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Kellomäki, S

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Effects of even-aged and uneven-aged management on carbon dynamics and timber yield in boreal Norway spruce stands: A forest ecosystem model approach

Kellomäki, S., Strandman, H., Peltola, H.¹)

University of Eastern Finland, Faculty of Science and Forestry, School of Forest Sciences, PO Box 111, FI-80101 Joensuu, Finland

¹) Corresponding author: Heli Peltola (email: heli.peltola@uef.fi; tel.: +358 40 5880005)

Abstract

We used a gap-type forest ecosystem model to study how even- and uneven-aged management affected the carbon dynamics and timber production in boreal Norway spruce stands. In business-as-usual management, the intensity of thinnings (from below) and single-tree selective cuttings followed those recommended for even-aged (BT) and uneven-aged management (BSC) in practical forestry in Finland. Moreover, higher or lower basal area thresholds, and shorter or longer production cycles, were used in simulations. We found that, the mean annual carbon uptake, volume growth, and carbon stock in trees and harvested timber, were nearly the same under even-aged (BT) and uneven-aged (BSC) management, when assuming full seed crop in latter one. However, the carbon stock in the soil and ecosystem and the mean annual net ecosystem exchange were slightly smaller under BT. The carbon retention time was longer under BSC. The net present value (NPV with interest rate of 3%) of timber production was clearly lower under BT, when the calculation was initiated at planting on clear-cutting area, in opposite to when initiating calculation a few years before the second thinning. Higher basal area thresholds and longer production cycles increased carbon stocks, carbon retention and timber yield, regardless of management system. On the other hand, the results of uneven-aged management (BSC) were very sensitive to the success of natural regeneration and ingrowth of seedlings, as a reduction of the seed crop by 25–75% from the full seed crop decreases the volume growth by 44–74% and timber yield up to 46%.

Keywords: Carbon exchange, carbon retention, carbon sequestration, economic profitability of forestry, even-aged management, uneven-aged management, boreal forests, gap-type forest ecosystem model
Introduction

In forest ecosystems, carbon cycles through uptake into storage in trees. Carbon further cycles through litterfall and dead trees into soil organic matter (SOM), further being emitted into the atmosphere through the decay of SOM. Carbon uptake and emissions define the net ecosystem exchange and balance. They are affected by the structure and dynamics of forest ecosystem, and edaphic and climatic properties of site. In forestry, intensity of management and wood harvesting also impact on the balance and retention of carbon in the ecosystem, respectively (e.g., Briceno-Elizondo et al., 2006a, b; Garcia-Gonzalo et al., 2007a, b, c; Jandl et al., 2007; Lorenz and Lal, 2010). This further applies for the supply of timber and forest biomass, which are used to substitute fossil-based materials and energy. In the perspective of climate change mitigation, such forest management regimes are needed, which can simultaneously enhance the removal of carbon from the atmosphere and storing and retaining carbon in forest ecosystems, and substituting fossil-based materials and energy.

In Northern Europe, Norway spruce (Picea abies Karst. (L.)) is ecologically and economically among the main tree species. In even-aged management, this shade-tolerant species is widely planted on medium-fertile and fertile upland sites. For example, in Finland planting of Norway spruce is usually followed by precommercial management, and two to three commercial thinnings during rotations of 70 to 100 years, depending on site fertility and region (Äijälä et al., 2014). Optionally, uneven-aged management, with selective cutting in every 15 to 20 years can be used in Norway spruce (Äijälä et al., 2014). In uneven-aged management, the production cycle extends from a selective cutting to another, allowing natural regeneration and ingrowth of seedlings in canopy gaps. In selective cutting, mainly larger (co-dominant and dominant) trees are harvested, but also dense groups of smaller trees can be thinned, if necessary.

There are only a few of comparative studies available on how uneven- and even-aged management affect simultaneously the carbon dynamics and timber production under boreal conditions. Nilsen and Strand (2013) found that, carbon storage in the trees and ecosystem was greater under even-aged than uneven-aged Norway spruce stands based on a long-term experiment. The amount of soil carbon was, however, smaller in even-aged stands, which may partly be explained by the faster decay of SOM in relation to clear-cutting than to that occurring after selective cutting (e.g., Jandl et al., 2007). Based on model simulations, Pukkala et al. (2011b) and Peura et al. (2018) showed that the total carbon storage in the ecosystem (trees and soil) might be of similar magnitude in Norway spruce forests under both uneven- and even-aged management. Paradis et al. (2019) also suggested that by increasing the rotation lengths under even-aged management and by using partial cut (to lesser extent), it may be achieved higher potential to mitigate climate change. This is due to increased carbon balance of forestry due to increased CO₂ storage in forest biomass and harvested wood products, and displacement of CO₂-intensive materials, respectively.

Based on extensive data from permanent long-term experiments established in 23 even-aged and 26 uneven-aged Norway spruce stands in southern and central Finland, Hynynen et al. (2019) showed that the basal area growth was on average 20% smaller for uneven-aged stands during the 15 years after cutting. The difference was the largest during the first 5 years after cutting. However, based on a long-term experiment, Nilsen and Strand (2013) found that the total timber yield in
uneven-aged Norway spruce stands was 95% of that in even-aged stands. As a comparison, several previous model-based studies have shown that timber yield under even-aged management is higher than that under uneven-aged management (e.g., Lundqvist et al., 2007; Tahvonen et al., 2010; Pukkala et al., 2011b; Tahvonen and Rämö 2016; Peura et al., 2018). However, the differences in results between previous studies may at least partially be affected by differences in volume of growing stock (stocking density) and intensity of harvesting in different management systems (see e.g. Lundqvist 2017; Hynynen et al. 2019).

