Long-term tree and stand growth dynamics after thinning of various intensities in a temperate mixed forest

Guillaume Moreau[a,b,c], David Auty[d], David Pothier[b], Jingning Shi[a], Jun Lu[e], Alexis Achim[c], Wei Xiang[a,*]

[a] Research Center of Forest Management Engineering of State Forestry and Grassland Administration, School of Forestry, Beijing Forestry University, Beijing 100083, People's Republic of China
[b] Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, QC G1V 0A6, Canada
[c] Centre de recherche sur les matériaux renouvelables, Département des sciences du bois et de la forêt, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec, QC G1V 0A6, Canada
[d] School of Forestry, Northern Arizona University, Flagstaff, AZ, United States
[e] Institute of Forest Resource Information Techniques, Chinese Academy of Forestry, 15 Beijing 100091, People's Republic of China

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ABSTRACT

In mixed forests, the presence of several tree species with various ecological characteristics leads to complex stand dynamics driven by the species-specific resource-use efficiencies that ultimately drive forest productivity. In this study, we applied the concept of stand growth dominance (GD), together with the growth rates of trees as a function of their allometric expectations (AE) under size-symmetric competition, as an analytical framework to identify the strong and weak contributors to the growth of thinned, mixed larch-spruce-fir stands. We used periodic surveys on approximately 2000 trees over a 25-year period following the application of four different intensities of thinning from below (TI): light (20% BA removed), moderate (30%), heavy (40%) and a control (0%). Results showed that stand GD became more negative with increasing TI and increased with increasing years since thinning except for the 20% TI, for which GD was always positive and had a small increase over time. Twenty-five years after treatment application, shade-intolerant larch trees contributed more to stand growth than their AE, particularly for medium- to large-sized trees, suggesting that they had acquired a large proportion of the available resources. Conversely, the shade tolerant coniferous and broad-leaved trees contributed less than their AE in all treatments, making them weak contributors to the overall stand growth. The analytical framework proposed in this study was useful to identify tree groups that were either weak or strong contributors to stand growth after partial cutting. This information can be used to help prioritise trees for removal during partial cutting operations and to identify successional pathways that will lead to the composition of the future stand.

1. Introduction

Commercial thinning is a widespread silvicultural practice that is used to extract a portion of the wood volume from dense premature forest stands undergoing imminent natural mortality (Boivin-Dompierre et al., 2017; Bose et al., 2018). Through the removal of trees, commercial thinning alters the competitive environment of the stand and redistributes site resources among residual trees (Bréda et al., 1995; Medhurst et al., 2002; Forrester et al., 2012; Forrester et al., 2013). The wood production objective of the treatment is to maintain stand yield while improving tree diameter growth, and thus increase the value of processed products at maturity (Boivin-Dompierre et al., 2017).

The effect of thinning on growth and yield have been widely studied in monocultures (e.g. Newton 1997; Sun 1999; Bradford et al., 2010; Soares et al., 2017). Among these studies, Bradford et al. (2010) proposed an approach based on stand growth dominance for assessing the efficiency of commercial thinning to reduce between-tree competition while promoting individual tree growth. Growth dominance is a stand-level metric that indicates the relative contribution of small and large trees to total stand growth, with a coefficient that ranges from −1 to 1. The resulting growth dominance coefficient takes a positive value when the growth of larger trees is proportionally greater than that of smaller trees, and a negative value when the relative contribution of smaller trees to total stand growth exceeds that of larger trees (Binkley, 2004). In shade-intolerant tree monocultures, stand growth dominance was observed to decrease with increasing thinning intensity, indicating that

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* Corresponding author.
E-mail address: wxiang@bjfu.edu.cn (W. Xiang).

smaller residual trees have benefited more from canopy openings than large ones (Bradford et al., 2010; Soares et al., 2017). However, the concept of growth dominance has rarely been used to analyse the growth dynamics of mixed-species stands (Binkley et al., 2003; Forrester, 2019).

In temperate mixed forests, several tree species with various ecological characteristics, such as longevity, shade tolerance and growth rate, share limited environmental resources. This leads to complex stand dynamics driven by the partitioning of resources among species based on their resource-use efficiencies that largely determine their competitive status within the stand (Richards et al., 2010; le Maire et al., 2013; Pretzsch et al., 2017). Among species-specific traits, shade tolerance is thought to be an important driver of stand growth dynamics (Jones et al., 2009; Prévost and Dumais, 2014; Bose et al., 2018; Pothier, 2019). While shade-intolerant, fast-growing species from the upper canopy of mixed stands tend to use a disproportionate share of resources even at advanced ages (Binkley et al., 1992; Kelty, 2006; Forrester et al., 2018), shade tolerant species in the understory can become stronger contributors to stand growth over time, resulting in an overall negative growth dominance (Pothier, 2019). In addition, shade-tolerant species generally can respond positively to small canopy openings (Jones et al., 2009), while larger openings are necessary to obtain a positive response from shade-intolerant species (Sakai, 1995).

To further our understanding of growth dynamics in mixed-species stands at the tree-level, Pothier (2019) recently proposed an approach that linked stand growth dominance with the prevailing mode of competition between trees. This method can be used to quantify the contribution of each tree, or group of trees, to overall stand growth. It allows a direct comparison, for any given tree size, of the contribution of different tree groups based on factors such as species, vigour, or stem quality. It is thus particularly well suited to study the growth dynamics of multi-cohort and/or mixed-species stands in which the contributions of trees to stand growth may vary as a function of a wide range of characteristics of individual trees that can be evenly or unevenly distributed among size classes (Pothier, 2019; Lemire et al., 2020). This method is therefore complementary to the use of a stand-level criterion such as the growth dominance coefficient.

