

Tree-level responses to commercial thinning in spruce-fir forests across northern Maine, USA

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ABSTRACT

Despite the widespread use of pre-commercial (PCT) and commercial thinning (CT) in spruce-fir (*Picea-Abies*) forests of North America, critical knowledge gaps exist on their long-term influences on individual tree growth and development. In this study, we used extensive repeated measurements from replicated experimental research sites across Maine ($n = 96090$ obs. from 7159 trees in 103 plots at 15 locations) to quantify the tree-level response of two shade-tolerant conifers: balsam fir (*Abies balsamea* (L.) Mill.; BF) and red spruce (*Picea rubens* Sarg.; RS) to contrasting thinning treatments in spruce-fir stands with and without a prior PCT (NoPCT). Treatments at the nine PCT sites included a combination of CT entry timings (immediate, 5-, and 10-year delay) and removal intensities (0, 33, and 50% relative density reduction). In contrast, at the six NoPCT sites, the CT treatments were a combination of thinning methods (dominant, crown, and low) and removal intensities (0, 33, and 50%). The results showed that compared to the unthinned control, BF in thinned NoPCT stands exhibited substantial increases in annual growth for basal area, merchantable volume, and aboveground carbon, ranging from 99 to 280%, 75 to 214%, and 104 to 312%, respectively. In comparison, RS showed more moderate increases of 36 to 121%, 6 to 81%, and 32 to 135%, respectively. Similarly, in thinned PCT stands, BF displayed annual growth increases of 11 to 139%, 28 to 87%, and 15 to 145% in basal area, merchantable volume, and aboveground carbon, respectively, while RS exhibited similar increases of 50 to 120%, 35 to 96%, and 51 to 122%, respectively. In addition, CT treatments in both PCT and NoPCT stands effectively reduced mean height-diameter ratios, while preserving live crown ratios and increasing tree-level growth efficiency. Overall, BF had a higher tree-level growth response than RS in NoPCT stands, while such differences were less pronounced in PCT stands. While stand-level growth and financial and operational factors should also be considered, our findings provide valuable insights into the long-term influences of both PCT and CT on individual tree growth, stability, vigor, and carbon sequestration potential in spruce-fir forests.

1. Introduction

Thinning is one of the most common silvicultural practices that involves the removal of selected trees from a forest to improve the remaining trees' overall health, quality, and productivity. Thinning is widely applied worldwide to achieve forest management objectives by

concentrating wood production on fewer stems through stand density regulation (Zhou et al., 2016; Saarinen et al., 2020). By reducing stand density, thinning can affect the expected growth of individual trees and the stand by manipulating the available growing space for residual trees. Thinning is generally believed to enhance the growth of residual trees by decreasing competition for resources such as light, water, and soil

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nutrients (Zeide, 2001; Cañellas et al., 2004; Bose et al., 2018b). It can also prevent potential volume loss due to competition-induced mortality by capturing that volume before it is lost (Emmingham et al., 2007; Powers et al., 2010; Bailey et al., 2015).

However, numerous long-term studies have reported a wide range of outcomes of different species that can vary with several factors, including thinning type, intensity, time since the last thinning, stand structure or age, and site conditions (Latham & Tappeiner, 2002; Soucy et al., 2012; Berrill & O'Hara, 2014; Bose et al., 2018a, 2018b; Dagley et al., 2023b). Several studies have shown that thinning is effective in accelerating the diameter and volume growth of individual trees, but does not necessarily increase the total production relative to unthinned stands (Curtis et al., 1997; Zeide, 2001; Cañellas et al., 2004; Mäkinen & Isomäki, 2004a, 2004b; Wagle et al., 2022). Despite a general expectation of enhanced growth of residual trees after thinning, it can also increase wind damage, water stress, and growth stagnation (Sharma et al., 2006; Lagergren et al., 2008; Kuehne et al., 2016). In particular, the response of shade-tolerant conifer species can be more complex and varied compared to shade-intolerant species, making developing general recommendations difficult (Bose et al., 2018a, 2018b). Consequently, long-term monitoring of replicated experimental designs in forest types composed of species with differing resource requirements is essential to determine the impact of thinning on tree growth and stand yield needed to achieve forest management objectives (Wagle & Sharma, 2012; Gauthier & Tremblay, 2019).

Spruce-fir forests, dominated by balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubens* Sarg.), trees, are common in the northeastern United States with significant ecological and economic value. Balsam fir and red spruce are the most abundant tree species in Maine, the most forested state in the USA with 89% of land under forest cover (Maine Forest Service, 2008). Maine's forest land contains over 50 species, where balsam fir alone represents around 33%, while balsam fir and red spruce together represent approximately 45% of the total number of stems (Woodall et al., 2022). These two species share a common niche and possess similar characteristics that "spruce-fir" is often used as if they were a single species (Seymour, 1992). Both species are shade-tolerant, shallow-rooted, vulnerable to windthrow, and can grow in various soil and moisture conditions (Blum, 1990; Frank, 1990). The cyclic outbreak of eastern spruce-budworm (*Choristoneura fumiferana* Clemens), a native insect that severely defoliates stands and causes widespread mortality, has been one of the historic forest disturbance agents in the region (Seymour, 1992; Olson et al., 2012; Bhattarai et al., 2022). Balsam fir is also susceptible to various stem rot fungi and its lifespan is often limited to 70 years (Frank, 1990; Seymour, 1992), whereas red spruce is long-lived, relatively resistant to insects and decay, and can remain suppressed for decades, with a lifespan of up to 400 years (Blum, 1990; Seymour, 1992).

Current spruce-fir forests in Maine are of two distinct types: a) naturally regenerated stands that were not influenced by the most recent large-scale spruce budworm outbreak in the region; and b) younger stands that were naturally regenerated after salvage clearcutting following the most recent devastating spruce-budworm outbreak from 1972 to 1986 (Clune, 2013). In many areas experiencing salvage clearcutting, herbicide applications occurred as release treatments to reduce competing vegetation and promote the natural regeneration of spruce-fir (Seymour, 1992; Olson et al., 2012). Since spruce-fir stands often regenerate at very high densities, pre-commercial thinning (PCT) usually occurs a few years after herbicide application. Although PCT has been applied extensively in younger spruce-fir stands, most older ones never had a PCT (Clune, 2013).

While thinning is a widely adopted silvicultural practice in the northeastern US and Canada to manage stand density, shift species composition, and improve forest health, the specific impacts on both stand- and tree-level growth are not yet fully understood in spruce-fir forests, particularly when PCT is combined with commercial thinning (CT). The few stand-level studies from the region have reported a range

of outcomes. For example, Pelletier & Pitt (2008) did not observe the benefits of either low or crown thinning in terms of total or merchantable volume gains in white spruce (*Picea glauca* (Moench) Voss) plantations in New Brunswick, whereas Soucy et al. (2012) observed 33% more merchantable volume with heavy CT (50% basal area removal) in naturally regenerated black spruce (*Picea mariana* (Mill.) Britton) stands compared to unthinned control, over the period covering 34–40 years after CT in Quebec. Thirty-two years after PCT in spruce-fir stands in central Maine, Weiskittel et al. (2011) found more larger and fewer small trees in thinned plots than unthinned controls. Similarly, Pitt et al. (2013) observed the production of more merchantable volume in PCT balsam fir stands compared to the stand that received no PCT. Hiesl et al. (2017a, 2017b) found no substantial economic benefit of CT compared to unthinned areas in spruce-fir stands dominated by balsam fir and red spruce with and without PCT. Bose et al. (2018b) observed higher relative growth in thinned spruce-fir stands than unthinned ones. Wagle et al. (2022) reported thinning from below being effective in improving log grades and producing more merchantable volume, whereas dominant thinning had a detrimental effect on stand-level responses of spruce-fir stands dominated by red spruce and balsam fir due to increased mortality. This wide range of prior findings is likely attributable to differences in the specific PCT and CT treatments applied, but it would also be related to stand structure and composition at the time of thinning and site productivity, which need to be evaluated better.

Several studies have demonstrated the positive effects of thinning on tree growth rates and structural attributes (e.g. Valinger et al., 2000; Blevins et al., 2005; Zhang et al., 2006; Weiskittel et al., 2011; Soucy et al., 2012; Bose et al., 2018b; Ward & Winkle, 2019). For example, Weiskittel et al. (2009a) observed that after PCT treatment, there was a significant increase in individual tree diameter, height growth, crown ratio, and crown width along with a reduction in height to diameter at breast height ratio (H:D ratio) for both balsam fir and red spruce. However, there is still a fundamental knowledge gap regarding how different CT types, intensities, and entry timing can affect the tree-level outcomes in spruce-fir. The Commercial Thinning Research Network (CTRN), established in 2000 by the University of Maine's Cooperative Forestry Research Unit (CFRU) provides a unique opportunity to study the effects of CT types and intensity in stands that had not received PCT (NoPCT), while the role of CT timing and intensity can also be examined in stands that had received PCT across the range of spruce-fir forest in Maine (Seymour et al., 2014; Kuehne et al., 2018). After ten years of treatment application in the CTRN study, Clune (2013) observed that BF responded to CT better than RS; crown and dominant thinning was better than low thinning in terms of diameter increment; and CT without delay in treatment application was more effective than the delayed CT treatments. However, Clune's (2013) assessment was constrained by the lack of growth response data, particularly for the delayed treatments of the PCT stands. In their analysis of CTRN data of the NoPCT stands, Bose et al. (2018b) found that thinned stands had higher relative volume growth both at tree- and stand-level than those in unthinned stands. However, their analysis did not include individual thinning treatments or explore the response of BF and RS separately, which is critical given the fundamental differences across these two species.

This study aimed to quantify tree-level responses to CT in spruce-fir stands that were not previously thinned; and in stands with a PCT history. We analyzed repeated-measures data from CTRN study sites to answer the following questions: (1) How does CT alter individual tree growth, crown ratio, H:D ratio, volume, and carbon? (2) What additional factors influence the response of spruce and fir to these treatments? and (3) Do spruce or fir respond differently to earlier vs delayed CT, different thinning methods (i.e., low thin, crown thin, and dominant thin), and contrasting thinning intensities? We hypothesized that different tree-level responses would be related to species, CT treatment type, time since treatment, initial tree size, site quality, and tree social position.

2. Materials and methods

2.1. Study area

The present study was conducted on long-term study sites ($n = 15$) established in early 2000s by the University of Maine's Commercial Thinning Research Network (CTRN). These sites are located across diverse geographic regions in northern Maine (Fig. 1) and fall within the Acadian forest, a mixed-wood ecosystem dominated by conifers that stretches across much of Maine and the Canadian Maritimes (Clune, 2013). The dominant species in these stands are balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubens* Sarg.), with other softwood species occurring in low densities, including white spruce (*Picea glauca* (Moench) Voss), eastern white pine (*Pinus strobus* L.), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), eastern hemlock (*Tsuga canadensis* (L.) Carrière) and northern white-cedar (*Thuja occidentalis* L.). Hardwood species include red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), paper birch (*Betula papyrifera* Marshall), and quaking aspen (*Populus tremuloides* Michx.). These stands cover a range of site conditions typical for the region, with drainage classes varying from poorly to well-drained and common soils being podzols with glacial till and alluvium as the parent material. Similarly, the elevation, mean annual temperature, and precipitation of the study area range from 44 to 652 m, 2.8 to 5.0 °C, and 1046 to 1185 mm, respectively (Kuehne et al., 2018; Wagle et al., 2022).

2.2. Experimental design and treatments

There are two types of installations in the CTRN thinning experiments: stands that had received PCT, and stands that had no history of PCT (NoPCT), replicated at nine and six sites, respectively (Fig. 1). Treatments in NoPCT experiment included a combination of thinning methods (low, crown, and dominant) and removal intensities (33 and 50% relative density reduction) giving six combinations: LOW.33, LOW.50, CRN.33, CRN.50, DOM.33, DOM.50. In the PCT experiment, the CT treatments were a combination of CT entry timings (immediate, 5-, and 10-year delay from the earliest (i.e., immediate) CT entry) and removal intensities (33, and 50%) giving six combinations: 0YR.33,

0YR.50, 5YR.33, 5YR.50, 10YR.33, 10YR.50. Each site of NoPCT and eight sites of PCT experiment had seven plots: six treated and one untreated (control), while one of the PCT sites consisted of five plots: immediate and 5-year delay treatments along with one control.

The low and dominant thinning treatments involved harvesting of trees beginning from the lower or upper end of the diameter distribution, respectively, until the desired residual density was reached. In the crown thinning treatment, crop trees were selected at one-third of the average height apart, and then dominant and co-dominant competitors surrounding each crop tree were removed until the desired reduction in relative density was accomplished (Kuehne et al., 2018; Wagle et al., 2022). The selection of PCT sites was based on stands ready for CT either in 2001–02 (six sites) or 2009–2010 (three sites). These sites were characterized by well-stocked and single-cohort stand structures, with a relative density >0.25 (Wilson et al., 1999), based on trees with diameter at breast height (DBH) >6.3 cm, and good to excellent site quality (Hiesl et al., 2017a). The timing of CTs applied in the six initial PCT stands in either 2001–02, 2006–07, or 2011–12 were defined as immediate (0YR), delayed 5 years (5YR), and delayed 10 years (10YR) treatments, respectively (Seymour et al., 2014; Wagle et al., 2022). For the three new sites included in the study in 2010, the 0YR and 5YR treatments were applied in 2010 and 2015, respectively, while 10-year delay treatments were not applied in those new sites until the last measurements of this study in 2018.