The economic profitability of uneven-aged management has usually been found higher than that of even-aged management. This is mainly because of the avoided costs of regeneration (e.g., soil preparation and planting of seedlings) and precommercial management (e.g., Pukkala et al., 2010, 2011b; Tahvonen et al., 2010; Tahvonen and Rämö 2016; Peura et al., 2018). The profitability of uneven-aged management can be further increased compared to even-aged management if higher interest rates and management costs, and/or lower timber prices are used in economic calculations (Andreasen and Øyen, 2002; Laiho et al., 2011; Juutinen et al., 2018). Based on these reasons, an interest in close-to-nature silviculture, and thus the use of selective cutting in Norway spruce, has recently increased in Finland, as elsewhere.

In uneven-aged management, the success of natural regeneration and ingrowth of seedlings have uncertainties. This is, because the amount of seed crop, success of dispersion of seeds, establishment of seedlings and ingrowth of seedlings in canopy gaps, affect all the success of uneven-aged management. In Norway spruce, the quantity and quality of seed crop vary substantially from year to year (Koski and Tallqvist, 1978; Saksa, 2004; Saksa and Valkonen, 2011). This increases uncertainty in the establishment of seedlings, compared to planting in even-aged management. However, several inventories show that the establishment of seedlings is likely large enough in a longer term for uneven-aged management (e.g. Lähde et al. 2002; Saksa, 2004; Saksa and Valkonen, 2011; Eerikäinen et al. 2014). On the other hand, there has been found a negative correlation between the level of ingrowth of seedlings (and other small trees) and overstory standing volume during the first 5-10 years after harvesting especially in dense stands (Lundqvist and Nilsson 2007; Lin et al. 2012). Canopy openness (gaps) has also been found to affect height increment of young spruce seedlings (height 0.1-2.0 m) and small trees (height 2.0-5.0 m) more than the average overstory basal area or standing volume (Chrimes and Nilson 2005). In overall, the establishment of seedlings might also occur over longer period under uneven-aged management than in natural regeneration with seed-tree and shelter-wood cuttings in even-aged management (Pukkala et al. 2011a; Saksa, 2004; Laiho et al., 2011; Saksa and Valkonen, 2011; Eerikäinen et al., 2014; Valkonen et al. 2017).

In this work, we used a process-based (gap type) forest ecosystem model to simulate how even-aged management (with thinnings from below, removing mainly suppressed and intermediate trees) and uneven-aged management (with single-tree selection cuttings from above, removing mainly dominant and codominant trees) affected the carbon dynamics and timber production in Norway spruce stands. The simulations were performed for medium fertile upland sites under middle boreal conditions in central Finland. In the simulations, we used varying basal area thresholds in thinning and selective cuttings, and varying lengths of production cycle (rotation, and the interval between...
subsequent selective cuttings). Additionally, we used varying seed crop potential in uneven-aged stands to evaluate their effects on results.

We hypothesized that the carbon sequestration and timber yield were of the same magnitude under even-aged management and uneven-aged management with full seed crop, when the basal area thresholds for the thinning and selective cutting, respectively, were those recommended for even-aged and uneven-aged management in practical forestry. Consequently, we hypothesized that the economic profitability of timber production is similar for both management regimes, if the economic calculations were initiated under even-aged management at the commercial thinning phase, instead of when planting on clear-cutting area. Additionally, we hypothesized, that the results for uneven-aged management are sensitive to the seed crop potential, and consequently to the natural regeneration success and ingrowth of seedlings, respectively.

Methods and simulations

Study layout and management options

In the simulations, we used a gap-type forest ecosystem model (SIMA) (Kellomäki et al., 2008). Under even-aged management, the production cycle extended from seedlings planted on clear-cutting area, through thinnings (from below), to clear-cutting at the end of the selected rotation length. Thereafter, the clear-cutting area was replanted, followed by the same management sequence as in the previous rotation. In the simulation of uneven-aged management, single-tree selection cutting, at a given interval, allowed the natural regeneration and ingrowth of seedlings in canopy gaps. In the baseline management under even-aged (baseline thinning, BT) and under uneven-aged (baseline selective cutting, BSC) management, the basal area thresholds were those recommended for use in practical forestry in Finland (Äijälä et al., 2014). In addition, higher or lower basal area thresholds, and shorter and longer production cycles, were used in the simulations.

All simulations were performed under the current climate in the middle boreal zone (62°N), central Finland, represented by a mean annual temperature sum of 1100 degree-days, precipitation of 540 mm, and atmospheric CO₂ concentration of 350 ppm. The simulations were performed for medium fertile (sub-mesic) sites (Myrtillus site type), on moraine soil with a volumetric water content of 25 m³ m⁻³ at field capacity, and 5 m³ m⁻³ at wilting point. The amount of soil organic matter (SOM), including litter and humus, was 68 Mg ha⁻¹ when initializing the simulations.

Under even-aged management, planting of 1800 seedlings ha⁻¹ with butt diameters of 2.5 cm (unimproved seedlings, no breeding gain assumed), was used to initialize the simulations at the clear-cut area. In the baseline thinning (BT) regime, thinnings from below were done when the dominant height was 12–22 m and the basal area 24–28 m² ha⁻¹. After thinning, the remaining basal area was 15–20 m² ha⁻¹, depending on the dominant height. In two additional thinning regimes, the basal area was kept ± 20% higher/lower (BT+20 and BT-20) than in the BT over a rotation. Clear-cutting was done at the end of the rotation. The simulations were performed over 525 years, using seven rotations (7 x 75 years). However, the three first 75-year rotations were excluded from the analysis in order to stabilize the effects of the initial stand conditions on the model output. Thus,
only four last rotations of 75 years, between years 225 and 525 (i.e., 300 years) was included in the data analysis.

