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Growth response of Norway spruce trees to selection harvest in continuous cover forestry stands on drained boreal peatlands

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ABSTRACT

Continuous cover forestry (CCF) has less environmental impacts than rotation forestry, but knowledge on growth responses of different tree cohorts to selection harvesting is scarce. In this study, tree-ring data of dominant and suppressed Norway spruce (*Picea abies* (L.) H.Karst.) trees representing CCF-managed drained peatland stands from north to south boreal forests were analysed with respect to selection harvest to basal area of 12–13 m^2/ha using generalized additive mixed models (GAMM). The first statistically significant impacts were seen in suppressed trees one year after thinning. In four out of five sites, the suppressed trees displayed significant impacts one year earlier than the dominant trees. In three sites, the post-thinning ring-widths of the suppressed trees were up to three to four times the predicted widths, three or four years after thinning, while dominant trees showed a 50–100 % increase. However, the growth response of the basal area increment of suppressed trees was smaller, since the suppressed trees were on average smaller than the dominant trees. Thus, the lower growth after selection cutting previously observed at stand-level studies of CCF is likely due to the removal of a large proportion of large productive trees, rather than a small or delayed response of suppressed trees. It seems that the elevated water table in the harvested plots through decreased evapotranspiration did not limit the post-harvest growth release in the case of the selection harvest experiment of the present study. If the elevated water table had any effect on the growth release, this mechanism was probably less counterproductive for suppressed trees which also benefitted from improved light conditions.

1. Introduction

Continuous cover forestry (CCF) is silvicultural system that avoid clearcuttings, promote stand structural diversity and mitigate negative environmental impacts associated to logging (Pommerening and Murphy, 2004; Nieminen et al., 2018; Mason et al., 2022; Laudon and Hasselquist, 2023). The overall area of forests managed by CCF, resulting in uneven-aged stand structures, in 31 European countries is approx. 40 million ha nowadays. This figure translates into ~ 22 percent of the forest area. Excluding Finland and Sweden, the proportion of CCF-managed forests appears to increase to ~ 30 percent (Mason et al., 2022). In these two countries CCF has only been accepted as a management approach quite recently (Mason et al., 2022; Pukkala et al., 2012). Yet, CCF is gaining popularity among forest owners and the need for new information on this alternative forest management method is increasing (Hänninen et al., 2020; Juutinen et al., 2020). Furthermore, CCF is suggested to be a management regime that results in lower greenhouse gas emissions on productive peatland forests than rotation forestry with clearcuttings (Nieminen et al., 2018; Shanin et al., 2021; Ahtikoski et al., 2022; Korkiakoski et al., 2023). In Finland, especially, drained peatlands play a significant role in operational forestry with ca. 20 percent coverage of the total area of productive forest land (Korhonen et al., 2021). However, large areas of boreal peatlands have been drained for forestry also in other northern European countries including Sweden, Russia, and Estonia (Nieminen et al., 2018). According to the latest national greenhouse gas inventory of Finland, the soils of drained peatland forests are an increasing source of emissions; in the peatlands of southern Finland soil greenhouse gas emissions are already larger than the carbon sink of the trees (Alm et al., 2023). Thus, forest management practices that may reduce soil emissions are needed while Finland is aiming to achieve legally binding climate targets incl. carbon neutrality target by 2035. This need calls for more detailed studies on management practices, with a focus on CCF on boreal drained peatlands.

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Table 1
Characterisation of drained peatland sites by the name of the site, its acronym and coordinates, the municipality where the site is located, the site type (following the classification of Vasander and Laine, 2008), timing of the harvest and sampling, and the pre-harvest basal area (Pre-BA). Site types Rhtkg I and II refer to Herb-rich Type I and II, Mtkgl I and II refer to *Vaccinium myrtillus* types I and II, and Ptkgl I refers to *Vaccinium vitis-idaea* type I. See text for more details.

Site name	Acronym	Latitude °N	Longitude °E	Municipality	Site type (Vasander and Laine, 2008)	Date of harvest	Date of sampling	Pre-BA m^2/ha
Lintupirtti	NORTH	66.18	25.66	Tervola	Rhtkg I	Mar 2015	Jun 2021	22–32
Vaarajoki	MID1	63.38	28.78	Juuka	Mtkg I – Ptkg I	Feb 2017	Sep 2021	19–24
Havusuo	MID2	62.54	24.57	Multia	Mtkg I – Ptkg I	Mar 2016	Jun 2021	25–31
Rouvanlehto	MID3	62.54	28.59	Heinävesi	Mtkg I, Mtkg II, Rhtkg I–II	Feb 2017	Sep 2021	22–24
Paroninkorpi	SOUTH	61.01	24.75	Janakkala	Rhtkg II	Feb 2017	Jun 2021	22–31

