



Multi-layered Scots pine forests in boreal Sweden result from mass regeneration and size stratification

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ABSTRACT

Understanding historic development of multi-layered Scots pine (*Pinus sylvestris* L.) stands and how they became multi-layered is essential for assessing the feasibility of using the selection system in these stands. To address this we measured trees (dbh \geq 4 cm) and saplings (height $>$ 0.5 m dbh $<$ 4 cm) and used increment cores from 244 sample trees to reconstruct stand structure development, ingrowth and basal area increment in four multi-layered Scots pine stands in Sweden. Age distributions were quite homogeneous, three of the four stands had age distributions that were dominated by one or two 20 year age classes, suggesting that the irregular diameter distributions displayed in 2013 had developed from more homogeneous distributions. Analyses of the historical ingrowth of Scots pine into the tree layer suggested that the multi-layered structure was created by mass regeneration followed by size stratification caused by differences in growth rates within even-aged cohorts of regeneration. Large reductions of the basal area in the past resulted in abundant regeneration and ingrowth of Scots pine. When the over-story increased in basal area over time, there was a growth differentiation among the saplings and small trees, gradually creating a multi-layered stand structure as some of the trees grew into the larger size classes while others remained in the smaller size classes. When the stands reached a basal area of about 13 m² ha⁻¹ the ingrowth of saplings past 1.3 m height essentially stopped but the size stratification among the small trees continued, further enhancing the multi-layered structure. The results indicate that to receive regeneration pulses and sustain a multi-layered structure in Scots pine forests, the basal area needs to be significantly reduced. The growth consequences of this need to be studied.

1. Introduction

The public in Europe is criticizing clearcutting of boreal forests and demanding that it should be replaced by continuous cover forestry (CCF). For Norway spruce (*Picea abies* (L.) H. Karst) the selection system is an accepted CCF method. It is a silvicultural system that requires and maintains multi-layered, full-storied forests (cf. Lundqvist, 2017). At relatively short intervals 20–30 percent of the growing stock is harvested, mainly among the largest trees. Remaining trees are continuously growing into larger size classes and the stem number is kept constant by saplings continuously growing past the ingrowth threshold into the tree stratum, and the saplings are in turn themselves being replaced by new seedlings continuously establishing under the dense forest.

However, about half of Europe's boreal forests are dominated by Scots pine (*Pinus sylvestris* L.), a species considered to be shade intolerant and which typically develops single-storied stands. If the selection system requires shade-tolerant species, like Norway spruce, which have the ability to establish, survive and grow in a semi-closed stand (cf. Schütz, 2001; Grassi et al., 2004; Redon et al., 2014), a large part of the boreal forests are unsuitable for CCF. Nevertheless, there are many examples from around the world where shade intolerant species have

been managed in a way that created and maintained multi-layered stand structures. They include shortleaf (*Pinus echinata* Mill.), longleaf (*Pinus palustris* Mill.) and loblolly pine (*Pinus taeda* L.) in the USA (Farrar and Boyer, 1991; Murphy et al., 1991; Baker et al., 1996), and Calabrian pine (*Pinus brutia* Tenore) in Italy (Ciancio et al., 2006). There are also examples of multi-layered Scots pine stands in Europe in e.g. Scotland, Sweden and Spain (Ågren and Zackrisson, 1990; Trasobares et al., 2004; Edwards and Mason, 2006). Together this suggests that Scots pine could potentially be managed with some modified version of the selection system.

Multi-layered stand structures can develop in several ways but in connection with silviculture, two principally different ways can be envisioned: (1) continuous regeneration and ingrowth from below, and (2) size stratification after mass regeneration. As established above, long-term use of the selection system requires alternative (1) (cf. Lundqvist, 2017).

With alternative (1) the size and age distributions in a stand should have a similar shape. There has to be a substantial seedling pool supplying the ingrowth and the level of ingrowth should gradually be lower if the threshold size is set at a gradually higher level, as shown by e.g. Lundqvist (2004) where the ingrowth in eight partially harvested uneven-aged sub-alpine spruce stands was 6–21 stems ha⁻¹ year⁻¹ past

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4 cm dbh but only 5–12 stems $\text{ha}^{-1} \text{year}^{-1}$ past 8 cm dbh. The cause for the drop in numbers is primarily mortality among the seedlings, saplings and small trees. Furthermore, this alternative requires that seedlings can continue to survive and grow also when stand density increases. However, studies in Scots pine shelterwoods show that growth of seedlings and saplings on undisturbed soil decreases with increasing shelterwood density and that to receive abundant Scots pine regeneration, the tree layer must be fairly open with a small basal area (Nilsson et al., 2002).

