

Tree pruning improves tree form but not understory plant production in mixed stands of Sitka spruce and western hemlock, USA

Kellen N. Nelson ^{1,*}, Jeffrey C. Barnard¹, Preston M. Massingham¹ and Justin S. Crotteau ²

¹Juneau Forestry Sciences Laboratory, Pacific Northwest Research Station, USDA Forest Service, 11175 Auke Lake Way, Juneau, AK 99801, United States

²Missoula Forestry Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 800 East Beckwith Avenue, Missoula, MT 59801, United States

*Corresponding author. Juneau Forestry Sciences Laboratory, Pacific Northwest Research Station, USDA Forest Service, 11175 Auke Lake Way, Juneau, AK 99801, USA. E-mail: Kellen.Nelson@usda.gov

Abstract

Precommercial thinning and tree pruning are frequently used together to improve timber quality and wildlife habitat in even-aged Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) stands. Thinning enhances crop tree growth and understory plant production; however, the benefits and drawbacks of tree pruning have received less attention. Tree pruning was investigated in two long-term experiments on the Tongass National Forest, Alaska, USA. Experiment 1 tracked four uniformly thinned sites for ~30 years that received 2.4, 3.6, and 5.2 m lift, and no pruning treatments. Experiment 2 tracked 11 sites for 16 years that received thinning/no pruning, thinning plus pruning (25% of trees), thinning plus pruning (50% of trees), and no thinning/no pruning treatments. We investigated (i) how pruning lift height affects tree form and understory production and (ii) how pruning density affects canopy closure and understory production. In Experiment 1, pruning reduced butt log taper and did not adversely affect diameter or height in either species. Pruning lift was visible in height-to-live crown measurements. Crown recession occurred first in low lift treatments and later in all treatments until crown form was similar after 28–31 years. Epicormic branching rates in Sitka spruce peaked 6–9 years after treatment before falling sharply. Deer forage declined through time and did not differ between lift treatments. In Experiment 2, canopy closure was lower shortly after thinning and pruning, but did not differ from the control after 16 years. Epicormic branching rates were greater shortly after thinning and pruning but did not differ from the control after 16 years. Deer forage declined with canopy closure and thinned and pruned treatments exhibited greater forage than the control. We conclude that pruning can improve log quality for timber applications but does not enhance understory plant biomass and deer forage over thinning treatment alone.

Keywords: pruning; thinning; understory production; Sitka spruce (*Picea sitchensis*); western hemlock (*Tsuga heterophylla*); coastal temperate rainforest

Introduction

Tree pruning and precommercial thinning are complementary silvicultural techniques used to achieve a wide array of management objectives. In even-aged Sitka spruce (*Picea sitchensis* [Bong.] Carr.) plantations growing in northern Europe (Macdonald and Hubert 2002) and even-aged mixed stands of Sitka spruce and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) growing in their native range in the Pacific coastal temperate rainforest of North America (Ruth and Harris 1979), these techniques are frequently used to manage growing stock to improve timber quality and provision for ecosystem services such as wildlife habitat and wild food subsistence harvest (e.g. blueberries, deer). Precommercial thinning has been shown to successfully open forest canopies and enhance crop tree growth and understory plant production during the stem exclusion phase of stand development (Crotteau et al. 2020b); however, the long-term benefits and drawbacks (i.e. epicormic branching; Deal et al. 2003) of tree pruning have received less attention, particularly in these species' native range.

The Pacific Northwest region of North America hosts the largest intact tract of coastal temperate rainforest globally where

Sitka spruce and western hemlock dominate stand composition across much of the ecoregion (DellaSala et al. 2011). Timber management during the twentieth century focused primarily on cutting and regenerating high-quality primary forest stands; however, contemporary forest management aims to balance ecological with economic objectives by sustainably managing second growth stands that are increasingly available across the region. Primary forests were predominantly harvested using clearcutting techniques and even-aged second growth stands re-established with abundant natural regeneration (Harris and Farr 1974, Ruth and Harris 1979). Understory vegetation responds favorably for a brief period following stand re-initiation but declines rapidly after canopy closure and is nearly absent during the prolonged stem exclusion phase of stand development (Wallmo and Schoen 1980, Alaback 1982). Therefore, density management practices are widely used for the dual purpose of enhancing crop tree growth and promoting understory vegetation for biodiversity and deer forage production by opening the forest canopy (Hanley et al. 2013, Crotteau et al. 2020b). Tree pruning in conjunction with precommercial thinning is an established

silvicultural practice that can be effective at improving wood quality (Henman 1963, Macdonald and Hubert 2002) and has also been prescribed in southeast Alaska to enhance understory plant production based on the assumption that pruning will enable additional light to penetrate to the forest floor.

The practice of tree pruning has long been applied to even-aged spruce–hemlock forests growing in their North American native range (Harris 1966) and Sitka spruce plantations across northern Europe (Henman 1963). Past research on pruning of both species indicates that branch occlusion occurs rapidly (Harris 1966, Petruncio 1994) and impacts on wood quality are varied depending on lift height (i.e. the height to which branches are pruned) and tree spacing (Deal et al. 2003, Newton and Cole 2012). Benefits of pruning on tree form and wood quality typically come at a minor cost to growth in the crop tree (de Montigny and Stearns-Smith 2001, Newton and Cole 2012, Baders et al. 2017) and include reduced taper, fewer branch intrusions in butt logs, and a higher proportion of late wood (Henman 1963).

In Sitka spruce, epicormic branching is common after stand improvement activities (Petruncio 1994, Deal et al. 2003) and natural disturbances (e.g. blowdown; Quine 2004) that alter the sub-canopy light environment. Epicormic branches arise from dormant or adventitious buds on the tree bole in response to heightened light levels and can result in pin knots, a defect that reduces the value of logs and lumber (Macdonald and Hubert 2002, Macdonald et al. 2010). Prior studies conducted 3–8 years following thinning and pruning in southeast Alaska demonstrate that sprout density is inversely related to tree spacing (Newton and Cole 2012) and suggest that Sitka spruce may be a poor candidate for pruning due to the species' propensity for numerous and large epicormic branches (Deal et al. 2003). To what extent emergent branches affect timber quality depends greatly on their longevity and retention, and a long-term view of their effects are needed to better understand the overall benefits of these treatments.