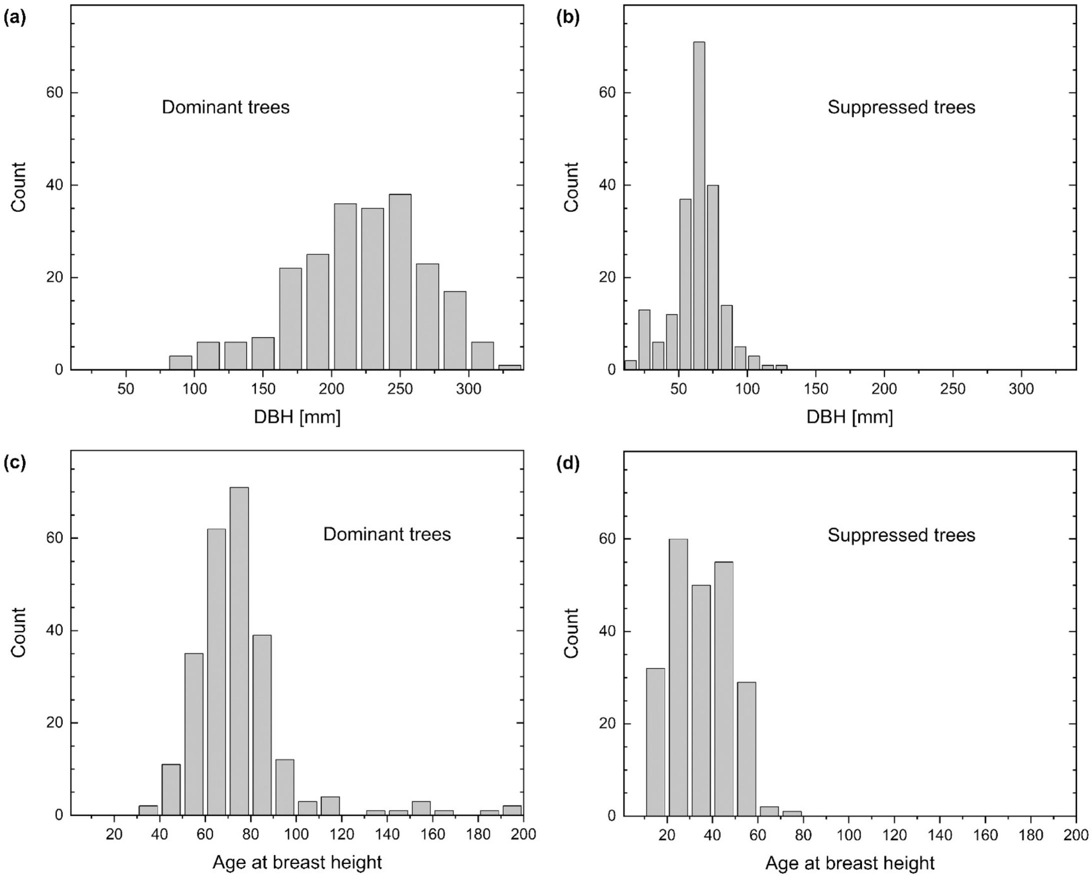

Fig. 1. Histograms of frequency distributions of sampled trees given as breast height measurements of size (a–b) and age (c–d). Diameters at breast height of dominant and suppressed spruce trees were measured in the field. Ages are determined from the number of identified tree rings as identified from dendrochronological samples.

Norway spruce stands on mineral soils are subjected to uneven-aged management with different harvest regimes. In a study at two sites in central and northern Sweden, the plots thinned from above were found to show consistently higher volume increments than plots thinned from below (Lundqvist et al., 2007). In Norway spruce stands in southern Norway, the long-term timber production in uneven-aged stand was measured to be 95 % of the even-aged stands (Nilsen and Strand, 2013). Bianchi et al. (2020a) compared the growth of Norway spruce in altogether 42 rotation forest management (even-aged, after first commercial thinning) and CCF (single-tree selection harvests) stands on mineral soils in southern Finland. The trees of CCF stand were found to have a consistently lower growth, which was explained by stronger effects of competition variables (diameter at breast height, tree basal area, live crown ratio (calculated as the ratio between the length of the stem with live crown), total height of the stem, height-diameter ratio (calculated between the total height and diameter at breast height)) in their analysis. Previously, Shanin et al. (2016) built an ecosystem simulation model calibrated against experimental data collected from a set of twenty managed, uneven-aged Norway spruce plots in southern Finland to model the volume of harvested timber and the stem volume growth. Lower harvest intensity increased the net ecosystem production, mean annual volume growth and indicators of sustainable management in their model simulating CCF regimes. Kellomäki et al. (2019) used a gap-type forest ecosystem model to simulate the timber yield in boreal Norway spruce stands. They found that the mean annual carbon uptake, volume growth, carbon stock in trees and harvested timber were nearly the same regardless of the management option (even-aged or uneven-aged). However, the uneven-aged management appeared very sensitive to the success of natural regeneration and ingrowth of seedlings. While the previous studies have concentrated on growth responses of trees growing on mineral soils, Juutinen et al. (2021) used the model of Shanin et al. (2016) to demonstrate that CCF provided a higher profit than rotation forest management (RFM), especially with a 15-year harvest interval, in drained peatland forests dominated by Norway

