



Release of retained oaks in Norway spruce plantations. A 10-year perspective on oak vitality, spruce wood production and ground vegetation

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ABSTRACT

This study explores the decade-long effects of release cutting around old retained oaks (*Quercus robur* L.) in a Norway spruce (*Picea abies* L. Karst) stand that was 33 year old when thinned. The impacts on both nature conservation values and spruce wood production were evaluated in a randomized block design. To release oaks from competition, stems of Norway spruce were cut around 33 oaks, in three different treatments: high release (HR), medium release (MR) and no release (NR). Trees within a circular sample plot (15 m radius from the oak) were measured at time of treatment and 10 years after. The treatment effects on stand development, oak vitality and understory vegetation were evaluated after ten years, using tree diameter, height measurements, oak crown and tree structure estimates as well as ground vegetation surveys. Release cutting did not impact spruce production within the sample plot, and given that there were no other obvious sources of spruce suppression in the stand, we speculate that release cutting has little to no impact at the stand scale. Oak crowns in the control plots (NR) became smaller after ten years, while the crowns expanded and colonized the gap in the release treatments. Simultaneously, the amount of dead wood in the crown increased among oaks in the control treatment, indicating dieback. Cover and species richness of vascular plants in the understory were significantly higher in the HR and MR treatments compared to NR. These results suggest that the creation of relatively wide gaps (greater than 2 m) around retained oak crowns is one efficient approach to maintain their conservation values in a spruce-dominated stand on a longer time frame. This will allow oaks to expand their crowns, increase their vitality and increase species richness and diversity of plants under the canopy. The economic loss of creating large gaps instead of no gaps may be negligible since the overall spruce production was not affected within 15 m of each oak.

1. Introduction

In northern Europe, intensive forest use and expansion of coniferous plantations has led to dramatic changes in the structure and composition of boreal and semi-boreal forests (Anderberg, 1991, Lindbladh et al., 2014). Old-growth and secondary deciduous forests, meadows and open woodland pastures have been reduced to a small part of their original coverage, replaced by homogeneous productive forests mostly lacking deadwood, old growth trees and other important features for biodiversity (Kuusela, 1994, Lindbladh et al., 2014, McGrath et al., 2015). The decline in old deciduous trees has diminished several species' habitats and populations, especially among insects and cryptogams

(Artdatabanken, 2020).

Improving conditions for biodiversity is needed in managed forests. The retention of older deciduous trees, or retention forestry, is a practice used in clear-cut systems which are applied in most European forests (Vanha-Majamaa and Jalonen, 2001, Gustafsson et al., 2019, Gustafsson et al., 2020). This approach to harvesting retains important structures, safeguards habitat continuity and thus positively affects biodiversity compared to clear felling (Gustafsson et al., 2010, Fedrowitz et al., 2014, Gustafsson et al., 2020).

Old oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) are frequently left as "retention trees" in conifer-dominated production forests. They provide valuable habitats and contribute to the diversity of

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many species groups, as solitary trees in the open landscape (Buse et al., 2007, Horak et al., 2014) or in forests (Tews et al., 2004, Widerberg et al., 2012, Parmain and Bouget, 2018). This is mainly due to the long lifespan of the oaks, and the fact that they provide a variety of habitats for epiphytic and saproxylic species on bark, in hollows and on dying and dead branches (Johansson et al., 2009, Lassaue et al., 2011). In northern Europe, many oak-associated species are on the Red List (Skarpaas et al., 2011, Mitchell et al., 2019, Mölder et al., 2019, Art-databanken, 2020), including many beetles (Jonsell et al., 1998, Jonsell et al., 2007, Carpaneto et al., 2015, Mitchell et al., 2019), fungi and lichens (Thor, 1997).

Maintaining both wood production and biodiversity in stands with old retained oaks poses challenges to forest management in Sweden. For example, release cutting during thinning may play a crucial role in preserving old oaks and their associated species as well as maintaining plant diversity on the ground. Release cutting around single trees improves oak vitality and habitat quality (Paltto et al., 2008, Götmark, 2009) by reducing competition from surrounding trees and bushes (Read, 1996). It can also mimic natural disturbances and affect ecological processes through gap dynamics (Muscolo et al., 2014). By increasing habitat diversity and structural complexity, release cutting create new niches, and stimulate the species diversity of both fauna (Widerberg et al., 2012) and flora (Gálhidy et al., 2006, McEwan et al., 2014).

Ground vegetation is an essential component of forest ecosystems because of its importance for soil processes, nutrient cycling, litter decomposition, forest succession, food chains, and ecosystem services like berry production (Nilsson and Wardle, 2005, Gilliam, 2007, Shields and Webster, 2007). Previous studies have shown the positive effect of gap creation on both ground layer diversity and abundance (Goldblum, 1997, Gálhidy et al., 2006, Fahey and Puettmann, 2007, Grandpré et al., 2011, Kelemen et al., 2012). The size of the gaps, soil characteristics and site history are important drivers of species composition. The development of the oak crown will affect gap dynamics and related ecological processes, making it important to understand how understory plant communities change as the canopy closes (Tsai et al., 2018).