With alternative (2) the age distribution should have most trees in a few distinct age classes. One would expect to find few seedlings in the stands as most of them would by now have either died or grown into larger size classes and ingrowth would be expected to drop over time because seedlings and saplings growing out of the smaller size classes would not be replaced by new regeneration. This could even result in higher ingrowth levels at higher threshold levels.

To assess the feasibility of managing Scots pine with the selection system we hypothesized that:

1. Multi-layered Scots pine stands are mainly a result of size stratification following mass regeneration and not of continuous ingrowth.
2. Abundant ingrowth into the tree layer only occurs while the stand basal area is below a threshold value.

2. Material and methods

We chose to limit our search for study stands to the experimental forests managed by the Swedish University of Agricultural Sciences (SLU), because almost all management done in the past has been recorded in more or less detail. Four stands were chosen for the study, two located in central Sweden and two in northern Sweden. The two southern stands (S1 and S2) were located at Siljansfors experimental forest (60°53' N, 14°22' E, 215 m a.s.l.) 20 km south of Mora, and the two northern stands (N1 and N2) close to each other at Svartberget experimental forest (64°14' N, 19°47' E, 190 m a.s.l.) 50 km northwest of Umeå.

Stand sizes varied between 1 and 12 ha. The stands were subjectively selected with the prerequisites of being visually multi-layered and with past management being known and documented.

In stand S1 the soil was a mesic sandy moraine, in S2 a dry sandy moraine, and in both N1 and N2 a mesic coarse silty-sandy moraine. All four stands had forest floor vegetation that mainly consisted of dwarf-shrubs with *Vaccinium vitis-idaea* L. as dominant species. Major additional species was *Vaccinium myrtillus* L., and in stand S1 also *Empetrum nigrum* L. and *Rhododendron tomentosum* Harmaja. Average annual temperature and annual precipitation at the time of inventory were approximately 3.9 °C and 670 mm at Siljansfors, and 3.0 °C and 649 mm at Svartberget (Ottosson-Löfvenius 2014).

At the inventory in 2013 all stands were dominated by Scots pine (*Pinus sylvestris* L.), 77–99% of the basal area, with the rest being scattered Norway spruce (*Picea abies* (L.) H. Karst) and birch (*Betula*

pubescens Ehrh and *Betula pendula* Roth) (Table 1).

Stand S1 was harvested in 1963, leaving approximately 60 seed trees ha^{-1} . The stand was then pre-commercially thinned twice: in 1977 to remove deciduous trees, and in 1993 to regulate stem density. The seed trees were never removed. Stand S2 had been subjected to high grading several times in the past and again in 1932, in which approximately 45% of the standing volume was removed, “creating a stand with low stem density and gaps”, having about 70 $\text{m}^3 \text{ha}^{-1}$ according to historical records. During the period 1945–1988 a total of 58 trees ha^{-1} were lost through wind damage, i.e. 1.3 stems $\text{ha}^{-1} \text{year}^{-1}$ but no harvests were done.

Stands N1 and N2 where initially part of one large compartment which was subjected to high grading in 1892, extracting timber for railroad sleepers. During the years 1908–1911 most Norway spruce and birch were harvested. The compartment was then divided into two separate stands, leaving stand N1 unmanaged since 1911 while N2 was subjected to high grading in 1936, and thinning in 1947 and 1957 but after that left unmanaged.

All measurements were done in the autumn of 2013. Two circular plots with an area of 1257 m^2 (20 m radius) were deployed in each stand. Within each plot, all trees with dbh \geq 4 cm (diameter over bark at breast height, 1.3 m above ground) were numbered and calipered. Total tree height (h , m), bark thickness (b , mm), and height to the first living branch (k , m) were measured on 1–3 randomly chosen trees of Scots pine and Norway spruce, respectively, within each 2 cm diameter class on each plot. An increment core was also taken at breast height on these sample trees, resulting in a total of 244 increment cores. The increment cores were stored in paper tubes at room temperature (around 20 °C) until further measurements.

Within the central 314 m^2 (10 m radius) of each plot, the total height and length of the last leading shoot (leader) were measured on all Scots pine and Norway spruce saplings (0.5–1.3 m in height) and small trees (0–4 cm dbh). For the pine saplings, total age was estimated by counting whorls, and the total length of the last 5, 10 and 15 leaders were measured and used to calculate the average annual height increment for the last three consecutive five year periods.