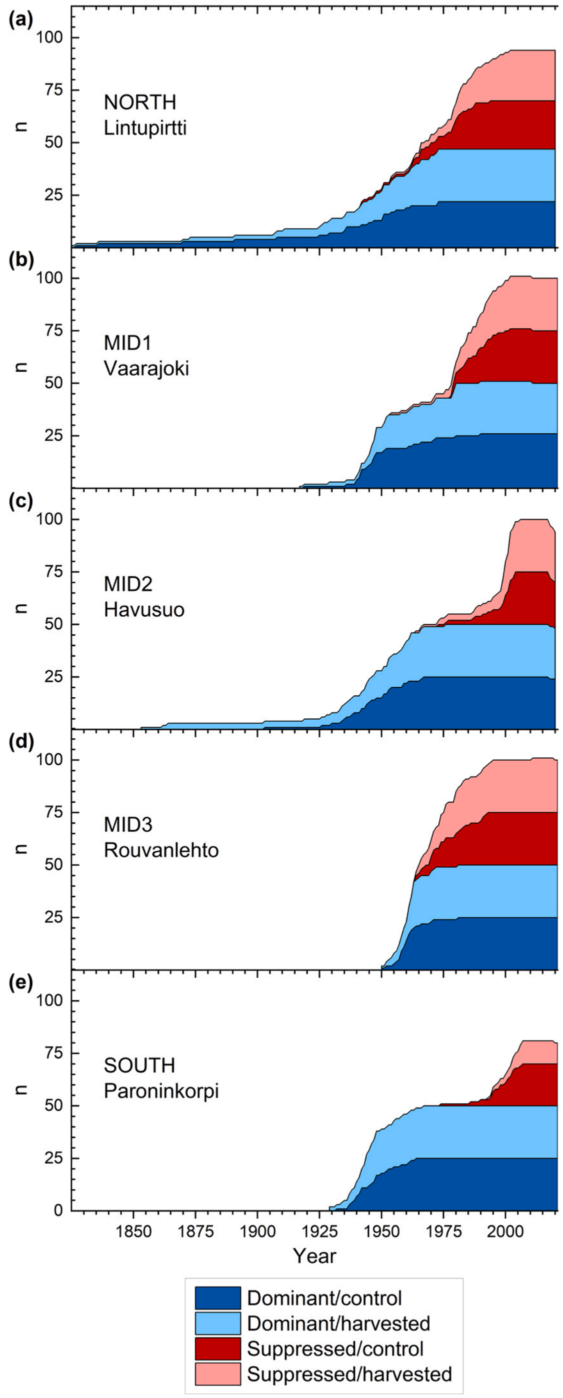

Fig. 2. Temporal changes in the sample size of tree-ring series shown for dominant and suppressed trees for harvested and control plots at each site.

spruce.

Collectively, Norway spruce stands managed by CCF appear to generally exhibit lower wood productivity in comparison to RFM, whereas CCF seems to maintain the economic profitability and multifunctionality of the forests considerably better than RFM (Lundqvist et al., 2007; Nilsen Strand, 2013; Hynynen et al., 2019; Bianchi et al., 2020a, 2020b). The observed deviations in wood productivity, on the other hand, may be affected by differences in the volume of growing stock and intensity of harvesting in different management systems (Hynynen et al., 2019; Kellomäki et al., 2019; Shanin et al., 2016) or by the types of variables used in the models (Bianchi et al., 2020a), between the studies. In general, tree size inequality may reduce forest productivity, since it may have negative effects on light use efficiency (Bourdier et al., 2016). However, competitive interactions in spruce are known to be more related to size-symmetric competition indicating that interaction might be more associated with competition for below-ground resources (Mina et al., 2018). Thus, reduced competition after selection harvesting (from all size classes) may benefit all size cohorts, while competition is related to resource depletion in size-symmetric competition (Cordonnier and Kunstler, 2015).

Apart from a few investigations (Juutinen et al., 2021; Lehtonen et al., 2023), the harvest responses in Norway spruce growth have so far been analysed merely on stands growing on mineral soils (Andreassen and Tomter 2003; Lundqvist et al., 2007; Nilsen Strand, 2013; Hynynen et al., 2019; Bianchi et al., 2020a, 2020b). Given the role of the peatland forestry as an essential component of operational forestry in the boreal region (Paavilainen and Päivänen, 1995) and knowing that 20 % of the most productive sites on drained peatlands may be regenerated or converted to CCF soon (Lehtonen et al., 2023, see their Supplementary Tables S6 and S7), there seems to be an apparent gap in knowledge of the harvest response and its characteristics especially with regards to CCF stands dominated by Norway spruce. It is essential to note that the harvesting of trees itself alters the hydrology of the drained peatland sites markedly raising the water table over the following years (Jutras et al., 2006; Hökkä et al., 2008; Leppä et al., 2020). This effect bears relevance also to CCF stands (Juutinen et al., 2021; Laudon and Hasselquist, 2023; Mäkipää et al., 2023) and impairs the comparability of growth data between the peatland and mineral sites. To this end, up-to-date records of tree growth are needed to demonstrate both the natural and managed variability in corresponding stand conditions to disentangle the climate-driven effects from the harvest response. This target is fulfilled here by producing an assemblage of Norway spruce tree-ring data from drained peatland sites from northern to southern Finland, between 66°N and 61°N, and hence a transect representative of boreal conditions. Previously, Lehtonen et al. (2023) analysed altogether 44 dominant and suppressed Norway spruce trees from a drained peatland forest site in southwest Finland. The results indicated ecophysiological responses of suppressed trees immediately after the CCF harvesting and increases in diameter growth two years later, with even stronger response in growth 3–4 years after the cutting.

The objective of this study was to compare harvest responses of dominant and suppressed CCF trees growing on drained peatlands. Our data was collected from drained peatland CCF stands 4–6 years after selection cutting with a target post-harvest basal area of 12–13 m^2 ha^{-1} (Laurila et al., 2021), in addition to data representing the unmanaged stands obtained from control plots. Given the sensitivity of CCF to the success of ingrowth of seedlings and suppressed trees, the analyses were carried out separately for tree-ring records representing the growth of dominant and suppressed trees. Our stands were harvested only recently (between 2015 and 2017), the post-thinning period thus providing quantifications of short-term effects on wood productivity under the selection harvesting regime. In particular, the comparisons between the harvest responses of dominant and suppressed trees were anticipated to throw light on the vitality and growth potential of trees that are released from competition for light and other resources as facilitated by CCF.

