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Original article

Wood density traits in Norway spruce understorey: effects of growth rate and birch shelterwood density

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Abstract – Effects of growth rate and birch shelterwood density (0, 300 and 600 trees ha^{-1}) on wood density traits in Norway spruce (*Picea abies* (L.) Karst.) understorey were evaluated for a trial in the boreal coniferous forest 56 years after establishment of the stand and 19 years after establishment of the trial. Wood density traits were measured by micro-densitometry for annual rings 21–30 extracted at breast height. In addition, ring width and mean density were measured for all annual rings. Growth rate was generally low with a mean ring width of 1.3 mm. Radial variations in ring width and density depended more on calendar year than on cambial age. The shelterwoods had moderate d fluctuations in ring width, but not in wood density. For annual rings 21–30, the mean density was 12 % higher in trees of the lowest growth rate compared to trees of the highest growth rate. Also, minimum density and latewood percentage were higher in trees with the lowest growth rate compared to all other trees, while there were no significant effects due to shelterwood treatment for any of the wood density traits tested. An increase in ring width from 1 to 2 mm resulted in an 18 % decrease in wood density. Latewood percentage explained 84 % of the variation in wood density. (© Inra /Elsevier, Paris.)

Norway spruce understorey / birch shelterwood / wood density / growth suppression / latewood percentage

Résumé – Caractéristiques de la densité du peuplement dans le sous-étage de sapin de Norvège : effets du taux de croissance et de la densité du peuplement de bouleaux résultant de la régénération par coupes progressives. Les effets du taux de croissance et de la densité du peuplement de bouleau résultant de la régénération par coupe progressive (0, 300 et 600 arbres ha^{-1}) sur les caractéristiques de la densité du peuplement de sapin de Norvège (*Picea abies* (L.) Karst.) sont évalués pour un essai dans la forêt de conifères boréale 56 ans après l'établissement du peuplement forestier et 19 ans après la mise en place de l'essai. Les caractéristiques de la densité forestière sont mesurées par microdensitométrie pour les anneaux annuels 21–30 extraits à hauteur de poitrine. En outre, la largeur et la densité moyenne des anneaux sont mesurées pour tous les anneaux annuels. On note un taux de croissance généralement faible, avec une largeur moyenne des anneaux de 1,3 mm. Il apparaît que les variations radiales de la largeur et de la densité des anneaux dépendent plus de l'année que de l'âge cambial. Les peuplements résultant de la régénération par coupes progressives présentent des fluctuations modérées dans la largeur des anneaux mais pas dans la densité. Pour les anneaux

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annuels 21–30, la densité moyenne est supérieure de 12 % pour les arbres ayant le taux de croissance le plus faible par rapport aux arbres dont le taux de croissance est le plus élevé. D'autre part, la densité minimale et le pourcentage de bois d'automne sont plus élevés pour les arbres dont le taux de croissance est le plus faible par rapport à tous les autres arbres, tandis que l'on ne constate aucun effet significatif résultant du mode de régénération par coupes progressives pour aucune des caractéristiques de la densité du peuplement étudiées. On note qu'une augmentation de la largeur des anneaux de 1 à 2 mm se traduit par une baisse de 18 % de la densité du peuplement. Le pourcentage de bois d'automne explique 84 % de la variation dans la densité du peuplement. (© Inra /Elsevier, Paris.)

sous-étage de sapin de Norvège / peuplement de bouleaux résultant de la régénération par coupes progressives / densité du peuplement / ralentissement de croissance / pourcentage de bois d'automne

1. INTRODUCTION

Several theories have been suggested regarding the influence of crown development on wood properties including mechanical, nutritional, water conductance and hormonal regulation, as reviewed by Lindström [28]. Silvicultural treatments that affect competition and crown development can thus be expected to affect wood properties [7]. Wood density is considered a key property, affecting for example pulp yield per unit of wood volume [54]. A high and uniform wood density is desirable for most products [41]. Generally, a negative correlation between annual ring width and wood density has been demonstrated for Norway spruce (*Picea abies* (L.) Karst.), suggesting that a low growth rate promotes the production of high-density wood [22, 40]. However, wood density also shows large variations within and between trees of the same species growing at similar rates [54].