Linear equations of bark thickness (b) as a function of dbh were calculated using data from the sample trees. Two equations, one for Scots pine and one for Norway spruce, were calculated and used for each location (Siljansfors and Svartberget). Double bark thickness for birch was calculated as 1/10 of the diameter at breast height, independent of location (Östlin, 1963).

Increment cores collected from the sample trees were swelled in water for at least one hour and then planed, whereafter ring widths were measured with a WinDendro scanner (Regent Instruments, Quebec, Canada) to the nearest 0.1 mm. For each site, increment cores for all trees in the same 2 cm dbh class were pooled to calculate an average ring width for each year. Historic diameters over bark were then reconstructed for all individual trees as:

Table 1
Stand characteristics at the time of measurement (2013).

Stand	Stem number (st ha^{-1})		Standing volume ($\text{m}^3 \text{ha}^{-1}$)	Basal area ($\text{m}^2 \text{ha}^{-1}$)	Species ³			Site productivity ⁴ ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$)
	Saplings & small trees ¹	Trees ²			Pine	Spruce	Birch	
N1	76	665	227	24	97	3	0	3.7
N2	0	1326	240	30	77	15	7	3.7
S1	287	1369	228	30	90	0	10	5.5
S2	60	573	127	16	99	1	0	4.7

¹ > 0.5 m in height and < 4 cm dbh.

² > 4 cm dbh.

³ Percentage of basal area.

⁴ Estimated from site characteristics and translated to site productivity according to Hägglund and Lundmark (1985).

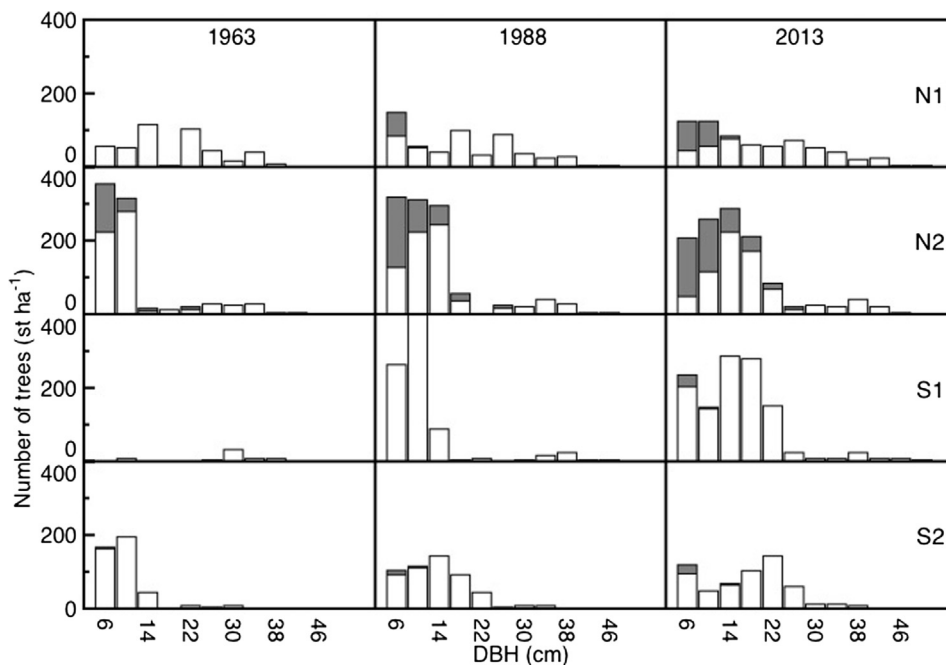


Fig. 1. Diameter distribution (4 cm dbh classes, 4–7.9, 8–11.9, etc) for Scots pine (unfilled) and Norway spruce (grey) in 1964, 1988 and at the time of measurements in 2013.

