

Evaluation of 10-year temporal and spatial variability in structure and growth across contrasting commercial thinning treatments in spruce-fir forests of northern Maine, USA

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Abstract

- Key message Detailed measures of growth pattern and structural heterogeneity applied in this study helped to quantify the immediate effects of various thinning regimes on forest structure and the resulting alterations in tree size as well as observed longer term stand dynamics.
- *Context* Forest management, stand structure, and tree growth are highly inter-correlated. Prior analyses, however, have resulted in mixed outcomes with limited success in revealing ecological mechanisms.
- Aims The study aimed at evaluating the relationship between forest structure and stand dynamics by applying several sophisticated measures of growth pattern and structural heterogeneity.
- *Methods* Data from a controlled and fully stem-mapped commercial thinning experiment with seven contrasting treatments including a non-thinned control at six locations across the Acadian Forest of Maine, USA, was used. Stand-level attributes examined included tree size and growth heterogeneity, spatial tree distribution, and growth dominance.
- Results Thinning generally reduced stand structural heterogeneity compared to the non-thinned control. In addition, the spatial arrangement of trees changed from fully random (non-thinned control) to a more clustered (removal of dominant and codominant individuals) or regular distribution (removal of intermediate and suppressed individuals). Overall, stand growth exhibited increasing (non-thinned control, removal of intermediate and suppressed individuals) or decreasing growth dominance of large trees (removal of co-dominant competitors). Forwarder trails increased basal area growth of individual trees up to a distance from the trail of approximately 5 m.
- *Conclusion* Findings of this study validate an earlier insight according to which interactions between management practices, forest structure, and tree growth form a permanent feedback loop.

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Contribution of the co-authors Christian Kuehne: data analysis and co-writing the manuscript.

Aaron Weiskittel: project idea and co-writing the manuscript. Ame Pommerening: data analysis and co-writing the manuscript. Robert Wagner: experimental design and study establishment.

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Keywords Stand structure · Spatial tree pattern · Growth dominance · Balsam fir · Red spruce

1 Introduction

Commercial thinning directly influences tree growth by releasing individual trees to achieve specific forest management objectives such as the promotion of desired species and the volume of utilizable woody material (Smith et al. 1997). The majority of thinning prescriptions, however, aims to concentrate total site productivity on fewer trees to optimize individual tree or stand growth.

In addition to the direct effect on individual trees, thinning also modifies overall forest stand structure. Depending on the method (Nyland 2002), thinning can alter variation in stem diameter, homogenize canopy stratification, or increase species mingling (Pretzsch 1998; Barbeito et al. 2009; Kuehne et al. 2015). More recently, thinning has been promoted as one means of enhancing structural heterogeneity in secondary forests due to thinning-induced changes in stand dynamics (Bauhus et al. 2009). The spatial arrangement of individual trees is an important aspect of forest structure, and its modification is of specific significance during thinning operations (Pretzsch 2009).

Forest structure has been defined as the spatial arrangement of the various components of a forest ecosystem, whereas forest structural heterogeneity refers to a measure of the variety and relative abundance of different structural attributes (Pommerening 2002). Changes in forest structure caused by management activities such as thinning can be measured and quantified to evaluate the effectiveness of the treatment. Depending on the spatial scale and availability of tree coordinates, a variety of spatially implicit and explicit tree neighborhood and stand metrics can be applied (Szmyt 2014). Using measures of forest structural heterogeneity, previous studies successfully differentiated between various forest management regimes including silvicultural systems (e.g., Saunders and Wagner 2008; Barbeito et al. 2009) and thinning treatments (e.g., Pretzsch 1998; Morrissey et al. 2015).

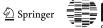
Quantifying forest structural heterogeneity and respective changes from management activities also allows for the subsequent evaluation of its influence on stand dynamics and hence stand and tree growth (Pretzsch 2009). The seemingly close inter-relationship among forest management, stand structure, and tree and stand growth has been analyzed in various studies (Pretzsch et al. 2015). Traditionally, the interconnectivity between these factors has been evaluated via the classical stand density-forest growth relationship (e.g., Assmann 1970). Other, more recent studies directly linked forest structure and stand (e.g., Lei et al. 2009; Kuehne et al. 2015) as well as tree growth (Mainwaring and Maguire 2004; Dănescu et al. 2016), or evaluated growth and stand dynamics

in different structural forest settings (e.g., Ngo Bieng et al. 2013; Pamerleau-Couture et al. 2015). These studies also included the examination of stand conditions shaped and defined by spatially restricted, hence small-scale structural, features such as artificial canopy openings (Arseneault et al. 2011) and harvester trails (Pukkala and Kolström 1991; Boivin-Dompierre et al. 2017).

Change in structure was often accompanied with increased growth rates in residual trees compared to a non-managed control in the abovementioned studies, but differences between varying management prescriptions were less obvious. In general, studies on the relationship of forest or tree growth and stand or neighborhood structural heterogeneity, respectively, have resulted in mixed outcomes with varying or limited success in revealing ecological or mechanistic rationale. Furthermore, treatments in most of these previous studies were not well replicated, which effectively limited their scope of inference and ability to detect general trends in the relationship between management regime and forest structure across treatments. In addition, effects of several different management regimes such as various thinning treatments on the relationship between forest structure and tree growth have only rarely been studied over longer, multi-year time periods to our knowledge (Pretzsch 1998; Crecente-Campo et al. 2009).