As the relative contribution of an individual tree to overall stand growth depends on its initial size, the mode of competition that prevails at a given time within a forest stand can be assessed using the linear relationship between annual stem mass increment and stem mass (Pretzsch and Biber, 2010; Pothier, 2017). A linear relationship passing through the origin indicates that the overall mode of competition between trees can be considered as 'size-symmetric' i.e. that the relative contribution of trees to stand growth is equal for all tree sizes (Pretzsch and Biber, 2010). A negative intercept indicates that large trees tend to contribute more than their share of the stem mass of the whole stand, while a positive intercept indicates that small trees are the largest relative contributors (see Pothier, 2017). Such size-growth relationships have been used to analyse growth partitioning in both monocultures and mixed-species stands (e.g. Pretzsch and Schütze, 2016; Forester, 2019). Further, size-symmetric competition was found to correspond to neutral growth dominance at the stand level (Pothier, 2017; Fernández-Tschieder and Binkley, 2018), which indicates that the relative contribution of trees to stand growth is equal for all tree sizes (Binkley, 2004).

Using this principle, Pothier (2019) defined the zero-intercept linear relationship between stem mass increment and stem mass in a given forest stand as the 'allometric expectation' of the relative contribution of individual trees to stand growth (Fig. 1). Following this principle, trees located above the zero-intercept linear regression line (i.e. positive residuals) grow faster than their allometric expectation, making them positive contributors to the overall stand growth (Fig. 1D–F). Conversely, trees with negative residuals contribute less to stand growth relative to their size (Fig. 1D–F). Even though this method has been effective for analysing growth dynamics in natural mixed-species

stands (Pothier, 2019), it has yet to be applied in thinned stands over a sustained period.

In this study, we applied the stand-level approach proposed by Binkley (2004) combined with the tree-level analysis developed by Pothier (2019) as a framework to evaluate the effectiveness of thinning treatments and to identify tree groups that are strong and weak contributors to the growth of thinned, mixed larch-spruce-fir stands. This common forest type in northeastern China often results from larch plantations that have been gradually enriched by new or pre-established seedlings of spruce, fir and broad-leaved species. Taking advantage of periodic surveys in a 25-year thinning experiment, we aimed to determine how the contribution of trees to stand growth changed over time and with thinning intensity. We hypothesized that i) the post-thinning growth of all-sized trees tends to approach their allometric expectations, resulting in stand neutral growth dominance; ii) the period of time during which the resulting neutral growth dominance is maintained increases with increasing thinning intensity; and iii) the growth of shade-intolerant species in the understory incrementally exceeds their allometric expectation with increasing thinning intensity.

2. Materials and methods

2.1. Sample plots and measurements

Permanent sample plot (PSP) data were collected from the Jingouling Experimental Forest Farm run by the Wangqing Forestry Bureau, in Jilin Province, located in the middle lower hill region of the Changbai Mountains in northeastern China (130°5′-130°20′E, 43°17′-43°25′N). Elevation ranges from 550 to 1100 m within the study area, with average annual rainfall and mean annual temperature of 650 mm and 3.9 °C, respectively. Mean monthly temperatures are ranged from 20.8 °C to −15.1 °C, with a 120-day growing season over the past two decades (China Meteorological Administration, 2020). Dark brown soils are the dominant soil type throughout the study area (Editorial Committee of Jilin Forest, 1988).

Plots were established in stands that originated from Changbai larch (*Larix olgensis* A. Henry) plantations following clearcuts applied between 1962 and 1964. Some fir (*Abies* sp.), spruce (*Picea* sp.) and broad-leaved trees were left standing after these cuts, which led to most stands developing a mixed composition, but over 60% of the combined basal area was occupied by larch by the time the experiment started in 1987 (Lei et al., 2007). These semi-natural larch-spruce-fir stands are composed of Changbai larch, Jezo spruce (*Picea jezoensis* var. *microsperma* (Lindl.) Cheng et L. K. Fu), Manchurian fir (*Abies nephrolepis* (Trautv. ex Maxim.) Maxim.), Korean pine (*Pinus koraiensis* Siebold & Zucc), Asian white birch (*Betula platyphylla* Sukaczev), Ussuri poplar (*Populus ussuriensis* Kom.), ribbed birch (*Betula costata* Trautv.), amur linden (*Tilia amurensis* Rupr.), elm (*Ulmus propinqua* Koidz.), maple (*Acer mono* Maxim.), manchurian ash (*Fraxinus mandshurica* Rupr.), and amur cork (*Phellodendron amurense* Rupr.).