In addition to improving tree growth and form, the maintenance and revitalization of understory vegetation is a poignant aspect of even-aged Sitka spruce–western hemlock forest management due to the long-acknowledged deleterious impact that naturally dense post-clearcut regeneration can have on understory plant communities (Wallmo and Schoen 1980, Alaback 1982). Productive understory communities are important for the maintenance of biodiversity and provide critical wildlife habitat for important species including Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), the Alexander Archipelago wolf (*Canis lupus ligoni*), and black bear (*Ursus americanus*) (Hanley 1993, Gilbert 2015). In addition, understory plant communities provide society with foraging opportunities for subsistence food resources across the ecoregion. Increased tree spacing achieved through thinning operations is an effective tool that improves understory plant diversity and deer forage production. Heightened benefits from thinning have been found when treatments are applied early in stand development, mitigating the effects of early canopy closure on understory plant communities (Cole et al. 2010, Crotteau et al. 2020b). Tree pruning may provide additional benefits to understory communities beyond thinning treatment alone by allowing additional light to pass through the forest canopy. No studies have addressed the effects of pruning activities on understory plant communities and an assessment is needed to determine the efficacy of pruning treatments for this purpose across the region.

The silvicultural application of tree pruning can affect tree characteristics and stand development in a variety of ways and

most research to date has evaluated crop tree response to pruning within a decade of treatment application (e.g. Petruncio 1994, Deal et al. 2003, Newton and Cole 2012). An understanding of longer-term effects of silvicultural pruning techniques are needed to guide management application of related prescriptions across young Sitka spruce–western hemlock forests of North America. In this article, we evaluate the efficacy of tree pruning in two long-term stand manipulation experiments implemented on the Tongass National Forest in southeast Alaska, USA (Petruncio 1994, Crotteau et al. 2020a, Nelson et al. 2022). In the first study, we evaluate how pruning lift height affects crop tree characteristics and understory plant communities through ~30 years of stand development on sites that were thinned twice to prevent canopy closure prior to pruning treatment application. In a second study, we evaluate how pruning density (the proportion of trees pruned) affects the rate of canopy closure and understory plant communities through ~15 years of stand development on sites that were thinned once at the time of canopy closure. Through these studies, we offer an evaluation of modern pruning prescriptions relevant to silvicultural practitioners of traditional and ecological forestry across the Sitka spruce–western hemlock coastal temperate rain-forest ecoregion.

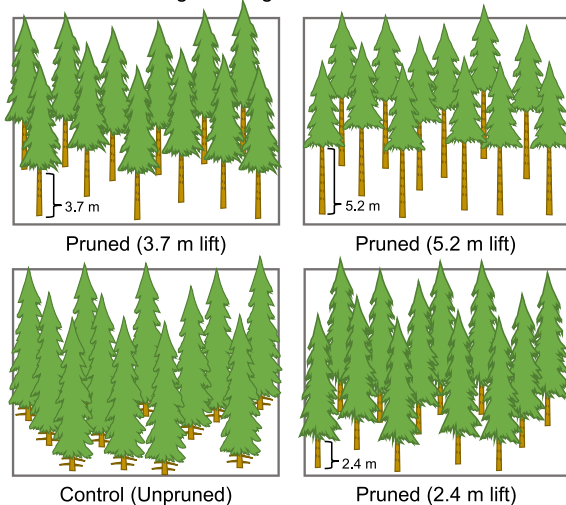
Methods

Experiment 1: Pruning lift height

Tree characteristics and understory vegetation were tracked across four sites that received manipulative pruning lift treatments at Cave Creek, Coffman Cove, and Salamander Lake on Prince of Wales Island and at Lemon Creek near Juneau, Alaska, USA (Petruncio 1994, Deal et al. 2003). Study sites were naturally stocked with Sitka spruce and western hemlock following harvest between 1968 and 1972. Precommercial thinning treatments occurred at 10 to 14 years of age to a uniform 4.9 m (16 ft) spacing or 420 trees ha⁻¹ (170 trees ac⁻¹). Pruning treatment plots were then established sequentially in 1990, 1991, and 1992 at ~22 years of age. Pruning lift treatments included 2.4 m (8 ft), 3.7 m (12 ft), 5.3 m (17 ft), and control (no pruning) and were applied to crop trees of both species using a pole pruner in four 0.22-ha (46.7 m × 46.7 m) adjacent experimental units (Fig. 1). A fifth site located at Falls Creek on Mitkof Island was also sampled but was excluded from analysis because tree spacing was not held constant in the preparatory thinning treatments.

At each site, tree data were collected in one square 0.08-ha (28.3 m × 28.3 m) fixed area sample plot centered in each treatment unit. A 9.1-m buffer was left between the sample plot and treatment unit boundary which resulted in a minimum 18.2-m buffer between sample plots. Treatments were located within a forested matrix and buffers were assumed to be sufficient to prevent confounding treatment effects. Tree measurements were collected before and immediately after each treatment unit was pruned and plots were remeasured in 1999, 2012, and 2021. Trees (>2.5 cm diameter) were sampled for species, diameter at breast height (diameter; 1.37 m height), height to crown base, total height, and live or dead status. On Sitka spruce trees, epicormic branches were counted up to 2.4 m (8 ft) height by size (i.e. ≤2 cm diameter, >2 cm diameter) and live or dead status. Three trees of either or both species were selected for butt and second log taper measurements in each plot (4.9 m (16') log lengths) and bole diameter was collected at 1.37 m, 5.2 m, and 10.1 m heights. Taper trees were required to be defect free and have a diameter within ±25% of the quadratic mean diameter of the eight largest spruce and hemlock trees observed in the plot. Wind damage

A: Experiment 1 – Pruning Lift Height



B: Experiment 2 – Pruning Density

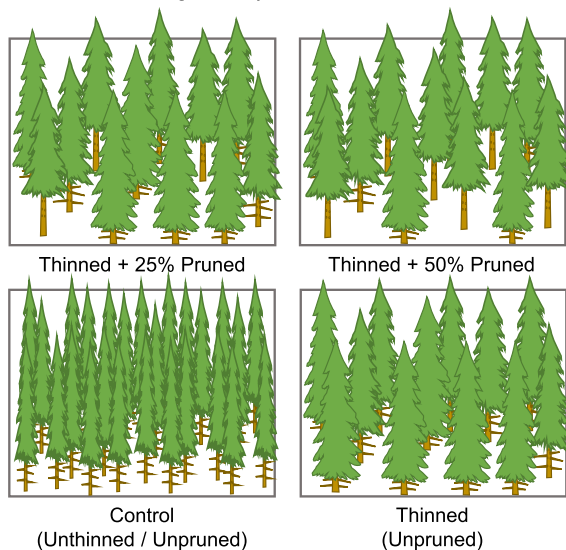


Figure 1. The effects of tree pruning were investigated in two manipulative experiments. Experiment 1 (A) evaluates pruning in thinned stands at 2.4 m (8 ft), 3.6 m (12 ft), and 5.2 m (17 ft) lift heights and a no pruning control. Experiment 1 was measured after establishment in 1991, 1992, and 1993, and remeasured in 1999, 2012, and 2021. Experiment 2 (B) evaluates pruning density and features combined thinning and pruning treatments. Prescriptions included thinning but no pruning, thinning plus pruning of 25% of trees, thinning plus pruning of 50% of trees, and a no thinning/no pruning control. Pruning lift height was 2.4 m (8 ft) and plots were measured 5 years after treatment in 2008 and again in 2013 and 2019.

affected crop tree spacing in the control treatment at Lemon Creek after 1999, and this plot was removed from all analyses for measurement years 2012 and 2021.