This study aimed at further evaluating the relationship between forest structure and stand dynamics by applying several detailed measures of growth pattern and stand complexity including spatial statistics of structural heterogeneity. Using 10-year measurements from a well-replicated, fully stemmapped commercial thinning experiment across the Acadian Forest in northern Maine, USA, we sought to answer the following research questions: (1) How do various thinning treatments modify stand structural heterogeneity and the spatial arrangement of trees compared to a non-thinned control? (2) How do potential changes in forest structure correlate with overall stand and individual tree growth? (3) How do forwarder trails as an additional structural feature of commercially thinned stands influence post-treatment individual tree growth?

The expected findings were that the range of thinning treatments would create distinctive spatial patterns within each stand, modify growth pattern at the tree and stand level, and in conjunction with the newly created forwarder trails potentially trigger new dynamics in forest structure and tree growth over the course of the 10-year study period. More specifically, we hypothesized that (1) thinning operations aimed at the removal of intermediate and suppressed trees will lower structural heterogeneity irrespective of thinning intensity and time since thinning (Soares et al. 2017), (2) thinning activities





focused on harvesting dominant and co-dominant trees reduce post-treatment size variability but the more aggregated post-thinning tree distribution pattern and increasingly variable growth rates among the small residual trees lead to higher structural heterogeneity in the longer term (Rozas et al. 2009), and (3) thinning operations that release dominant trees by removing co-dominant competitors promote higher levels of structural heterogeneity in the longer term (Pretzsch 1998).

2 Material and methods

2.1 Study sites and experimental design

We used six study sites of the Commercial Thinning Research Network (CTRN), which was initiated by the University of Maine's Cooperative Forestry Research Unit in the early 2000s. The CTRN study was implemented in naturally regenerated mixed red spruce (Picea rubens Sarg.)-balsam fir (Abies balsamea [L.] Mill.) stands of the Acadian Forest Region of Northern Maine to study the response of forest stand growth to commercial thinning (Kuehne et al. 2016). Low densities of white pine (*Pinus strobus* L.), eastern hemlock (Tsuga canadensis (L.) Carrière), or northern white cedar (Thuja occidentalis L.) also occurred in each stand. The stands covered a range of site conditions typical of the region. Soils were generally podzols with glacial till and alluvium as parent material and a mix of drainage classes that ranged from poorly to well drained. Elevation varied between 147 and 652 m above sea level, and mean annual temperature and mean annual precipitation were 2.8-5.0 °C and 1046-1185 mm, respectively. The resulting site index (red spruce top height at the age of 50 years) ranged from 13 to 22 m (Online Resource

Stands were between 32 and 68 years old when commercial thinning treatments were applied from autumn 2000 through to autumn 2002. None of the stands had been thinned before the study was initiated. Pre-treatment basal area and spruce-fir proportion ranged from 32 to 56 m² ha⁻¹ and from 34 to 99%, respectively (Online Resource 1). The experimental design was a randomized complete block with seven treatments and six replications, with the six study sites serving as blocks. Permanent 26.6 × 30.5 m (0.08 ha) research plots were established in the center of each of the seven 61 × 61 m (0.37 ha) treatment plots on each study site, and treatments were randomly assigned (Kuehne et al. 2016). In addition to a non-thinned control, thinning treatments included a factorial combination of thinning method (low, dominant, or crown) and intensities. The latter was assessed by the level of relative density (ratio of stand density index (SDI) and maximum SDI; Long 1985) reduction (33 or 50%). The low and dominant thinning treatments were defined as the removal of trees beginning at the lower or upper end of the diameter distribution,

respectively, until the target reduction in relative density was achieved. In the crown thinning treatment, crop trees were selected at approximately one third average tree height apart, and then, dominant and co-dominant competitors around each crop tree were harvested until desired residual density was reached.

Except for the non-thinned control, a 4-m-wide forwarder trail ran through the center and parallel with the shorter width of each research plot. Since forwarder trails were created approximately every 30 m, ghost trails used by the operating harvester only and running parallel with and at a distance of 8–10 m on each side of a forwarder trail also became part of the research plots.

All residual trees in each research plot were mapped by determining the x-y coordinate location of each living tree taller than breast height (1.3 m) after the commercial thinning treatments were completed. The diameter at breast height (DBH, cm) of all mapped trees was measured on an annual basis starting in the first year after the thinning and for 10 years. Tree data collected immediately after the thinning were not available.

2.2 Analytical approach

2.2.1 Differences in stand structural heterogeneity and variation in annual DBH growth

To study the relationship between overall stand structural heterogeneity and growth variability at the individual tree level, we calculated the spatially explicit structural complexity index (SCI, Zenner and Hibbs 2000). SCI is a measure of the vertical size differentiation and horizontal spatial positioning of triangles formed by considering x, y, and z coordinates of neighboring trees. The three-dimensional space is based on x and y coordinates of individual tree locations, and a selected measured individual tree characteristic such as total height or DBH used as the z variable. By connecting three adjacent points (trees) in the x, y, z space, a triangular surface is generated. When extended across a stand of trees, a network of nonoverlapping triangles forms a continuous faceted surface (Zenner 2000). SCI is the ratio of the continuous faceted surface, and the projected areas of the triangles forming the faceted surface and calculated as follows:

$$SCI = \frac{SCI_P}{AT_P} \text{ where } SCI_P = \sum_{k=1}^{N} \frac{1}{2} |a_k \times b_k|$$
 (1)

where k = 1, ..., N is the number of triangles in the research plot P, and $|a_k \times b_k|$ is the absolute value of the vector product of the vector AB with coordinates $a_k = (xb \ xa, yb \ ya, zb \ za)$ and the vector AC with coordinates $b_k = (xc \ xa, yc \ ya, zc \ za)$ (Zenner 2000). A graphical depiction of the approach is provided in Zenner (2000). SCI has a minimum value of 1 when