Treatments were applied within square plots measuring 3716 m² and each treatment plot contained a nested measurement plot of 809 m² positioned at its center, along with a forwarder trail running through the middle. Prior to treatment application, species and DBH were recorded for all trees >10.2 cm DBH. Height and height to crown base (the lowest live branch) were measured for sub-samples representing each diameter class, and missing heights were predicted using these measurements. In the first season after CT, each residual tree in each measurement plot was tagged, numbered and measured for DBH, total height and crown height. Subsequent measurements in the initial 12 sites were conducted on an annual or semi-annual basis until 2013, while only one site (PEF 23a) was measured in 2016 and the final measurement in all sites were made in 2018. Likewise, measurements were taken annually or semi-annually for the three most recent PCT sites until the last

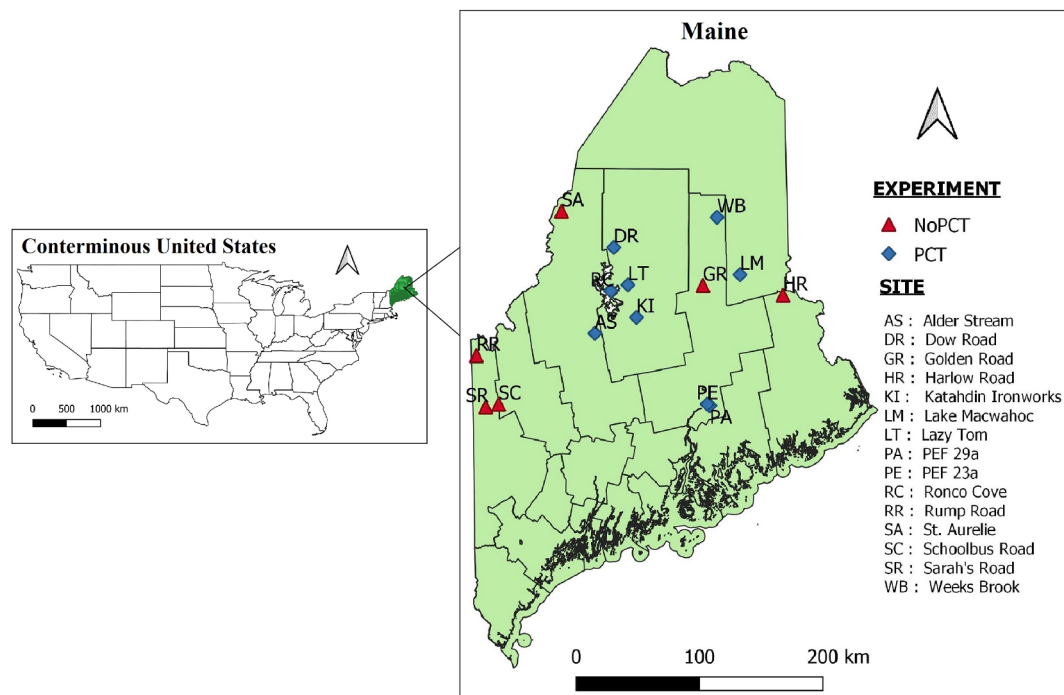


Fig. 1. Location of study sites.

measurement in 2018.

Two sampling schemes were employed for annual measurements: intensive post-treatment measurement (IM) and extensive post-treatment measurement (EM). In IM, each tagged tree's DBH, total height, crown height, and status were recorded, along with measuring ingrowth. On the other hand, EM involved measuring the DBH and status of each tagged tree and ingrowth. A more detailed description of the experimental design, treatments, and summary of stand information at the time of CT, just after CT and in 2018 can be found in Wagle et al. (2022) and Clune (2013).

2.3. Analysis

Missing heights were imputed by fitting a power equation (Equation (1)) using mixed-effects modeling with DBH as a fixed predictor of height and species, tree status, site, and plot as random effects. Similarly, missing height to crown base (HCB) was imputed by fitting the HCB, total height, and DBH to equation (2). Crown ratio was defined as a ratio between crown length (total height minus HCB) and total height for each tree. Leaf area of individual trees was estimated using DBH, height, and crown length based on species-specific parameter estimates following Weiskittel et al. (2009b).

$$H = b_0 D^{b_1} \quad (1)$$

$$HCB = \frac{H}{b_0 D + b_1 \log(D)} \quad (2)$$

$$TLA = b_0 D \left(b_1 + b_2 CL + b_3 \left(\frac{H}{D} \right) \right) \quad (3)$$

Where, H = total height (m); D = DBH (cm); HCB = height to crown base; CL = crown length; b_0 , b_1 , b_2 , and b_3 are regression coefficients.

Individual tree DBH and height were used to calculate the total and merchantable stem volumes using a Kozak (2004) taper function for the region (Li et al., 2012). Each tree was divided into 100 sections, with diameter predictions made at each section's height, and the volume for each section was calculated using Smalian's formula (Kershaw et al.,

2017). The total volume for an individual tree was determined by summing the volumes of each section. For merchantable volume, minimum DBH and top diameter were 12.7 cm and 7.6 cm, respectively (Wagle et al., 2022). Aboveground dry biomass was estimated using a local biomass equation for Maine (Equation (4)) (Young et al., 1980) and carbon concentration was estimated as 50% of the dry biomass.

$$Biomass = e^{(b_0 + b_1 \log(DBH))} \quad (4)$$

Where, biomass is dry weight (kg); DBH is the diameter at breast height in cm; b_0 and b_1 are species specific constants.

The growth data were annualized by dividing the observed periodic growth by measurement interval (year). Growth efficiency (GE) was calculated as a periodic annual biomass increment divided by leaf area for each tree.

A linear mixed-model analysis of covariance (ANCOVA) was used to evaluate the influence of treatments on the tree-level growth/attributes for BF and RS. In NoPCT experiment, time since treatment (TST) was considered as a covariate, while both TST and tree size, indicated by the DBH at the first measurement after CT, were included as covariates in the PCT experiment to account for the unequal post-treatment time and initial tree size. Random effects of trees nested within plot and plot nested within site were included to account for variation from unknown sources that may affect the dependent variables. Pairwise comparison tests among the treatments of the NoPCT experiment were performed using Tukey's method of multiple comparisons at 5% significance level ($p < 0.05$).

To evaluate the effects of CT on tree-level growth/attributes over the period, mixed-effect linear regression analysis was performed using measurements across all years. First, eight different model forms were developed with and without interactions of species (Spp), treatment (Trt), time since treatment (TST) and initial tree diameter (Size); and, those eight models were expanded to eighty models of various forms by including further terms ($\log(TST)$, TST^2 , $\log(Size)$, $Size^2$, Site index, and Basal area of larger trees (BAL)) as explanatory variables (Table 1). Continuous autoregressive (CAR1) function was included to account for serial autocorrelated errors. The performance of the eighty model forms was assessed with tree nested within plot, and plot nested within site as

Table 1
Models considered for the analysis of stand level attributes over the period.

Model form	Designation
$Y_{ijk} = Spp_{ijk} + Trt_{ijk} + TST_{ijk} + Size_{ijk} + u_i + u_{ij} + u_{ijk}$	M1
$Y_{ijk} = Spp_{ijk} * Trt_{ijk} + TST_{ijk} + Size_{ijk} + u_i + u_{ij} + u_{ijk}$	M2
$Y_{ijk} = Spp_{ijk} * TST_{ijk} + Trt_{ijk} + Size_{ijk} + u_i + u_{ij} + u_{ijk}$	M3
$Y_{ijk} = Spp_{ijk} * Size_{ijk} + Trt_{ijk} + TST_{ijk} + u_i + u_{ij} + u_{ijk}$	M4
$Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + u_i + u_{ij} + u_{ijk}$	M5
$Y_{ijk} = Spp_{ijk} * Trt_{ijk} * Size_{ijk} + TST_{ijk} + u_i + u_{ij} + u_{ijk}$	M6
$Y_{ijk} = Spp_{ijk} * Trt_{ijk} + Spp_{ijk} * TST_{ijk} + Size_{ijk} + u_i + u_{ij} + u_{ijk}$	M7
$Y_{ijk} = Spp_{ijk} * Trt_{ijk} + Spp_{ijk} * Size_{ijk} + TST_{ijk} + u_i + u_{ij} + u_{ijk}$	M8
Adding following explanatory variables in all models from M1 to M8, respectively	
$\log(TST_{ijk})$	M9 to M16
$(TST_{ijk})^2$	M17 to 24
$\log(Size_{ijk})$	M25 to M32
BAL_{ijk}	M33 to M40
SI_{ijk}	M40 to M48
$SI_{ijk} + BAL_{ijk}$	M49 to M56
$\log(TST_{ijk}) + (Size_{ijk})^2$	M57 to M64
$\log(Size_{ijk}) + (TST_{ijk})^2$	M65 to M72
$(Size_{ijk})^2 + (TST_{ijk})^2$	M73 to M80

Note: Y_{ijk} = response variable; Spp_{ijk} = species; Trt_{ijk} = Treatment; TST_{ijk} = time since treatment; $(TST_{ijk})^2$ = squared TST_{ijk} ; $\log(TST_{ijk})$ = log-transformed TST_{ijk} ; $Size_{ijk}$ = initial tree size (DBH); $(Size_{ijk})^2$ = squared $Size_{ijk}$; $\log(Size_{ijk})$ = log-transformed $Size_{ijk}$; BAL_{ijk} = basal area of all trees larger than the subject tree in the plot; SI_{ijk} = site index; u_i = random effects of i^{th} site; u_{ij} = random effects of j^{th} plot in i^{th} site; u_{ijk} = random effects of the k^{th} tree in j^{th} plot of i^{th} site. The interaction terms among variables were indicated by a * (e.g. $Spp_{ijk} * TST_{ijk}$).

Table 2

Species-wise mean $\pm$ standard deviation (minimum and maximum in parenthesis) of tree-level attributes for each treatment immediately after CT and for the last measurement in 2018.