2. Material and methods

2.1. Peatland study sites

Five sites belonging to the network of intensively studied drained peatlands stands with continuous cover forestry (CCF) experiments in Finland were visited for tree-ring sampling and to update the tree measurements (Table 1). These sites represent boreal conditions with the purpose to study the effects of CCF and clearcutting on ecosystem processes, as recently described in details by Laurila et al. (2021). The sites represent fertile Norway spruce (*Picea abies* (L.) H.Karst.) dominated peatland forests from north to south boreal forest zones. From

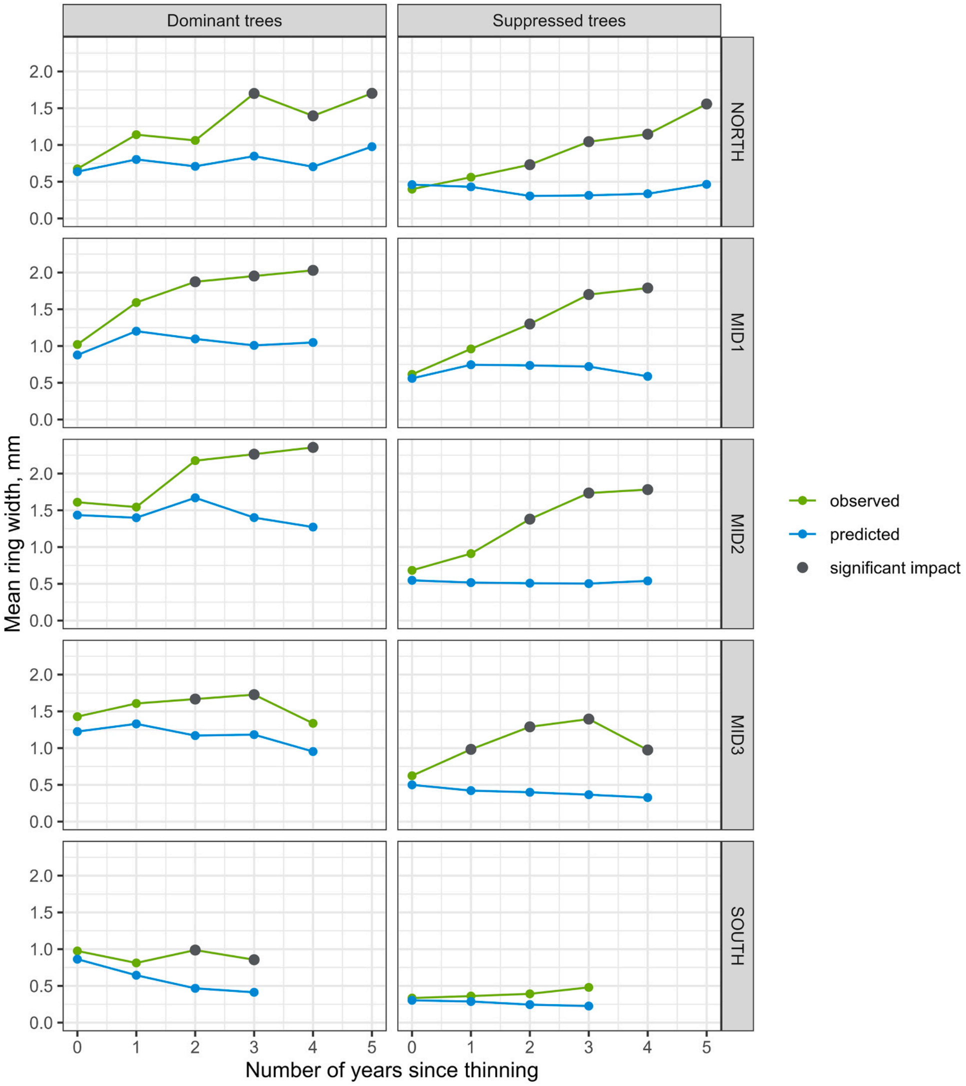

Fig. 3. Predicted and observed averages of ring width over the trees in the harvested plots after thinning. The black dots indicate statistically significant differences between the observed and predicted widths at 5 % significance level.

north to south these sites are Lintupirtti, Vaarajoki, Havusuo, Rouvanlehto, and Paroninkorpi, referred to hereafter as NORTH, MID1, MID2, MID3 and SOUTH, respectively. The northernmost site (NORTH) is located near the Arctic Circle. According to classification of the drained peatland forest types (Vasander and Laine, 2008), this site belongs to Herb-rich type I, which means that the bottom layer vegetation is sparse with common species from the family *Mniaceae* with scattered peat mosses (*Sphagnum*) on wet surfaces. Common species in the field layer are tall herbs, with several fern species. The MID1 and MID2 sites are characterised by *Vaccinium myrtillus* type I and *Vaccinium vitis-idaea* type I. In the former, peat mosses are typical with gradually changes to feather mosses, the field layer vegetation showing birch and other hardwoods, *Vaccinium myrtillus* being more common than *V. vitis-idaea*. In the latter, birch is typically a co-dominant tree species. The field layer also consists of tall shrubs. The MID3 site is located at the same latitudinal position as the MID2-site. It is also characterised by the *Vaccinium myrtillus* type I but also the type II and Herb-rich types I and II. In this way it differs from the more northern sites in that the bottom layer is relatively open with prevalent birch leaf litter after the peat mosses have disappeared. In the field layer, the number of dwarf shrubs may be considerable. In this respect the MID3-site resembles our southernmost site (SOUTH), which also belongs to Herb-rich type II. The stands were harvested during the late winter/early spring season (2015, 2016 and 2017), i.e. prior to growing season. The selection harvest treatments were carried out in 40 × 40 m square plots for a variety of post-harvest basal area levels, all the sites nevertheless containing plots harvested to a basal area of 12–13 m^2/ha (see Fig. S1–S5 for pre-harvest and post-harvest diameters at breast height), in addition to control plots with no harvest activity. This follows a standard randomised block design, with different treatments plus control plots. The number of plots with replicated basal area levels varied from two (MID1, MID2 and MID3) to four (NORTH) and five (SOUTH) per site. These plots (basal area of 12–13 m^2/ha and control) were sampled and used for the analyses of this study.

