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Height increment of understorey Norway spruces under different tree canopies

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Abstract

Background: Stands having advance regeneration of spruce are logical places to start continuous cover forestry (CCF) in fertile and mesic boreal forests. However, the development of advance regeneration is poorly known.

Methods: This study used regression analysis to model the height increment of spruce understorey as a function of seedling height, site characteristics and canopy structure.

Results: An admixture of pine and birch in the main canopy improves the height increment of understorey. When the stand basal area is 20 m2ha-1 height increment is twice as fast under pine and birch canopies, as compared to spruce. Height increment of understorey spruce increases with increasing seedling height. Between-stand and within-stand residual variation in the height increment of understorey spruces is high. The increment of 1/6 fastest-growing seedlings is at least 50% greater than the average.

Conclusions: The results of this study help forest managers to regulate the density and species composition of the stand, so as to obtain a sufficient height development of the understorey. In pure and almost pure spruce stands, the stand basal area should be low for a good height increment of the understorey.

Keywords: Advance regeneration; Continuous cover forestry; Growth model; *Picea abies*; Uneven-aged management

Background

Continuous cover forestry (CCF) and other near-natural forest management systems are gaining popularity in several countries (Brunner et al., 2006; Hasenauer, 2006; Schütz et al., 2012). In Finland, public opinion is against clear-felling, and also forest landowners are often unwilling to clear-cut their forests (Valkeapää et al., 2009). According to a recent survey, majority of forest landowners are interested in continuous cover forest management (Kumela and Hänninen, 2011).

Change in general attitude, encouraging results regarding the profitability of uneven-aged forest management (Tahvonen, 2009; Tahvonen et al., 2010; Pukkala et al., 2010, 2011a) and the decreasing importance of pulp and paper industries in Finland's economy have led to increasing criticism against the prevailing silvicultural practices. As a consequence, forestry legislation is being modified (Anonym, 2012), now allowing forest landowners to use CCF without any specific justification. Also, instructions for good forestry practice (Anonym, 2006) are being updated. As a result, forest landowners now have the freedom to pursue CCF if they decide so.

The sustainability of CCF depends on the amount and composition of regeneration and the survival and revival of the understorey trees. The first Finnish national forest inventory, conducted in 1921–1924, reported that on the basis of subjective assessments, only 3% of the forest area had a good-quality understorey (Ilvessalo, 1956). However, a closer look at the inventory results reveals that understoreys have been utilized in forest management much more than one would deduct from their reported occurrence. For example, 10-year old sapling stands covered 7% of forest land in 1921–1924, but 40 years later the percentage of 50-year old stands was 28% (Mikola, 1966), instead of 7%, suggesting that a majority of 50-year-old stands originated from a released understorey. Therefore, understoreys are more common than indicated by the inventory reports but, due to their spatial heterogeneity and size variation, they are seldomly evaluated as good enough starting points for

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even-aged stands. However, practical experience shows that almost all released understoreys develop into fully-stocked productive stands. Sarvas (1951) and Vuokila (1956) found that, in the 1950s, most spruce stands in Finland in fact originated from an understorey.

Looking at the diameter distributions of the sample plots of national forest inventories instead of subjective classifications, shows that there is plenty of advance regeneration in Finnish forests. For example, Lähde et al. (1999) calculated that in mature forests growing on mineral soil sites the total number of understorey Scots pine, Norway spruce and birches (from 50 cm height to 6 cm dbh) averaged 3000 trees/ha in the 1950s (see also Sarvas, 1944; Laiho et al., 2011)]. Plentiful regeneration was measured also later in both Finland (Lähde, 1992a,b; Lähde et al., 1999) and Sweden (Lundqvist, 1993; Lundqvist and Fridman, 1996; Lundqvist and Nilson, 2007). Pukkala et al. (2011b) calculated that only 5% of mature Finnish stands had less than 500 understorey trees of pine, spruce and birch per hectare, and 60% of stands had at least 2000 understorey trees at the end of the 1900s. When seedlings shorter than 1.3 m were excluded, almost 50% of stands still had at least 1000 undestorey trees per hectare.

