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RESEARCH

Swift adjustment of biomass allocation strategies in Scots pine after thinning

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Abstract

Our study aimed to evaluate the short-term effects of thinning in Scots pine (*Pinus sylvestris* L.) forests, with focus on above-ground biomass and allocation patterns within trees to compare between treatments. We have established four treatments: one control (unthinned), two moderate thinnings (from above and from below) and one heavy thinning from below, which were properly replicated across four blocks located at two sites in central Sweden. In addition to tree measurements in the field, we performed two destructive samplings, one before thinning in 2020 and another one three years after thinning (2023). We created above-ground biomass functions for each assessment and tree compartment, as well as leaf area and sapwood area functions, which were used for prediction of those variables for treatment effect comparisons on stand level. We found that, within three years after thinning, the dominant trees in the heavily thinned plots presented a significantly higher diameter at breast height (dbh) and leaf area increment, in addition to an increased leaf area-to-sapwood area ratio, than the control. These results indicate that Scots pine trees were able to quickly adjust their allocation strategies under intensive forest management, at least in the short-term, which further suggests that thinning can be a useful strategy in times of climate change and future extreme droughts, when adaptations would be necessary for retaining vital forests.

Keywords Scots pine · Thinning · Biomass allocation · Sapwood area · Leaf area · Forest management

Introduction

Thinning is one of the most relevant management practices in forestry. It has been traditionally used with the intent of increasing the number and size of valuable logs for the production of a variety of forest products e.g. sawn timber and veneer (Sabatia et al. 2009), while additionally improving the overall quality and health of the remaining trees (Wagle et al. 2023). Thus, by promoting competition release through thinning, there is an increased availability of resources, e.g. light, water and nutrients, for the retained trees (Coyea and Margolis 1992; del Río et al. 2017). Considering the better revenue from final fellings (Niemistö et al. 2018), thinning operations should primarily be seen as stand management and as investments for future gain, although there is a potential for provision of an early income for forest owners (Karlsson et al. 2015). The competition release in thinnings renders an increased diameter growth in remaining trees, which has been proven with measurements in long time series in thinning experiments (Nilsson et al. 2010; Segtowich et al. 2023; Mäkinen and Isomäki 2004a). Thinning can be done in different intensities e.g. higher or lower basal area removal, and in different forms e.g. from above and below. In this study, thinning from above refers to when the largest trees are removed, while the opposite is true for thinning from below, when the smallest trees are removed (Nilsson et al. 2010; Mäkinen and Isomäki 2004a, b). It can also be done systematically, with the use of corridors, for example (Mäkinen et al. 2005b; Nuutinen et al. 2021; Bergström et al. 2022; Segtowich et al. 2023).

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In boreal ecosystems, most cultivated forests are managed with one or more thinnings before final harvest (Valinger et al. 2019). In northern Europe, the rotation length for Scots pine (*Pinus sylvestris* L.) is usually in the range of 60–120 years, which explains the importance of the early stand management from an economical and ecological perspective. In the first thinning most of the harvested logs are sold as pulpwood (Demers et al. 2013), while other forest residues e.g. tops and branches are usually left behind (Titus et al. 2021).

Boreal forestry has undergone a major shift over the past decades, and such changes may continue in the coming years. With climate change and projections of a warmer climate, tree growth in the boreal zone is predicted to increase, at least for some species, and may even offset negative effects derived from such changes, as has been suggested by Wang et al. (2023). Appiah Mensah et al. (2021) reported increased height growth trends for Norway spruce and Scots pine in Sweden from 1986 to 2018, with growth being positively correlated to temperature, which was further confirmed in studies of stem radial growth (Ogana et al. 2024). Laudon et al. (2024) reported that Swedish forests have faced a recent decline in the previous rapid increase in growth from the last decade, which the authors suggest is most likely due to drought. Moreover, according to Spinoni et al. (2018), for the moderate emission scenario (RCP4.5), the frequency and severity of droughts are predicted to increase in a lot of regions in Europe, including Scandinavia.

Trees uptake resources, such as carbon, water and nutrients, which they can store for later usage or invest into the production of roots, leaves, stem, bark etc. (Bloom et al. 1985). Forests can serve as sinks or sources, when it comes to the balance involving the storage and release of carbon (Gower et al. 1994). The net exchange of CO_2 between terrestrial ecosystems and the atmosphere is characterized and driven by two main processes, net primary production through photosynthesis and heterotrophic respiration (Gower et al. 2001). Quantification of the tree biomass is, therefore, of the utmost importance, since it allows for estimations of the amount of carbon stored in different compartments of the tree, above- or below-ground, while also providing allometric equations on biomass, which are necessary and serve as basis for upscaling physiological parameters, understanding water relations and informing process-based models (Urban et al. 2015).

Individual tree growth is influenced by a number of factors, biotic or abiotic, including the amount of radiation intercepted by the canopy, i.e. amount of leaf area and its distribution along the crown (van Hees and Bartelink 1993), response to disturbances, like droughts (Bose et al. 2024), and management practices, such as thinnings (Nilsson et al. 2010; del Río et al. 2017; Segtowich et al. 2023). One important plant attribute is the leaf area-to-sapwood area ratio (A_L:A_S), which establishes a connection between photosynthesis and transpiration, since leaf area is linked to light interception, and sapwood area is associated with the hydraulic capacity of the trees being able to supply water to the leaves (Togashi et al. 2015).

The short-term response after thinning is important today for carbon budgeting (Aun et al. 2021), tree species diversity (Zhang et al. 2023) and for drought mitigation (Sohn et al. 2013, Sohn et al. 2016a, b). Some authors have suggested that the proportion of stem biomass is expected to increase with age for pine forests, while foliage biomass proportion decreases, regardless of climate conditions (Gower et al. 1994; Hu et al. 2020). However, stem density and the social status of a tree can also influence biomass allocation (Poorter et al. 2015; Wertz et al. 2020).

Therefore, we have raised three research questions: (i) what are the short-term thinning effects, if any, on diameter at breast height (dbh) and biomass allocation of Scots pine trees? (ii) how does thinning impact the standing above-ground biomass in the short-term? (iii) will the thinning treatments change allocation strategies in terms of leaf area-to-sapwood area ratio (A_L;A_S), height-to-diameter ratio (HDR) and live crown ratio (LCR)?

Using tree measurements in the field and a destructive biomass sampling of trees from an experiment, before thinning and three years after, we tested early effects of the thinning treatments compared to an unthinned control, formulated in the following hypothesis:

1) diameter at breast height (dbh) growth will be significantly higher for the dominant trees, which we here classified as the 300 largest (thickest) trees ha^{-1};
2) stem wood dry weight increment will be higher for the dominant trees, but thinning will significantly reduce standing above-ground biomass on stand-level;
3) similarly, individual tree leaf area increment will be higher, but not leaf area index (LAI), which will be higher for the control;
4) leaf area-to-sapwood area ratio will differ significantly for the dominant trees, i.e. with trees in the thinned treatments presenting higher values;
5) height-to-diameter ratio will be significantly higher for the control in comparison to the thinned treatments, while live crown ratio will be lower.

Material and methods

Study sites and experimental design

The study was done in two Scots pine (*Pinus sylvestris* L.) forest sites in central Sweden, Siljansfors (60°53′19.0″N 14°24′36.0″E) and Jädraås (60°51′34.4″N 16°25′19.9″E). Site index, according to dominant height at base age 100 years (SI_{100}) (Hägglund 1977), ranges from 25–27 to 28–29, respectively. Stand age when the experiment was established in 2020, before first thinning, was 40 years old in Siljansfors and 37 in Jädraås. In both sites, the soil rooting depth is more than 30 cm deep and the soils could be classified as sandy-till moraine soils.