Under uneven-aged management, the simulations were initiated in the same way as for even-aged management. Consequently, thinnings (from below) were done up to the year 75 from the initiation, but the clear-cutting was not done, allowing natural seeding to occur. Thereafter, single-tree selective cutting was done, one after another, following the given interval, thus gradually switching the even-aged management to an uneven-aged system. Selective cuttings were done whenever the basal area of a stand was ≥ 20 m$^2$ ha$^{-1}$, by reducing the basal area to 11 m$^2$ ha$^{-1}$. In addition to the baseline selective cutting (BSC), two additional selective cutting modes were used, representing ±20% higher/lower basal area thresholds (BSC+20 and BSC-20) than those used in the BSC over a production cycle. Also in this case, only the interval of simulations between years 225 and 525 (i.e., 300 years) was included in the data analysis, to allow for the stabilization of the variability in the structure of tree stand, and the amount and properties of the SOM. In all simulations, only sawlogs (stems with a diameter of ≥ 15 cm at the top), and pulpwood (diameter ≥ 6 cm at the top) were harvested. In opposite, the harvest residues (and small sized trees cut) were left on site to decay, regardless of management regime.

**Growth of trees under even- and uneven-aged management**

In the simulations, the carbon dynamics and timber production were affected by the regeneration success (naturally born or planted seedlings), growth, and mortality of the trees. Under both management systems, seedlings were established when their height was ≥ 1.3 m. The growth of established seedlings and more mature trees was calculated based on the diameter growth ($\Delta dbh$, cm yr.$^{-1}$):

$$\Delta dbh = \Delta dbh_0 \times M_{TS} \times M_L \times M_W \times M_N$$  \hspace{1cm} (1)

where $\Delta dbh_0$ is the maximum diameter growth (cm yr.$^{-1}$) under optimal conditions. The diameter growth was further scaled in the range of 0 to 1 in relation to prevailing temperature sum (TS in degree-days with +5°C threshold, $M_{TS}$), light conditions inside the stand ($M_L$), soil moisture ($M_W$), and nitrogen supply ($M_N$) (see for details, Table 1).

**Table 1.**

Maximum diameter growth under optimal conditions is dependent on tree diameter at breast height (dbh, cm, height ≥ 1.3 m) and atmospheric CO$_2$ concentration (ppm):

$$\Delta dbh_0 = \exp(a_1 \times \frac{b_1}{0.01 \times \text{CO}_2}) \times dbh \times e^{dgro \times dbh}$$  \hspace{1cm} (2)

where $a_1$, $b_1$, and $dgro$ are the parameters. Stem diameter was further used to calculate the height (m) of the trees (Kellomäki et al. 2008). Similarly, the mass (Mass(j), kg) of different organs (i.e., foliage, branches, stem, and roots) was calculated as the function of stem diameter:
\[ Mass(j) = \exp[a2(j) + b2(j) \times \frac{dbh}{c(j) + dbh}] \]  

(3)

where \( a2(j), b2(j), \) and \( c(j) \) are parameters specific to the mass component \( (j) \).

The initial amount of SOM, and the nitrogen available for growth, are related to the site type and regional mean temperature sum under the current climate (Kellomäki et al., 2008). Litter from any organ and deadwood (stemwood, branches, needles and leaves, stumps, and coarse to fine roots) transfers carbon and nitrogen into the soil, where litter and humus decay. Consequently, nitrogen is released for reuse in growth, and CO\textsubscript{2} is emitted into the atmosphere. The simulations were performed using the time step of one year and carried out on an area of 100 m\textsuperscript{2}. The simulations were based on the Monte Carlo technique. Each management scenario was repeated 100 times, but only the mean annual output values were used in the data analysis.

**Emergence and ingrowth of seedlings under uneven-aged management**

When using uneven-aged management with single-tree selection, large and mature trees (co-dominant and dominant ones) produced seeds for natural regeneration in canopy gaps. Following the approaches of Fox et al. (1983) and Pukkala (1987a, b), each seed crop indicates the potential number of emerging seedlings, but the scarcity of stockable area (open mineral soil/seedbed) and herbivory may limit the density of emerging seedlings. The properties of the seed crop may further limit the number of emerging seedlings, because only a fraction of the seeds is mature and capable of germinating (Kellomäki and Väisänen, 1995; Kellomäki et al., 1997):

\[ NS(t) = 10,000 \times f(SC(t)) \times f(SS(t)) \times f(UE(T)) \times f(FU(t)) \times f(MA(t)) \times f(GER(t)) \]  

(4)

where \( NS(t) \) is the number of emerged seedlings (seedlings ha\textsuperscript{-1} yr\textsuperscript{-1}) per the given seed crop \( SC(t) \) (seeds m\textsuperscript{-2}), \( SS(t) \) is the fraction of stockable area, \( UE(t) \) is the fraction of uneaten seeds, \( FU(t) \) is the fraction of full seeds, \( MA(t) \) is the fraction of mature seeds, and \( GER(t) \) is the fraction of germinated seeds.

Only a fraction of the seedlings \( \text{SURMUL}(t), (0,1) \) born in a given year \( t \) survives to year \( t+1 \). The initial growth of seedlings from each seed crop is followed through 12 years (Kellomäki et al., 1997). Over this period, the probability of survival increases, and the sensitivity of the seedlings to death decreases as a function of seedling age:

\[ \text{SURMUL}(t) = \text{SURPRB}(t) + YFL \times TOL(t) \]  

(5)

where \( \text{SURPRB}(t) \) is the probability of seedling survival, \( TOL(t) \) is the sensitivity of the seedlings to death, and \( YFL \) is a random number (0,1). Only a small fraction of emerged seedlings from each seed crop survive further, with the ingrowth into the existing canopy.