This study explores effects of release cutting in a Norway spruce (*Picea abies* L. Karst) plantation on the vitality of old retained oaks (*Quercus robur* L.), the growth of the surrounding Norway spruce and the diversity and abundance of surrounding ground vegetation over a ten-year period. To our knowledge, no previous study has simultaneously examined the decade-long effect of release cutting on oak vitality, the diversity of understory plants and conifer wood production. The overall objective of the study was to collect information to help improve management schemes for spruce stands with old retained oaks. Here we compare two different degrees of release cutting around old oaks in a dense Norway spruce stand. We hypothesize that release cutting will reduce spruce wood production within experimental plots around the oaks (H1). Release cutting will increase oak vitality, indicated by less dead wood in the oak crown and positive crown development (H2). Release cutting will also lead to higher ground vegetation cover compared to the control and a greater diversity of understory vascular plants species (H3).

2. Material and methods

2.1. Study area

The experiment is located in a 5.5 ha forest stand in the Asa Experimental forest in Sweden (57.138° N, 14.756° E). The site was planted with Norway spruce in 1975 with a 2 × 2 m spacing. Various deciduous trees that were present at the time of planting were retained and these constitute a part of the current overstorey. Pedunculate oak (*Quercus robur* L.), European aspen (*Populus tremula* L.) and Norway maple (*Acer platanoides* L.) are the most common broadleaved species in the stand. Retained oaks were, on average, 153 years old in the winter of 2018

(Drobyshev et al., 2019). According to historical pictures, the stand is an old wooded pasture. The site is quite fertile, with a site index of G39, which corresponds to a projected mean dominant height of the Norway spruce at the stand age of 100 years of 39 m (Hägglund and Lundmark, 1977). The site is located at around 220 m above sea level with an annual mean temperature of 6.6 °C and mean annual precipitation of 458 mm (reference years 1990–2019 from climate data from the SITES Asa research station). The site is located on a 10% slope facing west. Soil conditions are predominantly mesic (90% of stand area) and soil texture is sandy silt (80%) (Lindén, 2003).

The stand was first measured in 2003 by Lindén (2003) using a grid of sample plots to investigate how scattered large deciduous tree affected Norway spruce production. Therefore, all deciduous tree identifications were from this year. Thereafter the stand was thinned in 2008 and simultaneously a release cutting experiment was established by Koch Widerberg (2013) using oaks from Lindén (2003) broadleaved data. Koch Widerberg (2013) studied the effect of release cutting around retained oaks on saproxylic insects, and measured the focal crowns previous to thinning in 2007. In 2010, Altmäe (2012) investigated the effect of retained trees on the growth of Norway spruce, and some of the Norway spruce stand data was measured following Koch Widerberg (2013) sample plot method.

2.2. Experimental design

Eleven clusters of large oaks were identified from Lindén (2003), and were used as blocks in the experiment, evenly distributed over the entire stand. The study was designed as a randomized block experiment with three release cutting treatments, each treatment containing one focal oak, in total 33 focal oaks (Koch Widerberg, 2013). The treatments were created during the thinning of the stand in 2008, and defined as: 1) High release (HR), where all spruces were removed under the crown of the oaks and extended in a two meter zone; 2) Medium release (MR) where all spruces were removed directly under the crown of the oaks only; and finally 3) No release (NR) where no spruces were removed (Fig. 1). There was supposed to be no overlap between the 15 m radius plots within blocks. However, we discovered some overlap (ca 6 m) between two NR plots in different blocks and between a HR and MR plot from the same block. These overlaps were not corrected for in the analyses.

The crown radii sizes ranged from 2 to 10.3 m depending on the direction; therefore a sampling plot with a 15 meter radius was established around every one of the 33 focal oaks (corresponding to 0.07 ha, in total 42.4% of the total stand area). The individual focal oaks were considered as the center of the sample plot and marked with a permanent stick. Unfortunately, two oaks (111 & 166) were mismarked and thus excluded from the 2018 study, which left 31 plots (Appendix A). No further harvest of spruce or other tree species has been undertaken since the experimental treatments were applied.

2.3. Stand development

All trees above 1.3 m height within the sample plots were measured, including their distance to the focal oak stem, two years after the treatment in 2010 and eight years later, 2018. Diameter at breast height (DBH), 1.3 m above ground was recorded using a caliper. In addition, the heights of six sample trees of Norway spruce were measured systematically in each plot (two with the largest diameter and four in each of the smaller diameter groups). All Norway spruce trees were assigned an estimated height from the diameter-height function (Näslund, 1936) based on the measured sample trees.

In total our analysis includes 1294 trees, of which 1088 (84%) were Norway spruce and the rest broad-leaved species: Aspen (*Populus* sp.), Alder (*Alnus* sp.), Maple (*Acer* sp.), Oak (*Quercus* sp.), Lime (*Tilia* sp.), and Birch (*Betula* sp.) (Appendix B.1 and B.2). Of the 1294 trees, 1195 were also present in the 2010 inventory. DBH and basal area in 2010 and 2018 of missing (n = 49) and new Norway spruce trees (n = 42)