Treatment	SPP.	DBH (cm)		Height (m)		Crown ratio		Total volume (m ³)		Carbon (kg)	
		after CT	in 2018	after CT	in 2018	after CT	in 2018	after CT	in 2018	after CT	in 2018
LOW.33	BF	15.3 ± 3.6 (10.2; 29.0)	19.5 ± 5.0 (10.2; 36.6)	12.7 ± 1.9 (5.5; 17.7)	18.1 ± 1.3 (16.1; 19.3)	NoPCT 0.43 ± 0.12 (0.20; 0.83)		0.11 ± 0.07 (0.02; 0.45)	0.31 ± 0.10 (0.20; 0.50)	33.6 ± 20.2 (11.5; 142.2)	61.1 ± 38.9 (11.5; 249.1)
	RS	15.8 ± 3.5 (10.2; 31.5)	19.1 ± 4.5 (10.2; 36.6)	14.3 ± 1.9 (9.4; 18.9)	17.1 ± 1.9 (13.5; 20.1)	0.32 ± 0.08 (0.02; 0.55)		0.15 ± 0.08 (0.04; 0.66)	0.28 ± 0.13 (0.08; 0.47)	39.1 ± 21.9 (12.9; 180.3)	61.2 ± 34.9 (12.9; 255.5)
LOW.50	BF	16.0 ± 3.9 (10.2; 30.2)	21.1 ± 4.6 (10.2; 35.8)	13.9 ± 2.7 (6.8; 22.3)	16.4 ± 5.3 (7.0; 24.8)	0.42 ± 0.09 (0.18; 0.75)		0.16 ± 0.12 (0.04; 0.69)	0.36 ± 0.34 (0.03; 1.07)	37.9 ± 25.1 (11.5; 157.6)	71.6 ± 38.3 (11.5; 236.8)
	RS	18.1 ± 3.5 (10.2; 29.7)	22.5 ± 4.4 (12.2; 36.1)	15.7 ± 1.9 (8.8; 20.6)	17.7 ± 1.7 (15.2; 20.8)	0.34 ± 0.08 (0.14; 0.59)		0.21 ± 0.10 (0.04; 0.61)	0.39 ± 0.18 (0.18; 0.71)	52.5 ± 24.2 (12.9; 157.4)	87.3 ± 39.7 (19.7; 247.3)
CRN.33	BF	15.0 ± 3.5 (10.2; 27.9)	19.4 ± 5.5 (10.2; 34.0)	13.8 ± 1.9 (8.5; 20.6)	17.3 ± 3.4 (14.1; 20.8)	0.36 ± 0.13 (0.05; 0.67)		0.12 ± 0.09 (0.03; 0.56)	0.29 ± 0.25 (0.08; 0.57)	32.0 ± 20.5 (11.5; 130.5)	61.6 ± 39.0 (11.5; 209.6)
	RS	15.6 ± 4.5 (10.2; 30.5)	19.2 ± 6.2 (10.2; 35.8)	14.2 ± 2.2 (4.5; 19.8)	16.0 ± 2.7 (11.2; 20.5)	0.31 ± 0.10 (0.03; 0.64)		0.15 ± 0.11 (0.03; 0.68)	0.34 ± 0.25 (0.05; 0.83)	39.4 ± 28.6 (12.9; 167.0)	66.4 ± 49.1 (12.9; 243.2)
CRN.50	BF	15.0 ± 3.1 (10.2; 21.8)	20.8 ± 5.5 (10.2; 30.7)	13.7 ± 1.9 (10.0; 17.9)	16.2 ± 3.2 (12.8; 19.9)	0.38 ± 0.16 (0.03; 0.75)		0.12 ± 0.07 (0.04; 0.29)	0.22 ± 0.23 (0.07; 0.56)	31.1 ± 14.9 (11.5; 72.2)	71.7 ± 40.2 (11.5; 164.0)
	RS	16.7 ± 4.9 (10.2; 32.3)	20.7 ± 6.4 (10.2; 38.4)	14.3 ± 2.4 (8.0; 20.3)	16.6 ± 2.6 (12.2; 19.8)	0.32 ± 0.11 (0.05; 0.59)		0.18 ± 0.12 (0.03; 0.64)	0.38 ± 0.24 (0.13; 0.91)	46.4 ± 32.0 (12.9; 190.6)	77.8 ± 52.7 (12.9; 285.4)
DOM.33	BF	12.9 ± 2.0 (10.2; 18.5)	17.1 ± 4.2 (10.2; 25.4)	12.7 ± 1.9 (3.7; 17.7)	14.1 ± 2.5 (9.4; 16.8)	0.33 ± 0.13 (0.10; 0.77)		0.08 ± 0.03 (0.02; 0.22)	0.14 ± 0.08 (0.05; 0.25)	21.2 ± 8.0 (11.5; 48.7)	44.3 ± 25.2 (11.5; 103.8)
	RS	14.0 ± 2.6 (10.2; 21.1)	17.1 ± 3.9 (10.2; 26.4)	13.7 ± 2.0 (7.9; 18.2)	15.3 ± 1.5 (12.9; 17.5)	0.29 ± 0.08 (0.06; 0.70)		0.11 ± 0.06 (0.03; 0.29)	0.19 ± 0.09 (0.07; 0.35)	28.6 ± 12.8 (12.9; 70.7)	47.2 ± 24.3 (12.9; 119.6)
DOM.50	BF	12.3 ± 2.2 (10.2; 29.7)	16.2 ± 3.6 (10.2; 26.7)	13.2 ± 1.8 (9.7; 18.3)	15.6 ± 2.1 (13.1; 19.9)	0.36 ± 0.12 (0.15; 0.66)		0.08 ± 0.06 (0.04; 0.55)	0.21 ± 0.13 (0.06; 0.49)	19.1 ± 12.2 (11.5; 151.3)	38.3 ± 20.2 (11.5; 116.7)
	RS	13.5 ± 2.3 (10.2; 19.3)	17.5 ± 3.7 (10.2; 32.8)	13.6 ± 2.3 (6.1; 18.6)	14.4 ± 1.4 (11.8; 16.3)	0.28 ± 0.10 (0.02; 0.71)		0.10 ± 0.05 (0.03; 0.25)	0.19 ± 0.07 (0.08; 0.28)	26.2 ± 10.5 (12.9; 57.6)	49.1 ± 25.5 (12.9; 197.7)
Control	BF	12.7 ± 2.2 (10.2; 19.8)	15.2 ± 3.6 (10.2; 24.9)	12.0 ± 1.8 (5.9; 17.4)	17.6 ± 1.8 (15.1; 20.2)	0.41 ± 0.12 (0.19; 0.68)		0.07 ± 0.03 (0.02; 0.14)	0.17 ± 0.09 (0.07; 0.31)	20.6 ± 9.5 (11.5; 57.1)	33.2 ± 20.2 (11.5; 98.9)
	RS	14.9 ± 3.7 (10.2; 30.0)	17.0 ± 4.6 (10.2; 33.0)	14.8 ± 2.4 (8.8; 20.3)	16.1 ± 2.1 (13.0; 19.4)	0.31 ± 0.08 (0.08; 0.59)		0.16 ± 0.10 (0.04; 0.61)	0.18 ± 0.10 (0.07; 0.45)	34.5 ± 21.8 (12.9; 160.6)	47.7 ± 31.9 (12.9; 201.3)
0YR.33	BF	16.0 ± 3.1 (10.2; 27.4)	22.2 ± 4.7 (10.2; 34.3)	12.5 ± 1.7 (2.8; 16.9)	16.6 ± 2.3 (9.3; 20.9)	PCT 0.55 ± 0.10 (0.25; 0.84)		0.12 ± 0.06 (0.03; 0.43)	0.31 ± 0.15 (0.04; 0.71)	36.5 ± 17.1 (11.5; 124.8)	80.4 ± 38.5 (11.5; 213.4)
	RS	14.5 ± 3.5 (10.2; 27.2)	18.0 ± 4.2 (10.2; 33.0)	10.3 ± 1.8 (5.5; 14.8)	12.4 ± 2.0 (7.0; 17.5)	0.52 ± 0.10 (0.30; 0.78)		0.09 ± 0.06 (0.02; 0.40)	0.17 ± 0.09 (0.04; 0.38)	32.4 ± 19.8 (12.9; 127.8)	52.9 ± 30.5 (12.9; 201.3)
0YR.50	BF	16.0 ± 2.8 (10.2; 22.6)	23.9 ± 4.8 (10.4; 37.1)	12.1 ± 1.4 (7.3; 15.8)	17.0 ± 2.3 (9.7; 26.2)	0.61 ± 0.10 (0.25; 0.90)		0.12 ± 0.05 (0.04; 0.24)	0.39 ± 0.18 (0.04; 1.09)	35.9 ± 14.8 (11.5; 78.4)	95.4 ± 43.7 (12.2; 257.5)
	RS	15.1 ± 2.9 (10.2; 23.6)	20.1 ± 4.8 (11.2; 31.2)	10.0 ± 1.2 (6.6; 12.8)	13.2 ± 2.1 (8.7; 19.0)	0.57 ± 0.13 (0.27; 0.91)		0.09 ± 0.04 (0.03; 0.21)	0.22 ± 0.12 (0.04; 0.60)	34.2 ± 15.6 (12.9; 92.2)	68.8 ± 36.3 (16.1; 176.9)
5YR.33	BF	17.0 ± 3.1 (10.2; 29.7)	20.7 ± 4.5 (10.2; 34.8)	14.0 ± 1.6 (9.0; 18.8)	17.1 ± 2.2 (9.9; 22.8)	0.38 ± 0.08 (0.08; 0.57)		0.15 ± 0.07 (0.04; 0.52)	0.31 ± 0.16 (0.05; 0.91)	41.7 ± 18.4 (11.5; 151.3)	68.1 ± 34.6 (11.5; 221.0)
	RS	16.3 ± 4.1 (10.4; 27.9)	18.1 ± 5.0 (10.2; 31.0)	12.3 ± 1.9 (6.5; 17.0)	13.2 ± 2.7 (7.2; 19.0)	0.38 ± 0.08 (0.14; 0.69)		0.14 ± 0.09 (0.03; 0.48)	0.19 ± 0.14 (0.03; 0.63)	42.4 ± 25.6 (13.7; 136.3)	55.4 ± 35.6 (12.9; 173.6)
5YR.50	BF	17.1 ± 3.4 (10.2; 25.9)	22.3 ± 5.0 (10.2; 38.4)	13.7 ± 1.6 (9.0; 17.6)	16.3 ± 2.0 (11.1; 21.1)	0.42 ± 0.09 (0.12; 0.70)		0.15 ± 0.07 (0.03; 0.37)	0.35 ± 0.16 (0.05; 0.83)	42.7 ± 20.1 (11.5; 108.8)	82.1 ± 43.6 (11.5; 279.2)
	RS	15.8 ± 3.8 (10.2; 26.2)	18.0 ± 4.5 (10.4; 28.4)	11.0 ± 1.6 (6.4; 14.6)	12.9 ± 2.2 (6.6; 17.0)	0.43 ± 0.10 (0.17; 0.69)		0.11 ± 0.06 (0.03; 0.30)	0.20 ± 0.11 (0.03; 0.49)	39.4 ± 22.6 (12.9; 117.0)	53.6 ± 30.5 (13.7; 142.2)
10YR.33	BF	18.1 ± 3.4 (10.2; 28.2)	20.9 ± 3.9 (10.4; 31.5)	15.3 ± 1.8 (9.4; 20.3)	16.9 ± 2.2 (9.5; 23.0)	0.37 ± 0.07 (0.06; 0.54)		0.19 ± 0.09 (0.05; 0.52)	0.30 ± 0.14 (0.08; 0.79)	49.1 ± 22.6 (11.5; 133.3)	68.9 ± 30.4 (12.2; 174.0)

(continued on next page)

Table 2 (continued)

Treatment	SPP.	DBH (cm)		Height (m)		Crown ratio		Total volume (m ³)		Carbon (kg)	
		after CT	in 2018	after CT	in 2018	after CT	in 2018	after CT	in 2018	after CT	in 2018
10YR.50	RS	16.0 ± 3.2 (10.4; 24.1)	18.2 ± 4.0 (10.2; 28.2)	12.6 ± 1.7 (8.5; 16.0)	14.6 ± 1.6 (12.2; 17.6)	0.38 ± 0.08 (0.22; 0.53)	0.39 ± 0.06 (0.26; 0.49)	0.13 ± 0.07 (0.03; 0.34)	0.20 ± 0.09 (0.08; 0.38)	39.3 ± 18.7 (13.7; 96.9)	53.5 ± 27.2 (12.9; 139.2)
	BF	19.6 ± 3.4 (10.9; 27.2)	23.5 ± 3.8 (15.0; 33.8)	15.6 ± 1.7 (10.0; 18.7)	17.4 ± 2.0 (10.9; 26.7)	0.40 ± 0.06 (0.06; 0.54)	0.42 ± 0.08 (0.16; 0.65)	0.22 ± 0.09 (0.06; 0.47)	0.36 ± 0.13 (0.11; 0.82)	58.8 ± 23.0 (13.7; 122.1)	89.7 ± 33.7 (29.2; 205.8)
	RS	16.7 ± 3.6 (10.2; 25.9)	19.5 ± 4.1 (11.2; 27.9)	12.7 ± 1.7 (8.0; 15.8)	13.5 ± 2.7 (7.5; 17.3)	0.41 ± 0.06 (0.31; 0.57)	0.40 ± 0.10 (0.18; 0.59)	0.14 ± 0.07 (0.03; 0.36)	0.23 ± 0.13 (0.04; 0.47)	43.9 ± 22.0 (12.9; 114.3)	62.6 ± 28.7 (16.1; 136.3)
Control	BF	15.2 ± 3.3 (10.2; 30.5)	17.7 ± 4.3 (10.2; 35.3)	12.1 ± 1.7 (5.1; 18.1)	17.0 ± 2.2 (9.5; 22.9)	0.58 ± 0.12 (0.20; 0.95)	0.29 ± 0.08 (0.05; 0.64)	0.11 ± 0.06 (0.02; 0.50)	0.25 ± 0.15 (0.04; 0.97)	32.8 ± 17.8 (11.5; 160.8)	47.8 ± 29.1 (11.5; 228.9)
	RS	14.1 ± 3.4 (10.2; 38.9)	16.6 ± 3.9 (10.4; 27.7)	9.6 ± 1.7 (5.3; 17.8)	13.5 ± 2.1 (8.2; 19.2)	0.60 ± 0.10 (0.32; 0.96)	0.35 ± 0.10 (0.10; 0.69)	0.08 ± 0.07 (0.02; 0.96)	0.16 ± 0.09 (0.03; 0.46)	30.4 ± 21.9 (12.9; 294.3)	43.8 ± 24.6 (13.7; 133.5)

random effects. Best models based on AIC for each tree-level analysis were selected for further interpretation. Homogeneity of variance and normality was verified for all analyses using residual plots. Models for height growth of both PCT and NoPCT experiments and the growth efficiency model of the PCT experiment involved a log transformation of the dependent variable in satisfying the assumptions of homogeneity of variance and normality. Moreover, weight was applied in the height growth models of both PCT and NoPCT experiments using the square root of variance. All analyses were implemented in R version 4.0.4 (R Core Team, 2021), using nlme (Pinheiro et al., 2021), multcompView (Spencer et al., 2019), lsmeans (Lenth, 2016), and relaimpo (Grömping, 2006) libraries.

3. Results

Datasets for analysis ranged in size from crown ratio data (PCT stands: $n = 38286$ obs.; NoPCT: $n = 12071$ obs.) up to tree BA data (PCT: $n = 59894$ obs.; NoPCT: $n = 36196$ obs.). A wide range of RS and BF tree sizes and crown ratios were observed (Table 2). Analysis of covariance (ANCOVA) indicated that the thinning treatments had significant yet contrasting effects on the growth of tree-level attributes across species for both NoPCT and PCT stands. Key differences were noted across the various attributes examined by the different experiments, species, and

other influential factors, further summarized below.