The initial diameter at the stem butt \( (DButt) \) of emerged seedlings was assumed to be 0.1 cm. The potential growth of butt diameter was calculated using same Eq. (1), which was used for established
seedlings (height \(\geq 1.3\) m) and more mature trees. In the case of emerged seedlings, the dbh was replaced by \(D_{\text{butt}}\) in Eq. (1). The potential growth of butt diameter was used both for naturally born and planted seedlings until they reached height of 1.3 m. The butt diameter growth was further used to calculate the height growth of seedlings (height < 1.3 m): \(\text{PHEIHT} = \text{pdicn} \times D_{\text{butt}}\), where pdicn is a parameter. The ingrowth of seedlings was assumed to occur when seedling height was \(\geq 1.3\) m at the age of 12 years since emerging (if not exceeded the height limit, seedling dies). Time span of 12 years used in this study equals to the period, when the number of seedlings exceeded 80% of that established in the 30-year period since shelterwood cutting in the middle boreal zone in the study of Räsänen et al. (1986).

Over three to five years after harvesting, the decay of logging residues binds a part of nitrogen, which was available prior to cutting for tree growth. This reduces the diameter growth of seedlings and more mature trees over first few years after cutting. However, the diameter growth recovers in response to the increase of available nitrogen due to further decay of SOM (including the logging residues from the previous cutting). Light conditions, below dominating canopy, affect the growth of seedlings both before ingrowth and thereafter (e.g. Cajander, 1934; Greis and Kellomäki, 1981).

**Model performance**

Assessing model performance involved two main questions: (i) how well does natural seeding (regeneration) produce and maintain an acceptable size distribution of trees under uneven-aged management; and (ii) how are trees growing under uneven- and even-aged management through the production cycles? Figure 1 shows the simulated fraction of trees in different diameter classes (% of cases) over the 300-year simulation period for management option BSC, with seed crop of 0.25, 0.50, 0.75, and 1 of the full seed crop potential. The simulated size distribution (columns, SIMA model with full seed crop = 1) is well in line with the measured size distribution (solid line, Shanin et al., 2016), based on measurements for the ERIKA plots produced by the Natural Resources Institute Finland. The measurements represent sample plots prior to the next selection-cutting of the plots (with the average basal area of 23.8 m\(^2\) ha\(^{-1}\)). Moreover, the insert (small Figure) in Figure 1 shows a close correlation between the simulated (x-axis) and the measured (y-axis) tree size distributions.

**Figure 1.**

Several previous model validations have demonstrated good agreement between the simulated and the measured mean annual volume growth of Scots pine, Norway spruce, and birch on upland forest sites (the forest inventory plots) throughout Finland (Kellomäki et al. 2005, 2008). Simulations by the current model and the empirical growth and yield model MOTTI (Hynynen et al., 2002) have also showed good agreement for the mean annual volume growth for managed Norway spruce stands on medium fertile upland forest sites (Routa et al. 2011a, b). This also holds for single trees growing under uneven-aged management because the allometric growth of stemwood in single trees of the same size is similar under both management systems.

**Data analysis**
Based on the current simulations, we investigated how different management options affected: (i) the dynamics and structure of tree stands; (ii) the carbon dynamics; (iii) the amount of harvested timber; and (iv) the economic profitability of timber production. We also studied the effects of: (v) the size of the seed crop; (vi) the basal area thresholds for thinnings and selective cuttings; and (vii) the length of the production cycle on the carbon dynamics, timber yield, and economic profitability of timber production. The carbon dynamics were further assessed by considering net primary production, litterfall, and carbon emission from decaying SOM (see Figure 2). Based on these, the net ecosystem exchange (NEE) was calculated: \( \text{NEE} = \text{NPP} - \text{RH} \), where NPP is the net primary production and RH is the heterotrophic respiration from decaying SOM. The carbon in trees and soil indicates the carbon stock in the ecosystem, where carbon is retained for a while, indicated by the retention time (\( \tau \), years) (Kellomäki, 2017):

\[
\tau = \frac{\text{Capacity of a system to hold carbon}}{\text{Rate of carbon flow through a system}}
\]

The retention time begins when carbon enters the system and ends when carbon leaves the system.

**Figure 2.**

The economic profitability of timber production was calculated using the net present value (NPV), with an interest rate of 3%. In uneven-aged management, the stumpage prices for sawlogs and pulpwood were assumed equal to those used for thinning other than the first commercial thinning under even-aged management (Table 2). These values were higher than the stumpage prices for the first thinning, but lower than those for clear-cutting. In even-aged management, the regeneration cost was assumed to be 1066 € ha\(^{-1}\) for 1800 seedlings planted ha\(^{-1}\) including soil preparation, and the tending cost for seedling stands 400 € ha\(^{-1}\) five years after planting, based on the online statistics of the Natural Resources Institute Finland. Three different initial stand conditions were used for the NPV calculation under even-aged management over four 75-year rotation cycles, representing the 300-year period included in the data analysis: (i) initiation on clear-cutting area; (ii) initiation 6–7 years before the first commercial thinning (at an age of 20 years); and (iii) initiation 6–7 years before the second commercial thinning (at an age of 45 years). Under uneven-aged management, the length of the total simulation period was the same, as that under even-aged management.

**Table 2.**

**Timing management interventions and diameter distribution of trees**

Regarding both management systems, Figure 3 shows the timing of thinnings and selective cuttings, respectively, and the variability of the stemwood carbon, over the 300 years simulation period. Under even-aged management, thinning occurred at an interval of 20–30 years (the mean interval of 25 years between thinnings, equals BT) from the initiation of each rotation. Compared to the baseline thinning (BT), thinning was done earlier under lower basal area thresholds (BT-20) and later under higher basal area thresholds (BT+20), respectively. In uneven-aged management with full seed crop potential (seed crop fraction = 1), the interval between cuttings was 15 years in the baseline
selective cutting (BSC). A 20% reduction in basal area (BSC-20) thresholds produced an 11-year selective cutting interval, while a 20% increase (BSC+20) in thresholds gave a 23-year selective cutting interval, respectively.