The experiment had four treatments: control (unthinned), two moderate thinnings (thinning from above and thinning from below), which consisted of approximately 35% of basal area removal including strip roads, and heavy thinning from below (with 67% of intensity, including strip roads), which were randomized within blocks (Table S1). In the following tables and figures, we refer to the treatments simply as *control*, *above*, *below* and *heavy*, respectively. Treatments were not just thinnings. Firstly, all other tree species than Scots pine were removed from all plots, including the control. Furthermore, in the thinned plots, trees with damages that affect tree growth were removed, as well as trees in the strip road that went through the centre of these plots, no matter the size of trees. Finally, when the below or above thinning strategy was applied on the remaining stems, we also took into consideration the distribution of trees within the plot, to avoid unnecessary gaps in the canopy. Consequently, some of the bigger trees were also removed in the thinning from below, and some of the smaller trees were removed in the thinning from above, while still having a thinning ratio of less than 1 in thinnings from below and above 1 in thinning from above (Nilsson et al. 2010; Segtowich et al. 2023).

We established four blocks (two on each site). The selected stands started from the same baseline before thinning (Table 1). The plots within each block had a maximum coefficient of variation of 9% in basal area before thinning, which secured a small variation within each block. Moreover, the area of each plot was 0.1 ha. The mean stem density across all treatments ranged from 473 to 1798 trees ha^{-1} after thinning. Diameter in two directions at breast height (dbh, 1.3 m) was measured on all trees when the experiment was established. Tree height, height to the lowest living branch and bark thickness were measured on 20 sample trees per plot, where the five trees with highest diameter were mandatorily selected, and the other 15 randomly chosen. The sites were measured before thinning (spring 2020 in Siljansfors and autumn 2020 in Jädraås). Thinning operations were carried out between November 2020 and February 2021. A second measurement was done in the autumn of 2023, three years after thinning. Most sample trees were present in both measurements, but sample trees removed in the thinning were replaced using the same procedure as the first selection on the remaining trees, during the second measurement.

The dbh for all trees was used for calculations of quadratic mean diameter (QMD, cm), stand basal area (m^2 ha^{-1}) and annual dbh growth (cm $year^{-1}$). We ranked the trees from largest to smallest dbh within each plot in 2020, considering only the retained trees after the thinning. The ranking was used to determine the dominant trees that were kept in the stand after thinning, which in this study we consider as the 30 largest trees (equivalent to the 300 largest trees ha^{-1}). Height and dbh from the sample trees were used for year- and plot-wise height estimations for all trees using Näslund's function (Näslund 1936; Ogana et al. 2023). Dead trees were excluded from the analysis.

Biomass sampling and field assessment

The first destructive sampling for above-ground biomass quantification of individual trees was done in the autumn of 2020, before thinning. We sampled 16 trees in total across all treatments and blocks (one tree from each plot). The trees were selected based on the dbh distribution of the sites. From this data, we built functions with dbh as the independent variable and each above-ground biomass compartment (needles, stem wood, stem bark, living branches and dead branches) as the predicted variable. The second destructive sampling was performed in the autumn of 2023, three years after thinning. This time we sampled 38 trees in total, ten trees in the control, moderate thinning from below and moderate thinning from above treatments, respectively, and eight trees in the heavy thinning from below treatment. All trees were divided into three size classes (small, intermediate and big) and the sample trees were randomly selected within each of the classes. The classification of tree size was

Table 1 Mean plot attributes (N = 4) in 2020, before first thinning

Treatment	Stem density (trees ha^{-1})	Basal area (m^2 ha^{-1})	Leaf area (m^2)	Sapwood area (cm^2)		Quadratic mean diameter (QMD, cm)
				Breast height	Start of the living crown	
Control	1813 a	28.2 a	15.3 a	106.5 a	65.7 a	14.1 a
Above	1830 a	27.9 a	14.9 a	105.3 a	64.7 a	14.0 a
Below	1798 a	28.9 a	15.8 a	109.5 a	67.7 a	14.3 a
Heavy	1743 a	27.5 a	15.5 a	108.9 a	67.0 a	14.2 a

Mean leaf area (m^2) and sapwood area (cm^2) refer to results on individual tree level. Values in the same column followed by a common letter are not significantly different ($p > 0.05$)

done based on their dbh and the quantiles in the first revision (before thinning). We used the 25% quantile (11 cm) as the upper limit for the small tree class. Trees that had dbh values that laid between 25 and 75% (11–17 cm) were considered as intermediate trees. Big trees were considered as the ones higher than the 75% quantile (≥ 17 cm). We sampled 16 trees each in the intermediate and big size classes, evenly distributed among the blocks and treatments. Only six trees were sampled in the small size class, all within the control and moderately thinned plots. As for the heavy thinning from below, the small tree size class was not sampled at all due to there not being enough trees in this diameter class (< 11 cm) after thinning.

We registered the fresh weight of the above-ground compartments of the trees in the field by using a portable scale, in addition to later processing in the lab. The crown was divided in three equal parts (from the lowest living branch to the top, strata 1, 2 and 3) and we sampled four sample living branches in different directions of the canopy in the first destructive sampling and three in the second, for later processing in the lab, as well as four and three sample dead branches below the living crown, respectively. The stem was marked and cross-calipered at the base of the tree, breast height 1.3 m, 2 m and then at every 2 m, and was subsequently sectioned and discs were sampled at each of these markings.

Laboratory processing

Specific leaf area (SLA), leaf area (LA) and leaf area index (LAI)

From the living sample branches, we sampled 45 pairs of current (if fewer than 45 pairs, we sampled as many as there were), 1 and 2-year old needles (totalling at least 135 pairs of needles) for specific leaf area (SLA, $cm^2\ g^{-1}$) determination and later leaf area (LA, m^2) on tree and stand level and leaf area index (LAI, $m^2\ m^{-2}$) on stand level. The sample needles were scanned and the images were processed in the software ImageJ 1.53e for the calculation of flat Projected Area (PA). Using Goude et al. (2019)'s regression for Scots pine, we converted PA into Half Total Surface Area (HTSA). The samples were thereafter dried until constant weight at 70 °C and their dry weights were noted.

Once we had determined leaf area for the individual trees from the destructive samplings, we created functions, one for 2020 (Eq. 1, Table 2) and one for 2023 (Eq. 2, Table 2), with LA as the response variable, so we could estimate individual tree LA. Block and treatment were initially tested, but they were not significant and were removed from the models. Due to Eq. 1 being a non-linear model, we opted for using the Pearson correlation (r) between observed and predicted values to assess the goodness of fit, which was 0.91. Adjusted R^2 for Eq. 2 was 0.90. Since we used log transformations for the response variable in Eq. 2, when estimating LA for the individual trees, we used the correction factor proposed by Baskerville (1972), when back-transforming the values, to avoid systematic bias.

$$leaf\ area = a \cdot dbh^b \tag{1}$$

in which *leaf area* (m^2) is the area in 2020 (before first thinning), *dbh* (cm) is the diameter at breast height in 2020, and *a* and *b* are coefficients.

$$\log(leaf\ area) = intercept + \log(dbh) \cdot a + \log(baha) \cdot b \tag{2}$$

in which *leaf area* (m^2) is the area in 2023 (three years after thinning), *dbh* (cm) is the diameter at breast height in 2023, *baha* ($m^2\ ha^{-1}$) is the plot basal area in 2023, *a* and *b* are coefficients.