3.1. Basal area and height growth

Basal area growth (Δ BA) of both RS and BF in all thinning treatments of NoPCT experiment were greater compared to unthinned control (Table 3). However, pairwise comparison suggested that Δ BA of RS in both treatments of dominant thinning was not significantly different from the control ($p > 0.148$), whereas for BF, it was significantly different from the control in all treatments ($p < 0.009$). Within the same type of thinning, heavier thinning resulted in higher Δ BA compared to light thinning treatments. Likewise, the general ranking of Δ BA in terms of thinning types was found to be crown > low > dominant > control. Over the study period, both species had an initial increase in Δ BA for the first few years, followed by a peak and subsequent decline (Fig. 2A and 2B). Basal area growth of both species in the unthinned control consistently remained lower than trees in all the thinning treatments. The highest height growth (Δ HT) was observed in light crown thinning (CRN.33) for BF and in the unthinned control for RS. However, there was no significant difference in Δ HT between any pair of the treatments for BF ($p > 0.342$). On the other hand, the highest Δ HT of RS in unthinned control significantly differed from the lowest Δ HT observed in light crown thinning ($p = 0.031$). Both species exhibited relatively

Table 3

The adjusted mean of tree-level basal area, height, and crown attributes for each experiment (NoPCT and PCT) for all post-treatment measurements. The numbers in parentheses represent the percentage difference of the corresponding treatment from the unthinned control.

Treatment	Δ Basal area (cm ² yr ⁻¹)		Δ Height (m yr ⁻¹)		H:D Ratio		Crown ratio		Growth efficiency (gm/yr m ⁻²)	
	BF	RS	BF	RS	BF	RS	BF	RS	BF	RS
NoPCT										
	n = 11474	n = 24722	n = 3696	n = 8390	n = 3696	n = 8390	n = 3695	n = 8376	n = 3695	n = 8376
LOW.33	7.8(145)bc	5.9(56)b	0.29(16)a	0.20(-8)ab	90.9(-16)ab	91.2(-7)ab	0.41(32)bc	0.32(8)ab	111.0(62)b	93.9(55)b
LOW.50	9.6(203)cd	8.3(121)c	0.25(3)a	0.19(-12)ab	84.8(-22)a	84.1(-15)a	0.43(38)c	0.34(16)b	129.6(84)b	116.7(93)bc
CRN.33	7.9(150)bc	6.5(73)bc	0.27(9)a	0.15(-32)a	94.4(-13)ab	93.3(-5)ab	0.34(7)ab	0.29(-1)ab	137.0(93)bc	100.7(67)bc
CRN.50	12.1(280)d	8.3(120)c	0.25(2)a	0.16(-30)ab	90.3(-17)ab	85.9(-13)a	0.37(19)abc	0.33(12)b	187.7(153)c	121.4(101)c
DOM.33	6.3(99)b	5.1(36)ab	0.22(-11)a	0.17(-24)ab	98.5(-9)bc	96.0(-3)b	0.32(1)a	0.27(-9)a	127.1(81)b	97.7(62)bc
DOM.50	6.6(106)b	5.3(40)ab	0.20(-18)a	0.15(-30)ab	101.4(-7)bc	97.3(-1)b	0.32(4)a	0.27(-9)a	146.9(105)bc	104.8(73)bc
Control	3.2(-)a	3.8(-)a	0.25(-)a	0.22(-)b	108.5(-)c	98.5(-)b	0.31(-)a	0.29(-)ab	58.1(-)a	60.4(-)a
PCT										
	n = 49634	n = 10260	n = 31409	n = 6911	n = 31409	n = 6911	n = 31382	n = 6904	n = 31382	n = 6904
0YR.33	14.3(73)c	11.5(71)bc	0.33(-12)b	0.28(-17)ab	78.0(-4)b	70.1(-3)ab	0.49(4)d	0.52(8)cd	160.8(130)c	161.4(150)b
0YR.50	19.8(139)d	14.8(120)d	0.35(-7)bc	0.32(-5)bc	73.0(-10)a	65.2(-10)a	0.58(22)e	0.57(18)d	204.1(208)d	191.2(209)b
5YR.33	9.2(11)b	11.0(63)bc	0.32(-14)b	0.24(-31)a	86.5(6)d	78.4(8)c	0.39(-18)b	0.42(-14)b	166.8(141)c	170.9(169)b
5YR.50	12.6(52)c	11.2(67)bc	0.25(-32)a	0.21(-38)a	85.8(5)d	78.9(9)cd	0.41(-13)c	0.41(-15)b	213.2(225)d	189.6(206)b
10YR.33	13.3(61)c	10.1(50)b	0.34(-10)abc	0.36(6)abc	88.9(9)e	80.5(11)de	0.30(-37)a	0.33(-33)a	132.4(79)b	161.1(150)b
10YR.50	17.8(115)d	12.4(84)cd	0.37(-1)bc	0.41(20)bc	90.0(10)e	81.8(13)e	0.31(-35)a	0.34(-30)a	194.1(190)d	192.0(211)b
Control	8.3(-)a	6.7(-)a	0.37(-)c	0.34(-)c	81.6(-)c	72.4(-)b	0.47(-)d	0.48(-)c	88.9(-)a	85.7(-)a

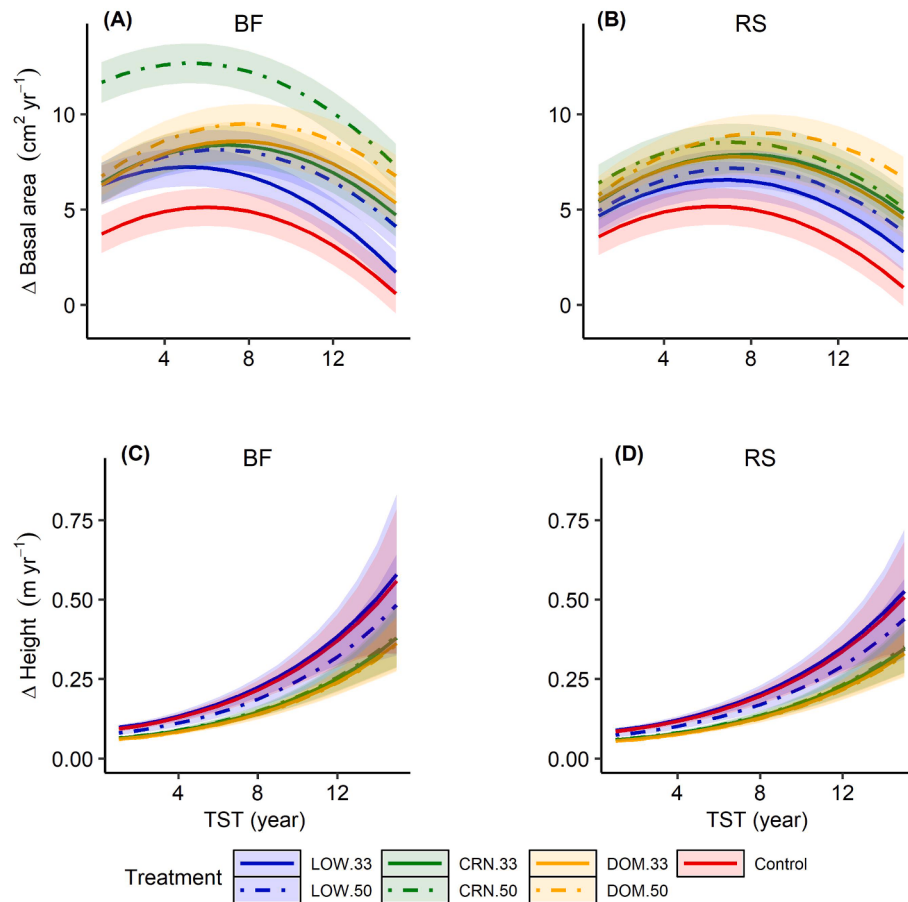


Fig. 2. Treatment-wise predicted individual tree basal area and height growth in NoPCT stands for a tree of 15 cm DBH of both species for different time since treatment (TST). Shaded areas correspond to $\pm 1\text{SE}$ calculated from the fixed effects of the respective models.

consistent ΔHT during the initial years after CT, followed by a more rapid increase throughout the study period (Fig. 2C and 2D).

In PCT stands, all CT treatments had significant effects on ΔBA for both BF and RS, with CT resulting in significantly higher ΔBA compared to the unthinned control (Table 3). Similarly, within the same timing of treatment, heavy CT resulted in higher ΔBA than light CT for both species. There was a slight decrease in ΔBA over time in the unthinned control and 0YR treatments, while it showed an increase in all delayed treatments for both species (Fig. 3A and 3B). Treatment-wise LS means of ΔHT for BF ranged from 0.25 (5YR.50) to 0.37 (Control) m yr^{-1} , and for RS, it ranged from 0.21 (5YR.50) to 0.41 (10YR.50) m yr^{-1} . Height growth of both BF and RS in control was significantly higher than that of the 5-year delayed treatments ($p < 0.001$). For both species, ΔHT in control and 0YR treatments of the PCT stands increased for the first few years after CT, reached a maximum, and then decreased gradually. However, all delayed treatments, except 5YR.33, showed a gradual decrease in ΔHT over the study period for both species (Fig. 3C and 3D).

3.2. Height-diameter ratio, crown ratio, and growth efficiency

LS means height-diameter ratio (H:D ratio) of BF ranged from 84.8 (LOW.50) to 108.5 (Control), while for RS, it ranged from 84.1 (LOW.50) to 98.5 (control) (Table 3). The highest H:D ratio for RS in the unthinned control was only significantly different from heavy low ($p < 0.001$) and heavy crown ($p = 0.002$) thinning. However, all four low and crown thinning treatments for BF resulted in significantly lower H:D ratios compared to the unthinned control ($p < 0.019$). During the duration of the study period, the H:D ratio of both BF and RS in thinned plots of NoPCT stands exhibited a gradual decrease, while in unthinned plots, it

was relatively stable for BF, and showed a slight increase for RS (Fig. 4A and 4B).

Crown ratio of BF in both treatments of low thinning were significantly higher than that of the control ($p < 0.008$) and dominant thinning ($p < 0.024$). In contrast, the crown ratio of RS in none of the treatments significantly increased compared to the unthinned control ($p > 0.1$; Table 3). On the other hand, both treatments of dominant thinning had significantly lower crown ratios for RS compared to heavy removal of both low ($p < 0.003$) and crown ($p < 0.017$) thinning. Despite marginal differences in the LS means of crown ratio between unthinned control and some of the CT treatments of NoPCT stands, both species in unthinned stands consistently exhibited declining CR over the period, while it slightly increased for BF or remained relatively stable for RS in thinned NoPCT stands (Fig. 4C and 4D). BF in unthinned stands showed a more rapid decline in CR than RS in unthinned stands. On the other hand, the BF crown ratio increased more rapidly in heavy thinning compared to light thinning. Unlike BF, differences in crown ratio trajectories between heavy and light thinning were less evident for RS (Fig. 4D).

In the PCT experiment, the H:D ratio of BF in control was significantly higher than that of the immediate treatments ($p < 0.032$; Table 3), but significantly lower than all delayed treatments ($p < 0.001$). Similarly, the H:D ratio of RS in unthinned control was higher than the immediate treatments (though not significant with 0YR.33), but lower than the delayed treatments. In thinned plots, the H:D ratio of both BF and RS showed a gradual decline, while in unthinned plots, it consistently increased for both species, throughout the study period (Fig. 5A and 5B). For both species, the CR was highest in 0YR.50, which was also significantly different from all other treatments including control for BF

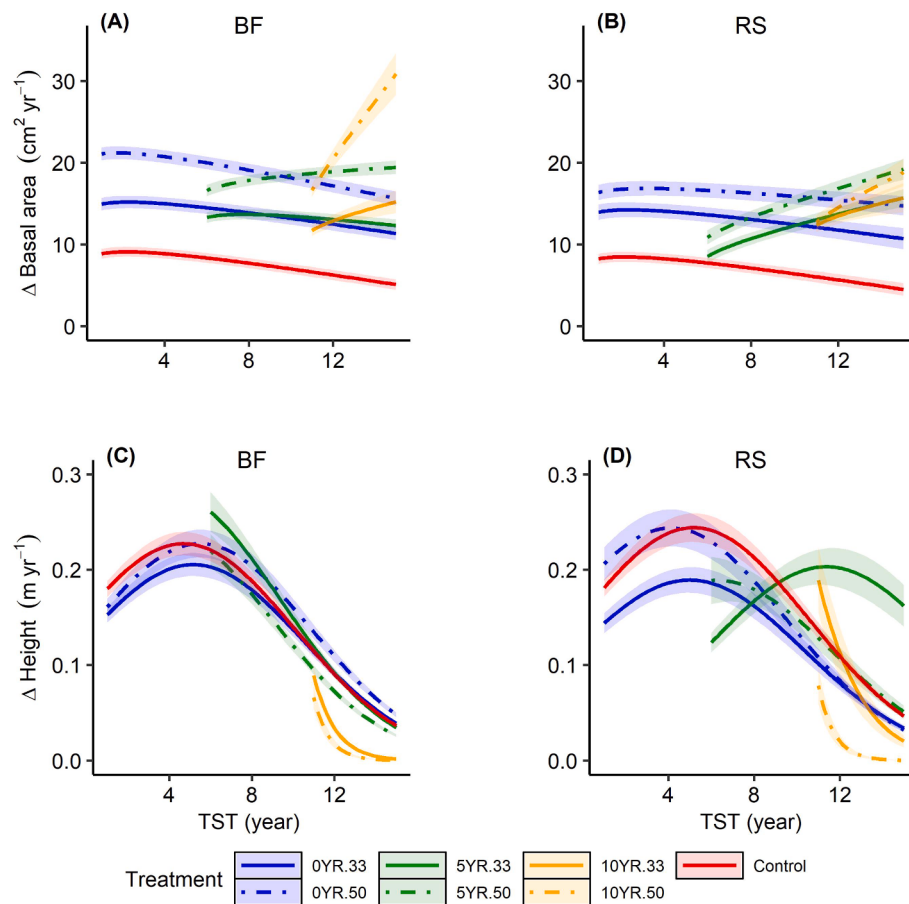


Fig. 3. Treatment-wise predicted individual tree's basal area and height growth in PCT stand for a tree of 15 cm DBH of both species for different time since treatment (TST). The x-axis is in reference to 0YR treatment; therefore, "10 (year) TST" should correspond to 5 and 0 (year) TST for 5YR and 10YR treatments, respectively. Shaded areas correspond to ± 1 SE calculated from the fixed effects of the respective models.