Figure 4 shows the mean diameter distribution for both management systems over the 300-year period. Under even-aged management, the diameter distribution spanned from just-planted seedlings to trees of 35–40 cm just before clear-cutting. The share of small trees (dbh < 5 cm) was similar, regardless of thinning regime used (BT-20, BT, BT+20). This pattern also held for large trees (dbh > 25 cm). However, the distribution was under even-aged management less skewed towards a dominance of small trees than that under uneven-aged management, when assuming in the latter case the full seed crop potential (seed crop fraction = 1). In the latter case, the share of small trees (dbh < 5 cm) was larger, and the share of larger trees (dbh > 25 cm) smaller. When using 20% higher basal area thresholds in selective cutting (BSC+20), the average number of small seedlings increased, in contrast to the use of 20% lower thresholds (BSC-20), due to higher seed crop and ingrowth of seedlings. A reduction of the seed crop by 25–75% reduced the number of small seedlings (dbh < 10 cm) under the BSC by up to 20–50%, compared to seedling numbers under full seeding potential.

Figure 3.

Figure 4.

Carbon uptake, stocks, and emission
The mean annual carbon uptake is shown in Figure 5, including the carbon in stems, branches, foliage, and roots over the 300 years simulation period. The mean annual carbon uptake was nearly the same under BT and BSC (seed crop fraction = 1). The mean annual carbon uptake was 10% lower for BT-20 and BSC-20, and 4–10% higher for BSC+20 and BT+20, compared to BT and BSC. Consequently, the mean carbon stock in trees was virtually the same under BT and BSC (Figure 5, Table 3) over the 300 years simulation period. The mean carbon stock was 12–17% lower under BSC-20 and BT-20, and 21–28% higher under BT+20 and BSC+20, compared to that under the BT and BSC. The carbon stock in soil was, on average, slightly greater under even-aged management.

Regardless of management regime, the carbon stock in soil was related to the litterfall, thus ultimately to the carbon uptake in trees, as further holds for the carbon stock in the ecosystem (trees and soil). The reduction in annual mean seed crop had a clear effect on carbon uptake and, consequently, on the total mean growth of stemwood, under uneven-aged management. The reduction in yearly seeding potential, by 25–75% of the full seed crop, reduced stemwood growth by 44–74%. On the other hand, carbon flows and stocks in the ecosystem (trees and soil) were less sensitive to the seed crop reduction. Even under 25% of the full seed crop potential, the carbon flows and stocks in the ecosystem would still be > 50% of those under the full seed crop. Differences in mean annual carbon uptake, emissions, litterfall, and carbon in the trees, between uneven- and even-aged (with seed crop fraction = 1) management were in general quite small. However, the carbon stock in the soil and ecosystem (trees and soil), were slightly lower under even-aged management.
Figure 5.

Table 3.

**Carbon exchange and retention time**

Carbon exchange (i.e., the NEE) was not sensitive to management system over the 300-year period (Figure 6). The carbon exchange was only 4–6% greater under BSC-20 (seed crop fraction = 1) than under BT-20. This held also for the BSC and BT. The carbon exchange was also nearly the same under the BSC+20 and BT+20. Under both management systems, lower stocking reduced NEE, while higher stocking produced the opposite effect.

Figure 6.

Carbon was retained in the ecosystem (in trees and soil) over 33 years (Figure 6, Table 4) when BT (with a 20-year thinning interval) under a 75-year rotation length was used. The prolongation of rotation length from 75-years to 100 years increased carbon retention to 37 years under BT. The thinning thresholds also affected the carbon retained in the ecosystem. Carbon retention increased from 36 to 42 years under BT+20 (with a 25-year thinning interval), when increasing the rotation length from 75-years to 100 years. The corresponding prolongation of the rotation length also increased retention under BT-20 (with a 15-year thinning interval), from 30 to 33 years.

Under BSC (seed crop fraction = 1), carbon retention was 15 years, and thus substantially less than under BT. An increase in basal area threshold in selective cutting (BSC+20) increased the retention to 23 years. A reduction in basal area thresholds (BCS-20%) reduced the carbon retention to 11 years. However, the carbon retention was affected also by the seed crop potential. A reduction in full seed crop potential for BSC by 25–75% reduced carbon retention by 5–16%. In overall, carbon retention was more sensitive to the basal area thresholds than seed crop potential.

Table 4.

**Carbon stock, amount of harvested timber, and economic profitability**

The carbon stock and total amount of harvested timber were nearly the same under even- and uneven-aged management (with seed crop fraction = 1), regardless of the basal area thresholds used in cuttings over the 300-year simulation period. However, the amount of sawlogs and their carbon stock were slightly higher under uneven-aged management, in opposite to those of pulpwood (Table 5). The use of a lower basal area threshold in cuttings reduced them, contrary to the use of a higher cutting thresholds, regardless of management system. The average sawlog share of the total harvest was 74–82% under uneven-aged management and 73–76% under even-aged management. The average shares of pulpwood for them were 18–26% and 24–27%, respectively. A reduction in full seed potential of 25–75% reduced the total timber yield by up to 46%, and the reduction was greater for pulpwood than sawlog yield.