Due to its ecological characteristics, Norway spruce does not thrive in open areas but regenerates easily and grows well under shade-intolerant pioneer species (Kalela, 1949). According to Valkonen (2000), a released spruce understorey may grow almost equally well as a spruce plantation, but the released understorey is more heterogeneous than the plantation would be. In a two-storied birch-spruce stand the volume growth of overstorey birches is often higher than the growth reduction of understorey spruces (Mielikäinen and Valkonen, 1995), making the two-storied stand more productive than either of the one-storied stands alone (see also Isomäki, 1979; Bergqvist, 1999).

According to official silvicultural instructions (Anonym, 2006) good-quality spruce understoreys can be used if they cover large enough continuous areas (at least 300–400 m^2), are dense and even-sized, and have at least 10-cm long annual shoots. Otherwise, the understorey should be removed, after which the stand should be clear-felled, and a new stand be established by planting. Those criteria, especially the 10-cm rule, are not supported by research, which shows that even a slow-growing stagnant understorey may start growing well (Vuokila, 1982; Ferlin, 2002). Old and large understorey trees revive slowly (Vaartaja, 1951) but may eventually grow as well as young seedlings and saplings (Näslund, 1944; Sarvas, 1951; Vuokila, 1970). According to Kneeshaw et al. (2002), height growth does not respond immediately to increased growth space, but growth reaction occurs first in roots. Typically, it takes 4–5 years for the Norway spruce to fully adapt to the new conditions (Metslaid et al., 2005). The requirement for homogeneity is not relevant in CCF management where uneven size, growth rate and gradual revival of the understorey are benefits rather than shortcomings (Lähde et al., 2010).

High risk of harvesting damages complicates the management of two-storied stands. According to Metsäteho (Kärnä, 2006), a spruce understorey of 6000 seedlings/ha decreases the productivity of harvesting by 5%. Niemistö et al. (2012) found that retaining the understorey spruces decreased the productivity of cutting by 6–17% as compared with clear cutting where the understorey was not considered. Damage to saplings may be as high as 50% (Surakka et al., 2011). Saplings near strip roads are vulnerable to additional injuries caused by hauling and forwarding. However, the high number of spruce stands that originate from advance regeneration demonstrates that the harvesting problems are manageable. A slightly more costly harvesting, as compared to clear-felling, is compensated for by savings in stand establishment costs, immediate stocking, soil protection, aesthetic values and benefits to fauna and flora, amongst other things (Ruel et al., 2000).

There are some Finnish studies on the revival and height increment of released Norway spruce understoreys (Koistinen and Valkonen, 1993; Valkonen, 2000) and on the growth of Norway spruce under birch (Mielikäinen and Valkonen, 1995) and spruce (Lin et al., 2012) canopies. Although much research has been done in other countries (see Metslaid et al., 2007 for review), quantitative knowledge about the effects of various factors on the growth of understorey Norway spruce, when they are not released, is very limited. More information and better predictive tools would make it possible to evaluate spruce understoreys from the perspective of CCF management, not only as the starting point of a new even-aged stand.

The aim of this study was to quantify the growth rate of Norway spruce (*Picea abies*) understorey under different canopies. In the case of abundant understorey the growth rate of the best individuals is relevant for future stand development and for CCF management. Therefore, growth variation among understorey spruces was also analyzed. A regression model was developed for describing the influence of site, canopy structure, and seedling height on the height increment of understorey spruces. The developed model was then used to illustrate the influence of various factors on the height increment of understorey.