Understory measurements were collected in 1999, 2012, and 2021 using 30 quadrats (1 m²) arranged uniformly along three transects within each plot. In each quadrat, tree seedlings were counted by species and size class (i.e. ≤10 cm height, 10 to 90 cm height, 90 cm height to <2.5 cm diameter). Aerial percent cover was estimated by species for all vascular plants and later summarized by life form (shrub, forb, and fern). Percent cover estimates were converted to forage biomass (kg ha⁻¹) estimates using allometric equations developed using data collected as part of Experiment 2 (see methods in Hanley et al. 2012, Hanley et al. 2013, Crotteau et al. 2020b). Forage biomass estimates were

entered into the FRESH deer forage calculator (Hanley et al. 2012; <https://apps.fs.usda.gov/FreshDeer/>) which calculates an estimate of deer days per hectare. Deer days are an estimate of the number of days that a Sitka black-tailed deer can meet their metabolic requirements with available forage. Metabolic scenarios included a single adult deer in summer, a lactating doe with one fawn in summer, and a single adult deer in winter with 20 cm of snow covering low stature vascular plants.

Hemispherical photos were collected at plot centers to estimate canopy cover using a Nikon D5000 in 2012 and a D5200 in 2021 with a Sigma 4.5-mm hemispherical lens. Canopy cover index was computed using hemispherical photos processed in SideLook (field of view: 120°; Nobis and Hunziker 2005) and Gap Light Analyzer (Frazer et al. 1999) software.

Experiment 2: Pruning density

Eleven study sites were established in 2002 and 2003 on Baranof, Chichagof, Prince of Wales, Revillagigedo, and Zarembo Islands as part of module 3 in the Tongass-Wide Young Growth Studies (TWYGS) project (Hanley et al. 2013, Crotteau et al. 2020a). The objective of module 3 was to evaluate the efficacy of precommercial thinning and pruning silvicultural prescriptions conducted 25–35 years after stand initiation. Treatments included thinning, thinning with 25% of crop trees pruned, thinning with 50% of crop trees pruned, and control (no thinning, no pruning) (Fig. 1). Thinning was applied at 4.9 m (16 ft) spacing or 420 trees ha⁻¹ (170 trees ac⁻¹) and pruning lift height was set at 2.4 m (8 ft). Treatment units were 4 ha (10 acres) or larger.

Tree and understory data were collected in five 0.05-ha (22.4 m × 22.4 m) fixed area plots per treatment at each site. Plots were randomly located >25 m from the treatment edge and >100 m apart. Measurements were collected in 2008, 2013, and 2019. Trees (>2.5 cm diameter) were sampled for species, diameter, height to crown base, total height, live or dead status, and presence of epicormics (same method as Experiment 1). In high-density control plots, a subsample of trees was measured in nine 9-m² subplots. Understory measurements were collected in each year using 12 quadrats (1 m²) in each plot or 60 per treatment unit. Analysis of the understory data followed methods described for Experiment 1.

Hemispherical photos were collected at plot centers to estimate canopy cover using a Nikon CoolPix 990 in 2008, a Nikon D5000 in 2013, and a D5200 in 2019 with a Sigma 4.5-mm hemispherical lens. Canopy cover index was computed using the same methods described in Experiment 1.

Statistical analysis

For each site in each study, measurement year was converted to time since treatment (years) to best convey stand developmental dynamics after treatment. In the pruning height study, measurements were assigned to time since treatment groups that spanned multiple years (i.e. 6–9, 19–22, and 28–31 years since treatment) due to the staggered nature of treatment implementation and subsequent sampling of all sites in single years. Analysis of variance with multiple pair-wise comparisons (Tukey's HSD, $\alpha = 0.05$) were used to evaluate the interacting effects of treatment and time since treatment on log taper, tree diameter, tree height, live crown height, live crown ratio, number of epicormic branches, canopy closure index, understory biomass, and deer days response variables. Log₁₀ transformation was used on number of epicormic branches, plant biomass, and deer days variables to ensure that residuals were normally distributed to