Needles, branches, stem wood and stem bark

Once the needles for LAI determination had been collected, the living sample branches of each tree were cut into smaller pieces and put in an oven for 24 h at 70 °C, after which the remaining needles were separated from the branches and put back in the oven until they reached constant weight. The dry weight of needles and branches was, therefore, separately taken. The processing of the stem sample discs included the removal of the bark before both parts were dried until constant weight. A dry to fresh weight ratio was calculated for each tree compartment (stem wood, stem bark, branches and needles) and each section e.g. the sectioned stem and crown parts. This ratio was used to estimate the dry weight of each section by multiplying it with their respective fresh weight, which was measured in the field. Later, the dry weight of

Table 2 Leaf area models for each assessment (2020 and 2023), in which dbh is diameter in cm, baha is basal area in $m^2\ ha^{-1}$ and leaf area is in m^2

Model	Year	Response variable	Parameters	Coefficients	Estimates	Std. Error	*p* value
1	2020	Leaf area	dbh	a	0.01246	0.01738	0.485
				b	2.65634	0.47195	6.23e−05
2	2023	log(leaf area)		Intercept	− 2.29019	0.48476	3.68e−05
			log(dbh)	a	2.20847	0.12566	< 2e−16
			log(baha)	b	− 0.22592	0.09743	0.0264

each tree compartment was summarized in order to obtain total tree dry weight.

Models used for predicting the above-ground biomass compartments for treatment comparison

To test the short-term effects of thinning on the different above-ground biomass compartments on stand-level, we created two Seemingly Unrelated Regressions (SUR) (one for each biomass harvest). We combined the individual above-ground functions (Eqs. 3–4, Tables S2 and S3) and their respective response variables i.e. dry weight (kg) of stem, bark, needles, living and dead branches and total above-ground biomass. The reasoning for using such approach is that we assume that the different compartments, which are measured within the same unit (i.e. tree), are not independent from each other (Siddique et al. 2021; Zhao et al. 2015; Trautenmüller et al. 2021). Therefore, by using SUR we are able to obtain the estimates simultaneously, while accounting for potential correlations between the error terms and ensuring additivity (Trautenmüller et al. 2021).

We linearized the models by using log or square root transformations for the response variables, as well as log transformations for dbh (independent variable) for most of the functions, except needle and stem functions in 2020, which we kept in the original unit (cm). If a log transformation led to heteroscedasticity, we opted for a square root transformation. Specifically for the biomass trees from 2023, which were sampled three years after the thinning had been performed, we used Theil's F-test, i.e. an F-test for joint hypothesis to test whether the inclusion of 'treatment' as a factor would significantly improve the model or not. For that, we ran the set of equations with and without the treatments to make such comparison, but we found no significance ($p =$ 0.1123), and, thus, it was not included. Moreover, we also calculated Akaike Information Criterion (AIC) for each of the models, and we found that the one without treatment was more suitable (AIC = − 227.68) than the one with it (AIC = − 216.62). Therefore, we only kept dbh as the predictor. Thus, model selection was done based on the results of Theil's F test and the AIC, while also ensuring the normality of residuals. When applied on different compartments and assessment years, the equation was separately adjusted to achieve normally distributed datasets by using either log or square root transformations (Eqs. 3 and 4). In the case of functions with response variables that have been log-transformed (Eq. 4), when calculating the predictions and back-transforming the values, we used Baskerville's (1972) correction factor to avoid systematic bias.

$$\mathrm{sqrt}(biomass\ compartment) = intercept + a \cdot dbh \tag{3}$$

$$\log(biomass\ compartment) = intercept + a \cdot \log(dbh) \tag{4}$$

in which the response variable *biomass compartment* is the dry weight (kg) of stem wood, stem bark, needles, living branches or dead branches; *dbh* is diameter at breast height (cm); and *intercept* and *a* are coefficients. The equation structure used for each compartment and assessment year can be found in Tables S2 and S3.

Sapwood area

During the destructive samplings, we collected two extra discs per tree, one in close proximity to breast height (1.3 m) and one at the start of the living crown of each tree. We applied an iodine solution on the disc surface, to enable a better distinction between sapwood and heartwood. The discs were then scanned and the images were processed in ImageJ 1.53e for sapwood area (cm^2) determination.

We later created a power function for each sampling year i.e. 2020, before thinning, and 2023, three years after thinning, using sapwood area at breast height (SA_{BH}) as a function of dbh for the analysed trees (Eq. 5, Table 3), which could be used for prediction of sapwood area for all the trees in the plots. For estimation of sapwood area at the start of the living crown (SA_{LC}), we linearized the functions by using log transformations of the response variable (SA_{LC}, cm^2) and the predictor (dbh, cm) (Eq. 6, Table 4). Similarly to Eqs. 2 and 4, due to the use of log transformations in the response variable for Eq. 6, we used a correction factor when back-transforming the predicted values (Baskerville 1972). Neither treatment nor block were significant, and thus they were not included in the models. Due to inconclusiveness on the differentiation between sapwood and heartwood for one of the discs at the start of the living crown in 2023, this sample was excluded from the analysis. Thus, for our SA_{LC} model in 2023 we used 37 trees, as opposed to 38.

Table 3 Model estimates for sapwood area at breast height (SA_{BH}), in cm^2, for each assessment (2020 and 2023), where dbh is in cm

Model	Year	Response variable	Parameters	Coefficients	Estimates	Std. Error	*p* Value
5	2020	Sapwood area	dbh	a	1.1069	0.1779	1.27e−07
				b	1.7351	0.5709	0.073
5	2023	Sapwood area	dbh	a	0.61798	0.14411	< 2e−16
				b	1.95076	0.07864	0.000129

Table 4 Model estimates for sapwood area at the start of the living crown (SA_{LC}) for each assessment (2020 and 2023)

Model	Year	Response variable	Parameters	Coefficients	Estimates	Std. Error	*p* value
6	2020	log(sapwood area)		a	− 1.1467	0.5170	0.0436
			log(dbh)	b	2.0002	0.1964	7.46e−08
6	2023	log(sapwood area)		a	− 1.7121	0.2907	1.08e−06
			log(dbh)	b	2.2120	0.1053	< 2e−16

Original unit of SA_{LC} was cm^2. For dbh, it was cm

$$sapwood\ area_{BH} = a \cdot dbh^{b} \tag{5}$$

in which *sapwood area*$_{BH}$ is in cm^2 either in 2020 (before first thinning) or in 2023 (three years after thinning), *dbh* (cm) is diameter at breast height in each assessment (2020 or 2023), *a* and *b* are coefficients.

$$\log(sapwood\ area_{LC}) = a + \log(dbh) \cdot b \tag{6}$$

in which *sapwood area*$_{LC}$ is in cm^2 either in 2020 (before first thinning) or in 2023 (three years after thinning), *dbh* (cm) is diameter at breast height in each assessment (2020 or 2023), *a* and *b* are coefficients.

Leaf area-to-sapwood area ratio (AL:AS)

We calculated leaf area-to-sapwood area ratio (A_L:A_S) before and after thinning by using the model estimates for tree leaf area (Table 2) and sapwood area at breast height (Table 3) and at the start of the living crown (Table 4). We performed the treatment comparison on stand level, taking into consideration all the trees that were retained after the thinning in the plots, as well as the dominant trees.

Height: Diameter ratio (HDR) and live crown ratio (LCR) based on measured sample trees

We used the sample trees that were present in both assessments (2020 and 2023) to calculate height-to-diameter ratio (HDR) and live crown ratio (LCR) in both revisions, with the latter being calculated as crown length divided by total tree height (Hasenauer and Monserud 1996). In total, we analysed 171 trees across all treatments. We compared the HDR and LCR of these trees in the first measurement, before first thinning, to test if there were any significant differences between plots aimed for a specific treatment, and then again three years after thinning. We used a mixed-effects model, with block as a random effect (Eqs. 7, 8 and 9), and the Tukey test for such comparisons.

$$\log(HDRyear) = intercept + treatment + \log(initial\ dbh) \cdot a \tag{7}$$

in which HDR_{year} is height:diameter ratio either in 2020 (before first thinning) or in 2023 (three years after thinning), *treatment* contains four levels (control, moderate thinning from below, moderate thinning from above and heavy thinning from below) and initial *dbh* is diameter at breast height (cm) in 2020. *Intercept* and *a* are coefficients.

$$\log\left(LCR_{2020}\right) = intercept + treatment + initial\ dbh \cdot a \tag{8}$$

$$LCR_{2023} = intercept + treatment + initial\ dbh \cdot a \tag{9}$$

in which *LCR* is live crown ratio either in 2020 (before first thinning) or in 2023 (three years after thinning), *treatment* contains four levels (control, moderate thinning from below, moderate thinning from above and heavy thinning from below) and initial *dbh* is diameter at breast height (cm) in 2020. *Intercept* and *a* are coefficients.