Methods

Altogether 262 temporary plots were measured in different stands on mineral soils in South Finland. Stands having advance regeneration of spruce were selected following a predefined target distribution of different stand types. A matrix of seven species compositions (pine, spruce, birch, pine-spruce, pine-birch, spruce-birch, pine-spruce-birch) and stand densities (< 10 m^2ha^{-1}, 10–30 m^2ha^{-1}, > 30 m^2ha^{-1})

was created. Then, 1–3 stands were measured for each class of stand composition and density, separately in two site class categories (herb-rich or better; mesic or poorer) and three different localities. The first 1–3 encountered stands per matrix cell having advance regeneration of spruce were measured in each locality and site category. A selected stand was entered, after which a random direction was chosen and 20 steps were taken to that direction, leading to plot center.

Forest site type and the degree paludification were assessed in the field. For easier modeling, forest site type was converted into site index (dominant height at 100 years) as follows (Vuokila and Väliaho, 1980): OMaT (mesotrophic herb-rich) 30 m; OMT (herb-rich) 27 m; MT (mesic) 24 m; VT (sub-xeric) 21 m; CT (xeric) 18 m. Intermediate values (e.g. MT^+ and MT^-, i.e., fertile and poor mesic) were given intermediate numerical values (25 m and 23 m). Afterwards, latitude of the site was obtained from a geographical map, and altitude of the stand was obtained from an elevation map. The basal area of canopy trees was measured separately for each species using relascope. The minimum, mean and maximum diameters of each species present in the canopy were measured from the relascope plot. Three trees per species were measured for diameter: the smallest, the largest, and the basal area median tree. The basal area median tree was selected visually, following the practices of Finnish compartment inventory.

At least 20 and at most 30 conifer seedlings and saplings (from 10 cm height to 4.5 cm dbh) closest to the plot center were measured for dbh, height, and height increment of the previous growing season. This resulted in 5811 spruce seedlings and 197 pines (pine seedlings are not analyzed in this study). When plots that had no overstorey trees were also removed from the data, 5601 observations remained for modeling (Table 1). About 50% of observations represented mesic growing sites, 38% represented herb-rich and better sites (OMaT and OMT), and 12% represented sub-xeric and xeric sites. Trees having dbh greater than 4.5 cm were defined as canopy trees and the remaining seedlings and saplings were defined as understorey trees.

A mixed-effects model was fitted to the data using SPSS software. Different transformations and combinations of predictors were carefully analyzed to find a model that describes the influence of site, canopy structure and seedling height on the height increment of understorey spruces. The mixed-effect model included a random plot factor, allowing us to divide the residual variation into between-plot and within-plot components.

Results

Model

The model for the height increment of understorey spruces was as follows:

$$\ln\left(ih_{ij}\right) = \mathrm{b}_0 + \mathrm{b}_1\sqrt{h_{ij}} + \mathrm{b}_2 SI_j + \mathrm{b}_3 P_j + \mathrm{b}_4 G_j + \mathrm{b}_5 G_{\mathrm{S}j} + \mathrm{b}_6\sqrt{D_j} + u_j + e_{ij}$$

where ih_{ij} the annual height increment of spruce seedling i in plot j (cm), h is height of the seedling (cm), SI is site index (m), P is paludification (percent coverage of peat land species among ground vegetation), G is basal area of canopy trees ($\mathrm{m^2ha^{-1}}$), G_S is basal area of canopy spruces ($\mathrm{m^2ha^{-1}}$), D is mean diameter of canopy trees (cm), $u_j \sim \mathrm{N}(0,\sigma_u^2)$ is random plot factor and $e_{ij} \sim \mathrm{N}(0,\sigma_e^2)$ is residual.

The degree of explained variance (R2) and the square root of the mean of squared errors (RMSE) were calculated from back-transformed non-logarithmic growth predictions (Table 2). The Baskerville (1972) correction was used in prediction. The correction was $s^2(e_{ij})/2 + s^2(u_j)/2$ for the fixed part of the mixed-effect model, and $s^2(e_{ij})/2$ for the full model. The residuals of the models were visually analyzed and they were found to be normally distributed with a constant variance across the ranges of predictors.