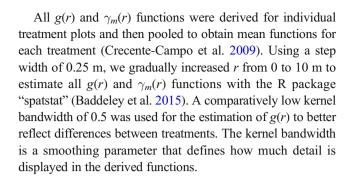


all trees have the same size, regardless of spatial pattern, and has no upper bound (Kuehne et al. 2015). In order to calculate SCI as a means to quantify spatial variability in individual tree size and growth, we used stem DBH and annual basal area increment (ΔBA , cm² year⁻¹), i.e., absolute growth rates. The programming software R version 3.3.1 (R Core Team 2016) and the "tri.mesh" function of the "tripack" package (Renka et al. 2016) were used to create the Delaunay triangulations. To improve interpretability and to effectively capture both the immediate and longer term response, SCI was averaged over the first 3 (1 to 3) and the last 3 years (8 to 10 years after thinning) of the study.

2.2.2 Spatial distribution of trees and spatial correlation of tree attributes

Contemporary spatial statistics have increasingly relied on second-order functions that depend on distances between all point locations in a point pattern instead of simple indices that are often based on limited nearest-neighbor data (Szmyt 2014). The two-dimensional arrangement of trees in a fully stem-mapped forest can be interpreted and hence analyzed as a realization of a spatial point pattern. Combining tree locations with individual tree attributes such as species or DBH creates spatial marked point patterns and allows interactions between trees to be identified (Penttinen et al. 1992). A variety of second-order summary characteristics exists to characterize and evaluate spatial point patterns and spatial marked point patterns. Here, we calculated several of these functions to gain further insights into the relationships between forest structure and growth. For this portion of the analysis, we focused on the 50% relative density reduction-level treatments because preliminary result indicated similar outcomes for the 33% reduction (less intense thinning treatments).

First, we evaluated horizontal tree distribution patterns using pair correlation functions. A pair correlation function g(r) is an inter-tree distance-dependent summary statistic that identifies the tree-to-tree distance r at which deviations from complete spatial randomness (Poisson distribution, g(r) = 1) occur and whether these deviations indicate clumping (g(r) > 1) or regularity (g(r) < 1) (Stoyan and Penttinen 2000). We then evaluated spatial differences between tree DBH using mark variograms. A mark variogram $\gamma_m(r)$ is a summary statistic for marked point patterns that helps in highlighting deviations from independence (no autocorrelation, $\gamma_m(r)$ = mark variance) occurs, and whether these deviations indicate positive (similarity, $\gamma_m(r) < \text{mark variance}$) or negative autocorrelation (dissimilarity, $\gamma_m(r) > \text{mark variance}$) (Stoyan and Penttinen 2000). Large $\gamma_m(r)$ values, for example, reveal high mark diversity at the tree-to-tree distance r, i.e., large differences in DBH between neighboring trees (Pommerening and Särkkä 2013).



2.2.3 Change of growth dominance over time

To further gain insights into the dynamics of treatmentinduced growth patterns at the stand level, we calculated the growth dominance statistic GD, which is a measure that detects and quantifies whether the larger or the smaller trees of a forest stand dominate total stand growth (Binkley et al. 2006). In mathematical terms, GD refers to the cumulative proportional contribution to stand growth by individual trees in relation to the cumulative proportional contribution of the sizes of those trees (West 2014). The calculation of GD requires the arrangement of trees in ascending order of size and results in values ranging between - 1 and 1 with GD values of 0 indicating no growth dominance, i.e., proportional contributions of each tree are the same for size as for increment. GD values greater than 0 signal growth dominance of larger trees (i.e., contribution to stand total growth by larger trees is greater than their contribution to stand total size), whereas negative GD values signal growth dominance of smaller trees ("reverse growth dominance"). Here, we used the numerical integration approach as in Eq. 2 in West (2014) to calculate GD with BA and ΔBA as tree size and tree growth measures, respectively:

GD =
$$1 - \sum_{i=1}^{n} (s_i - s_{i-1}) \times (d_i + d_{i-1})$$
 (2)

where s_i refers to tree sizes expressed as the cumulative proportions they make of plot-specific total size with

$$s_i = \frac{\sum_{j=1}^{i} BA_j}{\sum_{j=1}^{n} BA_j} \tag{3}$$

 d_i refers to tree growth expressed as the cumulative proportions they make of plot-specific total growth with

$$d_i = \frac{\sum_{j=1}^i \Delta B A_j}{\sum_{j=1}^n \Delta B A_j} \tag{4}$$

and n is the number of trees per plot. To improve interpretability, GD was averaged over the first 3 (1 to 3) and the last 3 years (8 to 10 years after thinning) of the study. Again, this should help to capture the immediate and longer term response to thinning.