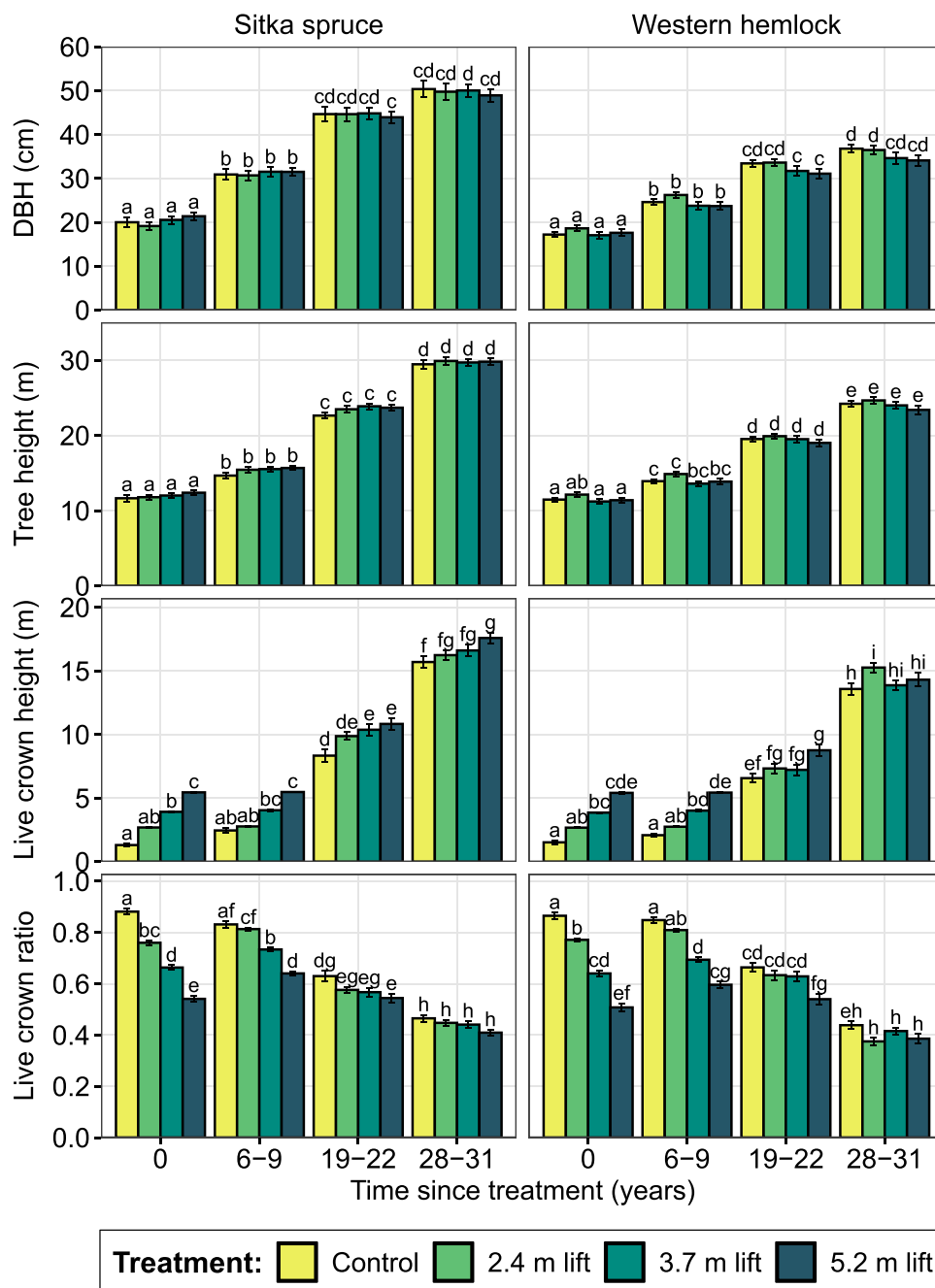


Figure 2. Sitka spruce and western hemlock diameter, height, live crown height, and live crown ratio response to pruning lift height treatment over ~30 years. Letters denote pair-wise statistical differences (Tukey's HSD, $\alpha = 0.05$).

meet model assumptions. Binomial logistic regression models with multiple pair-wise comparisons were used to evaluate differences in the proportion of trees with epicormic branches. Analysis of covariance regression models were used for Experiment 2 to fit models predicting understory plant biomass and deer days using treatment and canopy cover index as explanatory variables. Contrasts were set using treatment (i.e. dummy variable) coding where thinning and pruning treatments were compared against the control. Model assumptions were confirmed using standard regression diagnostic plots (e.g. residual versus fitted values, normal quantile–quantile (i.e. normal Q-Q), scale-location, residuals versus leverage plots). Outliers were identified for removal using Cook's distances. Data processing and statistical analysis were completed using the R statistical software (R Core Team 2022) with

doBy (Højsgaard and Halekoh 2023), multcomp (Hothorn et al. 2008), and tidyverse (Wickham et al. 2019) packages.

Results

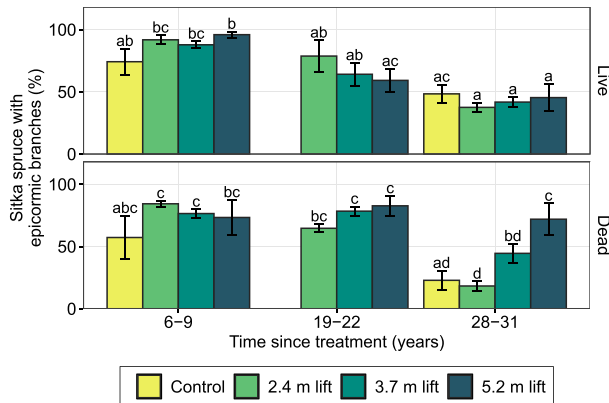
Experiment 1—Effects of pruning height

Mean tree diameter and tree height increased in both species over the course of the study and after ~30 years mean (± 1 standard error) Sitka spruce diameter was $27.8 \pm 3.1\%$ and height was $19.2 \pm 2.0\%$ greater than western hemlock (Fig. 2). Tree diameter and height did not differ by pruning height treatment for either species at any point during the study. In contrast, the effects of pruning height were evident on live crown height and live crown ratio in both species. The effects of pruning treatment

Table 1. Mean (± 1 standard error) Sitka spruce butt and second log taper 28–31 years after pruning lift treatment application.

	Log taper (cm per 4.9 m log length)			
	Control	2.4 m lift	3.7 m lift	5.2 m lift
Butt log	14.6 $\pm$ 1.3 ^a	12.0 $\pm$ 0.9 ^{ab}	10.6 $\pm$ 0.8 ^b	10.3 $\pm$ 1.1 ^b
Second log	3.9 $\pm$ 0.7 ^a	5.6 $\pm$ 0.5 ^a	6.0 $\pm$ 0.8 ^a	5.8 $\pm$ 0.9 ^a

Log length is 4.9 m (16').

**Figure 3.** Changes in the rate of epicormic branch occurrence on Sitka spruce by pruning lift height treatment over ~30 years. Letters denote pair-wise statistical differences (Tukey's HSD, $\alpha = 0.05$).

diminished with time indicating differences in crown recession rates between treatments (Fig. 2). In both species, crown recession was only evident in the unpruned control between 0 and 6–9 years after lift treatment. After that time, all pruning treatments appear to lift together until treatments became indistinguishable at 28–31 years post-treatment. For Sitka spruce, mean live crown ratio ranged from 0.88 ± 0.01 in the control treatment to 0.54 ± 0.01 in the 5.2 m pruning height treatment at year 0 and 0.46 ± 0.01 in the control treatment to 0.41 ± 0.01 in the 5.2 m pruning height treatment at years 28–31. Similarly, in western hemlock, mean live crown ratio ranged from 0.87 ± 0.01 to 0.51 ± 0.02 at year 0 and from 0.44 ± 0.01 to 0.38 ± 0.02 at years 28–31 between control and 5.2 m height treatments. Canopy closure index ranged from 79% to 91% at years 19–22 and 80% to 91% at years 28–31 (canopy closure was not measured earlier in the study) and did not differ between pruning height treatments. Thirty years after treatment, Sitka spruce butt log taper showed a declining relationship with pruning height (Table 1), but second log taper did not vary significantly with pruning height.