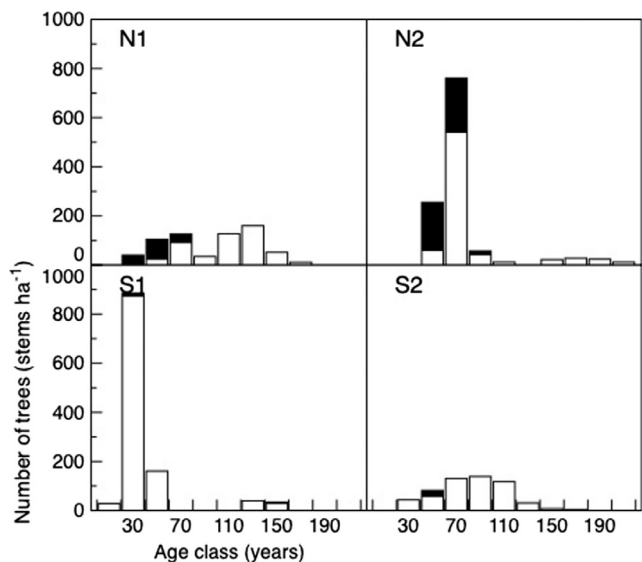


Fig. 2. Age distribution (20 year class width, 0–19, 20–39, etc) for Scots pine (unfilled) and Norway spruce (grey) at the time of measurements in 2013.

$$d_t = d - 2 \left(\sum_{i=1}^t \frac{w_i}{(1-c)} \right) \tag{1}$$

where d is dbh of each tree, t is the number of years before the survey, w_i is the calculated average annual ring widths, and c is the regression coefficient for the linear bark thickness equation. Historical diameter distributions were reconstructed 25 and 50 years backward in time from the year of inventory.

Age at breast height for the sample trees was estimated as the number of annual rings on the increment cores. To create age distributions, the following procedure was used. First, the sample trees were divided in 2-cm dbh classes. Next the age of each sample tree was given to its proportion of all trees within its dbh class. This means that with e.g three sample trees and fifteen trees in total within the 2-cm dbh class, the age of each sample tree was applied to ten trees. This way

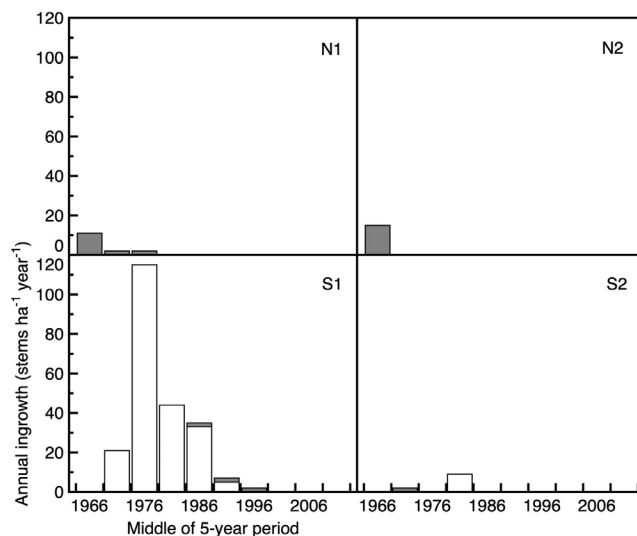


Fig. 3. Sapling ingrowth of Scots pine (black) and Norway spruce (grey), i.e number of saplings annually growing past 1.3 m height per five-year period during the last 50 years, 1964–2013.

trees of different dbh could be given the same age and trees with the same dbh could have different age.

Stem volume (v , dm^3) over bark for sample trees of Scots pine and Norway spruce were calculated with equations developed by Brandel (1990) using dbh, tree height, height to the live crown and (for Scots pine) bark thickness. Using sample tree volume (v) and dbh (d), separate volume equations were then calculated for each stand and species according to Hoffmann (1982):

$$\ln(v) = a_1 + a_2 \ln(d) + a_3 \ln(d)^4 + \varepsilon^2/2$$

where a_{1-3} are constants and ε is the mean residual error (to account for logarithmic bias). Volume for all calipered trees were then calculated using the plot- and species-specific equations and finally summed to get an estimate of the standing volume in each stand at the time of inventory.

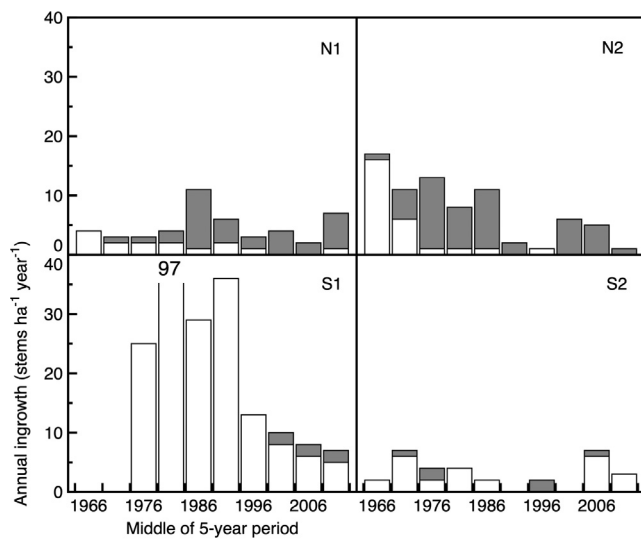


Fig. 4. Tree ingrowth of Scots pine (black) and Norway spruce (grey), i.e. number of small trees annually growing past 4 cm dbh per five-year period during the last 50 years, 1964–2013.