2.2.4 Effect of forwarder trail on basal area growth

To examine the effect of forwarder trails on individual tree ΔBA , we calculated the distance from each live tree to the forwarder trail (TDIST) using tree x-v coordinates. The effect of TDIST was first evaluated using a linear mixed-effects ANOVA and the "lme" function of the R package "nlme" (Pinheiro et al. 2016) and included DBH, species (balsam fir, red spruce), time since thinning, thinning treatment, as well as the interactions of TDIST with time since thinning and treatment, respectively, as fixed effects and CTRN sites as random effects. Because of the variation in stand age and site quality among the studied CTRN locations, the response variable ΔBA was relativized and transformed to percentage of species- and site-specific basal area growth of the respective control treatment (Rel Δ BA). Based on the outcome of the ANOVA, we further analyzed the TDIST and Rel Δ BA relationship to detect potential differences between species and treatments. Prediction performance of various model forms was preliminary assessed using the Akaike information criterion (AIC) as evaluation statistic with the logarithmic function resulting in the greatest prediction accuracy. Consequently, using the function nlme of the R package nlme, treatmentas well as species-specific non-linear mixed-effects models with CTRN locations treated as random effects of the following form were used to further examine the relationship:

$$Rel\Delta BA = a + b \times \ln(TDIST) \tag{5}$$

where *a* and *b* are estimated fixed parameters of the logarithmic function, and all other variables are described above. To improve interpretability and reliability, the models were derived using pooled data of the first 3 (1 to 3) and the last 3 years (8 to 10 years after thinning) of the study.

3 Results

3.1 Overall influence of thinning treatments

All commercial thinning treatments substantially reduced mean absolute stem density, and density further decreased between the first- and 10-year measurements (Table 1). Independent of the CTRN location, total post-treatment tree mortality over the course of the 10-year study was especially high in the crown and dominant thinning treatments averaging between 36 and 62% (Online Resource 2). In the control and low thinning treatments, mean cumulative mortality varied between 10 and 29% with the thinned plots exhibiting lower mortality rates on average. Across locations and treatments, no excessive mortality events were observed, and thus, mortality occurred continuously throughout the study period. In contrast to the control, where just 11% of all tree mortality was caused by wind storms

Mean (± standard deviation, minimum and maximum) of stand density (N, trees ha⁻¹), diameter at breast height (DBH, cm), and annual basal area growth (\DBA, cm² year⁻¹) for the different Table 1

CTRN	CTRN treatments 1 and 10 years after thinning $(n = 6 \text{ per treatment})$	er thinning $(n = 6 \text{ per treat})$	ment)				
	Control	33% Crown	33% Dominant	33% Low	50% Crown	50% Dominant	50% Low
1 year	l year post-treatment						
z	$4822 \pm 2169 \ (1963 - 7258) 1761 \pm 617 \ (988 - 2654)$	$1761 \pm 617 \ (988-2654)$	$2481 \pm 1123 \ (1407 - 4333) 1473 \pm 478 \ (1074 - 2185) 1446 \pm 550 \ (926 - 2432) 1979 \pm 1185 \ (1049 - 3975)$	$1473 \pm 478 \ (1074-2185)$	$1446 \pm 550 \ (926-2432)$	$1979 \pm 1185 \ (1049 - 3975)$	$874 \pm 187 \ (654 - 1197)$
DBH	$10.2 \pm 5.0 \ (0.8-47.8)$	$12.0 \pm 5.3 \ (1.0 - 30.5)$	$10.3 \pm 4.0 \; (1.3 - 23.1)$	$14.6 \pm 4.6 \; (1.3 - 35.1)$	$11.7 \pm 5.8 \ (1.3-32.3)$	$10.1 \pm 3.8 \; (1.3-29.7)$	$16.9 \pm 4.7 \ (2.5-31.2)$
ΔBA	ΔBA 1.98 ± 3.75 (0–40.28)	$3.43 \pm 5.40 \; (0-52.44)$	$2.65 \pm 3.87 \ (0-44.39)$	$4.94 \pm 5.74 \ (0-49.57)$	$5.00 \pm 7.17 \ (0-54.12)$	$2.93 \pm 4.86 \; (0-50.72)$	$6.93 \pm 6.91 \; (0-44.39)$
10 yea	10 years post-treatment						
Z	$3259 \pm 1076 \; (1703 - 4320)$	$1107 \pm 428 \ (506 - 1605)$	$1378 \pm 824 \ (568-2679)$	$1323 \pm 436 \ (951-2049)$	$796 \pm 462 \ (432 - 1691)$	$866 \pm 781 \; (173-2210)$	$710 \pm 212 \ (506 - 1062)$
DBH	$13.0 \pm 5.5 \ (1.5 - 52.6)$	$15.4 \pm 6.4 \ (2.0-36.3)$	$13.5 \pm 5.0 \ (1.5-29.7)$	$17.3 \pm 5.2 \ (2.3-43.9)$	$16.2 \pm 7.4 \; (1.3–36.1)$	$13.3 \pm 4.9 \ (2.5 - 32.0)$	$20.3 \pm 5.0 \ (4.8 - 36.6)$
ΔBA	$2.87 \pm 5.30 \; (0-73.37)$	$6.89 \pm 8.85 \; (0-65.11)$	$6.17 \pm 8.00 \; (0-72.97)$	$7.29 \pm 8.50 \; (0-64.61)$	$8.73 \pm 12.17 \ (0-88.17)$	$7.65 \pm 9.98 \; (0-78.44)$	$10.29 \pm 10.04 \; (0-61.57)$