3. Tree-ring materials

Tree-ring samples were extracted by increment borer from dominant and suppressed Norway spruce trees at the five sites. The classification of dominant and suppressed trees was based on their canopy status, describing the position of a tree, in particular its canopy, in the forest. According to the guidelines, the tallest trees in the experimental plot are selected as the starting point. They can be classified as dominant trees, the suppressed trees being those completely overtopped by surrounding trees (Mielikäinen, 1987). Each tree was cored at breast height (1.3 m) from one side only to avoid any possible damage to the trees. The tree

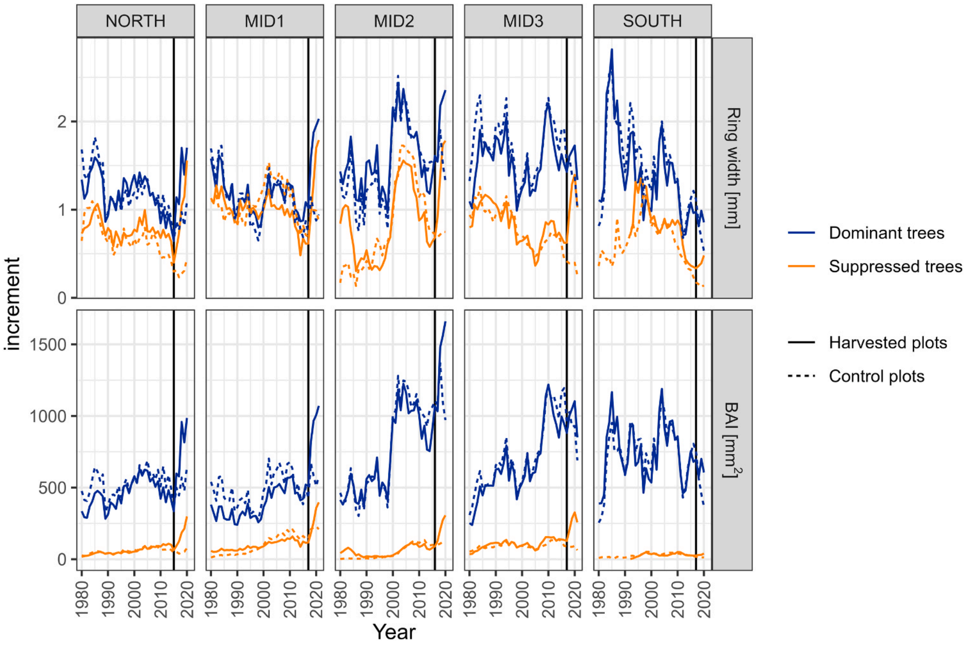

Fig. 4. Annual means of ring widths and basal area increments.

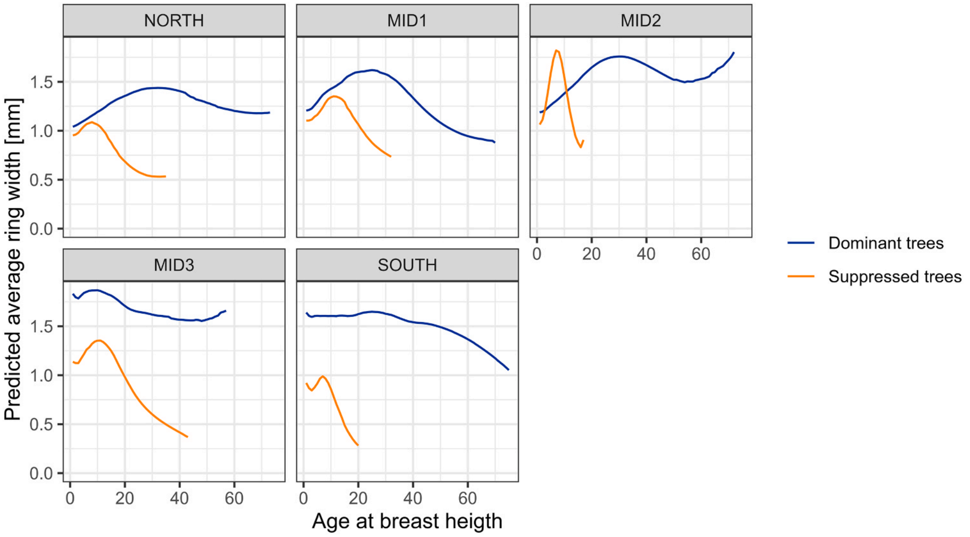

Fig. 5. Predicted ring widths from the GAMM model of the dependence of radial growth on tree age and breast-height diameter (DBH); see Supplementary Information, Eq. (1). For each age, the DBH was set to its median value over all trees in the relevant Site x Status group at that age.

stands had been measured in 2015 (MID2), 2016 (MID1, MID3 and SOUTH) and 2019 (NORTH), all trees higher than 1.3 m being marked and mapped (direction and distance from a reference point) (Laurila et al., 2021). These measurements provided the platform for the preselection of the trees to be cored. The designed protocol included 100 trees per site including 50 dominant and 50 suppressed trees half of them to be cored from the plots after selection harvest (basal area of 12–13 m^2/ha) and the other half from the control plots. In the field, however, it was recognised that some of the preselected trees had died between the field campaigns with no supplementary trees to replace the dead ones (generally avoiding trees with diameter lower than 5 cm at breast height) could be identified. As a result, the number of samples remained less than 25 for some of the site-wise categories especially in the case of suppressed trees from harvested sites. In all, tree-ring samples were collected from 477 trees representing five sites.