Shoot length

We measured apical shoot length on the trees harvested during the destructive sampling three years after thinning. The measurement was done on four years of tree growth i.e. before thinning (2020) and three years after (2021, 2022 and 2023). Since small trees were not sampled in the heavily thinned plots, for this analysis, we only kept the intermediate and big trees i.e. eight trees in total per treatment to avoid bias. We tested the treatment effect in shoot length in each year after thinning by using a linear model with current year shoot length as the response variable and previous year shoot length as a covariate (Eq. 10). For analysis of the shoot length in 2023, we used inverse transformation (1/shoot length$_{2023}$) to achieve normality of the residuals.

$$shootlength_{currentyear} = intercept + treatment + shootlength_{previousyear} \cdot a \tag{10}$$

in which *shoot length* is in cm. Therefore, *current-year shoot length* can be 2021, 2022 or 2023. Whereas, *previous-year shoot length* (cm) is the year prior to the current-year. *Intercept* and *a* are coefficients.

Analysis

The effects of the thinning treatments were tested on diameter and height increment, above-ground biomass after thinning and differences in allocation patterns, expressed in HDR and LCR, leaf area-to-sapwood area ratio (A_L:A_S) at breast height and A_L:A_S at the start of the living crown. To test the effects on individual trees sampled during the biomass harvest e.g. specific leaf area (SLA) and shoot length, we used a linear model. For individual tree and stand level comparisons (Table S4), we used mixed-effects models with block as a random variable. When block was not significant, we removed it from the model and ran a simple linear model instead. We used analysis of variance (ANOVA) or covariance (ANCOVA) and pairwise comparisons. The latter were done using the Tukey test (0.95 level of confidence) with the *emmeans* package in R (Lenth 2023). In addition to visual inspection, we used the Shapiro Wilk test to evaluate the normality of residuals. If residuals were not normal, we used transformations; log, square root or inverse. We calculated the Pearson correlation (r) to evaluate the relationship between SLA and dbh in 2023. We used Baskerville's (1972) correction factor only when back-transforming values from functions that were used for predictions and that had log-transformed response variables (Eqs. 2, 4 and 6). All analyses were done in the statistical software R (version 4.3.0) (R Core Team 2023).

Results

Tree growth

When the thinning treatments were established, basal area (m^2 ha^{-1}) became, by design, significantly different between treatments, except thinning from below and above ($p = 0.998$) (Table 5). These differences were maintained three years after thinning.

The thinning itself created an inevitable difference in dbh for the dominant trees (300 largest trees ha^{-1}), with the control and moderate thinning from below treatments presenting the highest mean dbh (20.2 cm and 19.2 cm, respectively) and differing to moderate thinning from above (18.2 cm) and heavy thinning from below (17.8 cm).

Table 5 Mean plot attributes (N = 4) for the retained trees after thinning in 2020 and in 2023

Treatment	Stem density (trees ha^{-1})		Basal area (m^2 ha^{-1})		Quadratic mean diameter (QMD, cm)	
	2020	2023	2020	2023	2020	2023
Control	1798 a	1738 a	28.1 a	30.6 a	14.1 bc	15.0 bc
Below	998 c	983 c	18.6 b	20.9 b	15.5 ab	16.4 ab
Above	1283 b	1263 b	18.8 b	21.1 b	13.7 c	14.6 c
Heavy	473 d	463 d	9.6 c	11.2 c	16.4 a	17.8 a

Values in the same column followed by a common letter are not significantly different ($p > 0.05$)

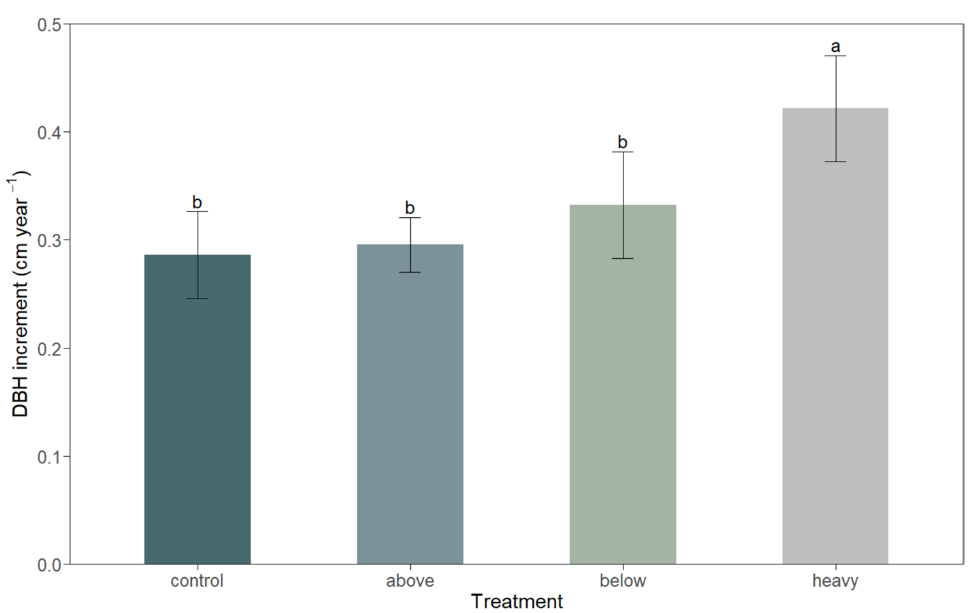


Fig. 1 Mean annual diameter increment at breast height (dbh) of the dominant trees (300 largest trees ha^{-1}) for each treatment three years after thinning. Error bars represent the standard error of the four blocks. Bars that have letters in common do not differ from each other ($p > 0.05$)

We found no treatment effect in height growth for the dominant trees three years after thinning (p = 0.320). However, we found a significant thinning response on dbh increment for the same trees in each plot, within the same time span (Fig. 1). The heavy thinning from below treatment presented the highest mean increment (0.42 cm $year^{-1}$) and differed significantly to all other treatments, followed by moderate thinning from below with an average of 0.33 cm $year^{-1}$ increment, which did not differ from moderate thinning from above ($p = 0.386$) or the control ($p = 0.220$). Moderate thinning from above (0.30 cm $year^{-1}$) did not differ significantly ($p = 0.972$) from the control (0.29 cm $year^{-1}$).

Treatment effect on above-ground biomass

The control treatment presented the highest total dry above-ground biomass (tons ha^{-1}) in both assessments, considering all the retained trees after thinning (Fig. 2, Table S5). Similarly to what has been previously stated, the treatments created a significant difference in total dry weight biomass, with the control presenting the highest amount. Most of the resource partitioning was stem wood, regardless of the treatment. On average, in 2023, 75.1% of the dry weight was stem wood, followed by living branches (10.4%), stem bark (6.4%), needles (4.9%) and dead branches (3.2%), respectively, across all blocks and treatments. When evaluating the dominant trees, the heavy thinning treatment presented a significantly higher stem wood dry weight increment (4.3 kg $year^{-1}$) in comparison to the control (3.3 kg $year^{-1}$, $p = 0.004$) and moderate thinning from above (3.2 kg $year^{-1}$, $p = 0.003$), but not thinning from below (3.7 kg $year^{-1}$, $p = 0.053$). No differences were observed among the other treatments.