Thinning treatments were applied to four blocks in a randomized-block design with three intensities determined by the percentage of basal area removed: light (20% BA removed), moderate (30%), heavy (40%) and a control (0%). In each case, thinning from below was applied manually with a chainsaw with log skidding by animals (Lei et al., 2007). In each experimental block, four rectangular PSPs corresponding to each treatment were established, ranging in area from 0.08 to 0.25 ha. Two plots (the 30 and 40% treatments) from block III were removed from the dataset as they were thinned for a second time in 1993, leaving a total of 14 plots. Tree species and diameter at breast height (DBH, 1.3 m above the ground) were recorded for all stems ≥ 5 cm at 3- to 5-year intervals from 1987 to 2012. Overall, the dataset consisted of approximately 2000 trees remeasured six times. Detailed information on the established plots is presented in Table 1.
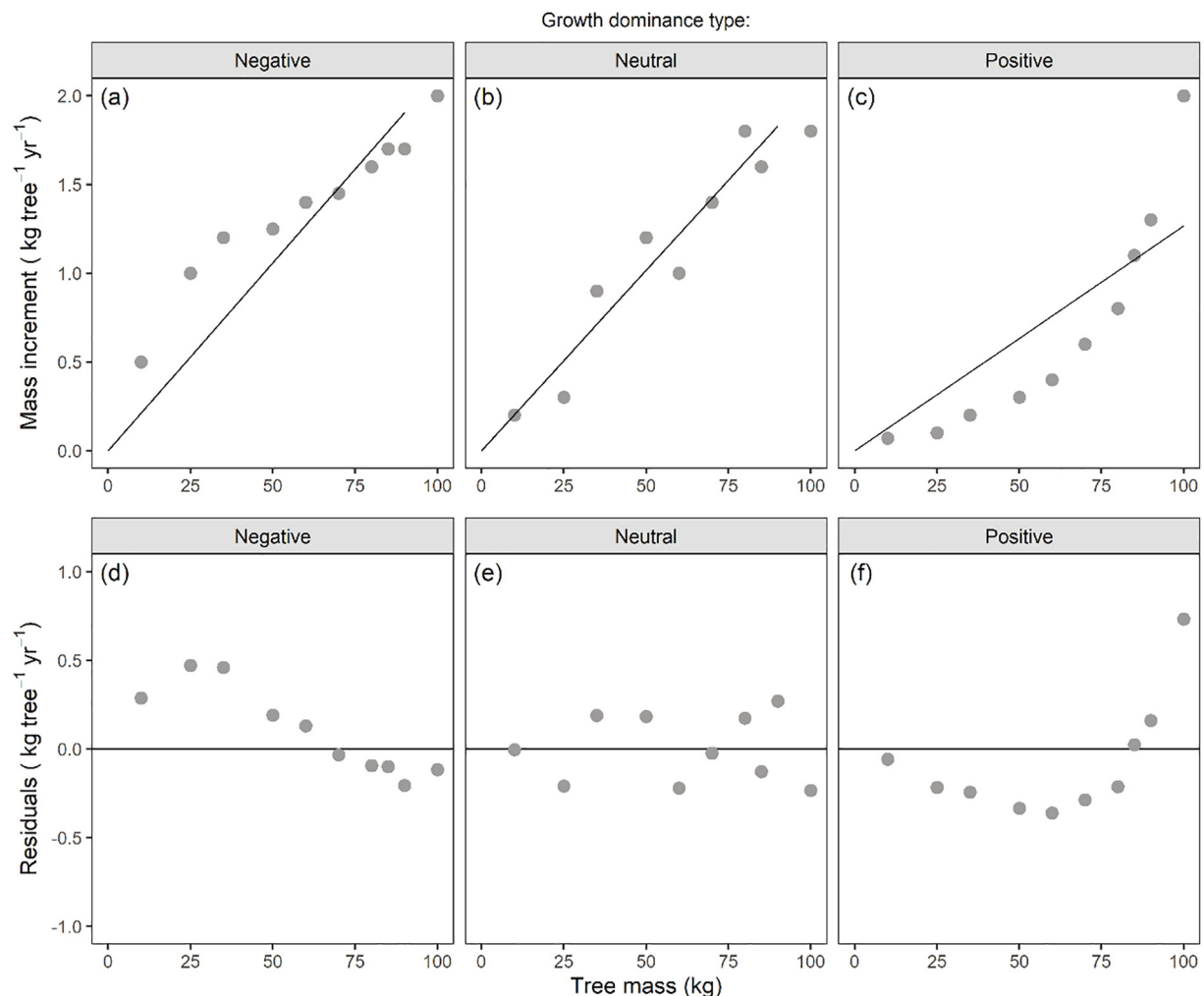
Fig. 1. Correspondence between the growth dominance and the zero-intercept linear relationship between stem mass increment and stem mass, defined as the 'allometric expectation' (A–C). The raw residuals (D–F), i.e. the differences between observed and predicted stem mass increment, were used to quantify the relative contribution of each tree to overall stand growth for a given measurement period.

2.2. Calculation of tree- and stand-level variables

For each PSP measurement, the volume of individual merchantable live trees was estimated with species-specific parameters of a model developed by Liu (2017) (Table 2). The estimated volume was then converted to stem mass using species-specific conversion factors that account for tree size (Cheng et al., 1992; Thomas and Malczewski, 2007; Kang et al., 2011). The annualized individual mass increment of each tree was computed using the repeated measurements performed within each PSP.

The growth dominance coefficient (GD) was computed using a method described in West (2014). For each site and remeasurement year, trees were arranged in ascending order of stem mass, and the cumulative increment in stem mass was plotted (y-axis) as a function of the cumulative stem mass (x-axis) to form a growth dominance curve (see Binkley (2004) or West (2014) for GD curve examples). GD was then calculated using a modified version of the trapezoidal rule that is used to estimate the area under a curve plotting the relationship between successive pairs of cumulative proportional values (West, 2014):

$$GD = 1 - \sum_{i=1}^{n} (s_i - s_{i-1})(\Delta_i + \Delta_{i-1})$$

$$(1)$$

where n is the number of live trees in the PSP, s_i is cumulative proportional stem mass (from 0 to 1) of tree i, and Δ_i is cumulative proportional stem mass increment (from 0 to 1) of tree i (see West (2014)

for a complete demonstration of the GD statistic calculations). Stands with a positive growth dominance, i.e. within which the relative contribution of small trees to total stand growth is lower than their relative contributions to total stem mass, were characterized by a GD > 0. Conversely, GD < 0 characterized a negative growth dominance, when the relative contribution of small trees to entire stand growth is larger than their relative contribution to stand mass. Finally, a neutral growth dominance, defined as GD = 0, is obtained when all trees contribute equally to stand growth relative to their size.