Norway spruce is considered to be a semi-shade tolerant species and can adapt to a wide variety of light conditions. Stratified stand mixtures, composed of shade tolerant late successional species in the lower strata and light demanding early successional species in the upper strata, have been recommended as a means of gaining a higher volume yield compared to a monoculture [3]. Norway spruce growing under a birch (*Betula* spp.) shelter is a common type of two-storied stand in the Scandinavian boreal forest [16].

Shelterwood systems are used in forestry worldwide mainly for regeneration purposes, and today this silvicultural method is the focus of increasing interest. Compared to conditions on a clear-cut area, a shelter will affect the availability of nutrients and water [16], temperature [13, 39, 43, 44] and wind speed [38] as well as quantity and quality of light [32] for the understorey trees. This in turn will affect their growth rate and crown development [12, 33, 50]. In frost-prone areas, the use of shelterwoods is of special interest as a means of raising the minimum temperature and reducing excess light, thereby reducing frost damage to the understorey trees [2, 30, 42].

A high wood density for spruce growing under shelter might be expected if, for instance, low spring temperatures under shelter results in a delayed spring flushing, since trees with early flushing show lower wood density compared to late flushing trees [25]. On the other hand, wood density is also positively correlated with light intensity when compared at the same ring width [10, 35]. Since a shelterwood will reduce light intensity for the understorey trees, this might also result in lower wood density for the understorey trees.

The objective of this investigation was to evaluate the effects of growth rate and birch shelterwood density on wood density traits for Norway spruce understorey in a trial in the boreal coniferous forest. Radial fluctuations in ring width and mean density from pith to bark, juvenile wood distribution and wood density traits (i.e. mean, minimum and maximum density, ring width, uniformity factor and latewood percentage) in annual rings 21–30 from the pith were examined by micro-densitometry on radial increment cores taken at breast height.

2. MATERIALS AND METHODS

2.1. Stand and trial description

The site is located in the province of Västerbotten, Sweden (64°18′30′′ N, 19°44′55′′ E, altitude 260 m) within the middle boreal forest zone [1]. Temperature sum (TS_5), i.e. the summation of all daily mean temperature values exceeding +5 °C is 828 degree days and the growing season averages 146 days according to Morén and Perttu [34]. The soil is till, sand-silt, and the field vegetation is dominated by *Vaccinium myrtillus* L., indicating site index G18, i.e. an 18-m dominant height of Norway spruce at 100 years of age [14].

Following clear-felling and prescribed burning in 1930, the stand was regenerated by direct seeding of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in 1938, using seeds of local provenance. The Norway spruce seedlings were soon overgrown by downy birch (*Betula pubescens* Ehrh.) and silver birch (*Betula pendula* Roth) suckers, and pre-commercial thinning among the birch suckers was performed in 1951. The field trial was established in 1973 and 1975. At the time of trial establishment, the number of birch and the few remaining Scots pine overstorey trees amounted on average to 2 000 ha^{-1}. The average height was 13 m. The average diameter at breast height (DBH; 1.3 m) over bark (o.b.) and average standing wood volume were 11–12 cm and 130 m^3 ha^{-1}, respectively, while the Norway spruce understorey totalled approximately 3 000 trees ha^{-1} with a mean DBH o.b. of 3–5 cm, an average height of 2–4 m and an average standing wood volume of 8–10 m^3 ha^{-1}. The following shelterwood densities were established: 1) dense shelterwood, 600 trees ha^{-1}; 2) sparse shelterwood, 300 trees ha^{-1}; and 3) no shelterwood. The shelterwoods consisted of silver birch and Scots pine, constituting 96 and 4 % of the total wood volume, respectively. Allotment of shelterwood treatments to plots was randomized. Removal of overstorey trees was performed during 1973, when four replications of each of the dense and no shelterwood treatments were established, and during 1975 when two replications were established for the sparse shelterwood treatment. All replications were 0.1 ha in size. Removal of excess Norway spruce stems took place in 1975 for all treatments and replications, leaving 1 500 trees ha^{-1} with an average DBH o.b. of approximately 3.5 cm, an average height of 3.5 m and an average standing wood volume of 6 m^3 ha^{-1}.