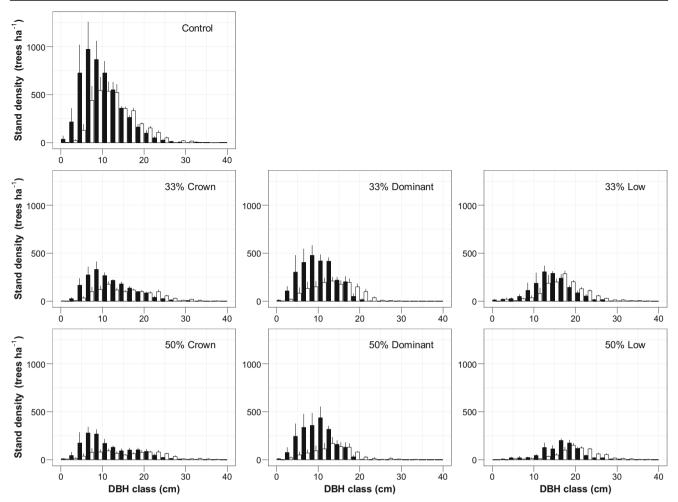


Fig. 1 Tree diameter distributions (2-cm DBH classes) for CTRN treatments 1 (black) and 10 years (white bars) after thinning. Distributions were derived as mean number of trees per diameter class

across the six CTRN locations with trees $>\!40$ cm DBH not shown. Error bars represent one standard error

on average, approximately 50% of all dead trees in the thinning treatments were either uprooted or snapped. Using first-year post-treatment data, plot-specific quadratic mean diameter (QMD) of dead trees were mostly smaller in comparison to QMD of live residual trees (Online Resource 3). In addition, pair correlation functions indicated random (control, dominant thinning) or regular spatial distributions of dead trees (low thinning) for the majority of treatments (Online Resource 4). Dead trees in crown thinning plots, however, appeared to be spatially clustered at inter-tree distances of 2 to 4 m.

Thinning in conjunction with post-treatment mortality had a strong influence on diameter distributions, particularly with the crown and low thinning treatments (Fig. 1). Consequently, mean DBH was higher in the crown and low thinning treatments by approximately 20 and 50%, respectively. In contrast, mean ΔBA increased by at least 30% in all thinning treatments when compared to the control (Table 1). Differences in DBH and ΔBA between thinned and non-thinned treatments either remained at the observed initial levels or further intensified towards the end of the study. Differences between

the 33 and 50% relative density reduction-level variants of the same thinning treatment were most evident in mean ΔBA and the low thinning (Table 1). The findings were consistent across the six CTRN locations.

3.2 Differences in stand structural heterogeneity and variation in tree growth

Irrespective of method and intensity, thinning reduced stand structural heterogeneity as reflected in lower DBH-based SCI when compared to the non-thinned control (Table 2). This was most evident in the dominant and low thinning treatments. Variation in ΔBA among trees in the different treatments generally followed trends observed for stand structural heterogeneity (Table 2). Initial ΔBA varied most in the control and was most homogeneous in the dominant and low thinning treatments, while crown thinning resulted in the most variation in ΔBA among the thinning treatments.

Stand structural heterogeneity mostly decreased marginally towards the end of the study except for the two low thinning



 4.78 ± 0.31 (3.18–7.45)

50% Low

Treatment YST Structural heterogeneity (SCIDBH) Growth variation (SCI_{ABA}) 1 - 38 - 101 - 38 - 10Control $5.81 \pm 0.08 \ (5.20 - 6.40)$ 5.58 ± 0.07 (5.20–6.13) 4.51 ± 0.17 (3.44–5.85) 4.94 ± 0.19 (3.32–6.45) 33% Crown 4.20 ± 0.19 (3.21–5.69) 4.18 ± 0.21 (2.91–5.68) 4.50 ± 0.35 (2.24–7.93) 5.22 ± 0.34 (2.75–7.67) 33% Dominant 3.47 ± 0.21 (1.99–4.89) 3.37 ± 0.31 (1.78–5.56) 3.81 ± 0.28 (2.56–7.45) 4.86 ± 0.51 (2.47–8.95) 3.07 ± 0.15 (2.24–4.25) 3.42 ± 0.16 (2.59–4.73) 4.25 ± 0.24 (2.39–6.04) 5.26 ± 0.36 (2.55–7.47) 33% Low 50% Crown 4.26 ± 0.17 (2.88–5.41) 3.91 ± 0.24 (2.85–5.87) 4.79 ± 0.33 (2.75–7.81) 5.30 ± 0.38 (2.75–8.28) 50% Dominant 2.76 ± 0.15 (1.94–3.68) 2.49 ± 0.23 (1.58–4.03) $3.82 \pm 0.40 \ (1.72 - 7.83)$ 4.73 ± 0.63 (1.65–9.97)

 2.53 ± 0.10 (2.19–3.47)

Table 2 Mean (\pm standard error, minimum–maximum) DBH-based stand structural heterogeneity and Δ BA-based tree growth variation in the different CTRN treatments (n = 6 per treatment) quantified using the structural complexity index (SCI) 1 to 3 and 8 to 10 years since thinning (YST)

treatments exhibiting slightly higher SCI 8 to 10 years after thinning (Table 2). A different trend was found for tree growth variation where heterogeneity in ΔBA increased in all treatments. The observed change in DBH heterogeneity and ΔBA variation was least pronounced in control and low thinning treatments.