Effect of seedling height and canopy structure

Height increment of understorey spruces increased as a function of seedling height (Figure 1). When the basal area of canopy trees was 20 $\mathrm{m^2ha^{-1}}$, a four-meter high seedling grew, on average, 50 cm per year under birch and pine canopies but a one-meter-high seedling grew only 10 cm/year.

The influence of overstorey tree species was very strong (Figure 1). In a sparse pine or birch stand (basal area 15 $\mathrm{m^2ha^{-1}}$) growing on mesic site, the average height increment of a 2-m-high spruce seedlings was 19 cm/year

Table 1 Description of modeling data (5601 spruce seedlings)

Variable	Minimum	Maximum	Mean	Standard deviation
Site index, m	18	30	24.84	2.47
Paludification,%	0	100	7.15	19.10
Canopy trees:				
Basal area, m^2/ha	2	52	19.38	10.10
•pine	0	43	4.24	8.35
•spruce	0	41	10.46	9.93
•hardwood	0	34	4.68	7.32
Mean diameter, cm	4.2	78	23.41	10.62
Harwood seedlings:				
Number	0	22043	2765.92	3420.73
Mean height, m	0	7	2.17	1.51
Spruce seedlings:				
Height, m	0.1	6.0	1.51	1.12
Height increment, m	0.0	1.0	0.12	0.13

Table 2 Model parameters. R2 and RMSE have been calculated for the back-transformed non-logarithmic height increment

Predictor	Coefficient	Estimate
Constant	b_0	–0.437
$\sqrt{h}$	b_1	0.162
SI	b_2	0.0138
P	b_3	–0.00653
G	b_4	–0.0108
G_s	b_5	–0.0335
$\sqrt{D}$	b_6	0.157
	$s(u_j)$	0.466
	$s(e_{ij})$	0.533
	R2 Fixed	0.510[1)]
	R2 Full	0.773[(2)]
	N	5601
	RMSE Fixed	9.45[(1)]
	RMSE Full	6.43[(2)]

[(1)]Calculated for the fixed part of the mixed-effects model.
[(2)]Calculated for the full mixed-effects model, including the random plot factor.

whereas the predicted increment was only 11 cm/year in a spruce stand. With a stand basal area of 30 m^2ha^{-1} the average growth would be 16 cm/year under pine and birch canopies but only 6 cm/year under a spruce canopy.

Mean diameter of canopy trees was also a significant predictor of height increment. With a given basal area, seedling increment improved with increasing diameter of the canopy trees (Figure 1). The result implies that seedlings grow better under a small number of large trees than under a larger number of smaller trees.