Two replications each of the dense shelterwood and no shelterwood treatments were randomly selected for this investigation, while both replications were included for the sparse shelterwood treatment. Wood sampling took place in October 1994, 19 growing seasons after trial establishment. At the time of sampling, the Norway spruce understorey trees were approximately 8–9 m tall, while the height of the shelterwood trees was 18–19 m (see *table I*).

2.2. Selection of sample trees and wood sampling

Prior to sampling, all Norway spruce trees in each shelterwood treatment were divided into three growth rate classes based on DBH o.b.: 1) high growth rate, over 11 cm DBH o.b.; 2) intermediate growth rate, 8–11 cm DBH o.b.; and 3) low growth rate, under 8 cm DBH o.b. A total of 90 trees, i.e. ten from each growth rate class within each shelterwood treatment were randomly selected. The sample trees surpassed actual mean DBH o.b. for the dense and sparse shelterwood by approximately 10 % (*table II*). From each selected tree, an increment core of 4.5 mm diameter was extracted from bark to pith at breast height, from a randomly selected compass direction. Branches were avoided.

2.3. Measurements

Wood density variations were measured on 1-mm thick samples prepared from the increment cores using a direct scanning micro-densitometer with automatic angle alignment and a resolution of 0.02 mm. Measurement precision was estimated to ± 5 %. Wood density was measured at 5.0 ± 0.62 % (mean ± SD) moisture content and normalized to oven-dry density. Samples were not extracted before measurement. Methods of sample preparation, measurement

Table I. Stand characteristics for the different shelterwood treatments at the time of sampling. Arithmetic averages for two replications per treatment.

	No. of trees (ha^{-1})	Diameter o.b.[a] (cm)	Average height[b] (m)	Wood volume[c] o.b. (m^3 ha^{-1})
Norway spruce understorey				
Dense shelterwood	1515	8.6	8.8	43.0
Sparse shelterwood	1495	8.6	8.2	39.8
Number of shelterwood	1485	9.8	8.6	53.9
Birch shelterwood				
Dense shelterwood	585	18.8	18.1	132.6
Sparse shelterwood	300	20.8	18.6	76.0

[a] Diameter corresponding to mean basal area at breast height over bark ($\sqrt{\sum d^2/n}$); [b] ($\sum d^2 h/\sum d^2$); [c]from stump to tip, calculated according to Brandel [6].

Table II. Arithmetic mean diameter (cm) at breast height o.b. for the Norway spruce understorey at the time of sampling for the different shelterwood treatments and growth rate classes, for all trees and for sample trees. One SE of the mean is given within brackets.

	Shelterwood			
Growth rate class	Dense	Sparse	No	Average
All trees				
High	12.0 (1.4)	12.2 (1.3)	12.3 (1.2)	12.2 (0.1)
Intermediate	9.4 (0.7)	9.2 (0.7)	9.4 (0.7)	9.4 (0.1)
Low	6.6 (0.9)	6.3 (1.1)	6.9 (1.1)	6.6 (0.1)
Average	8.6 (0.1)	8.6 (0.1)	9.8 (0.1)	9.0 (0.1)
Sample trees				
High	12.0 (0.4)	12.2 (0.3)	12.5 (0.5)	12.2 (0.2)
Intermediate	9.3 (0.2)	9.4 (0.3)	9.3 (0.2)	9.3 (0.1)
Low	7.1 (0.2)	6.9 (0.3)	7.0 (0.2)	7.0 (0.1)
Average	9.4 (0.4)	9.6 (0.4)	9.6 (0.5)	9.5 (0.2)

and normalization as well as the underlying theories and design of the equipment have been described in detail by Jonsson et al. [19], Larsson et al. [26] and Pernestål and Jonsson [45]. A total of 11 samples failed in the preparation process, leaving 79 scanned increment cores available for further analysis. The increment cores consisted of an average of 34 annual rings (*table III*); thus a total of more than 2 600 individual annual rings were scanned. For further analysis, annual rings with cracks or reaction wood were disregarded. Also the annual rings formed during 1994, i.e. those closest to the bark, were excluded from further analysis due to difficulty in distinguishing between density readings from wood and cambial tissue.