The NPV was 78–81% smaller under even-aged management regimes compared to corresponding uneven-aged management regimes with seed crop fraction = 1, when the production cycle under
even-aged management was initiated by planting on clear-cutting area (Figure 7). The NPV was also 22–28% smaller under even-aged management regimes when initiating the NPV calculation a few years before the first commercial thinning. However, initiating the calculations a few years before the second commercial thinning, resulted in 3-18% higher NPV under even-aged management regimes. The difference was the greatest when the BT+20 regime was used under even-aged management and the BSC+20 was used under uneven-aged management. Regardless of management system, the use of a lower basal area threshold reduced the NPV (by 5–15%), in opposite to the use of higher basal area thresholds, due to decrease in timber yield.

**Table 5.**

**Figure 7.**

**Discussion and conclusions**

**Evaluation of findings**

We carried out a comparative analysis on how different even-aged and uneven-aged management regimes affect the carbon dynamics and timber production in Norway spruce stands in the boreal conditions, based on simulations with a gap-type forest ecosystem model. The model combines the regeneration (planting or natural seeding), and the cohort-based growth and mortality of trees, allowing the development of both even-aged and uneven-aged forest structure as controlled by management. In even-aged management, the rotation was initiated by planting of seedlings on clear-cutting area, followed by thinnings from below, and ended in clear-cutting for the next rotation. In uneven-aged management, the emergence and ingrowth of seedlings occurred in canopy gaps, when dominating and co-dominating trees were removed in repeated single-tree selective cuttings. Under even-aged management, we did not assume any breeding gain in planting of seedlings, which would result in at least about 10% better growth for seedlings, compared to unimproved regeneration material (see e.g. Haapanen and Mikola, 2008; Haapanen et al. 2016). Additionally, it may also increase economic profitability of timber production due to enhanced tree growth and earlier cuttings, despite of the higher price of improved materials (see e.g. Ahtikoski et al., 2012, 2013).

In model based studies, the simulation of even-aged management with thinnings is less complex than that for uneven-aged management with selective cuttings. In the latter case, the ingrowth of seedlings represents the accumulation of seedlings over several years from natural seeding to established seedlings. However, the effects of different factors on regeneration success are often aggregated in simulation models for a lump estimation of emergence and ingrowth of seedlings (e.g., Pukkala et al. 2009; Tahvonen et al. 2010; Roessiger et al. 2016; Juutinen et al., 2018). We partially decomposed this aggregation by using the approach of Fox et al. (1983) and Pukkala (1987a, b), in which the seeding and germination of the seeds are affected in uneven-aged management by the properties of seed crop and seedbed, the prevailing climatic conditions, and the effects of herbivory, respectively. Only a few emerged seedlings per each annual seed crop become therefore established and grow to full maturity (Kellomäki and Väisänen, 1995; Kellomäki et al., 1987, 1997).
Our simulations produced the percentage age-distribution close to the inverse J-shaped form which is typical of forest growth under single-tree selective cuttings (e.g., Eerikäinen et al. 2014; Shanin et al. 2016). When assuming a full seed crop (seed crop fraction = 1), the annual mean growth of stemwood was in our study 4.5–6.0 m³ ha⁻¹ yr⁻¹ for uneven-aged management, the range being quite the same as for even-aged management. It was also in the same range as that found by Laiho et al. (2011) for uneven-aged Norway spruce dominated forests. On the other hand, Lundqvist (2017), based the meta-data analysis, and Hynynen et al. (2019), based on the field experiments, found use of uneven-aged management to reduce stemwood (or basal area) growth in Norway spruce stands compared to even-aged management. In the study by Hynynen et al. (2019), the basal area growth was 20% smaller under uneven-aged than under even-aged management during the post-treatment period of 15 years. However, the observed differences between management systems are also affected by the differences in their volume of growing stock (stocking density) and cutting intensity, which both affect forest growth per unit land area (see e.g. Lundqvist 2017; Hynynen et al. 2019). This could be seen also based on our findings, for example, when comparing the results for even-aged management with baseline regime (BT) against those of uneven-aged management with higher or lower basal area thresholds for cuttings (BSC+20 or BSC-20), instead of baseline regime (BSC).

Several previous model-based studies have shown that timber yield under even-aged management is equal or higher than that under uneven-aged management (e.g., Lundqvist et al., 2007; Tahvonen et al., 2010; Pukkala et al., 2011a, b; Lundmark et al., 2016; Tahvonen and Rämö 2016; Peura et al., 2018). In our study, the amount of harvested timber was quite same order under even-aged and uneven-management, when assuming full seed crop in the latter one (seed crop fraction = 1). Also, based on a long-term experiment by Nilsen and Strand (2013), the total timber yield in uneven-aged Norway spruce stands was 95% of that in even-aged stands.

The mean annual carbon uptake, emissions, litterfall, and carbon in the trees and harvested timber, were quite a same order under even-aged and uneven-management, when assuming full seed crop (seed crop fraction = 1). The carbon stock in the soil and ecosystem (trees and soil) and the mean annual net ecosystem exchange were, in general, slightly smaller under even-aged than uneven-aged management. On the other hand, the carbon retention time was shorter under uneven-aged management. The preference for higher stocking further increased both net carbon exchange and carbon retention, regardless of management system. Under even-aged management, the prolongation of rotation length, from 75 to 100 years, increased the NEE and carbon retention time, as found in previous studies (Kellomäki, 2017). Even a moderate prolongation of the rotation length can increase the capacity of the forest ecosystem to absorb carbon and enhance the retention of carbon in the ecosystem (Liski et al., 2001; Pukkala et al., 2011a, b; Kellomäki, 2017). Our findings on carbon stock in the soil and ecosystem (trees and soil) deviate from those of Nilsen and Strand (2013), who found based on an 80-year-long experiment, that the mean carbon storage in trees (including roots) was clearly greater in even- than uneven-aged Norway spruce stands. On the contrary, the amount of soil carbon was in some degree lower in the even- than the uneven-aged stand. Consequently, the total amount of carbon in the ecosystem (trees and soil) was higher in the even- than in the uneven-aged plots.
In our study, the share of saw-logs was also slightly greater, and pulpwood smaller, under uneven-aged management (seed crop fraction = 1), which is in line with the findings of Pukkala et al. (2011a, b), for example. As expected, uneven-aged management was substantially more profitable than even-aged management, especially when initiating the economic calculations from the clear-cutting area in the latter case. This is because in the former case, the costs of regeneration (e.g., soil preparation and the planting of seedlings) and precommercial thinning (e.g., Pukkala et al., 2010, 2011b; Tahvonen et al., 2010; Pukkala, 2016; Tahvonen, 2016; Peura et al., 2018) are avoided, unlike in the latter case. The situation was the opposite when initiating the NPV calculation a few years before the second commercial thinning. This emphasizes the importance of a time perspective, with proper initiation of calculations in comparative analyses. Thus, the initial structure substantially affected the outcome of comparison between different management regimes.