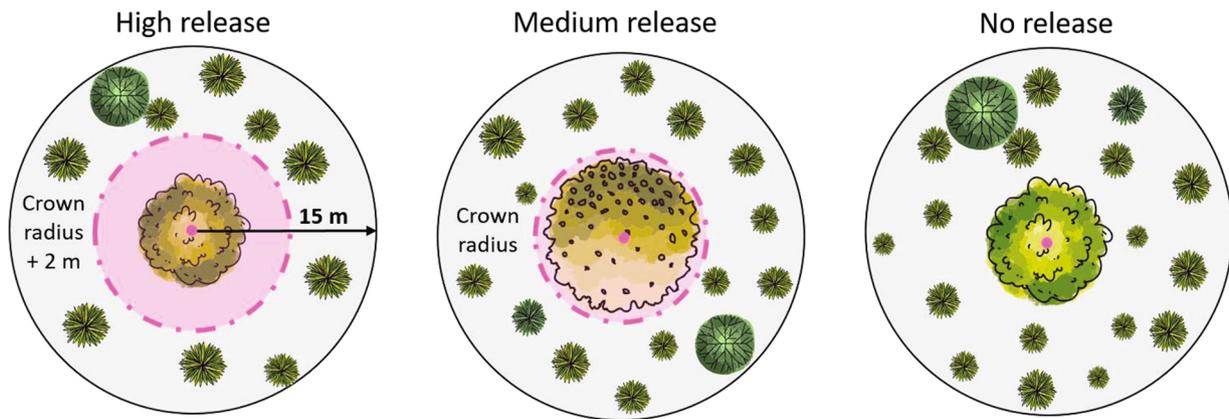


Fig. 1. Release cutting experiment. The left image shows the High Release (HR) treatment, the middle image shows the Medium Release (MR) treatment, and the right image shows the control No Release (NR). In dotted pink-line is the delimitation for the release cutting according to the treatment, and in light grey is the 15 m sample plot with a pink dot, or focal oak stem as the center. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respectively were reconstructed using linear regression (Appendix B.3). For every sample plot, dominant height (Appendix B.4), mean height, and mean DBH of Norway spruce were calculated. Basal area increment (BAI, $\text{m}^2 \text{ha}^{-1}$), DBH increment (DBHI, cm year^{-1}) were calculated using 2010 and 2018 values.

Treatment effects on Norway spruce DBH and BA for both years as well as DBHI and BAI were tested in R studio 3.4.3 (R development core Team, 2018) using REML linear mixed models (LMMs). The p-values were obtained using Satterthwaite's approximation using the 'lme4' and 'lmerTest' R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. For DBHI and BAI the initial 2010 DBH, or initial BA, were included as a covariate in the model in order to capture the variability in growth linked to initial stand values.

The interaction of tree size and competition from the focal oak, and how it is affecting the annual basal area growth of the tree was investigated, in a subset of the data only including the Norway spruce trees in the control plots (where trees from 1 to 15 m distance from the oak were present). The individual tree growth in terms of annual basal area growth (BAI) was tested in a mixed model using the plot as random variable.

$$\log(BAI_{ij}) = \mu + \beta_0 BA_{ij} \times \log(\text{Distance}_{ij}) + \beta_1 BA_{ij}^2 + \varepsilon_{ij}, \text{Plot}_j N(0, \sigma_{ij}^2) \quad (1)$$

Where BAI is the annual basal area growth, BA the initial basal area, Distance is the distance from the focal tree to the tree for tree 1 to i in each plot 1 to j . Transformations were made to reduce heteroscedasticity, and model selection was based on lowest AIC and smallest mean standard error. For model interpretation and visualization the trees were divided into three size classes: suppressed (smaller than mean DBH-1 standard deviation); dominant (larger than mean DBH + 1 standard deviation) and intermediate (in between).

2.4. Oak vitality

The focal oaks stem circumference was measured at breast height both in 2010 (Altmäe, 2012) and 2018 with a measuring tape and DBH (cm) was deduced (Appendix A). The focal oak's crown width from the stem to the edge of the crown was measured in four cardinal directions both in 2007 and 2018 (Fig. 2). Crown changes within this period were calculated by using the treatment mean crown width differences in each direction (crown growth) (Fig. 2). The crown area (i.e. the sum of all 4 triangles areas) for each focal oak (Fig. 2) was calculated for 2007 and compared to make sure the focal oaks did not have significantly different areas between treatments.

Canopy openness was estimated as the amount of visible sky between

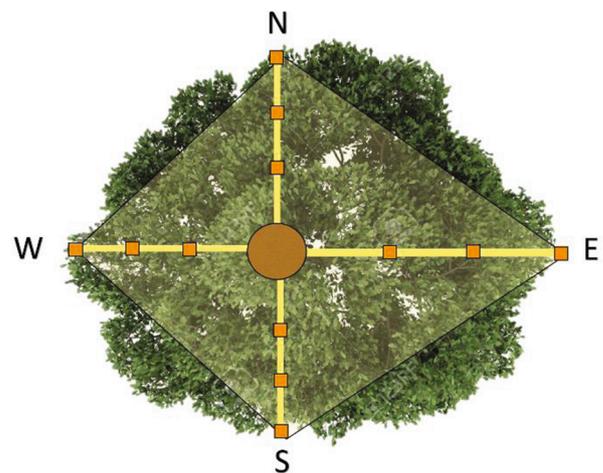


Fig. 2. Vegetation sampling design. Transects (yellow), area (shaded yellow) and quadrats (orange) are found up to the crown width limits in each cardinal direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the oak and the Norway spruce canopies using hemispherical pictures in a circle 1-meter from each focal oak stem. Eight photos were taken in the four cardinal and four intercardinal directions at the height of 1.8 m from the ground to capture the degree of canopy openness around each focal oak. Pictures were analyzed in the software Gap light analyzer (GLA) (Frazer et al., 1999) which transforms the pixels into a black and white representation in order to derive the percentage openness of the canopy (white pixels indicating visible sky). Each focal oak had a canopy openness value for each of the eight directions, and then the mean canopy openness per focal oak was computed to compare each treatment (with and without direction as a covariate).