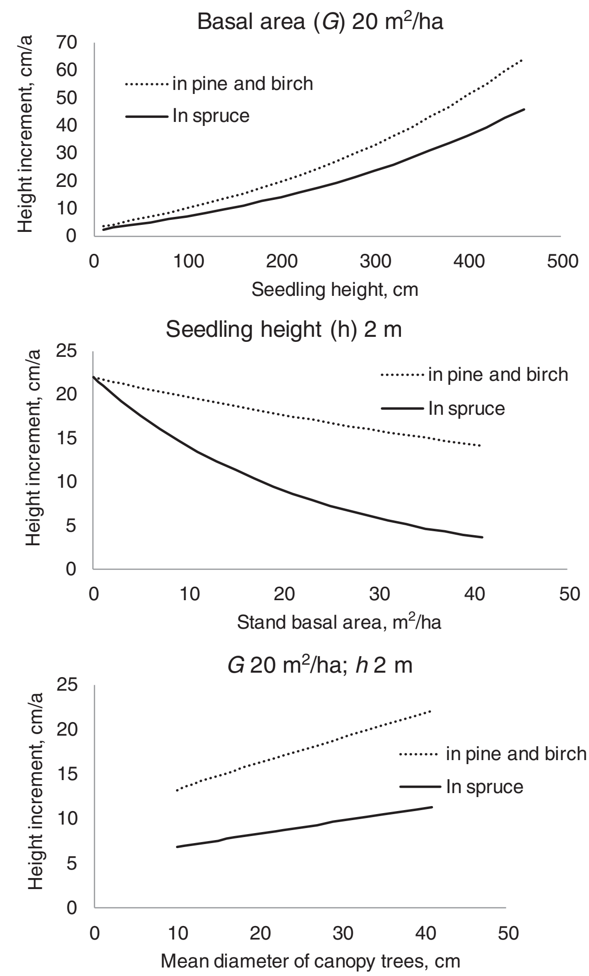

Figure 1 Effect of seedling height, stand basal area and mean diameter of canopy trees on the height increment of understorey spruces on mesic site. Paludification is 20%.

Effect of site

Improving site index (fertility) increased the height increment of understorey spruces but the influence was not strong (Figure 2). Height increment was only 8% better on a herb-rich site (OMT) than on a sub-xeric site (VT). Paludification also affected height increment, the predicted increment being 96% higher in case of no paludification as compared to a site where the coverage of peat land species in the ground vegetation was 100%. Latitude and elevation were not significant predictors, most probably due to their small range of variation in the modeling data (330 km in y coordinate; 167 m in elevation).

Growth variation within spruce understorey

Within- and between-stand variation in the height increment of understorey spruces was visualized by adding ± $s(u)$ or ± $s(e)$, i.e. standard deviation of random plot factor (u_j) or standard deviation of residual (e_{ij}), to the non-logarithmic prediction of the mixed-effect model. Predictions with $u_j = s(u)$ are referred to as 'good stand', $u_j = -s(u)$ as 'bad stand', $e_{ij} = s(e)$ as 'good seedling', and $e_{ij} = -s(e)$ as 'bad seedling'. About 1/6 of stands have the plot factor higher than $s(u)$, and another 1/6 of stands have u_j is less than $-s(u)$. Similarly, within a stand, the residual is between $-s(e)$ and $s(e)$ for about 2/3 of seedlings.

The visualizations (Figure 3) show that the variation unexplained by the fixed model predictors is very large, both among stands and among seedlings within a stand. A 'good seedling' grows twice as fast as a "bad seedling", and the average growth of understorey spruces is twice as much in a "good stand" as compared to a "bad stand" when the site index, paludification, amount of hardwood understorey and canopy structure are the same.

Discussion and conclusions

The study analyzed the dependence of the height increment of understorey spruces on seedling height, site properties and characteristics of the main tree canopy. A

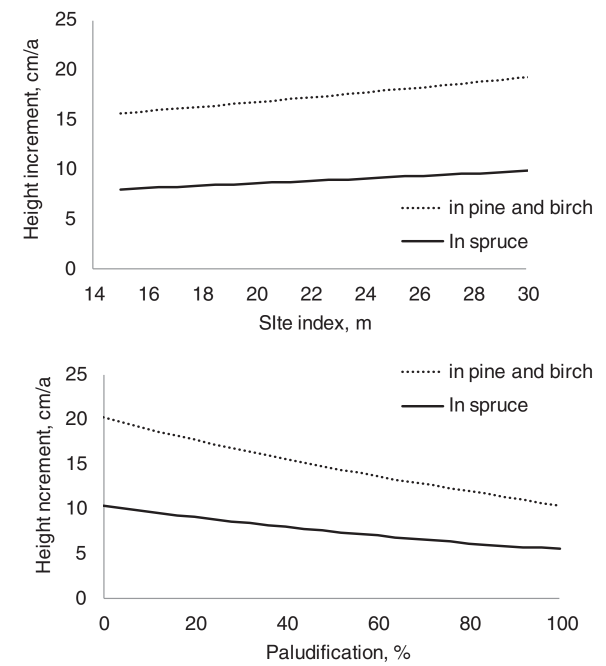

Figure 2 Effect of site fertility and paludification on the height increment of understorey spruces when the stand basal area is 20 m²ha⁻¹, mean diameter of canopy trees is 25 cm and seedling height is 2 m.