The fieldwork was carried out in the summer of 2021. The NORTH and MID2 sites were visited in June, whereas the fieldwork was performed at other tree sites (MID1, MID3 and SOUTH) in September. This means that the most recent tree-ring measurements to be used for growth estimations varied from site to site and represented the year 2020 for our NORTH and MID2 and the year 2021 for MID1, MID3 and SOUTH sites. The NORTH-site was harvested in 2015 and the thinning effects could thus be studied from tree-ring samples of that site over the post-harvest interval of six years. For other sites this interval is five years.

The cross-sectional surfaces of the tree-ring samples were sanded down and scanned for digital images from which the series of tree-ring widths were measured using the CooRecorder software (Maxwell and Larsson, 2021), except in the case of samples from the NORTH site, which were measured under a light-microscope using a computer-aided measuring system (Rinn, 2006). The obtained data of consecutive values were compiled into time-series of tree-ring widths and were cross-dated

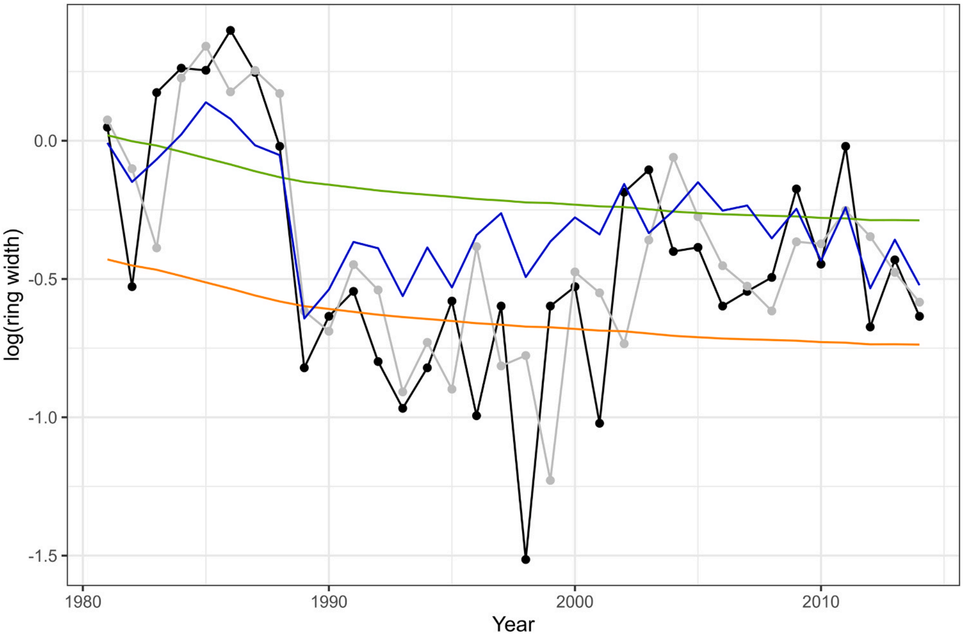

Fig. 6. Logarithms of measured ring widths of one tree (black), their predictions from our full model (grey) and various sub-models: a GAM model including only the age and breast-height diameter of the tree (orange), a GAMM model, including also the predicted tree effect ('green'), and a "calendar-year model" where the average residual of the year from the control plots is added to the GAMM prediction (blue).

both visually and statistically (Holmes et al., 1986; Rinn, 2006) prior to chronology construction and dendroclimatic analyses.

4. Statistical analyses

Generalized additive mixed models (GAMM) were used to analyse the harvest response. The response was analysed based on the differences of the ring widths measured after thinning to their predicted values, the expected ring widths under the counterfactual scenario of no thinning. The statistical models used in prediction were fitted separately for each site and status ("dominant" or "suppressed"), excluding the values representing the post-harvest period. The models included the impacts of tree age and breast-height diameter on radial growth, a tree-level random effect predicted from the pre-harvest data, and the annual growth variation estimated from the post-harvest ring widths measured in the control plots. Furthermore, the latest pre-harvest ring width of the target tree was utilized in the prediction, based on temporal autocorrelations of the model residuals estimated from the pre-harvest data.

Thus, the predictions of radial growth for the post-harvest period aimed at quantifying the tree-specific ring widths that would be expected without the thinning effect, taking into account the ages, sizes, and previous growth of the trees, as well as inter-annual growth variation in the control plots during the post-harvest period. The details of models and methods used in prediction are explained in Supplementary Information. As an aside, we note an alternative approach to detecting the harvest response simply as the ratio of the growth after thinning to the growth before thinning. Such an approach would not, however, account for natural variability between any two periods, inherent in the boreal ecosystems and affecting tree-ring data on timescales relevant to the harvest response. Accordingly, this approach was not pursued further.