Finally, the quantity of dead branches in the crown was assessed and used as an indicator of oak vitality. Dead wood was measured with the help of 2-dimensional tree architecture drawings (Appendix C). Each drawing was created in relation to the total tree height, which was measured with a Vertex IV ultrasound instrument system. In addition, an eight-meter reference stick was placed against the stem of each measured focal oak as an "eye-reference" for the drawings. For each focal oak, the total length of dead and living wood was calculated and related to the length of all branches on the tree drawing to obtain the proportion of dead wood. Oak 172 was not considered in this analysis and considered as an outlier value. The removal of this oak reduced the

standard deviation of the data by 35% within the NR treatment. This may be explained by the fact that the focal oak was located on the edge of the stand in an open area and not representative of a NR tree.

The impacts of retention level on oak vitality were tested by comparing the oak response variables (DBH both years, DBHI, crown width growth, mean canopy openness per oak, or dead wood proportion in the crown per oak) among treatments (HR, MR or NR) using REML linear mixed models (LMMs) (R studio 3.4.3 (R development core Team, 2018)). For each model, “block” was used as a random variable and for DBHI, the initial size (DBH 2010) was included as a covariate. The p-values were obtained using Satterthwaite’s approximation using the ‘lme4’ and ‘lmerTest’ R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. Pairwise comparisons between the groups were computed using Tukey’s post hoc test (function emmeans in package ‘lsmeans’ (Lenth and Lenth, 2018)). For all models, the assumptions were verified from inspection of plots of the residuals, and if necessary, transformation of the response variable was performed before statistical testing.

2.5. Vegetation inventory

The vegetation inventory was conducted in August 2018. For vegetation cover, north, south, east, and west cardinal directions were used to delimit four transects from the oak center. Three quadrats of 0.5 × 0.5 m were placed one third of the total distance apart along every transect, with the last plot being at the edge of the oak crown (Fig. 2). Each quadrat was inspected by a single experienced observer and percentage cover was visually estimated for each species within each quadrat. Sometimes species were layered and the total coverage can exceed 100%. In total 30 focal oaks were inventoried as one individual was dead (oak 68) and we discarded the two mismatched oaks (111 & 166). To be able to interpret edge effect, the distance between each oak and the edge of the stands were included as a covariate in the model. For tree seedlings, the percentage cover per seedling was set to 1% of a square plot area.

The percentage cover of each species in each of the 12 sample plots was summarized to one value per focal oak (oak level sum). A supplementary qualitative inventory was carried out by walking the plot in a circular spiral toward the oak. If a species was found within the 15 m radius of the sample plot during the qualitative inventory, but not in any of the 12 sample plots, it was listed with 0.001% total cover at the oak level. The species were classified into the following four habitat groups according to Heinken et al. (2019):

- *True herbaceous forest species* (1.1 & 1.2) (all taxa largely confined to forest): Including group 1.1 which contains taxa that are predominantly found in closed forests, as well as group 1.2 which are mainly species found on forest edges and in forest clearings.
- *Herbaceous generalist species* (2.1), herbaceous species and dwarf shrub species common in both forest and open land. A large

proportion of the species of group 2.1 probably had their original habitat in forests and have migrated from here into the open habitats.

- *Woody generalist species* (2.1), Tree and shrub species (excluding dwarf shrubs confined to the herbaceous layer).
- *Open land species* (2.2) are only occasionally found in the forest, and mainly occur in open habitat (dwarf shrub heaths, lime and sand-poor grasslands, wet meadows, etc.). Most species of group 2.2 are shade-intolerant.

The cover sum for each functional group was then calculated for each oak plot. Finally, the mean cover of each functional group per treatment was compared. Each species cover data was transformed into a binary presence/absence (1/0) to indicate how many species were associated with each oak. The impact of retention level on the mean number of species found at each oak was tested in R studio 3.4.3 (R development core Team, 2018) using REML linear mixed models (LMMs) to compare among treatments (HR, MR or NR). In the model, distance to the edge was added as a covariate to see if edge effect had an impact on species diversity, and then block was defined as a random effect. The p-values were obtained using Satterthwaite’s approximation using the ‘lme4’ and ‘lmerTest’ R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. Pairwise comparisons between the groups were computed using Tukey’s post hoc test P (function emmeans in package ‘lsmeans’ (Lenth and Lenth, 2018)). For all models, the assumptions were verified from inspection of plots of the residuals, and if necessary transformation of the response variable was performed before statistical testing.