 2.46 ± 0.07 (1.98–2.97)

3.3 Spatial distribution of trees and spatial correlation of tree attributes

The pair correlation function g(r) revealed spatial randomness in the control treatment 1 year after study initiation, while an aggregation of trees up to an inter-tree distance of 3 m was found in the dominant thinning treatments (Fig. 2). Clustering of trees also occurred in the crown thinning treatment at a distance between trees of approximately 1 m. However, trees became more regularly spaced at inter-tree distances of 2 to 3 m. Regularity was also observed in the low thinning treatment at inter-tree distances of approximately 4 and 9 m, respectively. Within the 10-year study period, the horizontal tree distribution patterns changed only marginally. There was a

slightly more clustered tree arrangement in the dominant thinning treatments at small inter-tree distances.

 4.15 ± 0.24 (2.65–6.17)

The mark variogram $\gamma_m(r)$ depicted a decrease in overall DBH variance for the dominant and low thinning treatments compared to the non-thinned control (Fig. 2). Across the 10-year period, overall DBH variance increased in the crown thinning treatments, where it remained relatively stable in the control and low thinning treatments. No or weak spatial correlation was found at the beginning of the study, but spatial patterns were more evident 10 years after thinning. Negative autocorrelation (significant variance in DBH of neighboring trees) up to an inter-tree distance of 2 to 3 m and weak positive autocorrelation (similarity in DBH of neighboring trees) at a distance of approximately 4 m was observed in the crown thinning. In contrast, weak negative autocorrelation became evident in the low thinning treatments at small inter-tree distances.

3.4 Change in growth dominance over time

Despite only marginal absolute differences, trends in GD showed variation among thinning treatments (Table 3).

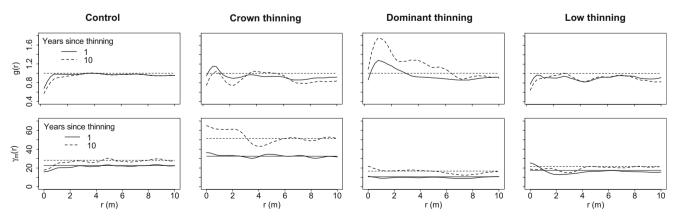


Fig. 2 Estimated mean pair correlation functions g(r) and estimated mean mark variograms $\gamma_m(r)$ for DBH (average mark variances are depicted as thin lines) of CTRN treatments (50% relative density reduction, n = 6 per treatment) 1 and 10 years after thinning



Table 3 Change in mean (\pm standard error, minimum–maximum) growth dominance GD in the different CTRN treatments (n=6 per treatment) 1 to 3 and 8 to 10 after thinning. GD values greater than 0 signal growth dominance of larger trees (i.e., contribution to total stand growth by larger trees is greater than their contribution to total stand basal area), whereas negative GD values signal growth dominance of smaller trees and GD values of 0 indicate no growth dominance, i.e., proportional contributions of each tree are the same for basal area (size) as for basal area increment (growth)

Treatment	Years after thinning		
	1–3	8–10	
Control	$0.15 \pm 0.02 \; (0.04 – 0.30)$	0.19 ± 0.02 (0.06–0.36)	
33% Crown	$0.11 \pm 0.02 \; (0.02 – 0.25)$	$0.10 \pm 0.02 \; (-0.04 - 0.28)$	
33% Dominant	$0.09 \pm 0.02 \; (-0.05 – 0.25)$	$0.12 \pm 0.02 \; (-0.04 - 0.29)$	
33% Low	$0.01 \pm 0.03 \; (-0.21 - 0.19)$	$0.10 \pm 0.02 \; (-0.12 - 0.23)$	
50% Crown	$0.06 \pm 0.02 \; (-0.06 – 0.21)$	$0.07 \pm 0.03 \; (-0.18 – 0.34)$	
50% Dominant	$0.05 \pm 0.03 \; (-0.13 - 0.31)$	$0.13 \pm 0.03 \; (-0.18 – 0.36)$	
50% Low	$-0.04\pm0.02\;(-0.130.14)$	$0.09 \pm 0.02 \; (-0.05 – 0.23)$	

Initially, comparatively large positive values signaling strong GD of larger trees in the control further increased in the second half of the 10-year study period. Irrespective of the level of relative density reduction, GD of large trees also increased in the low thinning treatments over time, but was not evident at the beginning of the study. In contrast, initial GD in larger trees in the crown and dominant thinning treatments remained stable or slightly increased over the course of the study, respectively.

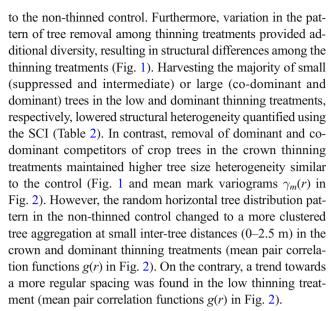
3.5 Effect of forwarder trail on tree growth

In addition to DBH, species, time since thinning, and treatment, forwarder trails also significantly influenced tree basal area growth quantified as relative percentage of species- and site-specific basal area growth of the control treatment (Rel Δ BA) (Online Resource 5). Regression analysis revealed that Rel Δ BA was reduced with increasing distance to trail. This effect was evident up to approximately 5 m from a trail irrespective of treatment and in both examined species with balsam fir exhibiting higher growth rates compared to red spruce (Fig. 3). Based on the slopes of the individual regression curves, the observed effect appeared to be greater in crown thinning treatments and towards the end of the study. Irrespective of treatment and species, observed data showed an increase in Rel Δ BA at a trail distance of approximately 8 to 9 m.