($p < 0.001$). Similarly, for RS, the CR in 0YR.50 was significantly different from control and all treatments ($p < 0.001$), except for the 0YR.33 treatment ($p = 0.284$). Heavy thinning resulted in a higher CR than light thinning of the same treatment timings. Similarly, according to the timing of treatment application, CR was ranked: 0YR > 5YR > 10YR for both species. Although all CT treatments in NoPCT stands were effective in maintaining (or increasing) the crown ratio over the study period, it gradually decreased in both of the 0YR treatments, and 5YR.33 of the PCT stands. However, the rate of decrease was much lower for the trees in thinned stands compared to that of the unthinned control stands (Fig. 5C and 5D).

CT treatments in both NoPCT and PCT stands had a significant effect on tree-level growth efficiency (GE) for both BF and RS, where trees in all thinned stands showed significantly higher GE than the trees in unthinned control ($p < 0.01$; Table 3). The highest GE in NoPCT experiment was observed in heavy crown thinning for both species. Heavier thinning generally showed higher, but insignificant GE compared to the NoPCT experiment's light thinning ($p > 0.077$). In the PCT experiment, BF trees in heavier thinning were significantly more efficient than trees in light thinning ($p < 0.001$), whereas the differences between light and heavy thinning were not significant for RS ($p > 0.119$). The GE for both species in all thinned stands, including both NoPCT and PCT stands, except for DOM.50 of the NoPCT, remained consistently higher than that of the unthinned stands throughout the entire study period (Fig. 4E, 4F, 5E and 5F).

3.3. Total volume, merchantable volume, and carbon growth

The response of trees in NoPCT experiment in terms of total (Δ Tvol)

and merchantable volume growth (Δ Mvol) were highest in CRN.50 and LOW.50 treatments for both BF and RS, respectively (Table 4). Among BF trees, the lowest growth in both Δ Tvol and Δ Mvol was observed in the unthinned control treatment. On the other hand, for RS, the Δ Mvol was lowest in the DOM.33 treatment, while the unthinned control treatment had the lowest Δ Tvol. The results of the pairwise comparison test indicated that, for both species, Δ Tvol and Δ Mvol were similar between both treatments of dominant thinning and the unthinned control ($p > 0.110$), except for the merchantable volume growth of BF between the control and DOM.50 treatment ($p = 0.015$). Similarly, volume growth between heavy and light thinning of the same thinning type was similar for both species, throughout the entire study period (Fig. 6A–6D).

All thinning treatments in NoPCT stands resulted in higher carbon growth (Δ C) compared to the unthinned control for both species, with the highest growth observed in CRN.50 treatment for BF and LOW.50 treatment for RS (Table 4). The lowest Δ C was observed in unthinned control for both species. However, there were no significant differences in Δ C between the dominant thinning treatments and the unthinned control for RS ($p > 0.466$). For BF, differences in Δ C between DOM.33 and the control were marginally significant ($p = 0.049$), while it was marginally insignificant between DOM.50 and the control ($p = 0.056$). Over the study period, there was an initial increase in Δ C of both species for the first few years, followed by reaching a peak and subsequently experiencing a decline (Fig. 6E and 6F).

In the PCT experiment, all CT treatments led to significantly higher total and merchantable volume growth when compared to unthinned control, for both BF and RS ($p < 0.007$; Table 4). Furthermore, heavy CT resulted in higher volume growth than light CT. Within the same

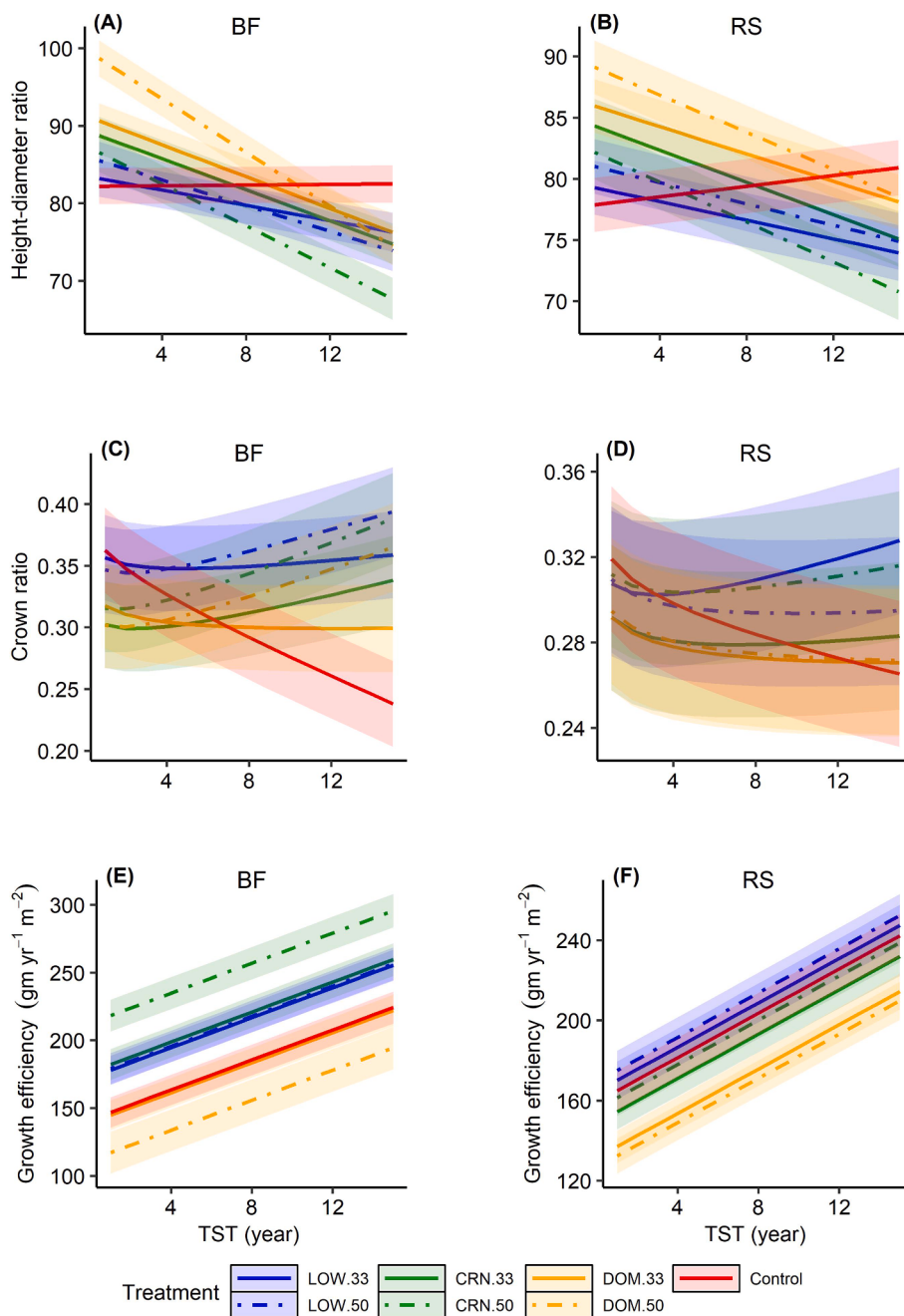


Fig. 4. Treatment-wise predicted individual tree's H:D ratio, crown ratio and growth efficiency in NoPCT stand for a tree of 15 cm DBH of both species for different time since treatment (TST). The basal area of larger trees (BAL) for the H:D ratio and GE models was set to 0, meaning that the tree with a DBH of 15 cm used should correspond to the largest tree in the plot. Shaded areas correspond to ± 1 SE calculated from the fixed effects of the respective models. Note: the y-axes differ to highlight trends.

treatment timings, the differences in both $\Delta Tvol$ and $\Delta Mvol$ between heavy and light thinning treatments were statistically significant for BF ($p < 0.005$), while these differences were less pronounced for RS ($p > 0.90$ for delayed treatments). After CT, both $\Delta Tvol$ and $\Delta Mvol$ gradually increased over the study period for both species in all treatments (Fig. 7A-7D). Carbon growth (ΔC) in all CT treatments of the PCT experiment was also significantly higher than that of the unthinned control for both species ($p < 0.002$; Table 4). Heavy CT treatments showed significantly greater ΔC compared to light thinning treatments of the same timing for BF ($p < 0.021$), except for a 10-year delay in RS ($p > 0.999$). ΔC was slightly decreased over the period in unthinned control and OYR treatments for both species, while it increased for both species in all delayed treatments (Fig. 7E and 7F). ($p < 0.007$; Table 4). Furthermore, heavy CT resulted in higher volume growth than light CT. Within the same treatment timings, the differences in both $\Delta Tvol$ and $\Delta Mvol$ between heavy and light thinning treatments were statistically

significant for BF ($p < 0.005$), while these differences were less pronounced for RS ($p > 0.90$ for delayed treatments). After CT, both $\Delta Tvol$ and $\Delta Mvol$ gradually increased over the study period for both species in all treatments (Fig. 7A-7D). Tree carbon growth (ΔC) in all CT treatments of the PCT experiment was also significantly higher than that of the unthinned control for both species. Heavy CT treatments showed significantly greater ΔC compared to light thinning treatments of the same timing for BF ($p < 0.021$), except for a 10-year delay in RS ($p > 0.999$). ΔC was slightly decreased over the period in unthinned control and OYR treatments for both species, while it increased for both species in all delayed treatments (Fig. 7E and 7F).

Models selected to describe the tree-level growth attributes over the study period for NoPCT stands had generalized R^2 of the fixed effects from 0.05 (ΔHT) to 0.62 (H:D ratio), and from 0.15 to 0.92 when including the random effects of tree, plot and site (Table 5). Similarly, the generalized R^2 of fixed effects of the models selected for PCT