3. Results

3.1. Stand development

The basal area (m^2ha^{-1}) for the Norway spruce adjacent to the focal oaks (15 m radius) was not significantly different among treatments (HR, MR, NR) directly after release cutting (Table 1). However, the arithmetic mean of Norway spruce DBH was smaller in NR compared to HR and MR (Table 1). The release cutting treatment had no effect on total stem growth of the Norway spruce around the focal oak in our sample plots, resulting in no significant difference in DBH, DBH increment, BA or BAI (Table 1).

For individual trees in the control plots, there was a significant increase in annual basal area growth with increasing distance to the focal oak treatment (F-value = 29.502, df/dendf = 1/333.31, $p < 0.000$) which interacted with initial tree size (F-value = 7.074, df/dendf = 1/334.89, $p < 0.008$). Including the squared initial basal area improved model fit (Fig. 3, Appendix E). Using the initial tree size classification for visualization of model behavior also highlighted the result that intermediate sized trees showed more growth dependency to the focal oak than suppressed trees (Fig. 3). Dominant trees were more or less absent in the nearest five meters from the focal oak.

Table 1

Effect of “Treatment” on the different Norway spruce variables at plot level (n = 31). The table shows means ± standard errors of the mean (SE) for each treatment (High release HR, Medium release MR and no releases NR). It also shows the F-value, degrees of freedom (df), denominator df (dendf) and p-values. P-values in bold are significant ($p < 0.05$). Means sharing a letter are means that are not significantly different from each other. *Growth variables (BAI, DBHI) all have respective initial measurement as covariates.

Response variable	Mean ± SE			F	df, dendf	p
	HR	MR	NR			
Stand BA 2010 (m^2/ha)	17.56 ± 1.31	17.89 ± 1.31	19.11 ± 1.45	0.40	1, 16.164	0.674
Stand BA 2018 (m^2/ha)	25.27 ± 1.96	25.86 ± 1.96	27.60 ± 2.17	0.43	1, 16.707	0.653
Mean DBH 2010 (cm)	21.69 ± 0.69 (a)	21.89 ± 0.69 (a)	18.92 ± 0.78 (b)	4.98	1, 28	0.014
Mean DBH 2018 (cm)	25.85 ± 0.89 (a)	26.19 ± 0.89 (a)	22.54 ± 1.00 (b)	4.43	1, 28	0.021
BAI ($\text{m}^2/\text{ha year}^{-1}$)*	1.37 ± 0.19	1.60 ± 0.19	1.61 ± 0.21	0.69	2, 17.791	0.516
DBHI (cm year^{-1})*	0.49 ± 0.018	0.51 ± 0.019	0.52 ± 0.022	0.45	2, 18.978	0.646

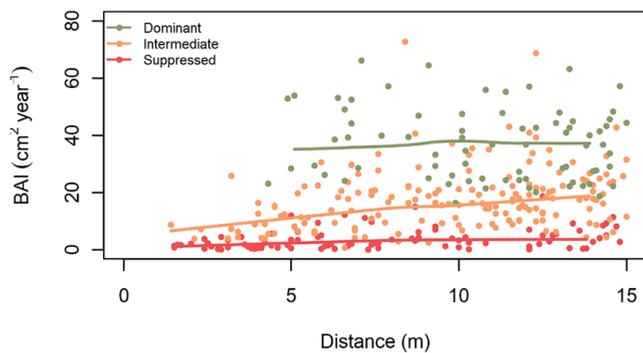


Fig. 3. BAI, annual basal area increment for Norway spruce trees at the different distance from the focal oak. The trees are grouped in colors based on suppressed, intermediate and dominant trees. The smoothed lines are predicted values from the model for the groups respectively (Eq. (1)).

3.2. Oak vitality

The stem diameter increment (DBHI) of the focal oaks did not differ among treatments neither did the initial DBH and the 2018 DBH (Table 2). The 2007 mean crown area did not differ between treatment (F-value = 0.119, df/dendf = 2/28, p = 0.888). The mean crown area in HR treatment (47.23 m² ± SE 5.73) did not differ compared to the mean crown area in MR (44.15.23 m² ± SE 5.73) or NR (Mean 43.39 m² ± SE 6.42). In addition, the crown length in the different direction was not significantly different between treatment (F-value = 0.274, df/dendf = 3/111.52, p = 0.761).

Mean crown width growth was about ten times higher in HR and MR treatments than in the NR treatment. The treatment effect was highly significant (Table 2). The canopy openness (open sky gaps) around the focal oaks did not differ among treatments eight years after release cutting (Table 2). Finally, the mean proportion of dead branches was affected by treatment (Table 2) with the highest proportion of dead branches in the NR treatment and the lowest in the HR treatment.

3.3. Vegetation

3.3.1. Cover data

The understory vegetation had a significantly different cover among treatments; with higher coverage in HR compared to MR and NR (F-value = 5.019, df/dendf = 2/114.632, p = 0.008). True forest herbaceous species mean cover is about three to four times higher in HR (76.86% ± SE 15.15) compared to NR (21.24% ± SE 16.07). The mean ground cover of generalist herbaceous species in the HR treatment (90.29% ± SE 41.02) was almost twice as high compared to NR (57.77% ± SE 41.44). The mean ground cover of generalist woody species was around three times higher in HR (113.57% ± SE 15.80) compared to NR (36.48 ± SE 17.50) and doubled in MR (62.77 ± SE 16.37) compared to NR. Finally, the differences in open land species cover among treatments are marginally non-significant. All habitat groups, except open land

Table 2

Effect of the different treatments on the different focal oak variables. The table shows means ± standard errors of the mean (SE) for each treatment (High release HR, Medium release MR and no releases NR). It also shows the F-value, degrees of freedom (df), denominator df (dendf) and p-values. P-values in bold are significant (p < 0.05). *For DBHI, initial DBH was used as a covariate in the model. Means sharing a letter are means that are not significantly different from each other.