2.4. Calculations and statistical analysis

Annual rings of cambial age 21 to 30 years were selected for the statistical evaluation of effects due to shelterwood treatment or growth

Table III. Number of Norway spruce understorey trees in the sample and their arithmetic mean total age at breast height at the time of sampling, with one SE of the mean given within brackets for the different shelterwood treatments and growth rate classes.

	Shelterwood			Total/
Growth rate class	Dense	Sparse	No	average
No. of trees in sample				
High	10	10	9	29
Intermediate	10	8	9	27
Low	8	6	9	23
Total	28	24	27	79
Total age at breast height (yr)				
High	35.5 (1.1)	38.4 (0.6)	36.8 (0.8)	36.9 (0.5)
Intermediate	33.0 (0.9)	36.4 (1.7)	30.8 (1.6)	33.3 (0.9)
Low	29,8 (0.6)	35.3 (0.8)	28.6 (1.0)	30.7 (0.7)
Average	33.0 (0.7)	37.0 (0.7)	32.0 (0.9)	33.9 (0.5)

rate class on wood density traits. This selection, rather than including all annual rings formed during the 19-year trial period, was performed in order to: 1) avoid comparing annual rings of different ages; 2) only include annual rings formed after the trial was established; and 3) only include mature wood. The following wood density traits were recorded or calculated; arithmetic mean ring width, arithmetic mean density, and minimum and maximum density. Latewood percentage was calculated as the percentage of all density values that exceeded 540 kg m^{-3}, the estimated equivalent to Mork's index on an oven-dry weight, oven-dry volume basis [15]. The uniformity factor, i.e. a measure of the variability in wood density, was calculated according to Olson and Arganbright [41]:

$$\frac{1}{\sum_{i=1}^{n}\left(S_i - S_{median}\right)^2} \cdot 200 \qquad (1)$$

where S_i are percentiles of the wood density values, n is 20, and S_{median} is the overall median density value for the whole material, in this case 367 kg m^{-3}.

One value for each density trait was calculated per tree; thus individual trees were used as observations in all statistical analyses. The average of 8.5 annual rings with an average cambial age of 25 years was included in the calculation of tree mean values (*table IV*).

In addition, arithmetic mean wood density and arithmetic mean ring width were calculated for all annual rings from pith to bark separately in order to examine radial variations, and the coefficient of variation (CV) for density and ring width was calculated for each tree. An attempt was made to manually establish a juvenile–mature wood boundary, based on the definitions of juvenile and mature wood given by Rendle [46] (i.e. "characterized anatomically by a progressive increase in the dimensions and corresponding changes in the form, structure and disposition of the cells..." and "the cells in general having reached their maximum dimensions and the structural pattern being fully developed and more or less constant..." for juvenile and mature wood, respectively).

Data were tested for homoscedasticity. Differences in arithmetic mean ring width, arithmetic mean density, minimum and maximum density, uniformity factor and latewood percentage (for annual rings 21–30) and CV for density and ring width (for all annual rings) due to shelterwood treatment or growth rate class were evaluated with two-way analysis of variance using the General Linear Model (GLM) procedure. The following model was applied:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk} \qquad (2)$$

where μ is the overall mean, α_i is shelterwood treatment, β_j is growth rate class, $(\alpha\beta)_{ij}$ is the interaction term and ε_{ijk} is the random error term. Both shelterwood treatment and growth rate class were regarded as fixed effects and type III sums

Table IV. Characteristics of annual rings 21–30 at breast height included in the statistical analyses of wood density traits for the different shelterwood treatments and growth rate classes. Arithmetic mean values with one SE of the mean given within brackets.