Dominant trees in the control had the significantly highest total biomass in 2020, differing to all other treatments ($p < 0.05$) (Fig. 3a). The differences were maintained three years after thinning, except for moderate thinning from below trees, which no longer differ to the control trees ($p = 0.095$) (Fig. 3b).

Specific leaf area (SLA)

There were no significant differences of SLA between the different treatments ($p > 0.05$), but SLA was negatively

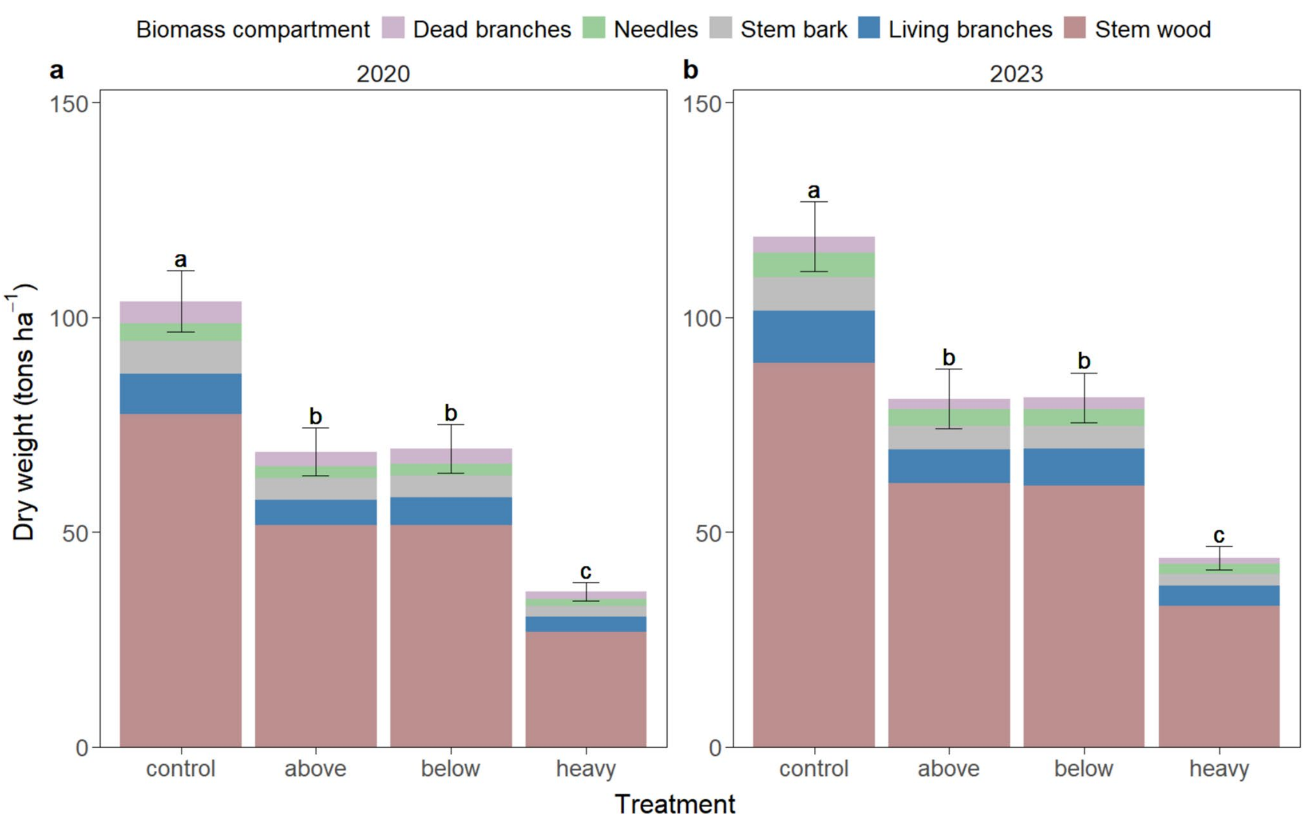


Fig. 2 Biomass partitioning among the different above-ground compartments (dead branches, needles, stem bark, living branches and stem wood) for all retained trees after thinning, 2020 (**a**), and three years after thinning, 2023 (**b**). Error bars represent the standard error of the total for the four blocks. Bars that have letters in common within the same year do not differ from each other ($p > 0.05$)

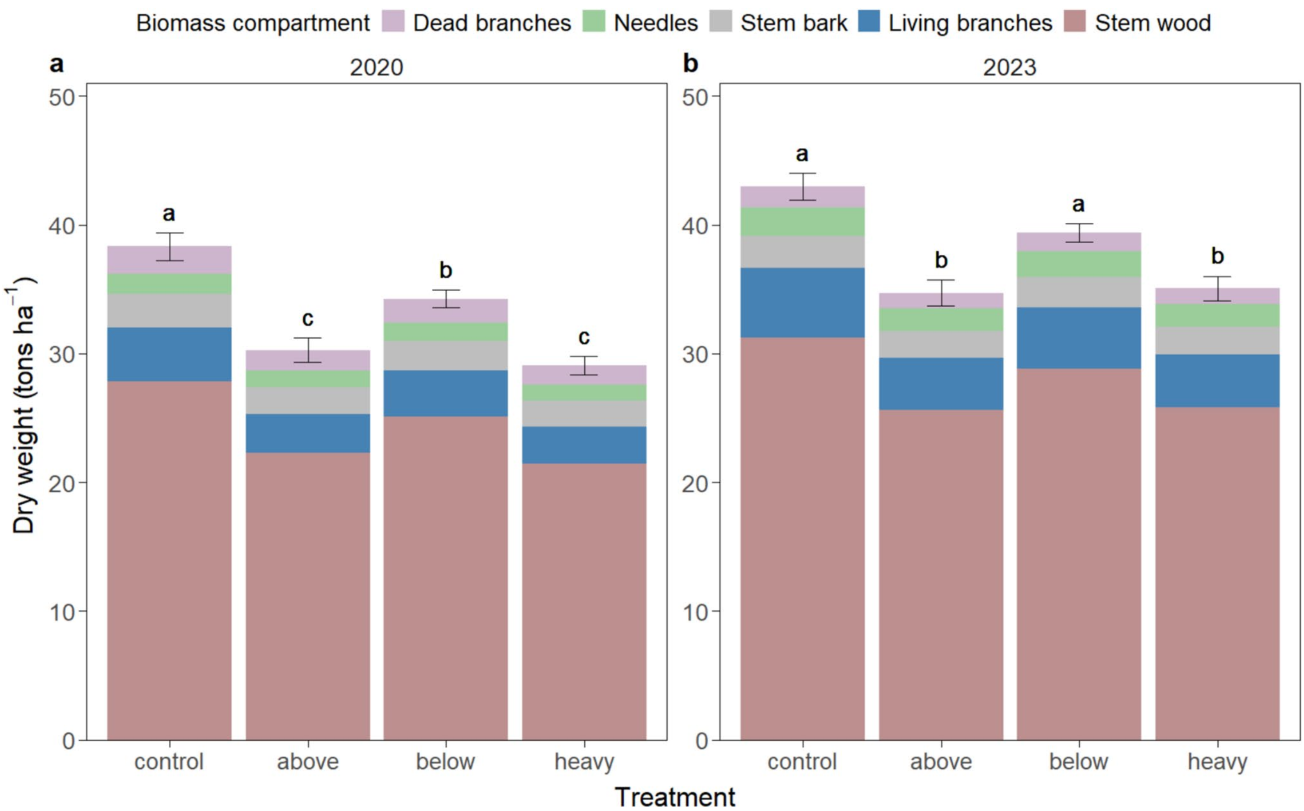
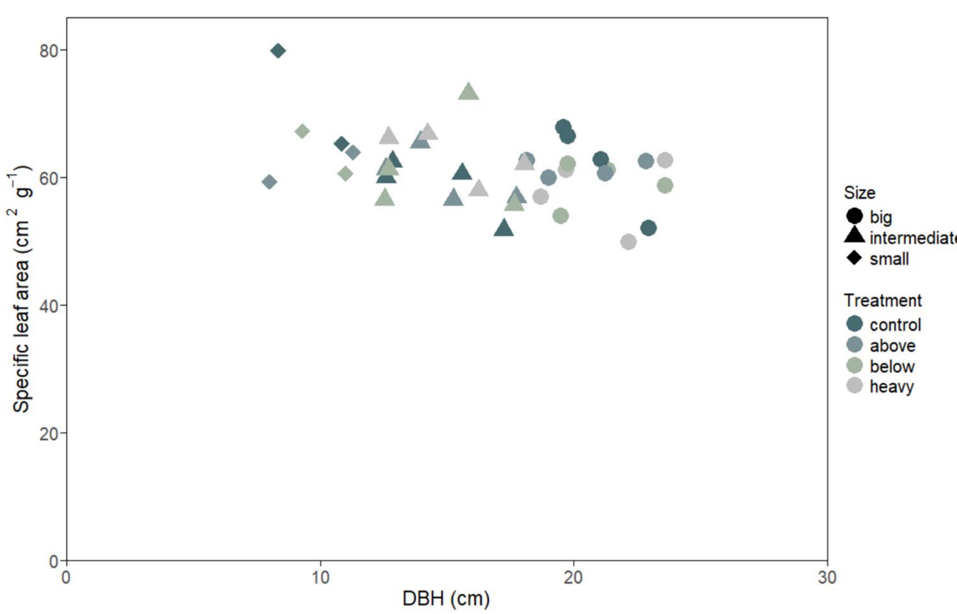