Conclusions

Based on our findings, uneven-aged management is promising management system in many ways. However, its success is in the long run very much depending on the success of natural regeneration and ingrowth of seedlings, as we demonstrated in this study. For example, a reduction of the seed crop by 25–75% from the full seed crop reduced the number of small seedlings (< 10 cm) under the BSC by up to 20–50%. As a result, also the volume growth decreased by 44–74% and timber yield decreased up to 46%, respectively. Carbon flows, stocks and retention were in some degree less sensitive to the seed crop reduction. In the future studies, it should be considered also the climate change and associated increase in various abiotic and biotic risks to forests (see e.g. Reyer et al. 2017). This is, because they may partly cancel the predicted increase in forest productivity under changing climate, regardless of management system.

Conflict of interest statement

None declared.

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Table 1. Explanation of environmental multipliers scaling maximum diameter growth in SIMA model.

<table>
<thead>
<tr>
<th>Multiplier</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature sum, $M_{TS}$</td>
<td>The multiplier for temperature sum is based on a symmetrical parabola, opening downwards through the minimum and maximum values. It defines geographical distribution for each tree species through the boreal zone (from the northern timberline forest to the northern parts of the hemiboreal zone in Finland).</td>
</tr>
<tr>
<td>Available light, $M_L$</td>
<td>The multiplier for light limits the growth of a tree, along with the vertical light gradient through the stand. It is based on the height and foliage mass of each tree, the cumulative foliage mass in trees taller than a given tree, and the proportion of light penetrating through the foliage of taller trees.</td>
</tr>
<tr>
<td>Dry days, $M_W$</td>
<td>The multiplier for soil moisture indicates the fraction of dry days in the growing season, with adequate/inadequate soil moisture for growth in relation to the balance between precipitation and evaporation at the site. Field capacity and wilting point define the maximal available soil water as a function of soil type.</td>
</tr>
<tr>
<td>Available nitrogen, $M_N$</td>
<td>The multiplier for nitrogen is related to the nitrogen content in foliage, which is a function of the available nitrogen in soil organic matter. Litter from any living organ and the mortality of whole trees transfer carbon and nitrogen into the soil, where the litter and humus decay, releasing nitrogen for tree growth.</td>
</tr>
</tbody>
</table>
Table 2. Stumpage prices of sawlogs and pulpwood as a function of cutting type (The Natural Resources Institute Finland. Available online at http://statdb.luke.fi/PXWeb/pxweb/en/LUKE/ Visited on November 17, 2017).

<table>
<thead>
<tr>
<th>Cutting per management regime</th>
<th>Sawlogs, € m$^{-3}$</th>
<th>Pulpwood, € m$^{-3}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Even-aged management</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First commercial thinning</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>Other commercial thinning</td>
<td>48</td>
<td>16</td>
</tr>
<tr>
<td>Final cutting</td>
<td>56</td>
<td>18</td>
</tr>
<tr>
<td>Uneven-aged management</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selective cutting</td>
<td>48</td>
<td>16</td>
</tr>
</tbody>
</table>
Table 3. Percentage differences in the values of carbon indicators under uneven-aged management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions (BSC, BSC+20, BSC-20), compared to the corresponding values under even-aged management (BT, BT+20, BT-20) with rotation length of 75 years. In both management systems, the values are based on a 300-year simulation period.

<table>
<thead>
<tr>
<th>Carbon indicators</th>
<th>Difference (%) for uneven-aged versus even-aged management</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BSC</td>
</tr>
<tr>
<td>Carbon uptake in trees</td>
<td>-1</td>
</tr>
<tr>
<td>Carbon stock in trees</td>
<td>-3</td>
</tr>
<tr>
<td>Carbon in litterfall</td>
<td>-4</td>
</tr>
<tr>
<td>Carbon stock in soil</td>
<td>-6</td>
</tr>
<tr>
<td>Carbon emission from soil</td>
<td>-3</td>
</tr>
<tr>
<td>Carbon stock in ecosystem</td>
<td>-4</td>
</tr>
</tbody>
</table>
Table 4. Carbon retention time under even-aged (BT, BT+20, BT-20, with rotation lengths of 75 and 100 years) and uneven-aged (BSC, BSC+20, BSC-20) management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions, respectively. Additionally, it is shown how use of higher and lower basal area thresholds affect carbon retention time, compared to the baseline management. In both management systems, the values are based on a 300-year simulation period.