The percent of Sitka spruce trees with live or dead epicormic branches did not vary with pruning lift height (Fig. 3), but the percent of trees with live epicormic branches declined with time across all treatments. Reductions in percent of epicormic branches were first detected 19–22 years after treatment in the 5.2 m lift treatment and all lift treatments exhibited reductions in the percent of trees exhibiting epicormic branches by 28–31 years after treatment. The percent of trees with dead epicormic branches also declined through time with reductions occurring in the 2.4 m and 3.7 m pruning lift treatment, but no change was observed in the 5.2 m lift treatment.

The average number of live or dead small epicormic branches per tree declined across all treatments from a high 6–9 years after treatment to a low 28–31 years after treatment (Table 2, Supplementary Fig. 1). Live large epicormic branches were found

Table 2. Mean (± 1 standard error) number of epicormic branches on Sitka spruce trees in the pruning lift height study.

		Time since treatment (years)		
		6–9	19–22	28–31
Live epicormics (tree ⁻¹)				
Small (<2 cm)	Control	20.6 $\pm$ 5.3 ^a		7.7 $\pm$ 2.0 ^b
	2.4 m lift	10.5 $\pm$ 1.9 ^a	4.2 $\pm$ 0.8 ^b	2.4 $\pm$ 0.4 ^b
	3.7 m lift	18.2 $\pm$ 2.7 ^a	5.6 $\pm$ 1.1 ^b	4.4 $\pm$ 1.0 ^b
	5.2 m lift	14.4 $\pm$ 1.5 ^a	4.9 $\pm$ 0.8 ^b	3.4 $\pm$ 0.9 ^c
Large (>2 cm)	Control	0.9 $\pm$ 0.6 ^a		0.6 $\pm$ 0.3 ^a
	2.4 m lift	0.6 $\pm$ 0.2 ^a	0.5 $\pm$ 0.3 ^a	0.0 $\pm$ 0.0 ^a
	3.7 m lift	4.0 $\pm$ 1.1 ^a	0.3 $\pm$ 0.2 ^b	0.1 $\pm$ 0.1 ^b
	5.2 m lift	8.3 $\pm$ 1.3 ^a	0.1 $\pm$ 0.1 ^b	0.1 $\pm$ 0.0 ^b
Dead epicormics (tree ⁻¹)				
Small (<2 cm)	Control	19.6 $\pm$ 4.2 ^a		1.6 $\pm$ 0.8 ^b
	2.4 m lift	7.9 $\pm$ 1.4 ^a	2.8 $\pm$ 0.5 ^b	1.3 $\pm$ 0.4 ^b
	3.7 m lift	7.4 $\pm$ 1.3 ^a	6.7 $\pm$ 1.2 ^a	3.2 $\pm$ 0.9 ^b
	5.2 m lift	3.1 $\pm$ 0.4 ^a	5.3 $\pm$ 0.6 ^b	4.3 $\pm$ 0.6 ^{ab}
Large (>2 cm)	Control	3.8 $\pm$ 1.3 ^a		0.0 $\pm$ 0.0 ^b
	2.4 m lift	0.0 $\pm$ 0.0 ^a	0.9 $\pm$ 0.3 ^b	0.0 $\pm$ 0.0 ^a
	3.7 m lift	0.1 $\pm$ 0.0 ^a	2.2 $\pm$ 0.7 ^b	0.2 $\pm$ 0.1 ^a
	5.2 m lift	0.0 $\pm$ 0.0 ^a	5.0 $\pm$ 0.9 ^b	2.4 $\pm$ 0.6 ^c

Letters denote pair-wise statistical differences in time since treatment (Tukey's HSD, $\alpha = 0.05$). Pruning height treatment effects did not differ significantly.

primarily 6–9 years after treatment in the 3.7 m and 5.2 m lift treatments, but the number of these branches declined abruptly in later measurements. Concordantly, the number of large dead epicormic branches spiked in the 3.7 m and 5.2 m lift treatments during the 19–22 years after treatment measurement but diminished by 28–31 years after treatment.

Understory plant biomass was highly variable in all treatments and measurement years (Table 3). Shrub biomass decreased substantially between 6–9 and 19–22 years after treatments but did not change between 19–22 and 28–31 years after treatment. Fern and forb lifeforms did not vary significantly with time since treatment.

Deer days decreased with time since treatment but did not differ between pruning lift treatments (Table 3). Assuming the metabolic demands for a single adult deer in summer, deer days decreased by nearly 65% in the unpruned control and 55% in the 3.6 m lift and 5.2 m lift treatments between 6–9 and 28–31 years since treatment. For a doe lactating one fawn in summer, deer days decreased by 73% in the unpruned control between 6–9 and 28–31 years since treatment, but no significant changes were found in the other treatments. Using a scenario of 20 cm of snow cover during winter, enough to cover all herbaceous plants thereby leaving only shrubs available as forage, deer days decreased by ~63% in the 2.4 m and 3.6 m lift treatments between 6–9 and 28–31 years since treatment, but no significant changes were found in the unpruned control and 5.2 m lift treatments.

Experiment 2—Effects of pruning density

Five years after treatment, the percent of Sitka spruce trees with epicormic branches was greatest in stands that received thinning and thinning plus pruning treatments over control plots. Control sites averaged (± 1 standard error) $29.4 \pm 6.5\%$ of Sitka spruce trees with epicormic branches whereas thinned sites averaged $80.2 \pm 3.3\%$, thinned plus 25% pruned sites averaged $80.3 \pm 3.7\%$, and thinned plus 50% pruned sites averaged $81.6 \pm 4.0\%$. Differences between groups became less evident through time and were

Table 3. Mean (± 1 standard error) understory plant biomass and Sitka black-tailed deer forage availability by pruning lift height treatment and times since treatment.