Fig. 3 Biomass partitioning among the different above-ground compartments (dead branches, needles, stem bark, living branches and stem wood) for the 300 largest retained trees ha^{-1} after thinning, 2020 (**a**), and three years after thinning, 2023 (**b**). Error bars represent the standard error of the total for the four blocks. Bars that have letters in common within the same year do not differ from each other ($p > 0.05$)

Fig. 4 Specific leaf area (SLA) per tree dbh in 2023. Each point represents one tree. The colours indicate their respective treatments and the symbols refer to the tree size classes (big, intermediate or small trees) in 2020, before thinning



correlated to dbh (r = − 0.41) (Fig. 4). Current and one-year old needles did not differ in SLA ($p > 0.90$), but SLA for two-year old needles was significantly lower than for younger needles ($p < 0.05$). SLA increased significantly ($p < 0.0001$) through the canopy within a tree, from top to bottom. Mean SLA in the upper part of the canopy (strata 3) was 55.1 $cm^2\ g^{-1}$, 62.7 $cm^2\ g^{-1}$ in the middle (strata 2) and 68.9 $cm^2\ g^{-1}$ in the lowest part of the crown (strata 1).

Leaf area (LA) and sapwood area (SA)

The establishment of the thinning treatments created an unavoidable difference in LA and SA, with the heavy thinning from below presenting the highest overall mean tree leaf area in 2020 (21.5 m^2) and differing significantly to the control and moderate thinning from above (Table 6). Among the dominant trees in 2020, the control treatment presented the highest mean LA (37.5 m^2), SA_{BH} (205.6 cm^2) and SA_{LC} (136.7 cm^2) and significantly differed to all the other treatments (Table 6). Three years after thinning, the individual tree LA for the dominant trees in the moderate thinning from above was significantly lower than the other treatments (Table 6).

The heavy thinning from below treatment presented the highest mean increment in LA (4.4 $m^2\ year^{-1}$) for the dominant trees and differed to all other treatments ($p < 0.001$) (Fig. 5), with the control presenting the lowest increment (1.2 $m^2\ year^{-1}$), followed by moderate thinning from above (2.3 $m^2\ year^{-1}$) and moderate thinning from below (2.5 $m^2\ year^{-1}$). The last two did not differ from each other ($p = 0.899$).

Leaf area-to-sapwood area ratio (AL:AS)

By the selections made in the thinning, the heavy thinning from below had a higher A_L:A_S, regardless of the position (breast height or start of the living crown), than the control ($p < 0.003$) and moderate thinning from above ($p <$

Table 6 Mean leaf area (LA) and sapwood area at breast height and at the start of the living crown (SA_{BH} and SA_{LC}, respectively) results for the treatments, considering all the retained trees after thinning and the dominant trees (300 largest trees ha^{-1}), in each respective assessment (2020) and (2023)

Selection of trees	Treatment	LA (m^2)		SA_{BH} (cm^2)		SA_{LC} (cm^2)	
		2020	2023	2020	2023	2020	2023
All	Control	15.4 b	19.4 b	107.1 bc	121.2 bc	66.0 bc	74.9 bc
	Above	13.9 b	19.7 b	101.6 c	114.7 c	61.8 c	70.1 c
	Below	18.6 ab	25.6 b	125.4 ab	144.8 ab	78.3 ab	90.7 ab
	Heavy	21.5 a	35.1 a	139.1 a	169.5 a	87.9 a	107.9 a
Dominant trees	Control	37.5 a	41.3 a	205.6 a	241.2 a	136.7 a	159.6 a
	Above	28.3 c	36.1 b	171.2 c	199.1 b	110.6 c	128.4 b
	Below	32.9 b	41.2 a	188.4 b	223.0 a	123.6 b	146.1 a
	Heavy	27.1 c	42.1 a	165.4 c	200.5 b	106.6 c	129.7 b

Values in the same column followed by a common letter are not significantly different ($p > 0.05$)

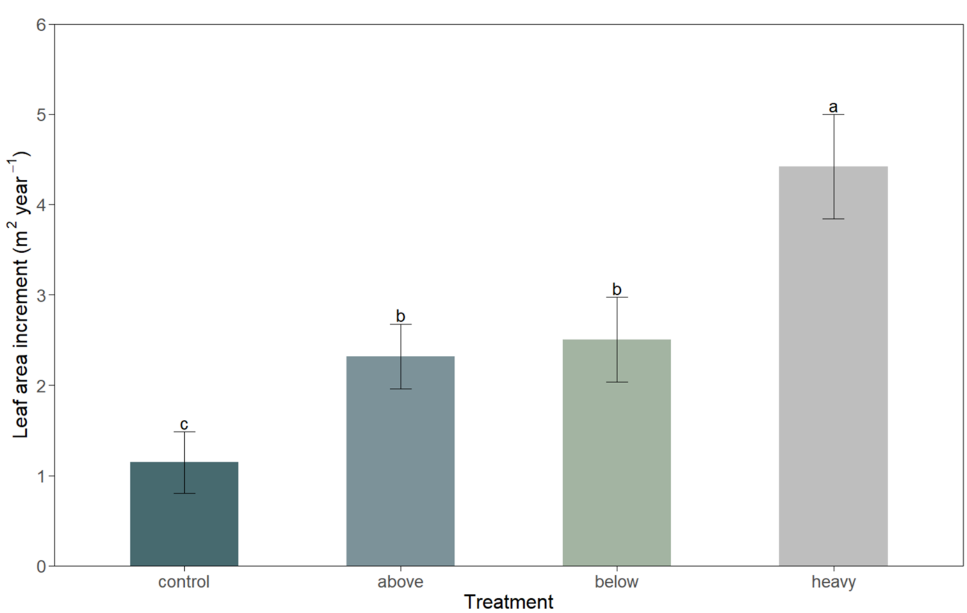


Fig. 5 Mean annual leaf area increment of the dominant trees (300 largest trees ha^{-1}) three years after thinning. Error bars represent the standard error of the four blocks. Bars that have letters in common do not differ from each other ($p > 0.05$)