To stabilize the variance-to-mean relation and to ensure non-negative increment predictions, the models were developed for log-transformed ring widths. Also the statistical significance of differences between the measured and predicted ring widths was evaluated in the log-scale based on a linear model with standardized difference of the measured and predicted log-widths as the response variable and all interactions of site, status, and number of years since harvest as categorical predictors. Standardization was required to avoid heteroskedasticity of the response variable, due to between-trees and between-years variation in precision of predictions. The precision is affected, for instance, by the length of the ring series (precision of tree-effect prediction), within-tree variance and autocorrelation in ring widths, and number of years since harvest (the smaller the better, since the latest pre-harvest ring width was used in prediction). The standardization was based on cross-validated predictions from the pre-harvest period (details in Supplementary Information).

The significance of the model mean from 0 was tested separately for each combination of site, status, and years since harvest, leading to t-tests of 60 individual null hypotheses. To counteract the multiple testing problem, we applied the conservative Bonferroni correction.

To quantify the thinning effect, we also computed the averages of observed ring widths and their back-transformed predictions for each combination of site, status, and years since harvest. On top of the conventional bias-correction of back-transformed predictions associated with the log-transformation (e.g., Miller, 1984), we applied a further correction, again based on cross-validated predictions from the pre-harvest period (details in Supplementary Information). The thinning effect was also quantified in the scale of basal area increments by applying transformations

$$\mathrm{BAI}_{i,t} = \pi\left[\left(\sum_{t'=1}^{t} w_{i,t'}\right)^2 - \left(\sum_{t'=1}^{t-1} w_{i,t'}\right)^2\right],$$

where $w_{i,t}$ is the width of the t'th ring of tree i and $\mathrm{BAI}_{i,t}$ the corresponding basal area increment.

The data and R-code are available at 10.5281/zenodo.15396269.

5. Results

5.1. Descriptive statistics

According to tree-ring samples, dominant trees were larger (Fig. 1a) and older (Fig. 1b) than suppressed trees (Fig. 1b, d). For dominant trees, the diameter at breast height averaged 220 mm (median = 223 mm), while the mean for suppressed trees was as low as 63 mm (median = 64 mm). On average, the tree-ring samples of dominant trees contained 74 rings (median = 72), while the suppressed trees had 35 rings (median = 33). The rings of dominant trees averaged 1.4 mm, while those of suppressed trees averaged 0.9 mm. Most of the suppressed trees were relatively young, but 85 % of them contained at least 25 rings (Fig. 2). The oldest trees were found at the northern sites. At our NORTH and MID2 site, a small number of trees had rings dated to the 19th century. The longest tree-ring sequence (from the NORTH site) covered the years from 1825 to 2020.

5.2. *Response to selection harvest*

Except the SOUTH site, observed post-harvest ring-widths of the suppressed trees were up to three to four times the predicted widths three or four years after thinning (Fig. 3). For the dominant trees, the observed widths were up to 50–100 % greater. The first significant impacts were seen in suppressed trees of site MID3 one year after thinning. In NORTH, MID2, and MID3 sites, the suppressed trees displayed significant impacts one year earlier than the dominant trees.

5.3. *Basal area increments*

Conversions of the ring-width data to basal area increments demonstrate the difference between the production of dominant versus suppressed trees (Fig. 4). Following the lower size of the stems, the increase in post-harvest radial increment of suppressed trees that equals or even exceeds that of dominant trees in control plots by the end of the study period, at least on the NORTH, MID1 and MID2 sites, did not result in similarly equal growth values in terms of basal area increment.

5.4. *Predictions of radial growth*

The assessment of harvest response relied on validity of model predictions as ring widths that would have been observed without thinning. According to our cross-validations, predictions utilizing tree age, breast-height diameter, predicted tree effect, year effect from the control plots, and the previous years' radial increment, explained on average 80 % of the pre-harvest variation in logarithmic ring widths of the harvested plots (for more details, see Supplement 1 for Table S2).

According to the fitted GAM's, average ring widths of dominant trees generally start to decrease at the age of about 30–40 years, while for suppressed trees this decline starts before ten years of age (Fig. 5). However, causal interpretation of these models is difficult due to the strong inherent correlation of size and age. On the other hand, this model component had a relative minor role in our predictions. Fig. 6 provides an example illustrating all components of the prediction models.

6. Discussion

Selection harvesting resulted in growth responses of both suppressed and dominant Norway spruce trees with a very short delay, one year after selection harvesting, and the post-harvesting growth values were up to three to four times the predicted growth. This result of the tree-level growth response to selection harvesting is consistent with recent findings that a temporal lag in growth response was negligible (Bianchi et al., 2020a). According to our results, the response of ring width growth of suppressed trees was higher than that of dominant trees. However, the response of basal area increment of suppressed trees was smaller, since the suppressed trees were on average smaller than dominant trees (Fig. 1). Thus, the lower growth after selection cutting previously observed in stand-level studies of CCF (e.g. Lundqvist et al., 2007; Hynynen et al., 2019; Bianchi et al., 2020a, 2020b) is likely to be due to the removal of a large proportion of large productive trees, rather than due to a small or delayed response of suppressed trees.