To address our third hypothesis, the relative contribution of every tree to overall stand growth was computed following the approach of Pothier (2019). Zero-intercept linear regressions between stem mass increment and stem mass were run for each plot and each measurement over the study period. These zero-intercept linear regressions refer to a theorical size-symmetric competition among trees, which has been found to correspond to neutral growth dominance at the stand level (Pothier, 2017; Fernández-Tschieder and Binkley, 2018). The regressions were thus computed as a proxy that indicates an equal contribution of all trees to stand growth relative to their size (Binkley, 2004). Accordingly, the raw residuals, i.e. the differences between observed and predicted stem mass increment of the zero-intercept linear regressions, were used to quantify the relative contribution of each tree to overall stand growth for a given measurement period (Fig. 1D–F). The residuals that were located above the zero-intercept linear relationship represented trees that grew faster than the allometric expectation,

Table 1
Stand characteristics of larch-spruce-fir plots established in 1987.

Block	Plot number	Area (ha)	Elevation (m)	Aspect	Slope (°)	Stem density (after thinning) (stems/ha)	Basal area (before thinning) (m²/ha)	Basal area (after thinning) (m²/ha)	Species composition by basal area (after thinning) (%)	Thinning intensity (%)
I	1	0.0775	760	Northeast (315°)	10	955	26.7	16.0	66L30C4H	40
	2	0.0775	760	Northeast (315°)	10	1535	26.1	26.1	45L42C13H	control
	3	0.13	760	Northeast (315°)	10	1085	23.9	16.7	47L40C13H	30
	4	0.0975	760	Northeast (315°)	10	903	21.6	17.3	67L18C14H	20
III	5	0.25	660	Northwest (315°)	6	1112	20.1	20.1	59L25C16H	control
	6	0.25	670	Northwest (45°)	10	840	24.1	16.9	47L39C15H	30
	7	0.25	670	Northwest (45°)	6	820	23.1	18.5	58L32C10H	20
	8	0.25	680	Northwest (45°)	10	896	26.8	16.1	51L38C11H	40
IV	9	0.1125	660	North (0°)	7	1680	24.0	24.0	63L32C5H	control
	10	0.1	645	North (0°)	7	1130	23.4	18.7	58L32C10H	20
V	11	0.1	615	Northeast (315°)	7	1280	21.4	17.1	62L31C7H	20
	12	0.1125	610	Northeast (315°)	7	880	23.0	13.8	73L21C7H	40
	13	0.1	605	Northeast (315°)	9	810	21.0	14.7	94L4C2H	30
	14	0.1	600	Northeast (315°)	9	1410	22.1	22.1	62L31C7H	control

Larch (**L**) refers to *Larix olgensis*. Conifers (**C**) represents *Picea jezoensis*, *Abies nephrolepis*, and *Pinus koraiensis*. Hardwoods (**H**) includes *Betula platyphylla*, *Populus ussuriensis*, *Betula costata*, *Tilia amurensis*, *Ulmus propinqua*, *Acer mono*, *Fraxinus mandshurica*, and *Phellodendron amurense*. For aspect, north was referred as 0°, west as 90°, south as 180° and east 270° Three thinning intensities were carried out according to the percentage of basal area removed: Light (LT, 20%), moderate (MT, 30%), heavy (HT, 40%) and a control (CT, 0%).

making them strong contributors to the overall stand growth, while residuals located below the line were weak contributors to overall stand growth (Fig. 1D–F).

2.3. Statistical analysis

To analyse the impact of thinning intensity (TI) and the number of years since thinning (YST) on stand growth dominance, we used a linear mixed-effects model with a block-level random effect using the *lmer* function in the *lme4* package (Bates et al., 2015) in the R statistical programming environment (R Core Team, 2019). The independent variables were TI, YST, the log-transformation of YST, and the interaction between TI and YST.

To investigate the influence of thinning intensity on individual tree growth, we modelled the effects of different potential covariates on the residuals of the zero-intercept model fitted to each measurement of each PSP. Because preliminary data exploration indicated that the relationships between some predictors and the model residuals were both linear and nonlinear, we modeled these variables using generalized additive models (GAMs) (Wood, 2017). This approach allows for flexible representation of functional relationships between predictors and independent variables by fitting both smooth and parametric terms in the models (Pedersen et al., 2019). Hence, GAMs are widely used to model complex ecological processes, such as predicting species distributions (Guisan et al., 2002), tree height-diameter relationships (Pya and Schmidt 2016; Zang et al., 2016), carbon storage (Gordon et al., 2018), and insect outbreaks (Haynes et al., 2018). In addition, GAMs can account for interactions between covariates and data with group-level variation or repeated measures.

For this analysis, we modelled species effects for the three most abundant species, i.e. larch, spruce and fir only, and grouped the remaining species together because they altogether represented less than 6% of the basal area of PSPs. To test the first two hypotheses, we modelled the residuals as smooth functions of individual tree mass (M) and years since thinning (YST), with the smooth term for YST varying for each level of TI. We also modelled the M × YST interaction using a tensor product interaction term; these give each term in the interaction its own smoothness penalty (Wood, 2006). To test the third hypothesis, we allowed the smooth term for M to vary by species and included a parametric TI × species interaction term. We used penalized thin plate regression splines as the basis for all smooth functions, and the significance of variables was assessed at the α = 0.05 level. All GAMS were fitted using the mgcv package (Wood, 2011) in the R statistical programming environment (R Core Team, 2019).