	Shelterwood			
Growth rate class	Dense	Sparse	No	Average
No. of annual rings in analysis				
High	9.2 (0.4)	9.4 (0.4)	10.0 (0.0)	9.5 (0.2)
Intermediate	9.2 (0.7)	8.8 (0.4)	7.8 (0.9)	8.6 (0.4)
Low	7.5 (0.5)	8.5 (0.8)	6.1 (1.0)	7.2 (0.5)
Average	8.7 (0.3)	9.0 (0.3)	8.0 (0.5)	8.5 (0.2)
Average cambial age of annual rings in analysis (year)				
High	25.6 (0.2)	25.8 (0.2)	25.5 (0.0)	25.7 (0.1)
Intermediate	25.2 (0.4)	25.8 (0.3)	24.5 (0.5)	25.1 (0.2)
Low	24.6 (0.4)	25.0 (0.4)	23.9 (0.5)	24.4 (0.2)
Average	25.2 (0.2)	25.6 (0.2)	24.6 (0.2)	25.1 (0.1)
Average year of ring formation				
High	1984	1981	1983	1983
Intermediate	1986	1983	1988	1986
Low	1989	1983	1989	1988
Average	1986	1983	1987	1985

of squares were calculated. Differences were considered significant at $P \leq 0.05$. When significant effects of shelterwood treatment or growth rate class were found, a Tukey post-hoc test was performed.

Regression curves, relating mean wood density to mean ring width for annual rings 21–30, were calculated using the density level regression developed by Olesen [40]:

$$R = a + \frac{b}{(c + RW)} = a + b\,RW' \qquad (3)$$

where R is wood density, RW is ring width, RW' is transformed ring width (this enables the use of linear regression) and a, b and c are positive constants. For constant c, the value of 2 was used in accordance with recommendations by Danborg [8]. Linear regression was also used to examine the relationship between mean wood density and latewood percentage for annual rings 21–30.

Regressions were calculated for each shelterwood treatment and each growth rate class separately, and differences were tested using dummy variables as described by Zar [53]. All analyses were performed using SPSS 7.0 for Windows [47].

3. RESULTS

Radial fluctuations in annual ring width and wood density were generally more affected by calendar year of ring formation than by cambial age (*figure 1*). No obvious systematic trends due to cambial age were apparent, and it was consequently not possible to establish a juvenile–mature wood boundary based on radial variations in annual ring width or wood density.

For spruce in the no shelterwood treatment, annual ring width increased abruptly by approximately 100 % and for approximately 5 years in response to the total release from overstorey trees in 1973 (*figure 1*). The coefficient of variation (CV) for annual ring width increased with decreasing shelterwood density and was 22.4 ± 1.10, 27.2 ± 1.00 and 36.7 ± 2.17 % (mean ± SE) for spruce in the dense, sparse and no shelterwood treatments, respectively. According to the ANOVA there was a strong significant effect of shelterwood treatment, but not growth rate class,