4 Discussion

4.1 Effect of thinning on forest structure

Our findings revealed that the studied commercial thinning prescriptions clearly modified forest stand structure relative



Thinning clearly increased post-treatment mortality rates compared to the non-thinned control in the crown and dominant thinning treatments and thus likely influenced the analyzed metrics and their change during the 10-year study period. Irrespective of treatment, dead trees were always smaller in size compared to the individuals still alive at the end of the study. The observed increase in mean DBH and annual basal area increment (ΔBA) in all treatments at the end of the study therefore are at least partly attributable to the observed mortality dynamics. Furthermore, SCI values calculated to quantify stand structure and growth variation could also have been lowered by higher mortality rates because the measure is related to stem density (Kuehne et al. 2015). However, we argue that the derived spatially explicit summary statistics were altered only marginally as a result of post-treatment mortality because dead trees were mostly randomly or regularly distributed throughout the research plots (Online Resource 4). Only the observed clumping of residual trees in the crown thinning might have been reinforced by post-treatment mortality patterns as dead trees also tended to form clusters at small intertree distances. Species-specific characteristics (shallow rooting patterns in both of the studied species and proneness to stem rot in balsam fir) and site specifics such as shallow soils and a high seasonal groundwater table likely contributed to the observed mortality levels (Seymour 1992). Consequently, post-thinning acclimation to higher wind loadings as a result of modified stem growth patterns failed to fully develop and therefore did not lead to improved wind firmness in all the trees of this study (Mitchell 2000, Bonnesoeur et al. 2016).

The pair correlation functions derived in this study evaluated the entire inter-tree distance range and not just nearest neighbor pairs allowing for a more detailed spatial analysis (Kint et al. 2003; Ruiz-Mirazo and Gonzalez-Rebollar 2013). For example, regularity at inter-tree distances of





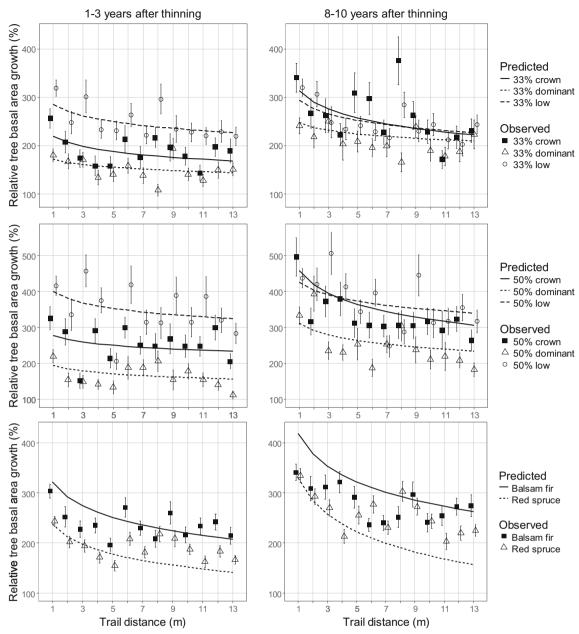


Fig. 3 Effect of distance to forwarder trail on relative annual tree basal area growth (cm² year⁻¹), percentage of species- and site-specific growth of control treatment with control = 100%) as a function of thinning

treatment and species 1–3 and 8–10 years after thinning. Depicted values represent classified means \pm one standard error

approximately 2 to 4 m in the crown and low thinning depicted the more uniform spacing of dominant and codominant trees released in these treatments (Pretzsch 2009). Thinning also changed spatial tree size diversity and thus tree size composition at the tree neighborhood level reflecting the differences in size and crown class of trees selected and harvested in the various thinning treatments. This effect was most apparent with crown thinning where negative autocorrelation (high DBH diversity) signaled close proximity of small and large trees at low to intermediate inter-tree distances (mean mark variograms $\gamma_m(r)$ in Fig. 2). In contrast, the control and dominant thinning treatments exhibited little if any tree size

diversity in neighboring trees. Overall, these findings are in agreement with the initial hypotheses and results of previous studies (Pretzsch 1998; Montes et al. 2004).

4.2 Effect of thinning on forest growth

Mean ΔBA in the low thinning treatments were among the highest measured in our study, likely a result of the prethinning dominant and co-dominant status of residual trees, as well as their relatively uniform spacing (Table 2 and mean pair correlation functions g(r) in Fig. 2). The non-thinned control, by contrast, exhibited the lowest ΔBA because of



high stand density and a large number of intermediate and suppressed trees (Fig. 1). Relatively minor changes in ΔBA in the control and low thinning as compared to crown and dominant thinning treatments likely were a result of the initial (post-treatment) stand structures that allowed no dynamic interactions among neighboring residual trees. Since no, or a very limited number of, dominant and co-dominant trees were removed, respectively, and post-treatment mortality levels were comparatively low, hardly any growing space became available in the upper canopy. Consequently, the observed initial stand structures remained fairly stable over the 10year study period, as reflected in the low and only slightly changing stand structural heterogeneity in these treatments (mean mark variograms $\gamma_m(r)$ in Fig. 2). This finding is again in agreement with our initial hypotheses and a previous study (Crecente-Campo et al. 2009).