<table>
<thead>
<tr>
<th>Management</th>
<th>Carbon retention, yr.</th>
<th>Carbon retention, % change from baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Even-aged, rotation length of 75 yr.</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BT</td>
<td>33</td>
<td>-</td>
</tr>
<tr>
<td>BT+20%</td>
<td>36</td>
<td>9</td>
</tr>
<tr>
<td>BT-20%</td>
<td>30</td>
<td>-10</td>
</tr>
<tr>
<td><strong>Even-aged, rotation length of 100 yr.</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BT</td>
<td>37</td>
<td>-</td>
</tr>
<tr>
<td>BT+20%</td>
<td>42</td>
<td>14</td>
</tr>
<tr>
<td>BT-20%</td>
<td>33</td>
<td>-11</td>
</tr>
<tr>
<td><strong>Uneven-aged</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BSC, thinning interval 15 yr.</td>
<td>15</td>
<td>-</td>
</tr>
<tr>
<td>BSC+20%, thinning interval 23 yr.</td>
<td>23</td>
<td>53</td>
</tr>
<tr>
<td>BSC-20%, thinning interval 11 yr.</td>
<td>11</td>
<td>-27</td>
</tr>
</tbody>
</table>
Table 5. Mean harvested amount of timber per year (sawlogs, pulpwood and total, m$^3$ ha$^{-1}$ yr.$^{-1}$) under even-aged (BT, BT+20, BT-20, with rotation lengths of 75 years) and uneven-aged (BSC, BSC+20, BSC-20) management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions, respectively. Under both management systems, the simulation period was 300 years. Corresponding carbon stock (Mg C ha$^{-1}$ yr.$^{-1}$) in timber is given in parentheses.

<table>
<thead>
<tr>
<th>Management regime</th>
<th>Even-aged, m$^3$ ha$^{-1}$ yr.$^{-1}$ (Mg C ha$^{-1}$ yr.$^{-1}$)</th>
<th>Uneven-aged, m$^3$ ha$^{-1}$ yr.$^{-1}$ (Mg C ha$^{-1}$ yr.$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sawlogs</td>
<td>Pulpwood</td>
</tr>
<tr>
<td>BT-20 or BSC-20</td>
<td>3.97</td>
<td>1.50</td>
</tr>
<tr>
<td>BT or BSC</td>
<td>4.46</td>
<td>1.63</td>
</tr>
<tr>
<td>BT+20 or BSC+20</td>
<td>4.92</td>
<td>1.56</td>
</tr>
</tbody>
</table>
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.
Figure captions

Figure 1. Simulated fractions of Norway spruce trees in different diameter classes over the 300-year simulation period. The values are based on baseline selective cutting (BSC) for uneven-aged management. The seed crop potential of 0.25, 0.50, 0.75, or 1 of the full potential was assumed in simulations. The solid line represents the size distribution, based on measurements of ERIKA plots in 2011, before the next selective cutting (Shanin et al. 2016). The insert in the main figure shows the correlation between the currently simulated (x-axis) distribution, assuming the full seed crop potential (i.e., a seed crop fraction = 1), and the distribution (y-axis) based on Shanin et al. (2016).

Figure 2. Outline of flows and stocks of carbon in the forest ecosystem.

Figure 3. Carbon stock in stemwood over the 300-year simulation period under even-aged (BT, BT+20, BT-20, with rotation length of 75 years) and uneven-aged (BSC, BSC+20, BSC-20) management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions, respectively.

Figure 4. Mean number of trees in different diameter classes and their proportion (% of cases) over the 300-year simulation period under even-aged (above: BT, BT+20, BT-20, with rotation lengths of 75 years) and uneven-aged (middle: BSC, BSC+20, BSC-20) management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions, respectively. Additionally, it is shown (below) mean number of trees in different diameter classes over the 300-year simulation period for baseline selective cutting (BSC), with seed crop of 25, 50, 75, and 100% of the full potential (i.e., a seed crop fraction = 0.25, 0.50, 0.75, or 1 was used).

Figure 5. Mean carbon fluxes and stocks in forest ecosystem over the 300-year simulation period under even-aged (BT, BT+20, BT-20, with rotation lengths of 75 years) and uneven-aged (BSC, BSC+20, BSC-20) management with full seed crop potential (seed crop fraction = 1), under baseline management and with higher and lower basal area thresholds for management interventions, respectively. Upper left: Mean annual carbon uptake in trees. Middle left: Mean annual carbon in litterfall originating from different tree organs. Below left: Mean annual carbon emission from soil (litter and humus). Upper right: Mean carbon stock in trees (including stems, branches, foliage, and roots). Middle right: Mean carbon stock in soil (litter and humus). Lower right: Mean carbon stock in the ecosystem (trees and soil).

Figure 6. Mean net ecosystem exchange between the atmosphere and forest ecosystem (upper left), mean retention time for carbon in the forest ecosystem (upper right), mean carbon retention time in the forest ecosystem under even-aged management as a function of rotation length (lower left), and mean carbon retention time in the forest ecosystem under uneven-aged management, with full seed crop potential (seed crop fraction = 1) (lower right) over the 300-year simulation period. Under both management systems, baseline regimes (BT and BSC), and lower (BT-20 and BSC-20) and higher (BT+20 and BSC+20) basal area thresholds were used for thinnings and selective cuttings, respectively.
Figure 7. Net present value (NPV, with an interest rate of 3%) for harvested timber under even-aged management (columns), when using baseline thinning (BT) and lower (BT+20) and higher (BT-20) basal area thresholds for thinning over a rotation length of 75 years. Under uneven-aged management (horizontal lines), baseline selective cutting (BSC) and lower (BSC+20) and higher (BSC-20) basal area cutting thresholds were used, with full seed crop potential (seed crop fraction = 1). Under both management systems, the simulation period was 300 years. Under even-aged management, the NPV calculations were initialized for: (i) clear-cutting area on which seedlings were planted in year 1 (scenario 1); (ii) the first thinning phase (scenario 2); and (iii) the second thinning phase (scenario 3).