Ingrowth past 1.3 m height (called ‘sapling ingrowth’) and past 4 cm dbh (called ‘tree ingrowth’) was calculated as the net difference in the number of saplings/trees between each year.

The time for saplings and small trees to grow through different height intervals was calculated by dividing the width of the height interval with the average annual height increment (average length of the last leader) of the sampled saplings/small trees within that height interval.

The time needed to reach 1.3 m and 4 cm dbh was calculated in two ways. First using the estimated age of the saplings and small trees, based on counting whorls, and secondly by using the estimated annual height increment for saplings and small trees of different height.

Hypothesis 1, that multi-layered Scots pine stands are mainly a result of size stratification following mass regeneration, was tested by (a) comparing the age distributions with the diameter distributions, (b) looking at the size of the sapling pool, and (c) the ingrowth past two different size thresholds. If the hypothesis is correct most of the trees should belong to a few age classes, there should be very few saplings and there should be higher annual ingrowth past higher threshold levels.

Hypothesis 2, that abundant ingrowth into the tree layer only occurs when stand basal area is below a certain level, was tested by correlating level of ingrowth with stand basal area and trying to identify such a threshold level.

Table 2
Mean annual ingrowth of Scots pine past two different size thresholds at different levels of stand basal area.

Threshold ¹	Stand	Time span ² (years)	Mean ingrowth (stems ha ⁻¹ yr ⁻¹) per basal area class (m ² ha ⁻¹) ³												
			3	5	7	9	11	13	15	17	19	21	23	25	27
1.3 m height	N1	74	–	–	–	–	6	0	0	0	0	0	0	–	–
	N2	56	–	–	–	12	2	0	0	0	0	0	0	0	
	S1	50	–	47	34	38	26	12	0	0	0	0	0	0	
	S2	50	0	0	5	0	0	0	0	–	–	–	–	–	
4 cm dbh	N1	74	–	–	–	–	1	2	4	1	2	0	0	–	–
	N2	56	–	–	–	6	6	15	3	0	1	0	1	0	0
	S1	50	–	13	95	44	6	34	37	14	10	8	7	4	4
	S2	50	0	4	3	1	0	4	3	–	–	–	–	–	–

¹ Ingrowth past 1.3 m height and past 4 cm dbh.

² N1: 1940–2013; N2: 1958–2013; S1 and S2: 1964–2013.

³ Middle of the 2 m² class denoted; a dash denotes that the stand did not have that basal area during the reconstructed period defined in note 2, a zero that the stand did have the basal area but no ingrowth occurred at that basal area level.

3. Results

The diameter distributions displayed in 2013 all indicated multi-layered stands (sensu Lundqvist 2017) (Fig. 1). In 1963, stands N2 and S2 had more than 80% of the trees in the two smallest diameter classes, and S1 had a diameter distribution that consisted almost only of the 60 seed trees ha⁻¹ with a majority having a diameter of 30–40 cm. N1 was the only stand that had trees over the whole diameter range in both 1963 and 2013.

In contrast to the diameter distributions in 2013, two of the four stands, S1 and N2, had age distributions where most of the trees were found in one 20-year age classes, indicating historical mass regeneration (Fig. 2). Stand S2 and N1 had a larger variation in tree ages, but few pine trees younger than 60 years, and the age distributions did not resemble the diameter distributions.

There were few saplings and small trees in the stands (Table 1). In the two northern stands there had been no ingrowth at all of Scots pine past 1.3 m height (Fig. 3) during the last 50 years but a little ingrowth past 4 cm dbh (Fig. 4). Stand S2 received a small addition of new pine saplings around 1980 (Fig. 3) resulting in a new wave of ingrowth past 4 cm dbh about 20 years later (Fig. 4). Stand S1 had a flush of ingrowth of Scots pine past 1.3 m height primarily during the 1970s and 1980s (Fig. 3) resulting in ingrowth past 4 cm dbh continuing throughout the remainder of the observation period (Fig. 4).