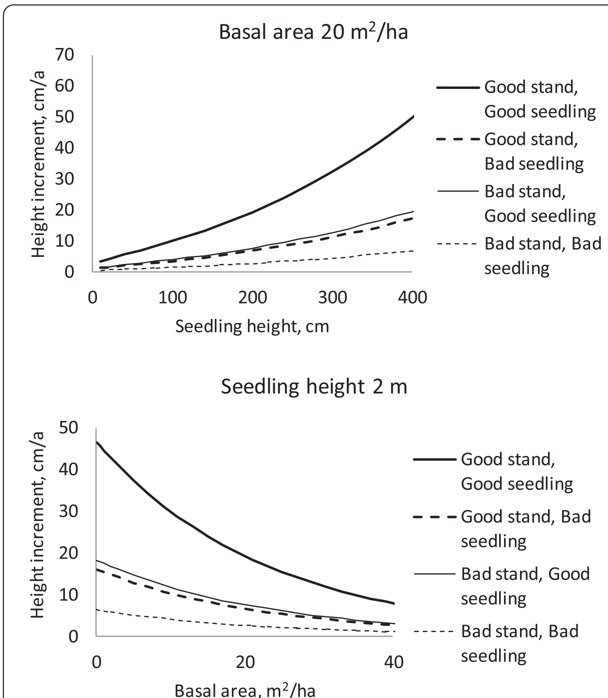

Figure 3 Variation in the height increment of understorey spruces among stands and individuals on mesic site when 50% of canopy basal area is spruce. Good stand, $u_j = s(u)$; Bad stand, $u_j = -s(u)$; Good seedling, $e_{ij} = s(e)$; Bad seedling, $e_{ij} = -s(e)$; $s(u)$ is standard deviation of random plot factor (u_j); $s(e)$ is standard deviation of residual (e_{ij}).

regression model was fitted that describes these relationships. This model should not be used to predict future understorey development because the used dataset is insufficient for genuine growth modeling. Height increment was measured in one year only, which may bring bias to the prediction due to the weather-induced annual growth variation. In addition, selection of the plots had subjective elements and measurement of the stand characteristics was not accurate enough for growth modeling purposes.

Results from this study indicate that 1–2 m tall spruces typically grow 15–20 cm/year under birch and pine canopies but only 5–10 cm under spruce canopies. The growth of understory trees improves when they get taller (Lieffers et al., 1996). Taking into account that spruces planted in open areas often need about ten years to reach breast height, the increment of understorey spruces is reasonably good. Given that height increment increases with increasing tree height the future increment would be slightly higher (usually 3–4%) than the past increment predicted by the model.

The height increment of the best-growing spruces under sparse pine and birch canopies is not slower than it would be in open area (Valkonen, 2000). This conclusion agrees with the result of Lieffers and Stadt (1994) who found that white spruces (*Picea glauca*) grow equally well under a canopy of trembling aspen (*Populus tremula*) as in full light if the light transmittance of the canopy is 40% or more. Comeau et al. (2003) found that the height increment of subalpine fir (*Abies lasiocarpa*) and white spruce was only weakly correlated with the light level under paper birch (*Betula papyrifera*) overstorey.

The results of this study showed that understorey spruces grow much faster under pine and birch canopies than under spruce canopies. Increasing percentage of spruce in the main canopy decreases the growth rate of understorey. Clear beneficial effects of birch and pine admixtures on the growth of larger spruces were recently reported (Pukkala et al. 2013). Earlier, positive mixture effects have been reported by several authors (Mielikäinen 1985; Pukkala et al. 1994; Liang et al. 2005 and Pretzsch et al. 2010). The practical conclusion that can be drawn from this study is that the density of birch and pine stands is not critically important for understorey development but spruce stands must be sparse for fast understory height increment.