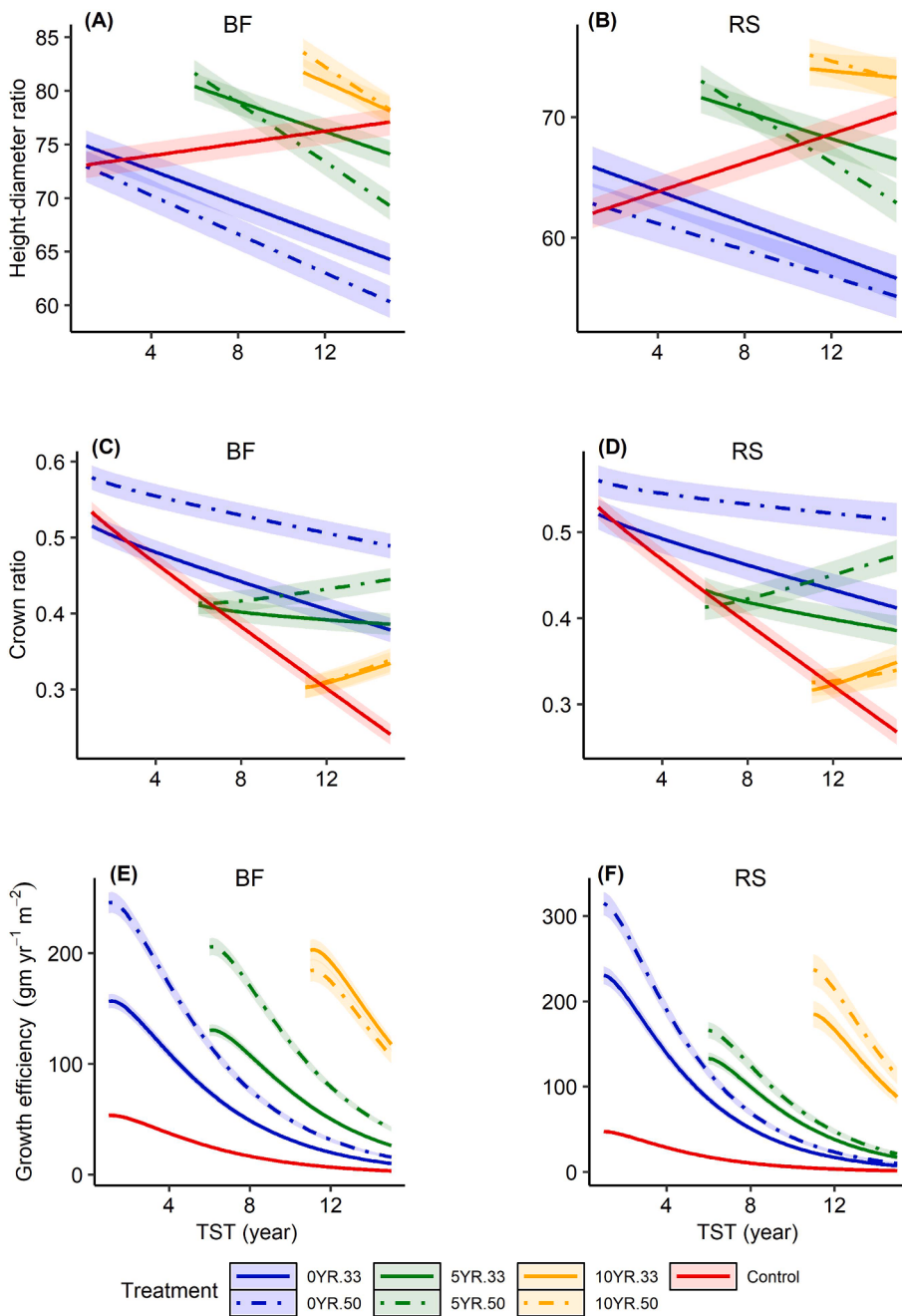


Fig. 5. Treatment-wise predicted individual tree's H:D ratio, crown ratio, and growth efficiency in PCT stand for a tree of 15 cm DBH of both species for different TST. The x-axis is in reference to 0YR treatment; therefore, "10 (year) TST" should correspond to 5 and 0 (year) TST for 5YR and 10YR treatments, respectively. The basal area of larger trees (BAL) for the H:D ratio model was set to 0, meaning that the tree with a DBH of 15 cm should correspond to the largest tree in the plot. Shaded areas correspond to $\pm 1SE$ calculated from the fixed effects of the respective models. Note: the y-axes differ to highlight trends.

experiment ranged between 0.02 (ΔHT) & 0.57 (H:D ratio) and an R^2 between 0.04 & 0.85 when including the random effects. Various factors exhibited different relative contributions to R^2 values for different growth metrics. In NoPCT stands, tree size had the highest relative contribution to R^2 for basal area, volume (both total and merchantable) and carbon growth, whereas it was the basal area of larger trees (BAL) for growth efficiency, and species for height growth and H:D ratio (Fig. 8A). In PCT stands, treatment demonstrated the highest relative contribution to the R^2 for ΔBA , ΔHT , and growth efficiency, whereas tree size and treatment showed similar contribution to ΔC (Fig. 8B). Similarly, tree size and BAL was more important for H:D ratio and volume growth, and crown ratio was mainly controlled by time since treatment.

4. Discussion

Commercial thinning had a positive influence on the growth of both BF and RS in stands with and without prior PCT. In general, tree size variables explained much variability in tree growth after CT in the NoPCT stands, whereas most variation in the PCT stands was explained by treatment differences and tree size variables. However, there were notable exceptions: crown ratio varied most among species in NoPCT stands, and according to time since treatment in PCT stands, while growth efficiency varied among treatments in PCT stands and according to basal area of larger trees in NoPCT stands. Our results indicated that 16–18 years after CT in NoPCT stands, ΔBA of BF trees following low, crown, and dominant thinning treatments were 174, 215, and 103%; and for RS, 89, 97, and 38% higher than the unthinned control, respectively. These results indicate that BF was generally more responsive to CT than RS. Differences in species-specific growth rates and their

Table 4

The adjusted mean of tree-level volume and carbon growth for each experiment (NoPCT and PCT) for all post-treatment measurements. The numbers in parentheses represent the percentage difference of the corresponding treatment from the unthinned control.

Treatment	Δ Total volume ($\text{dm}^3 \text{yr}^{-1}$)		Δ Merchantable volume ($\text{dm}^3 \text{yr}^{-1}$)		Δ Carbon (kg yr^{-1})	
	BF	RS	BF	RS	BF	RS
NoPCT						
	n = 3696	n = 8390	n = 3696	n = 8390	n = 11474	n = 24722
LOW.33	8.8(140) bc	6.2(29) ab	8.5 (119)bc	6.5(32) ab	1.7 (171)bc	1.3(58) b
LOW.50	10.2 (178)bc	9.2(91) c	9.6 (146)bc	8.9(81) c	2.2 (241)cd	2.0 (135)c
CRN.33	9.4(157) bc	6.3(30) ab	9.4 (141)bc	6.7(36) abc	1.7 (171)bc	1.5(79) bc
CRN.50	11.2 (207)c	7.8(62) bc	12.3 (214)c	8.1(64) bc	2.6 (312)d	1.9 (132)c
DOM.33	6.3(72) ab	4.6(-5) a	6.8(75) ab	5.2(6)a a	1.3 (104)b	1.1(32) ab
DOM.50	6.3(73) ab	4.7(-3) a	8.0 (105)b	5.4(11) a	1.3 (107)ab	1.1(35) ab
Control	3.7(-)a	4.8(-)a	3.9(-)a	4.9(-)a	0.6(-)a	0.8(-)a
PCT						
	n = 31409	n = 6911	n = 31409	n = 6911	n = 49634	n = 10260
0YR.33	11.7(35) b	8.9(33) b	12.2 (38)b	9.4(35) b	3.1(74) c	2.5(70) bc
0YR.50	15.1(75) cd	11.2 (69)cd	15.5 (75)c	11.8 (69)b	4.4 (145)d	3.3 (122)d
5YR.33	12.3(42) b	8.5(27) b	12.5 (42)b	9.9(42) b	2.9(61) c	2.3(51) b
5YR.50	14.1(63) c	9.4(40) bc	14.5 (64)c	11.4 (64)b	3.9 (120)d	2.7(84) cd
10YR.33	11.4(32) b	12.3 (85)cd	11.3 (28)b	11.8 (70)b	2.1(15) b	2.5(67) bc
10YR.50	16.7(93) d	13.5 (103)d	16.5 (87)c	13.7 (96)b	2.9(63) c	2.5(70) bc
Control	8.6(-)a	6.7(-)a	8.8(-)a	7.0(-)a	1.8(-)a	1.5(-)a

distinct resource utilization strategies could have played a pivotal role in shaping the observed patterns, wherein BF exhibited a more pronounced response compared to red spruce. Both species are tolerant of shade, but RS is commonly classified as tolerant while BF is very tolerant (e.g., Weiskittel et al., 2009b). Their growth rates and longevity differ (Blum, 1990). BF generally grows more rapidly than RS (Solomon and Frank, 1983; Frank, 1990) but is relatively short-lived (Seymour, 1992), so any advantages over RS are unlikely to endure with advancing stand age (Seymour and Hunter, 1992). We speculate that differences in morphology and physiology may allow BF to retain more leaf area under shade and therefore better respond to thinning. BF carries more leaf area than RS of a given size, and has a different vertical distribution of leaf area, which might allow for greater light interception after thinning (Weiskittel et al., 2009b). Furthermore, BF may have higher growth efficiency than RS after thinning that improves residual tree crown position, possibly explained by Seymour and Kenefic (2002) who reported the highest growth efficiency for RS with moderate crown size in mid-upper canopy positions as opposed to RS with relatively small or large crown size.

In terms of management implications, crown thinning might be a more effective method for promoting the growth of BF, while both low and crown thinning effectively promoted the growth of RS. It is also important to note that when comparing basal area increment between thinning treatments, it could be slightly higher after low thinning due to larger trees being retained in that treatment compared to dominant and crown thinning. This is because, with the same diameter increment but different initial diameters, larger trees have a higher basal area

increment compared to smaller ones. In PCT stands, Δ BA of BF following 0YR, 5YR, and 10YR delay thinning treatments were on an average 106, 32, and 88% higher than the control; and for RS, 96, 65, and 67% higher compared to the control, respectively. Greater Δ BA in the thinned stands is directly related to higher diameter growth due to increased resource availability and this is consistent with prior studies in the region (e.g. Pelletier & Pitt, 2008; Zhang et al., 2009; Weiskittel et al., 2011; Clune 2013).

Greater short-term response of 10-year delayed treatments over 5-year delayed treatments suggested that competition had intensified over time, garnering a greater response to a later release. This was consistent with the findings of Pelletier & Pitt (2008). They observed the greatest diameter increment in the double-entry thinnings, followed by the delayed single-entry, single-entry without delay, and the lowest in unthinned treatments. The magnitude of response to CT also depends on the time since treatment (Brix, 1981; Bose et al., 2018b), tree size, and age (Binkley et al., 2002, 2006; Seymour & Kenefic, 2002; Forrester, 2019). After 16–17 years following CT treatments in white spruce (*Picea glauca* (Moench) Voss) and red spruce plantations in New Brunswick, Pelletier & Pitt (2008) observed mean diameters 10 to 25% greater than the controls. While the initial response to thinning may vary over time, we lacked a long enough time series of the data following thinning to model the longer-term effects of delayed treatments in the PCT stands.

Mixed effects regression results showed that the rate of BA growth in NoPCT stands increased slightly over the first few years, reached a maximum then decreased gradually for both species. BF exhibited Δ BA well above all treatments after heavy crown thinning until 10 years after CT. Such differences among the treatments were less evident in RS. While the overall Δ BA was greater after low thinning than after dominant thinning, trees of the same size exhibited higher basal area increment throughout the measurement period after dominant thinning than after low thinning. These results indicated that the positive effect of thinning is greater among smaller trees previously dominated by large neighbors than among more dominant trees in the upper canopy. Thus, larger trees with more access to sunlight were less benefitted from the thinning. However, trade-offs between tree- and stand-level growth must be considered when selecting trees for retention or removal, since removing larger trees from the stand might cause higher mortality loss as observed by Pekol (2011) from the same stands of this study, while Emmingham et al. (2007) in Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) stands from the Pacific Northwest and Powers et al. (2010) in red pine (*Pinus resinosa* Ait.) stands in Northern Minnesota saw similar trends too. Wagle et al. (2022) from the same stands in this study reported that dominant thinning had the lowest standing and cumulative volume. Similarly, compared to unthinned control, there was no benefit of delaying CT after prior PCT in younger spruce-fir stands in terms of total merchantable volume and stand value (Wagle et al., 2022).

Many investigators have indicated that the diameter growth of individual trees is immediately affected (i.e. increased diameter growth) by thinning, whereas Δ HT is relatively unaffected by thinning (Lanner, 1985; Zhang et al., 2009; Swift et al., 2017). However, the effect of thinning on tree height growth, especially at very high thinning intensities is obvious (Zhang et al., 1997; Sharma et al., 2006; Deng et al., 2019). Zhang et al. (1997) found increased tree diameter and height growth by thinning in loblolly pine (*Pinus taeda* L.) plantations. However, thinning affected tree diameter growth more than height growth, resulting in lower H:D ratio after higher thinning intensity (Zhang et al., 1997). Brix (1981) and Ginn et al. (1991) have reported a short-term decrease followed by a long-term increase in Δ HT following thinning in Douglas-fir and loblolly pine stands, respectively. We also observed slow Δ HT for both BF and RS in NoPCT stands for the first few years, followed by increasing Δ HT over the study period. Despite the high shade-tolerance of RS and BF, our findings of short-term slowing in Δ HT after CT in NoPCT stands are consistent with responses of less shade-tolerant species (Brix, 1981; Ginn et al., 1991). However, there were