3. Results

3.1. Stand growth dominance

The interaction term between TI and YST was significantly related to stand-level GD (P < 0.0001) and explained 31% of its variation. Because the block random effect was not significantly different from 0, this term was removed from the model and only the site-level random effect and the fixed effects were retained. Overall, stand GD decreased with increasing TI and increased with increasing YST except for the 20% TI, for which GD was always positive with a small increase over time (Fig. 2). In unthinned stands, the GD value was initially close to zero and gradually increased to positive values after 25 years. For both the 30 and 40% TI, the stand GD was reduced immediately after the application of the treatment and gradually increased thereafter. However, GD values in the 40% TI remained negative for the entire study period.

3.2. Differences from allometric expectations against stem mass

All explanatory variables included in the model were significantly

Table 2
Local volume equations.

Species groups	Common name	Scientific name	Wood density (g/cm³)	Shade-tolerance class	Equations	Parameter					
						a	b	c	h1	h2	h3
Larch	Changbai larch	*Larix olgensis*	0.630	intolerance	**For volume**	8.47×10^{-5}	1.97	0.75	34.59	650.53	18
Conifer	Korean pine	*Pinus koraiensis*	0.467	shade tolerance	$V = a \times D^b \times H^c$	7.62×10^{-5}	1.90	0.86	21.84	309.16	14
	Khingan fir	*Abies nephrolepis*	0.336	shade tolerance	**For height**	5.79×10^{-5}	1.89	0.99	46.40	2137.92	47
	Yezo spruce	*Picea jezoensis*	0.394	shade tolerance	$H = h_1 - \frac{h_2}{D + h_3}$	5.79×10^{-5}	1.89	0.99	46.40	2137.92	47
Hardwood	Painted malpe	*Acer mono*	0.663	shade tolerance		4.88×10^{-5}	1.84	1.05	24.82	402.09	16.3
	Manchurian ash	*Fraxinus mandshurica*	0.694	shade tolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	Amur cork	*Phellodendron amurense*	0.515	intolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	White birch	*Betula platyphylla*	0.558	intolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	Amur linden	*Tilia amurensis*	0.388	shade tolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	Costata birch	*Betula costata*	0.662	shade tolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	Ussuri poplar	*Populus ussuriensis*	0.449	intolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7
	Siberian elm	*Ulmus pumila*	0.638	shade tolerance		5.33×10^{-5}	1.88	1.00	29.44	468.93	15.7

D, *H*, and *V* refer to tree diameter at breast height outside the bark (cm), tree height, and volume, respectively.

related to the differences from allometric expectations for a given stem mass (i.e. model residuals) calculated for each tree observation from each PSP measurement (Table 3). While the mean residuals of small trees (< 250 kg) tended to decrease over time for all treatments, there was a clear effect of thinning intensity on the temporal response of larger trees (Fig. 3). Generally, the stem mass residuals of larger trees were negative at the beginning of the study period but increased over time and with decreasing thinning intensity. At the end of the study
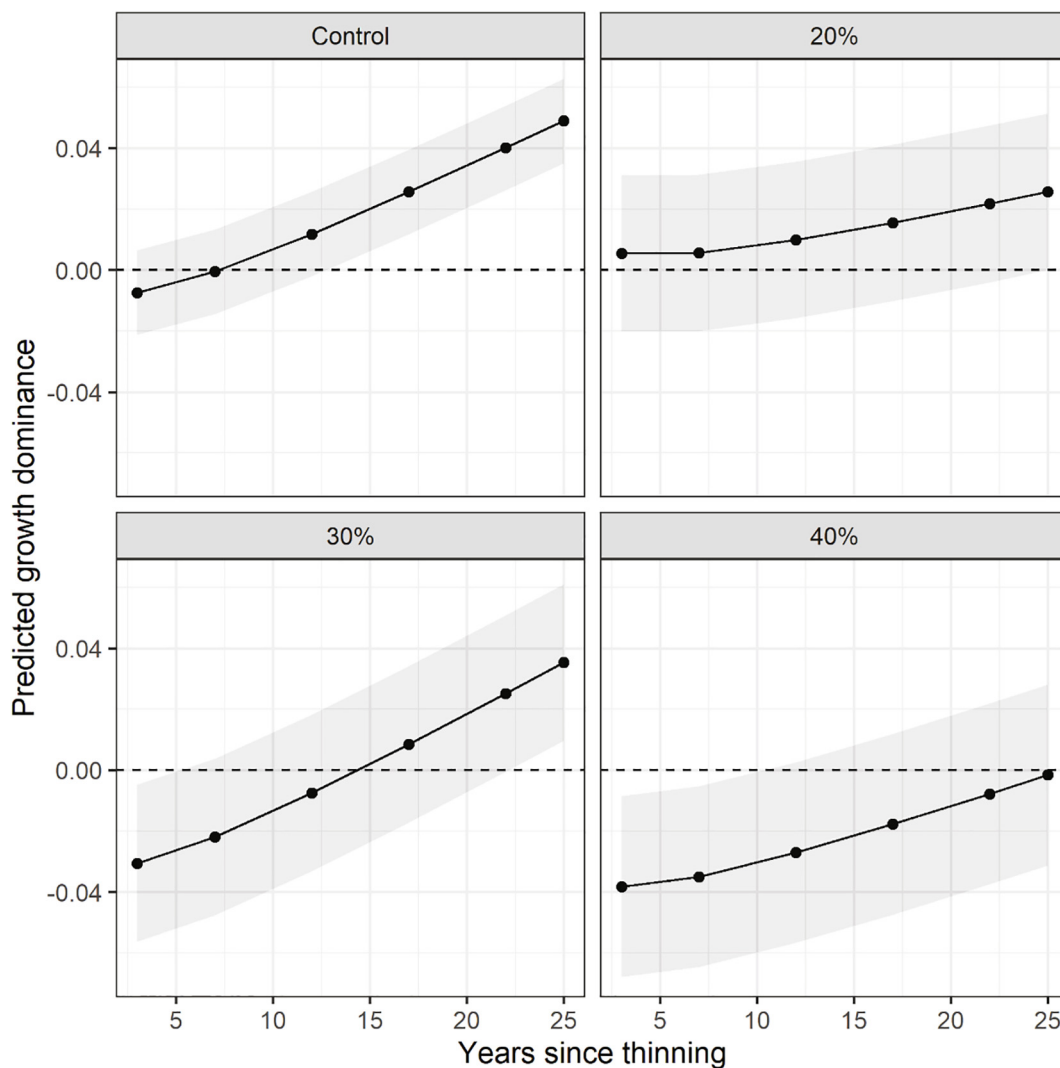