Focal oak variables	Mean ± SE			F	df, dendf	p
	HR	MR	NR			
DBH 2010 (cm)	63.75 ± 3.39	61.53 ± 3.59	56.62 ± 3.81	1.017	2, 27	0.375
DBH 2018 (cm)	67.33 ± 3.64	65.92 ± 3.84	60.69 ± 4.08	0.807	2, 27	0.456
DBH increment (cm)*	3.47 ± 0.87	4.41 ± 0.91	4.23 ± 0.98	0.180	2, 16.49	0.836
Crown width growth (m)	1.12 ± 0.26 (a)	0.72 ± 0.26 (a)	0.10 ± 0.26 (b)	6.1223	2, 119	0.003
Canopy openness (%)	16.11 ± 0.81	15.83 ± 0.83	15.55 ± 0.82	0.8683	2, 228.38	0.421
Dead wood proportion (%)	23.84 ± 2.95 (a)	27.88 ± 3.11 (b)	38.85 ± 3.54 (b)	5.640	2, 26	0.009

species, had higher cover in HR and MR treatments compared to NR treatment. The difference was statistically significant for HR vs NR (Fig. 4). The plot location in relation to the edge of the stand only affected open land species (F-value = 4.970, df/dendf = 1/11.293, p = 0.047).

Quercus sp. seedlings were observed adjacent to 11 of the sample plots out of the 30: four times in HR and four times in MR with a respective mean cover of 4.0% ± SE 1.2 and 1.3% ± SE 1.2, and three times in NR with a mean cover of 2.0% ± SE 1.4. Norway spruce seedlings were observed adjacent to 29 oaks, 11 times in HR with a mean cover of 19.4% ± 3.7, 10 times in MR with a mean cover of 8.6% ± SE 3.9 and finally eight times in NR with a mean cover of 6.6% ± SE 4.4.

3.3.2. Plant species richness

In total, 62 different species were inventoried, 45 species were found during the quantitative inventory in the quadrats and an additional 17 species were detected inside the full 15 m radius sample plots during the qualitative inventory (species list in Appendix D). In the HR treatments, 50 different species were found, in the MR treatments 50 species and in NR, 21 species. Some species were more frequent, such as *Oxalis acetosella*, which was found in all plots and treatments, compared to *Calamagrostis canescens*, *Solidago virgaurea*, and *Lysimachia vulgaris* which were only found in HR plots. All NR species were also found in MR treatments.

There was a significant difference in the mean number of species found in the three treatments (F-value = 6.4853, df/dendf = 2/18.022, p = 0.007). HR and MR treatments had significantly more species compared to NR (Fig. 5). HR had a mean number of species of 15.5 ± SE 2.0, compared to 13.3 ± SE 2.1 in MR and 7.2 ± SE 2.2 in NR. Distance was not a significant predictor of species diversity (F-value = 2.0654, df/dendf = 1/19.302, p = 0.167). The highest and lowest number of species found around a single oak was 29 and 3, respectively.

4. Discussion

This study generated novel information that can be applied to improve management of young conifer stands with old deciduous trees. The experiment shows that release cutting, including removal of commercially planted Norway spruce trees around large oaks, has positive effects on oak vitality and increase plant diversity and abundance. The release cutting had no detrimental effects on total Norway spruce wood production within a 15 m radius of the focal oak and over nine growing seasons. This indicates that releasing retained oaks during commercial thinning may be a way to balance production goals and conservation values.

4.1. Spruce wood production

This study demonstrates that removal of Norway spruce trees around old oak trees during the first thinning does not reduce growth or standing volume at the plot level over a 10-year period. The most obvious explanation of these results is that spruce trees under the oaks