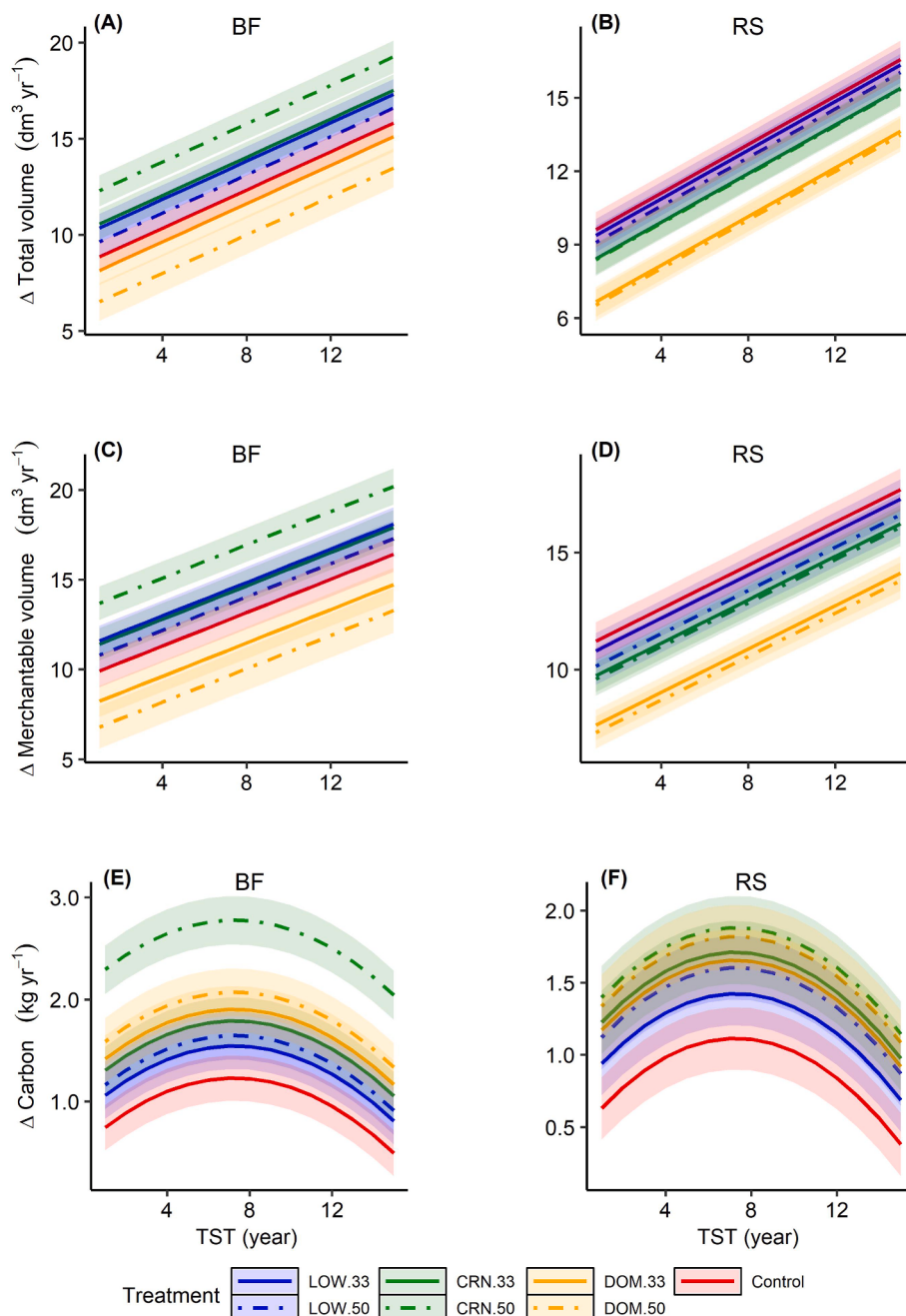


Fig. 6. Treatment-wise predicted individual tree's total volume ($\Delta Tvol$), merchantable volume ($\Delta Mvol$), and carbon growth (ΔC) in NoPCT stand for a tree of 15 cm DBH of both species for different time since treatment (TST). The basal area of larger trees (BAL) for both total and merchantable volume growths was set to 0, meaning that the tree with a DBH of 15 cm used should correspond to the largest tree in the plot. Shaded areas correspond to ± 1 SE calculated from the fixed effects of the respective models. Note: the y-axes differ to highlight trend.

no substantial differences in ΔHT between thinning treatments including control. In PCT stands, ΔHT over the study period exhibited a pattern of rise-peak-fall in 0YR treatments and unthinned control stands for both RS and BF, whereas all delayed treatments except 5YR.33 had slowing height increment over the study period for both species. The decrease in ΔHT after thinning might be due to the redistribution of photosynthate from height growth to the expansion of the lower crown after thinning (Ginn et al., 1991). Moreover, differences in ΔHT pattern with treatment timings might also be associated with tree age. On the other hand, it should also be noted that ΔHT data were relatively variable and the selected model had relatively poor fit statistics for both NoPCT and PCT stands.

Differences in H:D ratio immediately after CT was associated with the size of trees removed or retained, while the decreases in H:D ratio as observed in thinned stands over the period were related to treatment effects (i.e., higher diameter increment after CT) (Wonn & O'Hara,

2001; Pitt & Lanteigne, 2008; Saunders et al. 2008). For example, after dominant thinning, residual trees initially had the highest H:D ratio and needed approximately 9 years (for light removal) to 11 years (for heavy removal) of post-treatment growth for BF, and 11 years (for light removal) to 13 years (for heavy removal) of post-treatment growth for RS, to have H:D ratio similar to unthinned control. Over the study period, all thinning treatments showed substantial decreases in H:D ratios for both species, whereas in the unthinned control plots, it was more or less constant for BF and slightly increased for RS. In PCT stands also, all thinning treatments caused the H:D ratio to decrease substantially over the period for both BF and RS. Similar to trees' response in unthinned NoPCT stands, H:D ratio increased over the period for trees in the unthinned control plots of PCT stands. These results indicated that thinning treatments in both PCT and NoPCT stands were effective in promoting more stability and resistance against storm damage by reducing the H:D ratio for both BF and RS (Wonn & O'Hara, 2001).

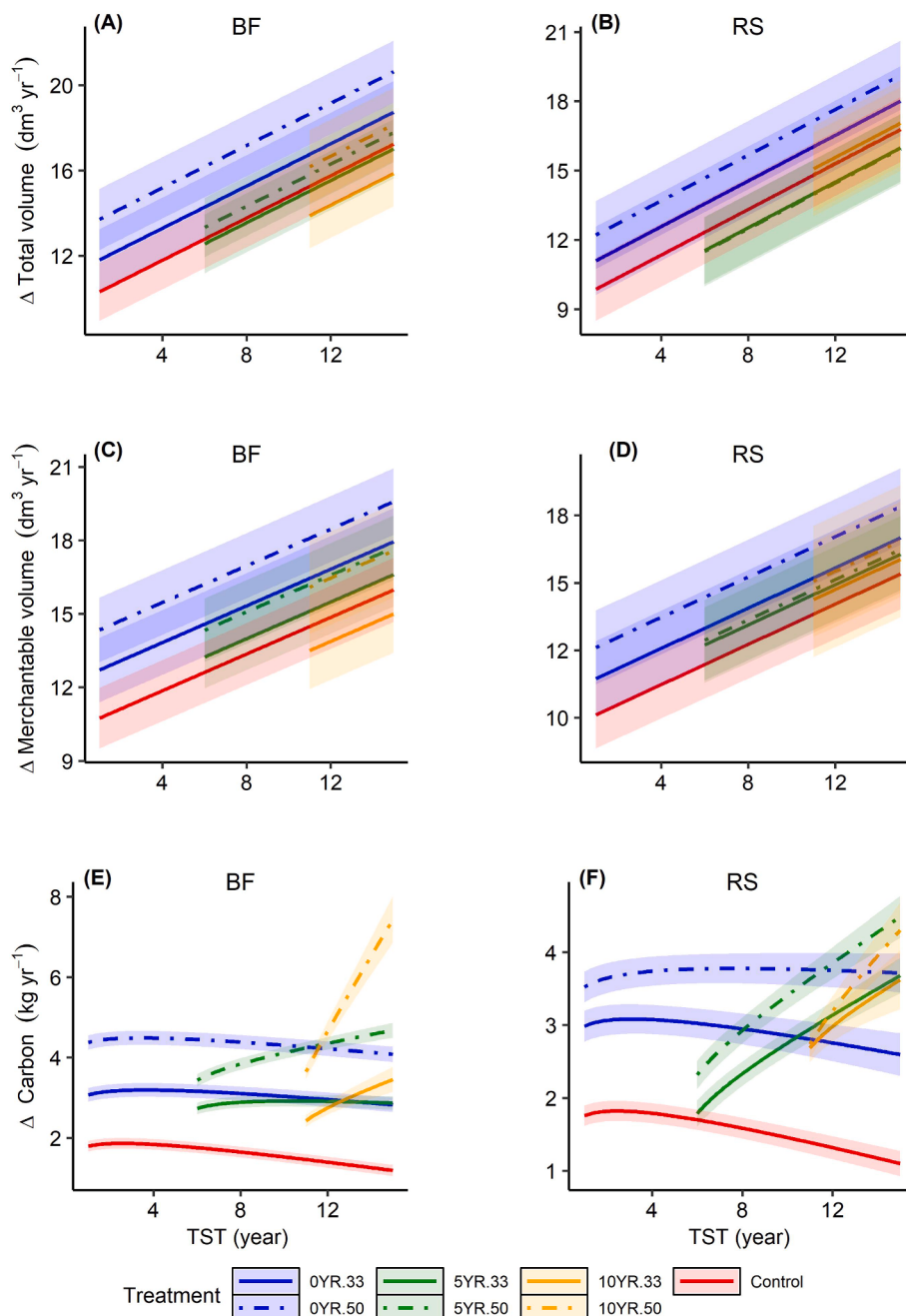


Fig. 7. Treatment-wise predicted individual tree's total volume ($\Delta Tvol$), merchantable volume ($\Delta Mvol$), and carbon growth (ΔC) in PCT stand for a tree of 15 cm DBH of both species for different TST. The x-axis is in reference to 0YR treatment; therefore, "10 (year) TST" should correspond to 5 and 0 (year) TST for 5YR and 10YR treatments, respectively. The basal area of larger trees (BAL) for the models of total and merchantable volume growth was set to 0, meaning that the tree with a DBH of 15 cm used should correspond to the largest tree in the plot. Shaded areas correspond to ± 1 SE calculated from the fixed effects of the respective models. Note: the y-axes differ to highlight trends.

However, removing larger trees and retaining smaller trees with an unfavorable H:D ratio as done in dominant thinning can cause substantial mortality from wind damage, particularly during the first few years after CT (Emmingham et al., 2007; Powers et al., 2010; Pekol, 2011).

Crown ratio is one of the measures of crown size (or tree foliage) which is commonly considered as an index of the crown's ability to supply sufficient carbohydrates for stem growth (Hynynen, 1995; Pretzsch, 2019; Poudel et al., 2021). Generally, larger crowns produce more carbohydrate to support stemwood volume growth (Long & Smith, 1990, 1992). Variation in crown ratio over the period in our study was associated with the relative rates of height growth and crown recession (Garber et al., 2008). Increasing crown ratio especially for residual trees after heavier thinning of NoPCT stands might be due to less crown recession than height growth in these stands. Brix (1981) reported slower height growth for the first two years after thinning; then, after

year five, both height growth and crown length increased (i.e., thinning slowed crown recession) for a Douglas-fir stand in British Columbia thinned at 24 years of age. Seven years after thinning in loblolly pine plantations, Short & Burkhardt (1992) found a significant effect of thinning intensity and time since treatment in crown height increment (i.e., crown recession) where the increment was ranked: unthinned > light thinning > heavy thinning. Using 10 years of data gathered after implementing the same CT experiment of our study, Clune (2013) also found crown recession decreased significantly after thinning for all treatments, where larger decreases were observed after heavier thinning. We also observed a higher crown ratio for the trees in heavier thinning treatments compared to light thinning and unthinned control. In contrast, higher crown recession (or lower crown ratio) for the trees in unthinned stands is expected given lower branches are lost after they die due to lack of light as a result of shading from neighbors (Assmann, 1970; Ryan et al., 1997; Ashton & Kelty, 2018).

Table 5

Selected models and their fit statistics to describe the change in tree-level attributes over the period.