Ingrowth past 1.3 m height only occurred when the basal area was small and there was no ingrowth of Scots pine past 1.3 m in any of the stands when the basal area exceeded 13 m² (Table 2). Ingrowth past 4 cm dbh occurred also at larger basal areas and was higher past 4 cm dbh than past 1.3 m height.

Annual height growth of Scots pine saplings was about 3 cm per year and for small trees about 6 cm per year. Assuming that the lower dbh limit for trees, 4 cm dbh, roughly corresponded to 4 m height, the average time needed by Scots pine saplings to grow from 0.5 m height to 4 cm dbh could be estimated to roughly 60–90 years. Most of the saplings and small trees found in the stands had thus established during a time when the stands had much lower basal area than today. Furthermore, saplings had lower height growth at the time of measurement than saplings of the same size had 40 years earlier.

4. Discussion

The diameter distributions displayed in 2013 had little resemblance with the age distributions. For two of the stands, which had trees mainly in a few age classes, the data do not falsify the hypothesis that size heterogeneity had primarily been created by size stratification caused by differences in growth rates within even-aged cohorts of regeneration, rather than by continuous ingrowth from below. This

conclusion is in line with results by Zackrisson et al. (1995) and Linder et al. (1997) who observed regeneration pulses and flushes of ingrowth in old growth Scots pine forests in Sweden. Similar results have also been observed in old-growth Ponderosa pine (*Pinus ponderosa* Laws.) forests in the central parts of the USA (Boyden et al., 2005). The other two stands had a larger variation in tree ages but few trees younger than 60 years at breast height, suggesting a more continuous establishment of pines in the past but not during the last decades when the basal area had increased.

The age distributions suggest that most of the pine trees had established during some special event when conditions for regeneration were favorable. Linder et al. (1997) found a relationship between observed regeneration pulses and forest fires and drew the conclusion that regeneration pulses occur after major disturbances. In the stands we studied there were no traces of major disturbances such as forest fires or severe storm damage during the last 100 years, nor were there any historical records of such events. However, the forest operations which had taken place in the stands may have played a role similar to major disturbances in the development of the stands. The flush of ingrowth in stand S1 was thus most likely a result of the regeneration pulse that occurred after the stand was harvested in 1963, leaving only seed trees. The flush of pine ingrowth past 4 cm dbh in stand N2 at the beginning of the observation period probably resulted from thinning done in 1947 and 1957. This conclusion is supported by data indicating substantial ingrowth past 1.3 m height before 1963. In stand N1, which had not been managed since 1911, most of the pines were older than 100 years and the last reconstructed ingrowth had occurred in the mid-1940s.

The level of annual ingrowth in a forest stand is determined by the number of seedlings, saplings and small trees below the ingrowth threshold, their growth and the mortality rates (Lundqvist, 1995). The mortality among Scots pine seedlings under shelterwoods is high when seedlings are small but decreases when the seedlings grow taller (Béland et al., 2000). However, growth of Scots pine seedlings on undisturbed soil decreases with increasing shelterwood density (Nilsson et al., 2002) which means that they will stay small for a longer time in denser stands. If both these relationships are valid also for multi-layered Scots pine stands, a conclusion would be that when stand density increases above a certain level, few saplings and small trees would reach the ingrowth threshold and grow into the tree layer. This corresponds with the observations in this study. There was also a rather clear basal area threshold above which no ingrowth occurred. Hypothesis 2, that abundant ingrowth of Scots pine only occur when the basal area is below a basal area threshold level, could thus not be falsified.

The more or less continuous ingrowth past 4 cm dbh could easily be interpreted as support for the ability of these stands to be managed with the selection system and remain multi-storied. However, to be managed with selection system there has to be a continuous ingrowth also past 1.3 m height and the ingrowth past that level needs to be higher than the ingrowth past 4 cm dbh to compensate for mortality among the saplings. None of the studied stands had a continuous ingrowth past 1.3 m height. In fact, three of the stands had no or very little ingrowth at all past 1.3 m height during the last 50 years. The lack of continuous ingrowth past 1.3 m height give further support to the hypothesis that the multi-layered structure was a result of historical mass regeneration followed by size stratification.