Fig. 2. The variability in growth dominance of mixed larch-spruce-fir stands in relation to thinning intensity (%) and the number of years since thinning. Shaded areas correspond to 95% prediction intervals calculated from the fixed effects of the growth dominance model.

Table 3
Type III ANOVA table for the final model of mass increment residuals showing degrees of freedom, F-values and p-values for the parametric terms, and the estimated degrees of freedom, F-value and p-value for the smooth terms in the model.

Parametric terms			
	df	F	p-value
TI	3	0.88	0.45
Species	3	42.47	< 0.0001
TI:Species	9	2.91	0.002
Approximate significance of smooth terms			
	df	F	p-value
s(mass):Larch	5.57	28.34	< 0.0001
s(mass):Fir	5.28	34.12	< 0.0001
s(mass):Spruce	5.39	28.07	< 0.0001
s(mass):Others	11.13	28.26	< 0.0001
s(YST):TI00	1.00	14.96	0.0001
s(YST):TI20	1.00	12.34	0.0004
s(YST):TI30	1.01	11.97	0.0005
s(YST):TI40	1.81	6.08	0.0016
ti(mass,YST):TI00	4.43	3.43	0.0026
ti(mass,YST):TI20	2.98	2.19	0.0544
ti(mass,YST):TI30	4.03	4.33	0.0012
ti(mass,YST):TI40	7.46	11.42	< 0.0001
s(block/site)	8.21	6.27	< 0.0001

Hierarchical smooth terms for mass, years since thinning (YST), and their tensor-product interaction varied by Species, Thinning intensity (TI), and TI, respectively.

period, the residuals of the largest trees were positive for all treatments except for the 40% TI, for which they were still strongly negative (Fig. 3).

The residuals of the planted larch trees increased with increasing stem mass and were generally positive for all treatments except for the largest trees of the 40% TI (Fig. 4). In this treatment, the larch residuals peaked for medium-sized trees, and reached their lowest values for the largest trees. The residuals of the other species groups were negative and generally decreased with increasing stem mass (Fig. 4). However, the residual patterns of spruce trees were slightly different from those of the other shade tolerant companion species in thinned stands, with U-shaped residuals reaching minimum values in medium-sized trees.

4. Discussion

Immediately after treatment application, a neutral growth dominance characterized unthinned stands and those treated with a low intensity thinning, suggesting that limited between-tree competition resulted in an efficient use of the available resources for all-sized trees (Bradford et al., 2010). With time, however, unthinned stands developed positive growth dominance, which indicates that the growth partitioning to dominant trees increased, and thus exceeded their allometric expectations. This increasing dominance suggests that dominant trees either obtained more resources, used them more efficiently, or both (Fernández-Tschieder and Binkley; 2018; Forrester, 2019). These results support the hypothesis of Binkley (2004), which stipulated that stand growth dominance would increase from neutral in young stands to positive after canopy closure, when the resource use efficiency of large dominant trees is high. They are also consistent with observations of near-zero growth dominance values in young unthinned stands (< 50 years), which then increased over time (Binkley et al., 2006; Bradford et al., 2010). However, it is worth mentioning that increasing growth dominance with age is not universal and that neutral and negative growth dominance values were both observed for a wide range of ages (Binkley et al., 2006; Binkley and Kashian, 2015; Looney et al., 2018).

In line with our first hypothesis, there was a sustained neutral

growth dominance after the application of a low-intensity thinning, which indicates that the growth of all-sized trees was close to their allometric expectations. Therefore, it seems that the removal of about 20% of the initial basal area using thinning from below was enough to increase the growth partitioning to smaller trees such that their growth per unit size was similar to larger trees. Accordingly, this treatment stimulated the growth of small- to medium-sized trees through a better sharing of resources among residual trees (Nyland, 1998; Bradford et al., 2010; Bose et al., 2018). The site resources were even more evenly shared between trees after a thinning of 40% of the basal area was performed, in such a way that 25 years after its application, stand growth dominance was still negative. In this thinning treatment, the negative allometric residuals associated with large trees should not be interpreted as resulting from a growth decline of large trees, but rather from a marked growth improvement in small- to medium-sized trees (Jones and Thomas, 2004; Prévost and Dumais, 2014). Indeed, the negative growth dominance of this treatment implies that the zero-intercept regression caused positive residuals for small trees and negative residuals for large trees, even if the growth of large trees was similar among treatments (Fig. 1A, D). In the 30% thinning intensity, the growth dominance values shifted rapidly from being negative to positive with increasing stand age. This might be induced by a rapid improvement in light availability for small- to medium-sized trees immediately after treatment (Forrester et al., 2013; Gspaltl et al., 2013), followed by a gradual increase in competition between these trees. As suggested by the slower rate of increase of growth dominance in the 40% thinning intensity, the removal of several small trees likely allowed the others to contribute substantially to the overall stand growth over a longer period.