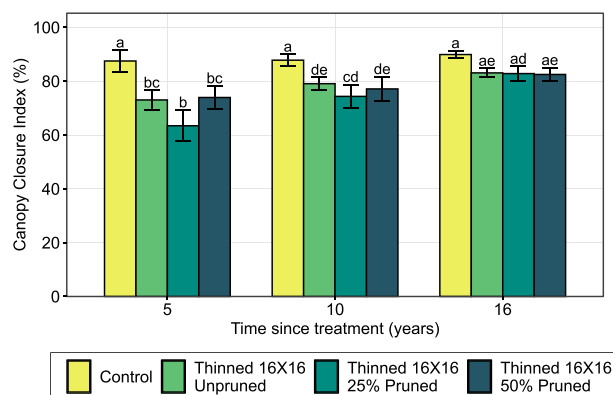
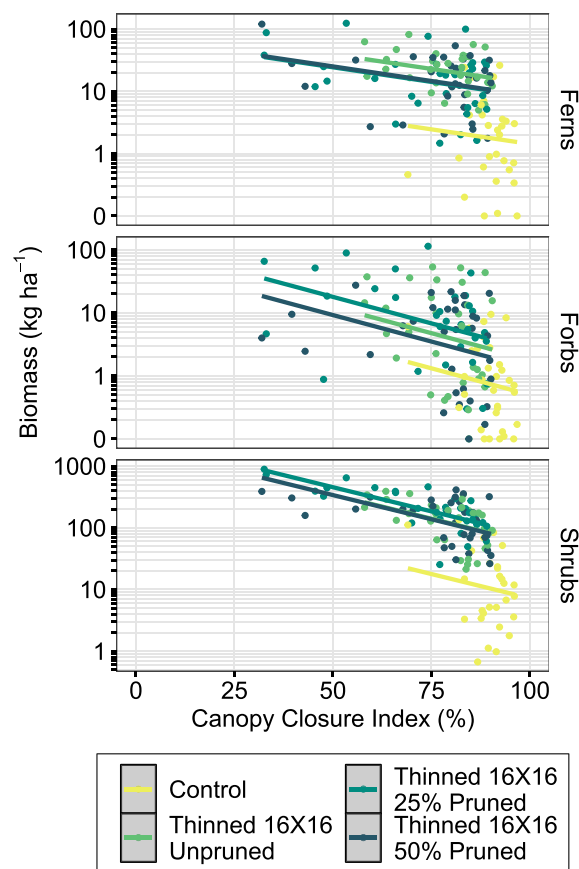
		Time since treatment (years)		
		6–9	19–22	28–31
Biomass (kg ha^{-1})				
Ferns	Control	54.9 $\pm$ 25.1 ^a	37.1 $\pm$ 19.1 ^a	73.1 $\pm$ 23.6 ^a
	2.4 m lift	11.2 $\pm$ 6.7 ^a	37.9 $\pm$ 21.4 ^a	54.4 $\pm$ 26.2 ^a
	3.7 m lift	60.1 $\pm$ 29.6 ^a	37.1 $\pm$ 19.1 ^a	87.3 $\pm$ 36.0 ^a
	5.2 m lift	15 $\pm$ 5.1 ^a	32.5 $\pm$ 15.0 ^a	60.0 $\pm$ 18.8 ^a
Forbs	Control	60.1 $\pm$ 58.0 ^a	11.9 $\pm$ 6.2 ^a	2.9 $\pm$ 2.7 ^a
	2.4 m lift	6.1 $\pm$ 5.8 ^a	19.6 $\pm$ 10.1 ^a	4.2 $\pm$ 3.0 ^a
	3.7 m lift	42.3 $\pm$ 37.8 ^a	3.6 $\pm$ 2.1 ^a	13.5 $\pm$ 9.7 ^a
	5.2 m lift	33.1 $\pm$ 32.9 ^a	12.0 $\pm$ 4.9 ^a	2.0 $\pm$ 1.2 ^a
Shrubs	Control	366.6 $\pm$ 77.9 ^a	70.1 $\pm$ 31.0 ^b	52.7 $\pm$ 21.7 ^b
	2.4 m lift	313.4 $\pm$ 63.6 ^a	70.5 $\pm$ 11.4 ^b	91.3 $\pm$ 23.1 ^b
	3.7 m lift	390.3 $\pm$ 38.3 ^a	80.2 $\pm$ 16.9 ^b	111.1 $\pm$ 17.0 ^b
	5.2 m lift	395.7 $\pm$ 64.1 ^a	106.4 $\pm$ 32.3 ^b	91.8 $\pm$ 48 ^b
Deer days (ha^{-1})				
Summer (one deer)	Control	339.4 $\pm$ 46.3 ^a	136.2 $\pm$ 40.5 ^{ab}	119.2 $\pm$ 62.2 ^b
	2.4 m lift	258.6 $\pm$ 50.4 ^a	134.3 $\pm$ 37.3 ^a	170.5 $\pm$ 55.7 ^a
	3.6 m lift	407.9 $\pm$ 40.9 ^a	148.9 $\pm$ 30.1 ^b	185.3 $\pm$ 33.0 ^b
	5.2 m lift	300.2 $\pm$ 42.2 ^a	175.1 $\pm$ 23.1 ^{ab}	140.7 $\pm$ 23.9 ^b
Summer (doe with one fawn)	Control	179.9 $\pm$ 57.8 ^a	86.2 $\pm$ 41.3 ^{ab}	48.2 $\pm$ 39.4 ^b
	2.4 m lift	111.0 $\pm$ 42.2 ^a	64.9 $\pm$ 31.8 ^a	74.9 $\pm$ 35.8 ^a
	3.6 m lift	228.9 $\pm$ 46.6 ^a	71.4 $\pm$ 25.5 ^a	115.4 $\pm$ 37.7 ^a
	5.2 m lift	149.5 $\pm$ 55.1 ^a	78.8 $\pm$ 19.5 ^a	55.3 $\pm$ 13.6 ^a
Winter (one deer, snow depth: 20 cm)	Control	103.8 $\pm$ 39.1 ^a	20.2 $\pm$ 12.9 ^a	20.1 $\pm$ 10.2 ^a
	2.4 m lift	116.4 $\pm$ 34.7 ^a	23.3 $\pm$ 2.9 ^b	44.1 $\pm$ 9.0 ^{ab}
	3.6 m lift	131.4 $\pm$ 31.9 ^a	56.1 $\pm$ 23.8 ^{ab}	24.6 $\pm$ 6.8 ^b
	5.2 m lift	129.0 $\pm$ 52.4 ^a	58.7 $\pm$ 26.1 ^a	45.7 $\pm$ 21.3 ^a

Letters denote pair-wise statistical differences in time since treatment (Tukey's HSD, $\alpha = 0.05$). Pruning height treatment effects did not differ significantly.

insignificant after sixteen years of stand development. At that time, control sites averaged $49.1 \pm 10.0\%$ of Sitka spruce trees with epicormic branches whereas thinned sites averaged $79.0 \pm 8.6\%$, thinned plus 25% pruned sites averaged $75.5 \pm 8.0\%$, and thinned plus 50% pruned sites averaged $76.9 \pm 7.2\%$. We also found that a larger proportion of pruned trees had epicormic branches than unpruned trees. Five years after treatment, epicormic branches were found on $91.7 \pm 2.6\%$ of pruned trees versus $75.9 \pm 3.4\%$ of unpruned trees. This relationship was no longer evident 16 years after treatment. At that time, epicormic branches were found on $79.3 \pm 5.0\%$ of pruned trees versus $74.8 \pm 5.7\%$ of unpruned. No difference in epicormic branching rates were detected between the thinning plus 25% pruning and thinning plus 50% pruning treatments.