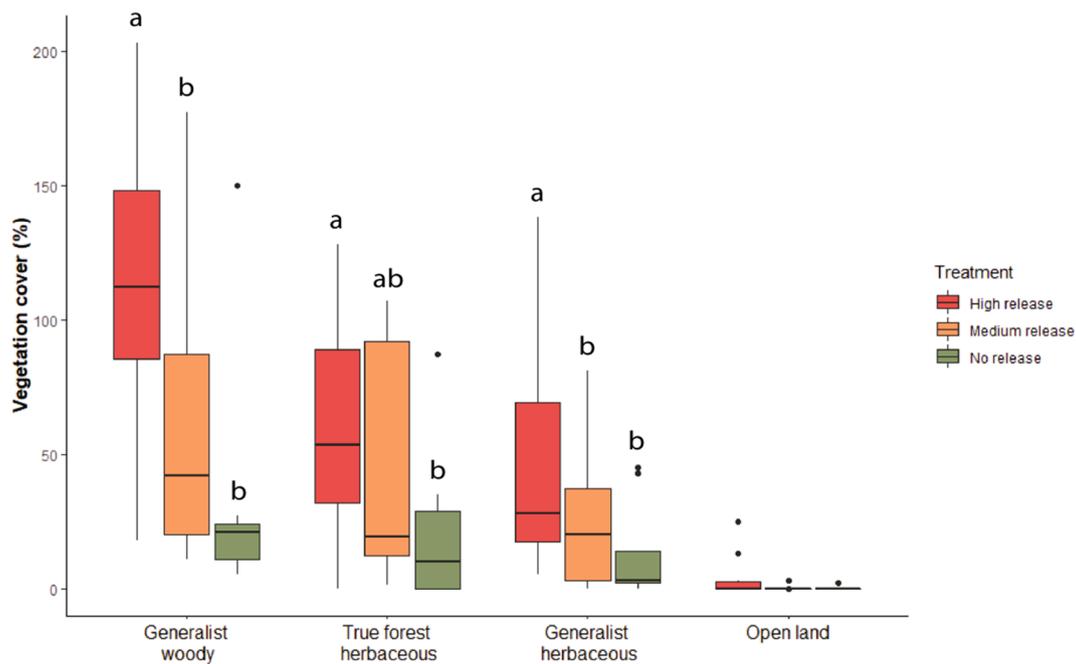


Fig. 4. Distribution of the ground vegetation cover (in percentage) per habitat group and treatment. The boxplot shows the distribution of the data and the black line shows the median values among blocks in the data set. The letters indicate the pairwise comparisons of means. Boxplots sharing a letter have means that are not significantly different from each other.

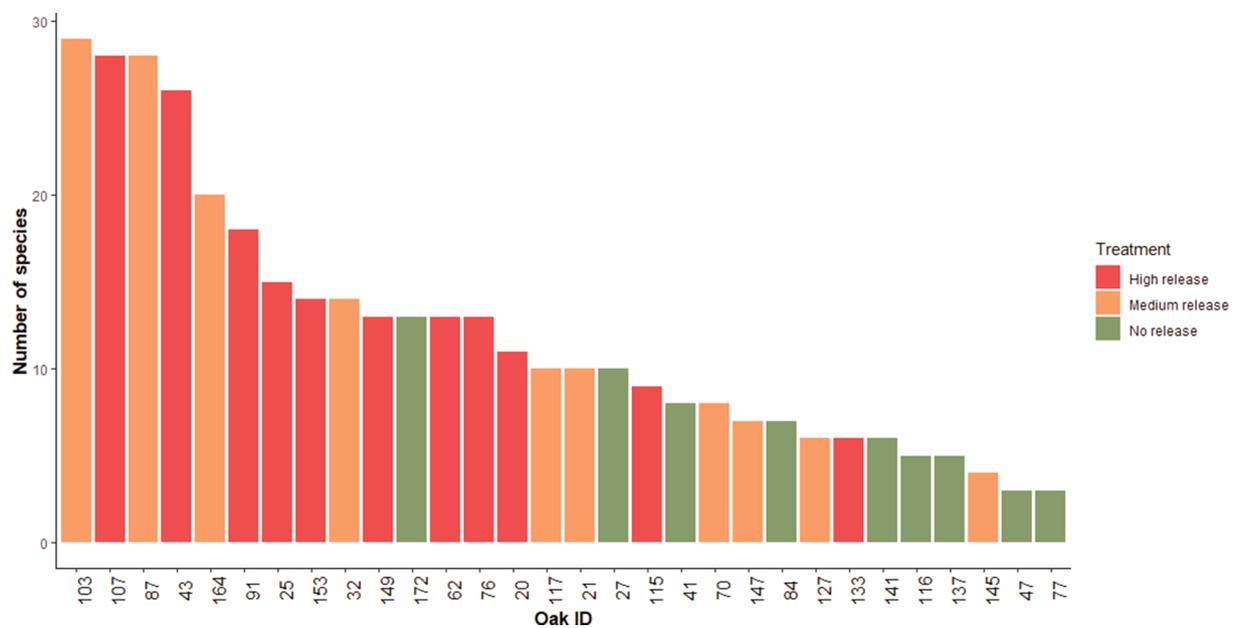


Fig. 5. Species richness for each focal oak (n = 30), represented by its oak ID on the x axis and treatment (HR, MR, NR). Species richness is ordered from the richest oak on the left to the poorest oak on the right. The richest oaks on the left are mostly red (HR) and orange (MR). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were small and suppressed and contributed very little to the overall growth in the plots. This is reinforced by the fact that control plots had significantly smaller mean Norway spruce DBH compare to the other treatments. Our study is in agreement with results by Lindén (2003) who studied the same stand 10 years prior to the release cutting. When comparing oak retention to the alternative of clear-cutting, Lindén (2003) reported that substantial growth losses in Norway spruce stands can be anticipated, depending on density and size of retained oaks. Our study indicates that growth losses can be anticipated within 5 m from the retained oaks. Our results are in line with the results by Elfving and

Jakobsson (2006), who found that Scots pine (*Pinus sylvestris* L.) volume was decreasing within a 5–10 m competition zone depending on fertility. Spruce is a shade tolerant species (Kantola and Mäkelä, 2006) and belowground competition could be an explanation to the reduction of growth. In our data the effect of oak competition was significantly decreasing with distance to the oak and size of the tree basal area, which was primarily visible on the intermediate trees. This may be explained by suppressed trees being outcompeted also by the other Norway spruce trees throughout the stand. Dominant trees were missing in the nearest five meter radius of the oaks, which corresponds to an area of c. 80 m² in

which Norway spruce production is severely reduced meaning that at a density of e.g. 10 large oaks per ha, about 8% of the area for effective spruce wood production is lost. This exemplifies a significant cost in keeping oaks within spruce production stands.

