, and 20 years post-treatment. *F*-values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures. Significant values in bold text.

Plant group	PCT only						PCT + FERT					
	<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> _{3,12}	<i>P</i>	<i>F</i> _{3,36}	<i>P</i>	<i>F</i> _{9,36}	<i>P</i>	<i>F</i> _{1,14}	<i>P</i>	<i>F</i> _{3,42}	<i>P</i>	<i>F</i> _{3,42}	<i>P</i>
Graminoids	0.13	0.94	5.01*	<0.01	1.11*	0.38	7.46	0.02	16.48*	<0.01	5.72*	<0.01
Forbs	0.43	0.74	3.66	0.02	0.85	0.58	6.88	0.02	5.77*	0.01	6.16*	<0.01
Total herbs	0.13	0.94	6.06*	<0.01	1.28*	0.29	8.09	0.01	10.48*	<0.01	6.77*	<0.01
Total shrubs	1.57	0.25	3.46	0.03	1.10	0.39	0.04	0.85	1.19*	0.32	0.63*	0.53
Total herbs+shrubs	0.34	0.80	6.03	<0.01	1.38	0.24	6.13	0.03	9.96*	<0.01	6.82*	<0.01

List of Figures

Figure 1. Mean ($n = 4$ replicate stands; $n = 2$ for year 0) $\pm$ SE biomass production (kg/ha) of (a) graminoids, (b) forbs, and (c) total herbs at 0, 2, 5, 10, 15, and 20 years post-treatment (pre-commercial thinning) among four densities (stems/ha) of lodgepole pine: low (500), medium (1000), high (2000), and unthinned.

Figure 2. Mean ($n = 4$ replicate stands; $n = 2$ for year 0) $\pm$ SE biomass production (kg/ha) of (a) shrubs, and (b) total herbs and shrubs (understory) at 0, 2, 5, 10, 15, and 20 years post-treatment (pre-commercial thinning) among four densities (stems/ha) of lodgepole pine: low (500), medium (1000), high (2000), and unthinned.

Figure 3. Mean ($n = 8$ replicate stands) $\pm$ SE biomass production (kg/ha) of (a) graminoids, (b) forbs, and (c) total herbs at 0, 5, 10, 15, and 20 years post-treatment in unfertilized and fertilized lodgepole pine stands. F = fertilization.

Figure 4. Mean ($n = 8$ replicate stands) $\pm$ SE biomass production (kg/ha) of (a) shrubs, and (b) total herbs and shrubs (understory) at 0, 5, 10, 15, and 20 years post-treatment in unfertilized and fertilized lodgepole pine stands. F = fertilization.

Figure 5. Mean ($n = 2$ replicate stands) biomass production (kg/ha) of (a) graminoids and (b) forbs annually from 1993 to 2003 and at 5-year intervals from 2003 to 2013 for four densities (250, 500, 1000, 2000 stems/ha) of unfertilized and fertilized lodgepole pine stands, and an unthinned pine stand. F = fertilization.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.