Canopy closure index in thinned stands was lower than in control stands (Fig. 4), but no difference was observed between thinning and thinning plus pruning treatments. The effect of treatment on canopy closure index lessened through time. Differences were present at 5 and 10 years after treatment, but a significant effect was no longer observed when sites were remeasured 16 years after treatment.

Understory plant biomass differed between plant life forms with shrubs containing ~ 10 times greater biomass than fern or forb life forms on average across all years (Fig. 5). Understory biomass varied negatively with canopy closure index and thinning, and thinning plus pruning treatments exhibited greater biomass than untreated control plots across fern, forb, and shrub life forms (Fig. 5, Supplementary Table 1). Thinning and thinning

**Figure 4.** The effects of thinning and pruning density treatment on canopy closure index over 15 years. Letters denote pair-wise statistical differences (Tukey's HSD, $\alpha = 0.05$).**Figure 5.** Linear regression models predicting understory plant biomass with canopy closure index and thinning and pruning treatment. Note biomass (y-axis) is $\log_{10}$ scaled.

plus pruning treatments did not differ from one another across life forms.

Deer forage availability (deer days) was greatest in summer when the largest number of plant species were available as forage and were lowest in the 20 cm snow scenario where herbaceous plants were covered by snow (Fig. 6). Deer days varied negatively with canopy closure index across all treatments. In all scenarios, the control treatment produced significantly fewer deer days than the thinning treatments; however, the thinning and thinning plus pruning treatments did not differ from one another (Fig. 6, Supplementary Table 2).

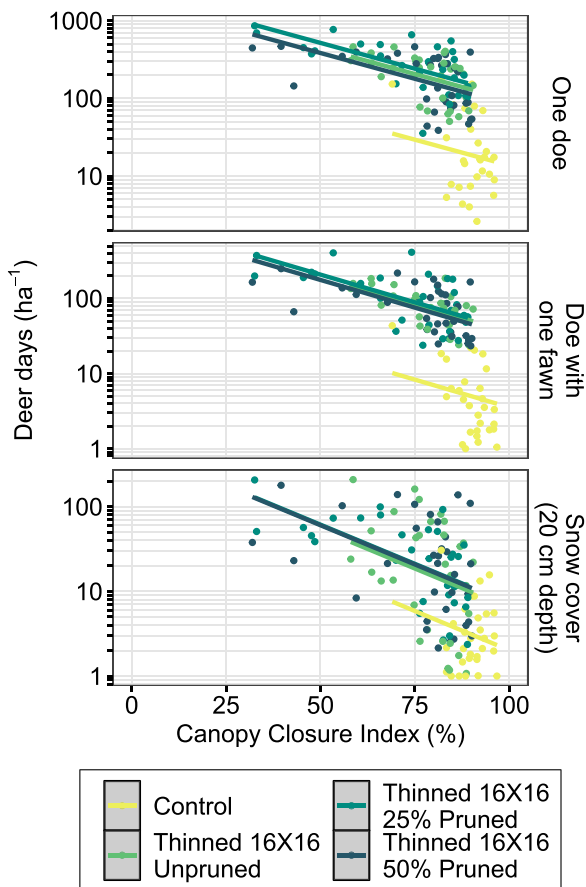


Figure 6. Linear regression models predicting Sitka black-tailed deer forage availability (deer days) by canopy closure index and thinning and pruning treatment. Note deer days (y-axis) is $\log_{10}$ scaled.

Discussion

Stand tending techniques such as tree pruning are frequently used to enhance benefits of early stand improvement treatments in silvicultural systems. In southeast Alaska, possible benefits of tree pruning include improving the quality of Sitka spruce and western hemlock logs, and provisioning for ecosystem services such as wildlife habitat that are restricted during the prolonged stem exclusion phase of stand development. In this article, we evaluated the effects of tree pruning in two long-term stand manipulation studies located on the Tongass National Forest. These studies indicated that appropriately applied pruning can provide lasting improvements in tree form without loss of diameter and height growth. Tree pruning does not appear to promote understory vegetation production over precommercial thinning treatment alone in the prescriptions we evaluated.

Treatment effects on tree characteristics

Both studies provide insights into stand dynamics in Sitka spruce–western hemlock forests following thinning and pruning. In the pruning height experiment, treatment effects on height to live crown and live crown ratio were evident after pruning application in both species; however, crown characteristics steadily converged through time with natural crown recession and treatment effects were indiscernible after ~30 years of stand development. In these stands, pruning lift treatments did not reduce live crown length by more than 50%, a guideline noted across conifer species that can be associated with reduced radial growth (O'Hara 1991,

Gartner et al. 2005, Waring and O'Hara 2005, Amateis and Burkhart 2011, Nyland 2016, York 2019) or height growth (Pinkard et al. 2004, Amateis and Burkhart 2011). While we did not evaluate annual ring increment using tree cores, we found no evidence of tree diameter or height falling behind in either species following pruning application.

Thinning in Sitka spruce–western hemlock forests is widely applied to accelerate the production of large trees and can affect tree characteristics and wood properties (Harris and Farr 1974, Ruth and Harris 1979). As with other conifer species (Nyland 2016, Barrette et al. 2023), greater crop tree spacing increases tree taper and crown depth, and leads to larger branches (Mitchell 2000, Moore et al. 2009, Auty et al. 2012, Newton and Cole 2012), all of which make log processing less efficient and more costly (Macdonald and Hubert 2002, Macdonald et al. 2010). Studies investigating the impact of thinning on wood quality in these species also report reductions in modulus of elasticity (i.e. wood stiffness), bending strength, and wood density (Wang et al. 2001, Moore et al. 2009, Krajnc et al. 2019); however, investigators evaluating lumber grade and recovery found no difference between trees sourced from thinned and unthinned stands (Christensen et al. 2002, Lowell et al. 2012). Tree pruning can complement thinning treatment with the aim of improving tree form and wood quality (O'Hara 1991, Macdonald and Hubert 2002). In this study, pruning application was effective at reducing stem taper in the lower sawlog portion of Sitka spruce trees like what has been seen in other conifers (Henman 1963, Staebler 1963). Stems with lower taper are recognized as having improved stiffness and strength through lower grain angles and improved value recovery in timber operations (Macdonald and Hubert 2002, Macdonald et al. 2010). Pruning also accelerates crown recession and branch occlusion which reduces the number of large open-grown branches and associated knots on the lower bole (Petruncio et al. 1997, Macdonald and Hubert 2002, Mäkinen et al. 2003, Baders et al. 2017). Large knots lead to poor mechanical properties in wood products through reduced wood stiffness and strength (Moore et al. 2009, Auty et al. 2012, Krajnc et al. 2019) and can lead to higher log harvesting and processing costs (Macdonald et al. 2010). Thus, pruning accomplished the primary improvements to tree form important to traditional forestry objectives.