Our investigation revealed the influence of size-asymmetric competition between Norway spruce trees when the suppressed trees displayed considerably lower growth rate throughout in comparison to dominant trees. Size-asymmetric competition means that the resources available for trees in a stand are not taken proportionally to the tree size, but by increasing proportions by larger individuals (e.g. Peltoniemi and Mäkipää, 2011). An exception in this comparison was our MID1 site where the tree-ring widths of the dominant and suppressed trees did not indicate any noticeable differences in their growth levels (see Fig. 4). Size-asymmetry is known to be more pronounced on light-limited fertile sites than on poor sites, where competition for nutrients is prevailing limiting factor (e.g. Pretzsch and Biber, 2010). In our study, the pre-harvest basal area was lowest for the MID1 site (Table 1), which means that light competition before the treatments was modest on that site and growth might be predominantly limited by soil nutrient availability and moisture.

Our study sites were harvested to a basal area of 12–13 m^2/ha, suggesting that the growth reducing effects from soil wetting may have been largely mitigated by evapotranspiration. In other words, the water table that elevated in the harvested plots through decreased evapotranspiration (Leppä et al., 2020) may not in any case have critically impaired the post-harvest growth. It would follow that the harvest response we observed is expected to primarily represent the release from resource competition, rather than from compound effects from water relations. This evaluation is judged by the results by Juutinen et al. (2021), who coupled the growth of Norway spruce to fluctuations in the water table in their recent model of CCF. In their most profitable CCF alternative, the water table could be kept below the critical level with no need for ditch network maintenance, by using the effects from evapotranspiration (see Leppä et al., 2020). Based on these results, Juutinen et al. (2021) concluded that the ditch network maintenance was needed to promote stand growth on drained peatlands only when the post-harvest basal area was below 10 m^2/ha. The response we observed to selection harvesting can be compared to post-harvest growth on the control plots, where the growth of suppressed trees continued at markedly low level. Although our study did not involve post-harvest basal areas other than 12–13 m^2/ha, the growth response to less intensive selection harvest could be expected to remain at a level intermediate to that of our harvested and control stands. Additional quantification of growth under different selection harvest intensities remains an important target for future work.

The growth release of suppressed trees was more vigorous in our large dataset than in those by Lehtonen et al. (2023). The first significant impacts were seen in suppressed trees of MID3 sites one year after thinning. According to Lehtonen et al. (2023), whose data originated from a drained peatland site in southwest Finland, the growth response of the suppressed Norway spruce to harvesting (from mean basal area of 27 m^2/ha to mean basal area of 11 m^2/ha) occurred after an average delay of two years, with strongest values found three to four years after the selection harvesting.

The suppressed trees displayed significant impacts one year earlier than the dominant trees, in NORTH, MID2, and MID3 sites, which could demonstrate that their resource supply was less altered by harvesting. Light availability is directly affected by the reduction of standing trees and this effect is more pronounced in the lower canopy layers than in the prevailing canopy layer of dominant trees. It has also been observed that asymmetric competition is commonly observed on Norway spruce stands and larger trees tend to dominate resource use on light-limited sites, but in nutrient-limited conditions competition is more symmetric (e.g. Pretzsch and Biber, 2010). On drained peatlands in southern Finland, nutrient deficiencies may limit the growth of trees and the K storage of the peat soil is low in comparison to the nutrient demand of the trees (Laiho et al., 1999). The slow growth response of dominant trees could likewise be explained by reduced evapotranspiration if the roots of these trees were more affected by elevated water table, especially because the harvesting has been shown to alter the water table more profoundly in the southern than in northern Finland (Leppä et al., 2020).

Regarding the suppressed trees, our findings are consistent with those of Lehtonen et al. (2023) who, using stable carbon isotope data, found a non-delayed increase in carbon uptake for their suppressed Norway spruce trees after the selection harvesting. In our data, such an immediate carbon uptake could contribute to the observed harvest response. The foregoing increase in carbon uptake observed for the drained peatland site in southwest Finland was inferred from ^{13}C enrichment in the post-harvest tree rings using the Farquhar equations (Farquhar et al., 1982; Francey and Farquhar, 1982). Generally, the less negative δ^{13}C values could result from increasing irradiation, warmer temperatures and/or from anomalous hydroclimatic conditions driving the combination of stomatal and photosynthetic responses. In this regard, it can be expected that thinning from above increases the incoming solar radiation when the trees harvested are close enough and tall enough to shade the suppressed ones and that this change in irradiance best explains the subsequent warming of both air and surface temperatures (c.f. Berry et al., 2013).

On the other hand, as the harvesting of drained peatland stands also elevates the water table (Leppä et al., 2020), the situation could be seen to somewhat mimic that observed previously for boreal riparian old-growth Scots pine trees of which carbon uptake and growth were reduced following the rise in lake level despite of positive trends in irradiance and temperature over the same period (Helama et al., 2018). In contrast to the ^{13}C enrichment in the post-harvest tree rings observed for suppressed Norway spruce trees (Lehtonen et al., 2023), this comparison would reinforce the interpretation of largely non-stomatal limitations for photosynthesis in similar CCF trees. Correspondingly, the value of irradiance has been emphasised for Norway spruce sapling density and thus for the ingrowth of the CCF stands (Vencurik et al., 2020). As the growth of dominant trees did not increase as vigorously as that of suppressed ones and the isotopic analyses focussed on suppressed trees (Lehtonen et al., 2023), the relative roles of stomatal and photosynthetic responses behind the less intensive response in dominant trees could not be similarly inferred but the investigation remains a target for the future.

CRediT authorship contribution statement

Samuli Helama: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Juha Heikkinen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Aleksi Lehtonen:** Writing – review & editing, Funding acquisition. **Raisa Mäkipää:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Conceptualization.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122816.

Data availability

Manuscript includes statement: "The data and R-code are available at https://doi. org/10.5281/zenodo.15396269."

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