4.2. Oak vitality

Release cutting increased vitality of the focal oaks. Crowns were small in the control plots while they expanded and colonized the space made available in the release treatments. Simultaneously, the amount of dead wood in the crowns increased among oaks in the control treatment, indicating dieback. In a similar experiment conducted by Götmark (2009) with oaks in broadleaf-dominated conservation forests in Sweden, openness around oaks was a positive predictor of oak vitality and similarly he used the amount of dead wood in the crown as a negative predictor of growth vitality. Götmarks and our findings confirm an earlier finding that *Quercus* sp. is shade intolerant, have high crown plasticity, but low competitive ability when growing with other species (Le Due and Havill, 1998, Pretzsch et al., 2013). Control oaks in our study probably suffered from competition and crowding with the surrounding trees, leading to increasing amount of dead crown and reduced crown expansion, which potentially affected photosynthetic ability and the overall tree vitality. Götmark (2009) also mentioned that release cutting increased the mean relative basal area growth of large oaks after four growing seasons. Such an increase was not found in our study, as treatments had no effect on diameter increment of the focal oaks.

4.3. Vegetation

Overall, mean plant cover increased with treatment in order NR, MR and HR for all species groups. The creation of a gap in the canopy can be seen as simulation of natural disturbances at a local spatial scale impacting the understory through the alteration of important resources for plant growth (Muscolo et al., 2014). The alteration of the horizontal structure of the forest (including small gaps or thinning) will most importantly change the light environment and according to the theory of gap dynamics, changes in ground vegetation cover occur quite quickly after the creation of the gap since open conditions facilitate vegetative reproduction (Dai, 1996, McEwan et al., 2014, Muscolo et al., 2014). Tree cutting increases not only light but also nutrient and often soil moisture availability for understory plants, which usually boosts their abundance (Matula et al., 2020). However, as also regeneration of woody species, including Norway spruce, was favored by release cutting, the cover of herbaceous species may gradually decrease again until a new release cut is done.

The removal of spruce favoured the growth of both true forest species with low light requirements (e.g. *Oxalis acetosella*, *Maianthemum bifolium*, *Lactuca muralis*), generalist species with higher light requirements and even some indicators of the historical land use (pasture) (e.g. *Veronica chamaedrys*, *Anthoxanthum odoratum*, *Alchemilla acutiloba*, *Ranunculus repens*, *Hypericum maculatum*) (Tyler and Olsson, 2013, Milberg et al., 2019). These findings are in accordance with previous studies on effects of partial cutting which showed positive effects on a majority of species (Brunet et al., 1996, Götmark et al., 2005). Many of the species found in both the HR and MR treatments are habitat generalists, whereas none of those disturbance-tolerant species were found in the control. Instead, the control was characterized by low cover of true forest-species or/and species with low light requirements.

We also found a higher number of species in the MR and HR treatments compared to NR, including both light demanding generalists and shade tolerant forest species. This may be explained by the fact that shade tolerant species are able to survive where there is very low light availability, but also grow better with increasing light (Gaudio et al., 2008). However, the observed gradient of treatment effect (HR > MR > NR) may indicate that, as the gap closes in the future, species richness may decrease again (Dai, 1996, McEwan et al., 2014, Muscolo et al.,

2014). Previous studies have found that grassland species can survive as small remnant populations in forested areas, and that this can facilitate colonization of new sites after canopy opening (De Graaf and Roberts, 2009, Jonason et al., 2016). The extent of this establishment over time remains unknown. It has been documented that it can take more than one decade for management legacies to disappear and they can sometimes even be permanent (Dupouey et al., 2002, Cuddington, 2011). Repeated release cutting could be a suitable management strategy for long-term conservation of a diverse forest ground vegetation in conifer-dominated production forests. Knowing that coniferous forests generally provide less diversified vascular plant understories than broadleaved and mixed forests (Barbier et al., 2008, Felton et al., 2010), this study highlights the importance of considering understory dynamics in forest management practices.

5. Conclusions and management implications

In plantation forestry, the creation of gaps influences a considerable number of biological processes and will provide habitat and new structures that will enhance the vegetation cover and species richness in a long-term perspective. Leaving more space around retention trees when conifers are being planted or releasing the oaks at the time of the first commercial thinning will reduce the competition with Norway spruce and increase oak vitality and conservation value. The felling of the suppressed spruce trees will increase harvesting costs but the impact on spruce wood production is negligible. We suggest that release cutting practices could be developed to support plant diversity, for example, by the creation of larger gaps in early thinnings where old trees are present. The retention and management of old oaks and other deciduous broadleaf trees can ensure the survival and development of some species of the ground vegetation, but further research is needed to study the extent of the long-term effect in this specific setting. More actions may be needed in the future to maintain wood production, oak vitality and plant diversity.

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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Appendices. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118670>.

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