If these Scots pine stands were to be managed with selection system the stand basal area would have to be reduced well below $13 \text{ m}^2 \text{ ha}^{-1}$ at the harvests in order to give the stands a chance to produce a sufficient amount of new pine regeneration. For full-storied Norway spruce stands it has been established that volume increment is proportional to the standing volume (Lundqvist, 2017). If this is true also for multi-layered Scots pine stands, such a large reduction of the basal area would cause an equally large reduction of stand volume increment. If the basal area was kept at a higher level, to maintain a high level of volume increment, repeated thinning from above would continuously reduce the stem number as harvested trees would not be replaced by saplings

growing into the tree layer. This would eventually cause the multi-layered structure to disappear and the stand would become single-storied.

A disadvantage with reconstructions is that only trees that survived during the whole reconstructed time period are included (Lundqvist, 2004). Depending on the size of mortality rates this could potentially bias the results, and the bias would increase with increasing length of the reconstruction period. The total number of trees at the beginning of the reconstruction period would be underestimated, leading to an overestimation of the ability of the stand to re-create a large stem number at the end of the reconstructed period. However, annual mortality rates in mature Scots pine stands are usually rather low. Rouvinen et al. (2002) reported mortality rates in old-growth Scots pine forests in the western parts of Russia to be 0.6–1.2 percent of the living standing volume, in average $3.7 \text{ trees ha}^{-1} \text{ year}^{-1}$. In a nation-wide series of thinning experiments in Scots pine forests in Sweden, non-thinned control plots had annual mortality rates of 0.8–1.8 percent of the stems (Elfving, 2010), and mainly small trees had died. It takes up to 80 years for dead Scots pine trees to decompose and disappear (Mäkinen et al., 2006), and since few dead trees were found during the fieldwork, we believe the mortality rates in our stands corresponded to or were even lower than the mortality rates reported by Elfving (2010) and Rouvinen et al. (2002). The general trends observed in this study should, therefore, be reliable in spite of the absence of data on mortality.

Put together, the data suggest that these multi-layered Scots pine stands were created by mass regeneration followed by size stratification caused by differences in growth rates within even-aged cohorts of regeneration. Large reductions of the basal area in the past, down to $4\text{--}8 \text{ m}^2 \text{ ha}^{-1}$, resulted in abundant regeneration and ingrowth of Scots pine. When the over-story increased in basal area over time there was a growth differentiation among the existing seedlings, saplings and small trees, gradually creating a multi-layered stand structure as some of them grew into the larger size classes while others remained in the smaller size classes. When the stands reached a basal area of about $13\text{--}14 \text{ m}^2 \text{ ha}^{-1}$ the ingrowth of saplings past 1.3 m height essentially stopped but the size stratification among the small trees continued, further enhancing the multi-layered structure.

We only studied four different stands at two different locations. However, in spite of having rather different prior histories, the stands showed obvious similarities in their development during the last 50 years. This suggests that to create and maintain multi-layered Scots pine stands it is necessary to heavily reduce the basal area and then leave the stand for several decades, where after the harvest can be repeated. The cost for this kind of management could be a substantial loss of stand growth but further studies are required to verify and quantify this.

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Conflict of interest statement

None declared.

References

- Ågren, J., Zackrisson, O., 1990. Age and size structure of *Pinus sylvestris* populations on mires in central and northern Sweden. *J. Ecol.* 78, 1049–1062.