These results are consistent with previous observations in eucalypt plantations that were thinned from below, in which GD decreased in proportion to thinning intensity, while subsequent increases in GD decreased with thinning intensity (Soares et al., 2017). However, GD values in the current study are lower than those observed in thinned even-aged eucalypt monocultures (Soares et al., 2017), and in natural mixed Douglas-fir stands (Binkley, 2004). Fast-growing species such as eucalypt are known to increase resource acquisition and resource use-efficiency by developing large crowns and root systems, which in turn decreases the availability of resources for the suppressed trees (Binkley et al., 2010). The lower GD values of the current study rather indicated a smaller difference in resource efficiencies and/or resource uptakes between dominant larch and subdominant trees. A sharing of photosynthates between trees via root grafts could explain this limited growth dominance development (Binkley et al., 2006), and this is worth exploring in future work. In addition, northeastern China is characterized by the frequent occurrence of strong winds, with effects amplified by the occurrence of snow damage during the winter (Zhu et al., 2006; Li et al., 2018). This disturbance regime may play a role in mitigating the dominance of larger trees by limiting leaf area expansion and light interception (Binkley et al., 2006).

Twenty-five years after treatment application, the analysis of the tree-level allometric residuals indicated that the relative contribution of the shade-intolerant larch to overall stand growth was much larger than the other tree species, particularly for medium- to large-sized trees. In the 40% thinning intensity, the positive allometric residuals of medium-size larch trees indicated that they markedly improved their growth. This result is in line with our third hypothesis and indicated that large openings induced by the removal of about 40% of the initial basal area were effective to stimulate the growth of the shade-intolerant larch trees of the understory. For their part, the shade-tolerant coniferous and broad-leaved trees contributed less than their allometric expectation in all treatments. However, in thinned stands, the residuals of large spruce trees tended to be closer to zero than other companion species. This may be related to its mid-shade tolerance compared to the shade tolerant fir and other hardwoods (He et al., 2002). A species with intermediate tolerance to shade like yezo spruce may have the capacity to be
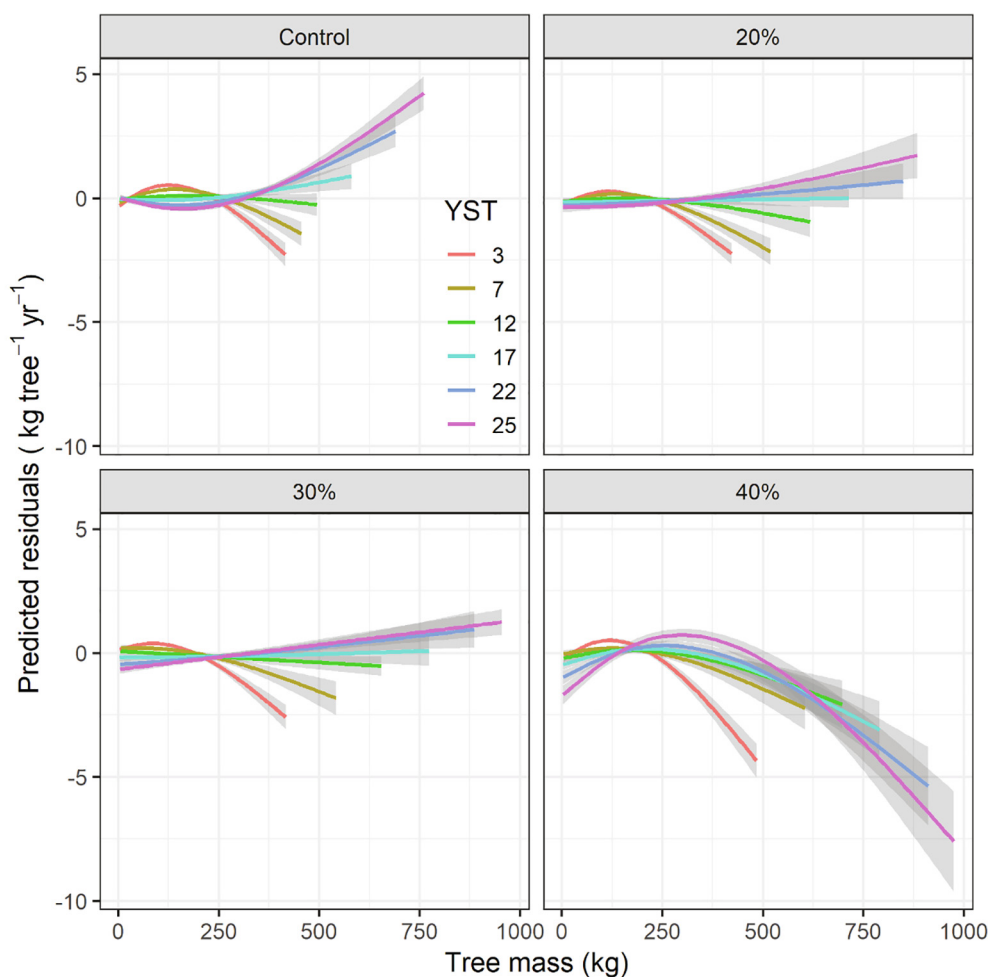
Fig. 3. Mean predicted relative contribution of each tree against tree mass for the four different treatments over time. Shaded areas around each curve correspond to 95% confidence intervals. YST: Years since thinning.

more responsive to the increase in light induced by thinning than shade-tolerant, understory species (Sakai, 1995). This suggests that spruce may succeed to larch as the dominant species of these stands in the long term. This dynamic should eventually lead to the development of a mixed coniferous and deciduous forest dominated by a shade tolerant coniferous species, which is closer to the primary vegetation in northeastern China (Lei et al., 2007). Given the increasing importance of natural forest rehabilitation and restoration in China (Zhou, 2004; Lei et al., 2007), the conversion of larch plantations to natural mixed forest with complex structure is stated as a management objective for the region (Lei et al., 2007). Based on our observations, a succession cut that prioritizes the harvest of dominant larch trees could be used in the future to accelerate stand conversion and meet such an objective.