Table 7 Leaf area-to-sapwood area ratio (A_L:A_S) in two different positions in the trunk i.e. at breast height and at the start of the living crown, in 2020 and 3 years after thinning (2023) for all the retained trees after thinning and the dominant trees

Position	Treatment	A_L:A_S			
		All trees		Dominant trees	
		2020	2023	2020	2023
Breast height	Control	0.122 bc	0.152 d	0.180 a	0.170 c
	Above	0.120 c	0.165 c	0.163 c	0.181 b
	Below	0.136 ab	0.172 b	0.172 b	0.184 b
	Heavy	0.144 a	0.203 a	0.160 c	0.208 a
Start of the living crown	Control	0.204 bc	0.259 c	0.271 a	0.259 c
	Above	0.201 c	0.282 b	0.253 c	0.282 b
	Below	0.221 ab	0.282 b	0.262 b	0.282 b
	Heavy	0.230 a	0.325 a	0.249 c	0.324 a

Values in the same column followed by the same letter are not significantly different ($p > 0.05$)

0.001), but not moderate thinning from below ($p > 0.200$) (Table 7), due to the changes in diameter distribution. In comparison of the dominant trees only, the control presented the highest A_L:A_S at breast height and at the start of the living crown in 2020 ($p < 0.05$) (Table 7). However, three years after thinning the thinned treatments had a significantly higher A_L:A_S ratio compared to control, in both positions of the trunk (breast height and start of the living crown) ($p \leq 0.0001$). Furthermore, the heavy thinning had a significantly higher ratio than the moderate thinning treatments ($p < 0.0001$).

Leaf area index (LAI)

Stand leaf area index (m^2 m^{-2}), estimated from direct measurements (Gower et al. 1994; Goude et al. 2019), and considering only the retained trees after thinning, was significantly higher for the control in comparison to the thinned treatments, both in 2020 (2.75 m^2 m^{-2}) and in 2023 (3.35 m^2 m^{-2}) (Table 8). The control was followed by the moderate thinnings from below and from above, which did not differ significantly from each other ($p > 0.900$), and heavy thinning from below. The latter presented the lowest LAI in both measurement periods 0.98 m^2 m^{-2} and 1.57 m^2 m^{-2}, respectively.

Height-to-diameter ratio (HDR) and live crown ratio (LCR)

HDR did not differ between treatments at the time of the first measurement in 2020, before thinning ($p = 0.403$) (Fig. 6a). However, we found a significant effect on HDR already three

Table 8 Leaf area index (LAI) in 2020 and three years after thinning (2023), considering only the retained trees after thinning

Treatment	LAI (m^2 m^{-2})	
	2020	2023
Control	2.75 a	3.35 a
Above	1.78 b	2.48 b
Below	1.86 b	2.51 b
Heavy	0.98 c	1.57 c

Values in the same column followed by the same letter are not significantly different ($p > 0.05$)

years after thinning, in 2023 ($p = 0.004$). The heavy thinning from below treatment presented the lowest mean HDR of 0.83 and differed significantly to the control (1.00), moderate thinning from above (0.99) and moderate thinning from below (0.93). The other treatments did not differ from each other.

Similarly, there were no differences in LCR in 2020 for the same set of trees (Fig. 6b). However, in 2023, heavy and moderate thinnings from below presented the highest mean LCR (0.50 and 0.48, respectively) and differed to the control ($p < 0.002$), but not to moderate thinning from above ($p > 0.1$).

Shoot length

There was no thinning effect in shoot length in 2021 and 2023. We only found a difference between treatments in 2022 ($p = 0.015$), with the control presenting a significantly higher ($p = 0.013$) mean shoot length (44.2 cm) than the heavy thinning from below (28.3 cm), but not differing to the moderate thinnings from below (39.9 cm, $p = 0.817$) and above (31.5 cm, $p = 0.220$).

Discussion

Allocation patterns

In future climate scenarios, with a shift towards increased temperature and reduced precipitation during the growing season, thinning can be a way to increase resources for the retained trees. This is why climate change adaptations for boreal forests must include mid-rotation measures. In our study we highlight the initial growth response after thinning in Scots pine stands, and our results show that already after three years, competition release has shifted the biomass allocation within trees towards an increased stem wood production, as well as an increase in leaf area increment and A_L:A_S. The trees in the heavy thinning invested more in diameter growth, as opposed to height growth, than the lower intensity thinning and unthinned treatments. It was further confirmed by the significantly higher dbh increment for the

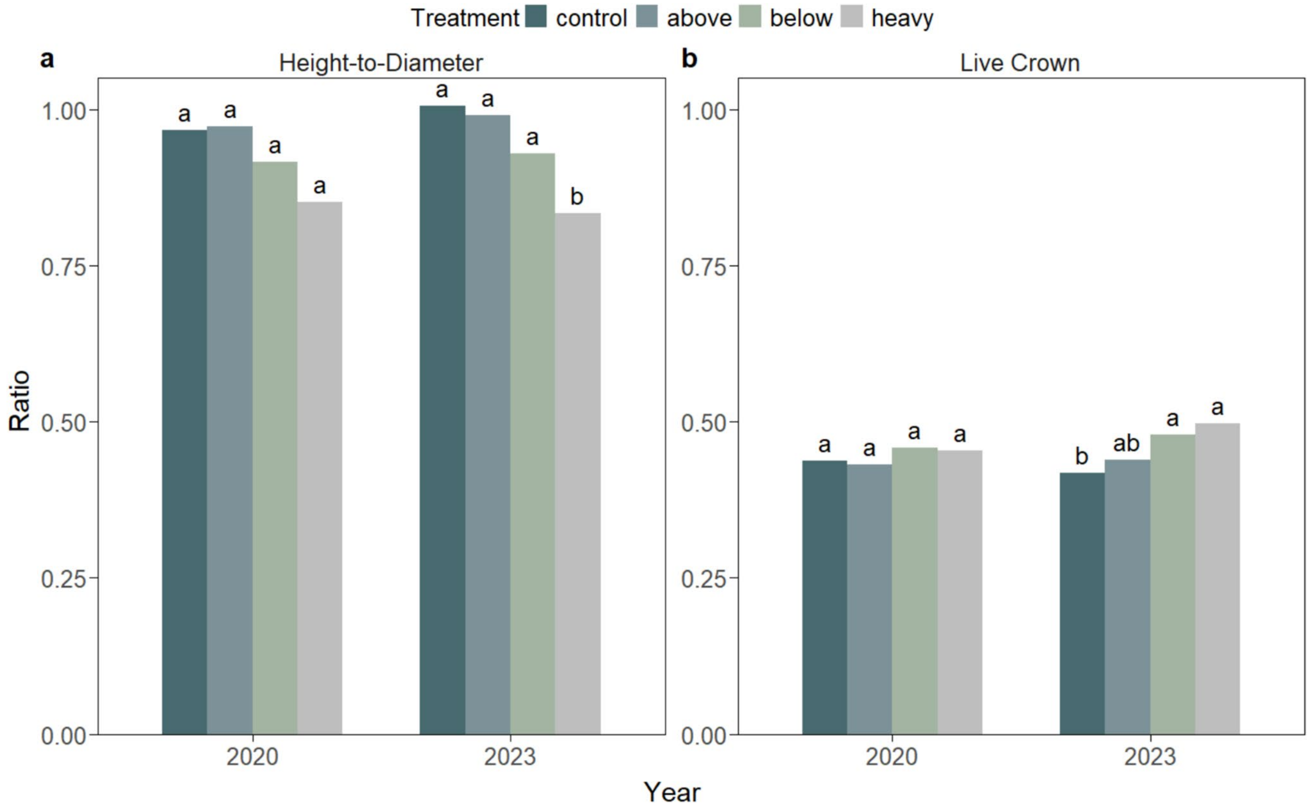


Fig. 6 Mean height-to-diameter ratio (HDR, **a**) and live crown ratio (LCR, **b**) for the sample trees* before thinning (2020) and three years after thinning (2023). Bars that have letters in common within the same year (2020 or 2023) and variable (HDR or LCR) do not differ from each other ($p > 0.05$). *The sample trees used here were present in both assessments