The production of epicormic branches is widespread across coniferous and deciduous species (Meier et al. 2012), and their size, density, and longevity tend to increase with the severity of crown removal (Collier and Turnblom 2001, O'Hara et al. 2008, O'Hara and Berrill 2009), tree spacing (Deal et al. 2003, Newton and Cole 2012), or canopy gap size (Quine 2004), and can vary depending on the seasonal timing of crown disturbance (O'Hara et al. 2008). Epicormic branches sprout as a result of tree stress and wounding, reduced vigor, and heightened light conditions, and contribute to the recovery of crown architecture that supports light capture and production of photosynthate (Meier et al. 2012). The pruning height experiment offers a nearly three-decade view of epicormic branch dynamics following silvicultural intervention. We found that the proportion of trees with epicormic branches nearly halved and the number of live epicormic branches decreased by a factor of five or more since Deal et al. (2003) evaluated these sites 6–9 years after treatment. Unfortunately, low sample size (i.e. low statistical power) limited our ability to detect treatment effects in the pruning height study. Results from the pruning density study were robust and showed that thinning and thinning plus pruning treatments resulted in a higher proportion of trees exhibiting epicormic branches over the unthinned control. This effect degraded as epicormic branching rates rose in the

unthinned control through time, perhaps due to natural crown thinning from density dependent mortality. Both pruned and unpruned trees exhibited high rates of epicormic branching, but pruned trees exhibited a slightly greater propensity. Our findings demonstrate that heightened epicormic branching is ephemeral following thinning and pruning activities and returns to background levels with time as stands develop. The two primary management approaches that can be applied to minimize the occurrence and impacts of epicormic branching include limiting pruning severity below 40%–50% crown removal (O'Hara and Valappil 2000, Collier and Turnblom 2001, Waring and O'Hara 2005) and increasing stand densities and/or canopy cover (Quine 2004, Newton and Cole 2012). Staggering thinning and pruning implementation across several years (O'Hara and Berrill 2009) and timing pruning activities during the growing season (O'Hara et al. 2008) may also help mitigate excessive epicormic sprouting. To what extent epicormic branches compromise Sitka spruce wood quality is unknown; however, the impact of epicormics is likely restricted to small knots that do not pose a long-term detriment to log quality, aside from appearance-grade applications (Macdonald et al. 2010). Ultimately, wood quality and grade need to be evaluated in a milling and sort yard study to fully understand the effects of pruning on clearwood development and knot reduction.

Understory plant production

Precommercial thinning has been widely found to improve understory plant production in the Pacific coastal temperate rainforest during the stem exclusion phase of even-aged forest stand development (Doerr and Sandburg 1986, Lindh and Muir 2004, Cole et al. 2010, Hanley et al. 2013, Crotteau et al. 2020b). Such treatments attenuate light and resource limitation by opening the forest canopy and reducing tree competition and offer an alternative successional pathway that supports greater understory plant production and wildlife forage. Results from the pruning density study clearly demonstrated that thinning 25–35 years after stand initiation led to less canopy cover for at least a decade (see also Crotteau et al. 2020b), although we anticipate that the rate of canopy recovery varies with site productivity (a variable not evaluated in this study). Plant biomass responded favorably in all thinning and thinning plus pruning treatments, producing more than 10 times as much biomass in thinned plots over unthinned plots across all plant functional groups. Interestingly, plant biomass in thinned and unthinned prescriptions both exhibited negative relationships with rising canopy cover; however, control stands with low canopy cover produced substantially less biomass than thinned stands with higher canopy cover. This supports the assertion that thinning not only produces a substantial pulse in understory plant biomass, but the effects can be relatively long-lasting, declining slowly even as canopies close after treatment (Alaback and Herman 1988). Continued monitoring will be required to determine how long understory communities can persist in stands with high canopy closure and when subsequent intermediate treatment might be warranted to revitalize understory plant communities.

Tree pruning has been implemented in southeast Alaska as a supplement to precommercial thinning with the partial objective of further reducing canopy cover to benefit understory plant communities. Results from both our pruning height and density studies suggested that these tree pruning intensities do not provide an additional benefit over precommercial thinning alone in terms of plant production. One explanation might be that progressive canopy cover reduction has a diminishing effect on understory plant production and the addition of pruning in thinned stands

does not reduce canopy cover enough to have a measurable benefit to understory plant communities. It remains possible that more intensive or frequent pruning application or pruning in stands with higher tree densities may produce measurable benefits to the understory, but such prescriptions may not be financially feasible or operationally tractable. These experiments, taken together, illustrate that operational pruning in Sitka spruce–western hemlock stands does not increase canopy openness above and beyond that of thinning, nor does it delay the recovery of canopy closure following treatment. Therefore, we conclude that the pruning prescriptions evaluated in this study appear to have no practical benefits to canopy cover nor understory production.

Conclusion

Timber management in southeast Alaska historically focused on cutting primary forests using clearcutting techniques. Natural stand regeneration has led to widespread even-aged stands with high density across the region that provide limited ecosystem services during the prolonged stem exclusion phase of stand development. Stand improvement silviculture can achieve a span of management objectives as stands develop. Precommercial thinning is commonly used across the region to boost crop tree growth rates and improve understory plant production and wildlife forage availability, and tree pruning is effective at improving tree form and log quality. In this study, we evaluated the effects of pruning lift height and density of trees pruned in two experimental studies on the Tongass National Forest. We found that tree pruning can improve log quality for timber applications but does not appear useful as a supplementary treatment for the purpose of enhancing understory plant biomass and forage availability when done in conjunction with precommercial thinning.

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Author contributions

Kellen Nelson (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing), Jeffrey Barnard (Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Supervision, Writing—review & editing), Preston Massingham (Investigation, Software, Writing—review & editing), and Justin Crotteau (Conceptualization, Data curation, Funding acquisition, Writing—review & editing)

Supplementary data

Supplementary data is available at *FORESJ* Journal online.

Conflict of interest

None declared.

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Data availability

Data presented in this paper will be published in the USDA Forest Service Research Data Archive (<https://www.fs.usda.gov/rds/archive/>).

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