Attributes	Selecte dmodel	R ²				MB	MAB	%MAB
		Fixed	Site	Plot	Tree			
NoPCT								
ΔBasal area (cm ² yr ⁻¹)	M69	0.22	0.32	0.32	0.53	7.9 × 10 ⁻¹⁰	3.33	51.6
ΔHeight (m yr ⁻¹)	M57	0.05	0.12	0.15	0.15	0.079	0.14	69.1
H:D ratio	M53	0.62	0.65	0.69	0.92	0.005	3.17	3.4
Crown ratio	M61	0.13	0.53	0.56	0.79	-0.002	0.04	12.7
ΔTotal volume (dm ³ yr ⁻¹)	M54	0.43	0.43	0.47	0.64	-3.8 × 10 ⁻¹⁰	2.50	38.7
ΔMerch. volume (dm ³ yr ⁻¹)	M54	0.23	0.23	0.25	0.29	-1.8 × 10 ⁻⁹	4.02	59.2
ΔCarbon (kg yr ⁻¹)	M72	0.26	0.35	0.35	0.56	7.5 × 10 ⁻¹¹	0.73	51.6
Growth efficiency (gm yr ⁻¹ m ⁻²)	M54	0.24	0.24	0.28	0.63	7.0 × 10 ⁻⁹	35.0	34.8
PCT								
ΔBasal area (cm ² yr ⁻¹)	M13	0.34	0.36	0.38	0.54	-0.001	4.74	44.2
ΔHeight (m yr ⁻¹)	M69	0.02	0.03	0.04	0.04	0.169	0.26	71.1
H:D ratio	M37	0.57	0.63	0.65	0.85	-0.167	3.53	4.4
Crown ratio	M13	0.36	0.45	0.48	0.56	-0.003	0.06	13.0
ΔTotal volume (dm ³ yr ⁻¹)	M54	0.37	0.38	0.41	0.50	-4.1 × 10 ⁻¹⁰	4.37	43.1
ΔMerch. volume (dm ³ yr ⁻¹)	M54	0.20	0.20	0.22	0.27	1.5 × 10 ⁻⁹	5.69	55.3
ΔCarbon (kg yr ⁻¹)	M61	0.38	0.40	0.42	0.58	-1.8 × 10 ⁻⁴	1.03	44
Growth efficiency (gm yr ⁻¹ m ⁻²)	M63	0.10	0.14	0.15	0.27	52.866	72.7	57.6
M13: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + \log(TST_{ijk}) + u_i + u_{ij} + u_{ijk}$								
M17: $Y_{ijk} = Spp_{ijk} + Trt_{ijk} + TST_{ijk} + Size_{ijk} + (TST_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								
M37: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + BAL_{ijk} + u_i + u_{ij} + u_{ijk}$								
M53: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + SI_{ijk} + BAL_{ijk} + u_i + u_{ij} + u_{ijk}$								
M54: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * Size_{ijk} + TST_{ijk} + SI_{ijk} + BAL_{ijk} + u_i + u_{ij} + u_{ijk}$								
M57: $Y_{ijk} = Spp_{ijk} + Trt_{ijk} + TST_{ijk} + Size_{ijk} + \log(TST_{ijk}) + (Size_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								
M61: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + \log(TST_{ijk}) + (Size_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								
M63: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} + Spp_{ijk} * TST_{ijk} + Size_{ijk} + \log(TST_{ijk}) + (Size_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								
M69: $Y_{ijk} = Spp_{ijk} * Trt_{ijk} * TST_{ijk} + Size_{ijk} + \log(Size_{ijk}) + (TST_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								
M72 : $Y_{ijk} = Spp_{ijk} * Trt_{ijk} + Spp_{ijk} * Size_{ijk} + TST_{ijk} + \log(Size_{ijk}) + (TST_{ijk})^2 + u_i + u_{ij} + u_{ijk}$								

Note: Merch. volume = merchantable volume, MB = mean bias, MAB = mean absolute bias, %MAB = percentage mean absolute bias; Variables defined in Table 1.

All thinning treatments were effective in maintaining (or enhancing) crown ratio of both RS and BF in both NoPCT and PCT stands. Earlier thinning treatments of the PCT stands slowed down the trend of decreasing crown ratio, whereas all treatments in NoPCT stands caused crown ratio to increase over the period. At the beginning of the study period, the crown ratio in PCT stands was much higher than that of NoPCT stands because trees in PCT stands were younger, had increased inter-tree spacing due to early PCT, and had therefore experienced less competition-induced crown recession. Unlike in PCT stands, trees were much older in NoPCT stands, and may have already undergone extensive crown recession. Work by Garber et al. (2008) examining crown recession patterns in white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) and Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) indicated that crown recession probability increased among trees with high initial crown ratio and decreased with increasing tree age. At the end of our study period, the range of crown ratios was not much different between PCT and NoPCT stands, as trees in thinned NoPCT stands were able to maintain or increase their crown ratio over the period, while the crown ratio in PCT stands was higher initially but then decreased gradually following earlier CT treatments.

Our study confirms Bose et al.'s (2018b) findings that trees in thinned stands have higher growth efficiency (GE) than trees in unthinned stands. However, the ability of a tree to utilize growing space depends on several factors, including species, age, size, crown position, site index, and competition within the stand (Ryan et al., 1997; Binkley et al., 2002; Seymour and Kenefic, 2002; DeRose and Seymour, 2009; Bose et al., 2018a). DeRose and Seymour (2009) found that the growth efficiency in BF significantly increased with site index, while it remained unaffected by site index in RS. Bose et al. (2018b) reported that thinned stands showed higher relative volume growth for various species, from shade-intolerant loblolly pine to highly shade-tolerant spruce-fir. They also

found that the growth efficiency of shade-intolerant loblolly pine and moderately shade-tolerant Douglas-fir was positively related to the increased thinning intensity, while the extent of removal was less important for highly shade-tolerant spruce-fir. In our study, we found that the GE of RS was not significantly different between heavy and light thinning in both PCT and NoPCT experiments, similar to the findings of Bose et al. (2018b). In contrast, for BF, we observed that GE was similar in heavy and light thinning in the NoPCT experiment but significantly higher after heavy thinning than after light thinning in the PCT experiment. These results suggest that BF trees in the relatively young PCT stands were more capable of utilizing growing space resulting from thinning than RS trees, while both species were less capable of utilizing growing space created by the heavier thinning in the older NoPCT stands. These differences could be due to age-related decline (Binkley et al., 2010, 2013). Our findings further emphasize the importance of considering species-specific responses to thinning in forest management practices.

The increase in resource availability, combined with the increased growth efficiency of the trees in thinned stands, further contributed to enhancing volume and above-ground carbon growth of trees in both NoPCT and PCT stands (Blevins et al., 2005; Boivin-Dompierre et al., 2017). The effects of thinning treatments on volume and biomass growth rates have been extensively studied in comparison to no thinning, with most studies reporting a significant increase in these rates following thinning (e.g. Valinger et al., 2000; Blevins et al., 2005; Zhang et al., 2006; Soucy et al., 2012; Bose et al., 2018b; Ward & Winkle, 2019). In both PCT and NoPCT experiments, the percentage difference in above-ground carbon growth between unthinned and thinned plots was substantially higher than the percentage difference in volume (both total and merchantable volumes) growth between control and thinned plots for both species. These findings indicate that the impact of CT treatments on above-ground tree carbon growth is even stronger than their

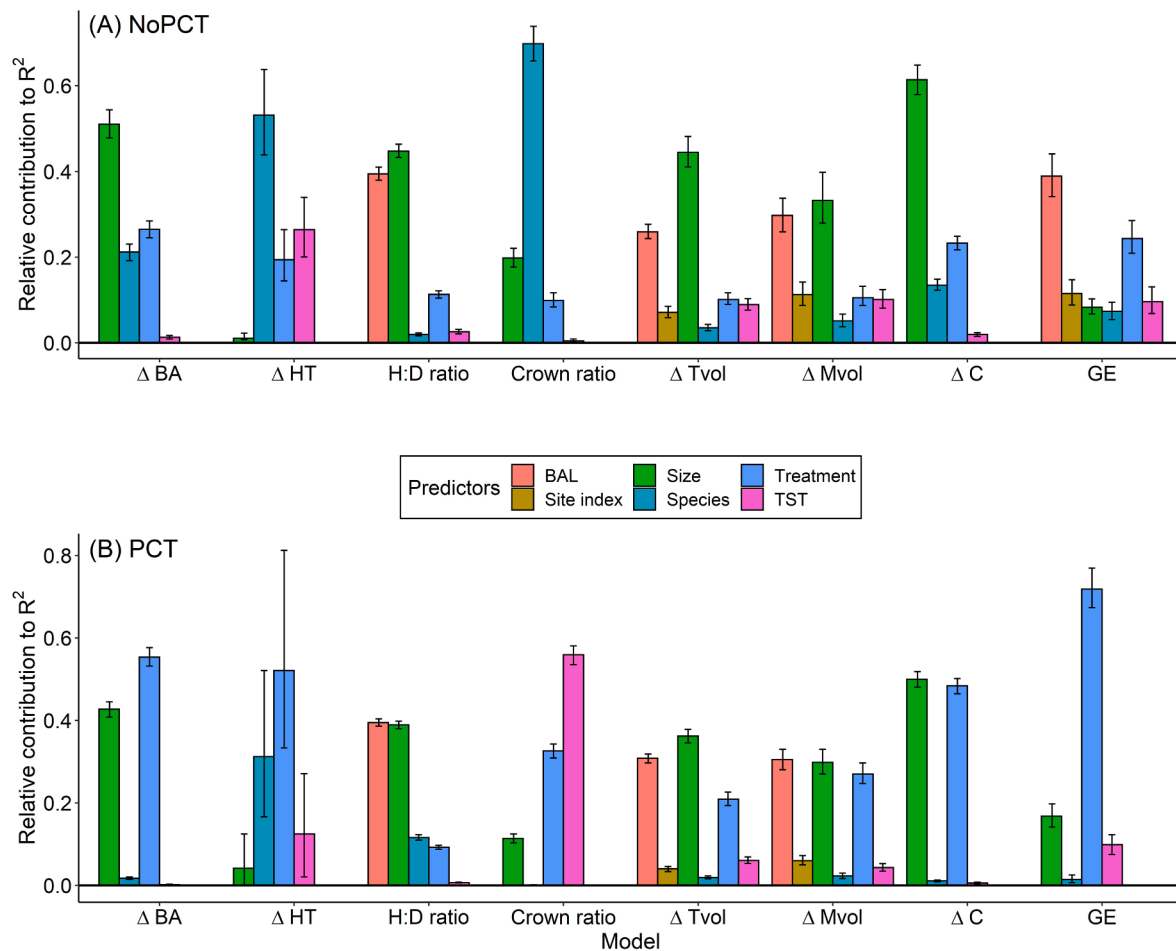


Fig. 8. Relative importance of predictor variables for each model selected. Bars represent 95% confidence intervals obtained from 1000 bootstrap replicates (Grömping, 2006).

impact on volume growth for both BF and RS. However, we caution that tree carbon estimates may be overestimated for rapidly-growing trees in thinned stands where CT enhanced diameter increment but not height increment. Our carbon estimates were derived from diameter-based equations, such that the estimated enhancement in carbon sequestration of trees in thinned stands is linked to enhanced diameter increment (ignoring height) whereas stemwood volume increment was derived from a subset of trees having data for both diameter and height needed for stemwood volume estimation. Similar problems might arise when using allometric equations to obtain estimates of tree leaf area for GE calculations if leaf area prediction models were not fitted to representative data collected from thinned stands.

Carbon sequestration is an important ecosystem service provided by forests, and increasing the carbon storage capacity of forests is an important strategy for mitigating climate change (Gren & Zeleke, 2016; Smith et al., 2019; FAO, 2020). However, the forest ecosystem is vulnerable to the changing climate, which can disrupt its stability through altered patterns, frequencies, intensities, and associated risks of disturbances (Stăncioiu et al., 2021). Therefore, enhancing carbon sequestration rates along with ensuring forest stability and resilience against climate-induced disturbances such as wind, drought, snow and ice, insects, pathogens and fire should be an important forest management strategy in the changing climate scenario (Garcia-Gonzalo et al., 2007; D'Amato et al., 2013; Seidl et al. 2017; Dagley et al., 2023a). Fundamentally, forest managers must compromise between lighter CT favoring stand-level growth and carbon sequestration per hectare versus heavier CT promoting individual-tree growth, vigor, size, and stability (Woodall and Weiskittel, 2021). Our results show that CT has both

increased tree-level carbon sequestration rates as well as encouraged the development of tree-level attributes associated with vigor (greater crown dimensions) and stability (lower H:D). As a result, these rates and carbon stocks are potentially more resilient to climate change than those observed in unthinned stands where trees have lower vigor and stability (Stăncioiu et al., 2021).

5. Conclusion

The results of this study provide evidence that both BF and RS exhibit a positive response to CT, as indicated by enhanced diameter increment leading to lower H:D ratio, and increasing tree crown ratio, growth efficiency, basal area, and volume increment, and carbon sequestration, with BF trees being generally more responsive to CT than RS. Tree growth responses to thinning differed according to residual tree size, highlighting the importance of the decision to cut or retain smaller or larger trees (i.e., thinning method and intensity). Tree-level responses to the method of thinning differed between species. Balsam fir responded most after heavy crown thinning, whereas red spruce growth was most enhanced in heavy low thinning treatments. In general, tree-level growth increases with thinning intensity for both BF and RS. Nonetheless, a trade-off exists between tree- and stand-level responses to CT, as heavier thinning may lead to understocked stands.

Overall, tree-level growth attributes for both species were higher in young PCT stands distributed across better quality sites than for older NoPCT stands located on relatively poor sites. However, when compared to their respective controls, the tree-level growth response to CT was found to be greater in NoPCT stands compared to PCT stands for both

species, except in terms of growth efficiency responses. This suggests that reducing competition by CT is more important for the NoPCT stands than PCT stands.

In summary, our findings have important implications for forest management practices, highlighting the potential benefits of CT for enhancing tree growth and form. In addition to the tree-level responses reported here, forest managers should simultaneously consider stand-level responses including productivity and carbon sequestration. Furthermore, financial and operational challenges should also be considered when deciding whether to thin, when to thin, and when designing thinning prescriptions in spruce-fir forests dominated by balsam fir and red spruce.

CRediT authorship contribution statement

Bishnu Hari Wagle: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **Aaron R. Weiskittel:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Visualization, Data curation, Supervision. **John-Pascal Berrill:** Methodology, Writing – review & editing. **Anil R. Kizha:** Writing – review & editing, Funding acquisition, Supervision. **Anthony W. D'Amato:** Writing – review & editing. **David Marshall:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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