- Baker, J.B., Cain, M.D., Guldin, J.M., Murphy, P.A., Shelton, M.G., 1996. Uneven-Aged Silviculture for the Loblolly and Shortleaf Pine Forest Types. General technical report SO-118. USDA Forest Service, pp. 65.
- Béland, M., Agestam, E., Ekö, P.M., Gemmel, P., Nilsson, U., 2000. Scarification and seedfall affects natural regeneration of Scots pine under two shelterwood densities and a clear-cut in southern Sweden. *Scand. J. For. Res.* 15, 247–255.
- Boyden, S., Binkley, D., Shepperd, W., 2005. Spatial and temporal patterns in structure, regeneration and mortality of an old-growth ponderosa pine forest in the Colorado front range. *For. Ecol. Manage.* 219, 43–55.
- Brandel, G., 1990. Volymfunktioner för enskilda träd [Volume Functions for Individual Trees], vol. 26, 183.
- Ciancio, O., Iovino, F., Menguzzato, G., Nicolaci, A., Nocentini, S., 2006. Structure and growth of a small group selection forest of calabrian pine in Southern Italy: a hypothesis for continuous cover forestry based on traditional silviculture. *For. Ecol. Manage.* 224, 229–234.
- Elfving, B., 2010. Natural mortality in thinning and fertilisation experiments with pine and spruce in Sweden. *For. Ecol. Manage.* 260, 353–360. <https://doi.org/10.1016/j.foreco.2010.04.025>.
- Edwards, C., Mason, W.L., 2006. Stand structure and dynamics of four native Scots pine (*Pinus sylvestris* L.) woodlands in northern Scotland. *Forestry* 79 (3), 261–277. <https://doi.org/10.1093/forestry/cpl014>.
- Farrar, R.M., Boyer, W.D., 1991. Managing longleaf pine under the selection system – promises and problems. General Technical Report SO-70 In: Proceedings of the 6th Biennial Southern Silvicultural Research Conference, October 30–November 1, 1990, Memphis, Tennessee. USDA Forest Service, pp. 357–368.
- Grassi, G., Minotta, G., Tonon, G., Bagnaresi, U., 2004. Dynamics of Norway spruce and silver fir natural regeneration in a mixed stand under uneven-aged management. *Can. J. For. Res.* 34, 141–149.
- Hägglund, B., Lundmark, J.-E., 1985. Handledning i bonitering med skogshögskolans boniteringssystem, Del 2 Diagram och tabeller. [Manual in Site Productivity Estimation with the College of Forestry system, Part 2 Figures and Tables]. Skogsstyrelsen, Jönköping.
- Hoffmann, C., 1982. Die berechnung von Tarifen für die Waldinventur. *Forstwissenschaftliches Centralblatt* 101 (1), 24–36.
- Linder, P., Elfving, B., Zackrisson, O., 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *For. Ecol. Manage.* 98, 17–33.
- Lundqvist, L., 1995. Simulation of sapling population dynamics in uneven-aged *Picea abies* forests. *Ann. Bot.* 76, 371–380.
- Lundqvist, L., 2004. Stand development in uneven-aged sub-alpine *Picea abies* stands after partial harvest estimated from repeated surveys. *Forestry* 77, 119–129.
- Lundqvist, L., 2017. Tamm review: selection system reduces long-term volume growth in Fennoscandic uneven-aged Norway spruce forests. *For. Ecol. Manage.* 391, 362–375. <https://doi.org/10.1016/j.foreco.2017.02.011>.
- Mäkinen, H., Hynynen, J., Siitonen, J., Sievänen, R., 2006. Predicting the decomposition of Scots pine, Norway spruce and birch stems in Finland. *Ecol. Appl.* 16, 1865–1879.
- Murphy, P.A., Baker, J.B., Lawson, E.R., 1991. Selection management of shortleaf pine in the Ouachita mountains. *South. J. Appl. For.* 15, 61–67.
- Nilsson, U., Gemmel, P., Johansson, U., Karlsson, M., Welander, T., 2002. Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. *For. Ecol. Manage.* 161, 133–145.
- Östlin, E., 1963. Barkuppgifter för tall, gran, björk m.fl.; Del 1 Barkuppgifter för län, regioner. [Bark Data for Pine, Spruce, Birch, etc.; Part 1 Bark Data for Provinces and Regions]. Rapporter och uppsatser, Institutionen för skogstaxering, Skogshögskolan.
- Ottosson-Löfvenius, M., 2014. Referensmätningar av klimat vid skogliga försöksarkerna. Årsrapport 2013. Sveriges lantbruksuniversitet, Enheten för skoglig fältforskning (in Swedish).
- Redon, M., Luque, S., Gosselin, F., Cordonnier, T., 2014. Is generalization of uneven-aged management in mountain forests the key to improve biodiversity conservation within forest landscape mosaics? *Ann. For. Sci.* 71, 751–760.
- Rouvinen, S., Kuuluvainen, T., Siitonen, J., 2002. Tree Mortality in a *Pinus sylvestris* Dominated Boreal Forest Landscape in Vienansalo Wilderness. Eastern Fennoscandia, *Silva Fennica*, pp. 36.
- Schütz, J.-P., 2001. Der Plenterwald und weitere Formen strukturierter und gemischter Wälder. [The Selection Forest and Other Types of Structured and Mixed Forests]. Parey Buchverlag, Berlin, pp. 221.
- Trasobares, A., Pukkala, T., Miina, J., 2004. Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain. *Ann. For. Sci.* 61, 9–24.
- Zackrisson, O., Nilsson, M.-C., Steijlen, I., Hörnberg, G., 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. *J. Ecol.* 83, 469–483.