300 largest trees ha^{-1} in the heavy thinning from below in comparison to the other treatments. The initial response to heavy thinning seems to be a disproportional investment in stem growth, resulting in a decrease in height-to-diameter ratio, HDR, which is further confirmed in other studies in plantations of Pinus species (Deng et al. 2019; Mäkinen and Isomäki 2004b; Naidu et al. 1998). Despite the significantly higher increase in mean shoot length in 2022 for the control, in comparison to the heavy thinning from below, no difference in mean annual height growth was found for the dominant trees between any of the treatments. We also found a thinning effect on live crown ratio, LCR, with the control presenting the lowest crown ratio, similarly to what has been seen by Mäkinen et al. (2005a), in which the authors found that the mortality of the lowest branches was quicker on Scots pine stands with the highest stem density i.e. 1200 stems ha^{-1}. In our study, on average, the control had a stem density of 1798 stems ha^{-1}. Wagle et al. (2023), although working with spruce-fir forests, suggest that the increase in LCR for trees in heavier thinnings could be due to less crown recession (i.e. needle loss) than height growth in their stands, which we argue could be the case for our study, since we found no height difference between treatments within three years after thinning. This means that the thinned treatments, particularly moderate thinning from below and heavy thinning from below, are possibly retaining living branches for a longer time. Similarly, Hynynen (1995) found a thinning response on LCR in Scots pine stands five years after thinning, and we were able to detect such response within three years.

We detected a response in individual tree leaf area, LA, for the dominant trees, with all the thinned treatments presenting a significantly higher increment than the control (Fig. 5). Crown characteristics heavily influence access to resources and the capacity to compete with neighbouring trees (Pretzsch 2019), with the amount of photosynthesis a tree does being dependent on the amount of light intercepted by its leaves (Givnish 1988). Moreover, in stands with lower LAI, as is the case for the thinned treatments in our study, the intercepted radiation per unit leaf area is expected to increase, similarly to what has been found by Mencuccini and Grace (1996) in their study with Scots pine in mature stands. Thus, with more light readily available, the dominant trees in the thinned treatments seem to be increasing their leaf area in order to be more efficient, without necessarily increasing the allocation towards needle biomass production at this stage, but rather stem wood—a response which we already detected for the heavy thinning treatment within three years after thinning. Interestingly, these responses were significant despite the two blocks in Siljansfors having one growing season before thinning included in the calculations.

Specific leaf area was influenced by crown depth and age, but not thinning

We observed that specific leaf area, SLA, was not impacted by the treatments, but was significantly influenced by position in the crown (lower, middle and upper parts) and needle age. SLA increased with crown depth i.e. higher mean value in the lower third of the crown, which also has been found in other Scots pine studies (van Hees and Bartelink 1993; Goude et al. 2019; Xiao et al. 2006; Kellomäki and Oker-Blom 1981). SLA is expected to increase with lower light intensity (Kellomäki and Oker-Blom 1981), and such behaviour can be considered as an adaptive mechanism, so that the tree can maximize the capture of solar radiation in more light-limited environments e.g. the base of the crown (Blanche et al. 1985). Kellomäki and Oker-Blom (1981) suggest that this happens due to considerable light penetration in the upper part of the canopy and higher light capture in the lower parts.

Shift in leaf area-to-sapwood area ratio (AL:AS) three years after thinning

The increase observed in A_L:A_S for the dominant trees in the thinned treatments, especially heavy thinning from below, likely indicates an increased water availability promoted by thinning, as has been suggested by Giuggiola et al. (2013), when they worked in xeric Scots pine stands. Thus, deepening our understanding on the biomass allocation patterns of trees and the factors influencing them (Valinger 1993) as an effect of thinning could be relevant for future decision-making in forestry. Within a climate change scenario, in which the frequency and intensity of droughts in Europe are likely to increase (Spinoni et al. 2018), this kind of adaptive behaviour by Scots pine trees showcases the potential of this species to quickly adjust their allocation strategies under intensive forest management, at least in the short-term. It is important to note that such benefits may not hold in the long-term, unless further competition release occurs e.g. for dealing with drought specifically, Sohn et al. (2016a) recommend shorter thinning intervals. Additionally, such responses may differ depending on site-specific characteristics. For example, forests in the southern-most region of Sweden, where maximum summer temperatures are the highest, are generally considered more prone to drought damage risks (Aldea et al. 2024; Ogana et al. 2024) than the central (the case for our study sites) and northern regions. Thus, the advantages derived from thinning, in terms of drought stress mitigation, may be even more prominent in lower water availability sites (Sohn et al. 2016b).

Effect of thinning form (above or below) and thinning intensity on above-ground biomass

Within three years after thinning, thinning form did not affect standing above-ground biomass, dbh and leaf area increment of the dominant trees, as both moderate thinnings from above and below, which had the same amount of basal area removal, performed similarly so far. Choosing one thinning form over the other would rely on one's objective. Performing thinning from above as the first commercial thinning could be an economically viable option due to the removal of the largest trees, which is generally performed to a lower cost and, thus, generating a higher income at an early stage, especially in systems with long rotations (Nilsson et al. 2010). From an economic standpoint, subsequent thinnings from above would result in longer rotation time or lower gains in the final felling (Nilsson et al. 2010). From an ecological perspective, the longer rotations could help preserve biodiversity e.g. lichen community composition and ectomycorrhizal mushrooms (Petersson et al. 2023; Roberge et al. 2016), in addition to promoting deadwood through natural mortality and increasing the size of retention trees in final fellings (Koskela et al. 2007).

Stronger thinning intensity, as represented here through heavy thinning from below, presented a bigger response, both in terms of higher individual tree dbh and stem wood dry weight increment, but also in the significant reduction in the total standing above-ground biomass in comparison to the unthinned and moderate thinning treatments. While working with a long-term experiment in Sweden, Nilsson et al. (2010) found a small but significant decrease in net volume production for Scots pine in a one-time heavy thinning treatment in comparison to the control. Similarly, Bianchi et al. (2024) have shown that the heavy thinning significantly reduced total carbon intake and wood production of Scots pine in Finland in the long-term, which is one of the major disadvantages of heavier thinnings, as the one we have in our study.

Conclusions

The first commercial thinning in Scots pine in the boreal forests usually happens from 30 to 50 years after regeneration, and the stands are planned for further growth and thinnings in many decades after this before final harvest. Our findings show that Scots pine trees responded to thinning within three years and that such response primarily happened in terms of dbh, stem wood dry weight and leaf area increment. The early thinning response in these Scots pine stands demonstrates how competition release can be an increasingly important management practice in forests exposed to stress or resource limitations. Thus, further research evaluating how thinning affects ecophysiological parameters, such as transpiration and water use efficiency, will be beneficial for an increased understanding of tree behaviour in response to drought periods of varying levels and other extreme events.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-025-01788-z.

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Availability of data and materials Plot level data summary in this study is available in https://www.silvaboreal.com, accessed on 21 August 2024. Other data can be made available upon request to the corresponding author.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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