It is commonly believed that birch is the best canopy for spruce understorey and birch is the best admixture in a spruce stand. However, the current study showed that this is not necessarily the case; if the effects of stand basal area and site fertility are removed, the growth is equally good or even better (Pukkala et al., 2013) under pine than under birch. The common belief of the smaller competitive effect of birch may be partly due to lower stand basal areas and better site fertility of birch stands, as compared to pine stands. Due to fertile site and low stand basal area, understorey spruces often grow well under birch canopies although the competitive effect of pine would be fairly similar with the same basal area.

Increasing size of canopy trees improved the height increment of understorey spruces when stand basal area was constant. The result suggests that open space below the crowns of canopy trees may improve the height increment of spruce understorey. When the vertical distance between the main canopy and understorey is large, the shading effect of canopy trees is more uniformly distributed than in stands where the crown bases are near ground (Kuuluvainen and Pukkala, 1991). Therefore, the beneficial effect of large tree size in the main canopy may be related to more uniform light conditions for understorey spruces.

A result relevant for CCF management was the improving height increment with increasing seedling height (Lieffers et al., 1996). This means that height differences among understorey spruces tend to increase when the understorey develops. The understorey becomes uneven-sized even when it is even-aged. Also the high within-stand variation in height increment and the positive temporal autocorrelation of annual growths of consecutive years (Miina, 1993; Pasanen, 1998; Metslaid et al., 2005) contribute to the differentiation of tree size.

According to Lin et al. (2012) the height increment of the best 100 understory spruces per hectare decreases from 50 to 5 cm/year when the stand volume of a spruce-dominated stand increases from 50 to 400 m^3/ha. The result agrees well with the predictions of our model. When the height of spruce seedling is 1–3 m and the basal area of overstorey birches is less than 20 m^2/ha, our model gives fairly similar predictions as an earlier model (Mielikäinen and Valkonen 1995) for two-storied spruce-birch stands. Increasing overstorey basal area decreases height increment more in Mielikäinen and Valkonen (1995) than predicted by the model of this study. It is noteworthy that, similarly to this study, the model of (Mielikäinen and Valkonen 1995) also predicts that increasing tree size in overstorey improves the height increment of spruce understorey if stand basal area remains unchanged. The relationships found in this study are similar to the ones reported earlier for other spruce species (e.g., Filipescu and Comeau 2007). Bergqvist (1999) found that diameter increment of understorey Norway spruces is reduced more than height increment by the competition caused by birch overstorey.

In CCF stands where spruce understorey is abundant, its average growth rate is less relevant than the growth rate of the best individuals (e.g., the best 10 or 30%, depending on the density of understorey). According to this study, the growth of the best 1/6 of seedlings is at least 50% better than the average. In sustainable CCF management, only the removed trees need to be replaced by well-growing understorey trees. If the high thinning removes 333 trees/ha, and the density of understorey is 2000 trees/ha, only 1/6 best growing understorey trees are required to take the place of the removed trees. These understorey trees grow at least 50% faster than a population-averaged model prediction.

Between-stand variation in height increment was also high. This implies, for example, that bad experiences (slow growth) in one forest do not mean that the growth of spruce understorey is always slow. In the best stands, the growth is at least 50% faster than in an average stand and 100% faster than among the poorest stands. Therefore, overall recommendations about the utilization of spruce understorey in CCF management cannot be given only on the basis of site characteristics and overstorey stand structure. Instead, the manager needs to assess the vitality of the understorey in the field and adapt the management to the specific conditions of each stand.

Other practical conclusions of the study, from the viewpoint of CCF management, can be summarized as follows. Species composition of the canopy is critically important for the height development of spruce understorey. An admixture of birch and pine should be maintained in the stand as long as possible. If the canopy is a pure spruce stand, it should be thinned to a low basal area for fast understorey development. Between- and within-stand variation in understorey height development is high, which should be taken into account in growth and yield prediction. Using population-averaged model prediction in simulations may lead to biased results and conclusions.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
OL and EL collected the data. TP fitted the regression model. All authors participated in writing. All authors read and approved the final manuscript.

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