In contrast, different stand structural development was evident following crown and dominant thinning treatments where growth rates increased substantially in relative terms towards the end of the study. The rapid and distinct change in ΔBA indicates that crown and dominant thinning-induced changes in larger DBH size classes modified the competitive status and likely the vigor of most residual trees in these treatments (Fig. 1). Exploiting more resources as a result of lower competition and newly available growing space eventually triggered growth acceleration in the released residual trees as reflected in higher ΔBA at the end of the study period. In addition, higher stem taper as a result of greater exposure to wind and related mechanical stress may have also contributed to the observed trend (Gardiner et al. 1997).

Commercial thinning-induced patterns of individual tree growth also influenced, and thus were reflected in, stand-level GD of each treatment (Table 3). Although differences between treatments as well as changes over time were often small, several trends were evident. Large dominant trees accounted for the majority of stand growth (cumulative DBH growth) in the control and crown thinning treatments. This finding was consistent with the distinctive canopy stratification reflected in high DBH heterogeneity (Table 2). GD was therefore mainly driven by disproportionally low relative growth rates of intermediate and suppressed trees caused by strong size-asymmetric inter-tree competition (Barnes et al. 1998, Weiner et al. 2001).

GD in the dominant thinning slightly increased over time. This is in agreement with the observed substantial increase in ΔBA variation reflecting greater growth rates, most likely in some of the larger released individuals in the dominant thinning treatments (Tables 2 and 3). Previous studies have shown the size dependence of the growth response in shade-tolerant understory trees or advance regeneration released from strong overstory competition with taller individuals exhibiting a more pronounced and often more rapid increase in growth rates (e.g., Claveau et al. 2006).

In contrast, growth rates of the more evenly spaced former dominant and co-dominant residual trees of the low thinning treatments resulted in the lowest GD values of any treatment. This suggests comparable growth rates across all residual trees especially at the beginning of the study, which was not as clearly reflected in variation of ΔBA quantified using SCI (Table 3). Ten years after the thinning, however, reoccurring or strengthened inter-tree competition in the retained, and thus mostly intact upper canopy, likely caused changes in resource allocation leading to higher variation in relative growth rates and thus the observed but unexpected increase in GD. Nevertheless, our findings of mid-term changes in GD have been partly verified in previous studies where similar trends were reported for non-thinned control and lowthinning treatments (Bradford et al. 2010; Keyser 2012).

4.3 Effect of forwarder trails

Forwarder trails added another structural element to the forest structures modified by commercial thinning prescriptions. Irrespective of thinning treatment and tree species, trails had a beneficial effect on the relative basal area growth (Rel Δ BA) of individual trees up to 5 m from the trail (Fig. 3). However, the observed effect became more pronounced towards the end of the study when trees had adjusted to and were fully capable of exploiting the improved growing conditions created in close proximity of the forwarder trails. Increased tree growth (DBH, basal area, volume) has also been reported in other studies analyzing the effect of linear clearings including hydro lines and built roads (e.g., McCreary and Perry 1983; Stempski and Jabłoński 2014). As in our study, the observed effect was often restricted to distances ranging between 3 and 5 m from the trail edge (see overview in Bowering 2004; Mäkinen et al. 2006).

In contrast to the regression analysis used in our study, previous studies often categorized distance to road or clearing and thus investigated growth response in pre-defined zones. This approach may not have allowed the detection of finescale differences in tree growth at greater distances from the trail edge. As a result of our approach, for example, we found an additional and spatially limited peak in observed growth rates at a trail distance of about 8 to 9 m, which most likely was caused by ghost trails created during thinning in the interspaces between forwarder trails (Boivin-Dompierre et al. 2017). The lack of clear differences in magnitude and extension of the trail effect among treatments is at least in partial disagreement with findings from a previous study (Van Laar et al. 1990 in Bowering 2004). Therefore, our findings may indicate that growing conditions in proximity of the trail were not merely improved by increased radiation levels (Wallentin and Nilsson 2011).





5 Conclusions

This is one of the very first studies that used a strongly replicated and multi-treatment thinning experiment as well as a number of detailed stand- and tree-level metrics to evaluate the effects of various silvicultural manipulations on forest structure and growth pattern over the longer term. Applying sophisticated measures and statistics used in this study helped to uncover and better quantify the dynamic effects of commercial thinning on forest structure as well as their long-lasting influences on observed tree and stand growth patterns (Hui and Pommerening 2014).

Overall changes in forest structure and growth observed in our study highlight the interrelationship of forest management, stand structure, and tree growth (Pretzsch et al. 2015). As management activities manipulate stand structure, individual tree growth patterns are altered at the same time. The resulting ongoing alterations in tree morphology, size, and mortality affect the observed stand dynamics and in turn the constantly changing forest structure and its substantial impact on small-scale growing conditions (Suzuki et al. 2008, Bayer et al. 2013). Although potentially confounded by high post-treatment mortality rates in some of the thinned stands, our findings therefore vividly validate an earlier insight according to which interactions between management practices, forest structure, and tree growth form a permanent feedback loop (Pretzsch 2009).

The influence of forwarder trails in thinning experiments has probably not received the attention it deserves given our findings here. Given the complexities of thinning, continued investigation using the various measures used in this analysis is recommend for other species and forest types.

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