5. Conclusion

By linking the concepts of stand-level growth dominance with tree allometric expectations, we were able to deepen the understanding of changes in growth partitioning after thinning as a function of both tree size and species. While the growth dominance analysis first suggested that thinning was effective in stimulating the growth of small trees through a better partitioning of resources among residual trees, the use of tree-level allometric residuals revealed that this result was caused by the thinning response of small- to medium-sized, shade intolerant larch trees. This approach has thus allowed us to identify tree groups that were major contributors to stand growth after thinning treatments and, conversely, those that grew below average. It may be interesting to use

this approach not only to identify tree groups based on species, but also by grouping trees according to their functional traits, stem or crown defects, or any individual characteristics. This information can be used to help target trees for removal during partial cutting operations and to identify successional pathways that will lead to the composition of the future stand. Such information is crucial to predict long-term forest productivity and to help achieve short- and long-term management objectives such as maximising the value of end-use wood products, restoring depleted stands, or altering tree species composition.

CRediT authorship contribution statement

Guillaume Moreau: Writing - original draft. **David Auty:** Formal analysis, Data curation, Writing - review & editing. **David Pothier:** Writing - review & editing. **Jingning Shi:** Data curation, Formal analysis. **Jun Lu:** Resources. **Alexis Achim:** Conceptualization, Methodology, Writing - review & editing. **Wei Xiang:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.
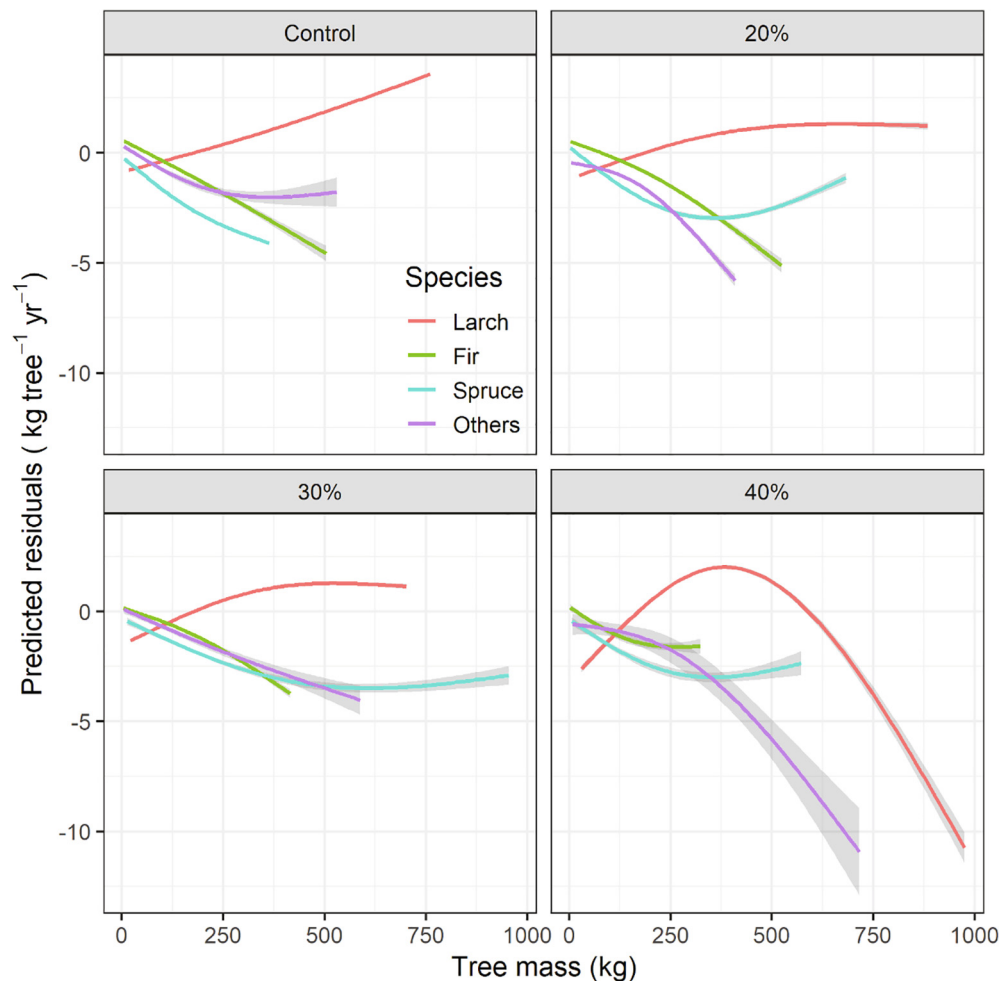
Fig. 4. Mean predicted relative contribution of each tree for the four different treatments as a function of individual tree mass and species group twenty-five years after treatment application. Shaded areas around each curve correspond to 95% confidence intervals. Larch: Changbai larch, Fir: Manchurian fir, Spruce: Jezo spruce, Others: all remaining species.

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.

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