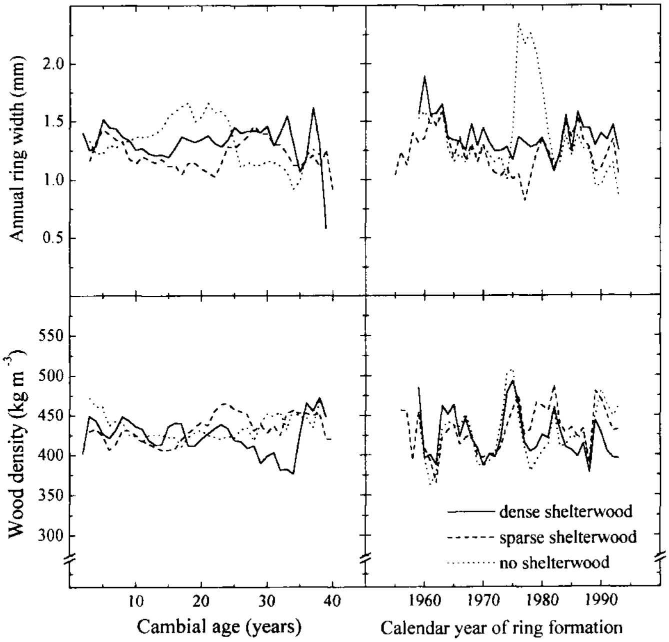

Figure 1. Radial variations in annual ring width (top) and wood density (bottom) at breast height for Norway spruce understorey in the different shelterwood treatments, due to cambial age (left) and calendar year of ring formation (right). Lines are based on the arithmetic average values of all trees in each treatment.

on CV for annual ring width (*table V*) with CV for Norway spruce in the no shelterwood treatment being significantly higher than that of the other treatments according to the Tukey test.

Radial fluctuations in wood density were generally smaller than fluctuations in ring width, and were not significantly affected by shelterwood density or growth rate class (*table V*). The CV was 13.6 ± 0.52, 11.3 ± 0.62 and 12.5 ± 0.83 % (mean ± SE) for spruce in the dense, sparse and no shelterwood treatments, respectively.

According to the ANOVA, the shelterwood treatment had no significant effect on any of the wood density traits tested for annual rings 21–30, while there was a strongly significant effect of growth rate class on all variables tested except for the maximum density and uniformity factor (*table VI*). Generally, a large proportion of the total sums

Table V. Effects of shelterwood treatment (S) and growth rate class (G), individually and in combination on the coefficient of variation (CV) for radial fluctuations in ring width and wood density for all annual rings at breast height, according to analysis of variance with sums of squares expressed as percent of total SS.

Source of variation	d.f.	%	*F*	*P*
CV for annual ring width (%)				
S	2	37.3	24.36	0.000
G	2	1.0	0.66	0.517
S × G	4	6.7	2.20	0.078
Error	70	55.0		
Total	78			
CV for mean density (%)				
S	2	6.6	2.75	0.070
G	2	0.0	0.06	0.940
S × G	4	6.0	1.25	0.299
Error	70	87.4		
Total	78			

of squares was attributed to the error term, suggesting a pronounced tree to tree variability in the wood density traits tested.

Table VI. Effects of shelterwood treatment (S) and growth rate class (G), individually and in combination, on wood density traits in annual rings 21–30 at breast height, according to the ANOVA with sums of squares expressed as percent of total SS.

Source of variation	d.f.	%	*F*	*P*
Annual ring width (mm)				
S	2	2.0	1.22	0.301
G	2	38.3	24.01	0.000
S × G	4	5.2	1.64	0.173
Error	70	54.5		
Total	78			
Mean density (kg m^{-3})				
S	2	3.5	1.53	0.224
G	2	12.3	5.31	0.007
S × G	4	1.9	0.42	0.793
Error	70	82.3		
Total	78			
Minimum density (kg m^{-3})				
S	2	0.4	0.02	0.981
G	2	14.8	6.66	0.002
S × G	4	6.8	1.54	0.201
Error	70	78.0		
Total	78			
Maximum density (kg m^{-3})				
S	2	1.6	0.60	0.552
G	2	2.6	1.00	0.375
S × G	4	3.3	0.63	0.644
Error	70	92.5		
Total	78			
Uniformity factor				
S	2	0.4	0.15	0.858
G	2	1.0	0.38	0.688
S × G	4	3.1	0.57	0.686
Error	70	95.5		
Total	78			
Latewood percent (%)				
S	2	3.2	1.30	0.279
G	2	8.6	3.52	0.035
S × G	4	2.4	0.33	0.858
Error	70	85.8		
Total	78			

The arithmetic mean ring width for annual rings 21–30 was 58 % greater for the fast growing trees compared to the slow growing trees (*table VII*). Differences were highly significant between all growth rate classes.

Mean wood density for annual rings 21–30 increased with decreasing growth rate, and was 12 % higher for the slow growing trees compared to the fast growing trees (*table VII*). This was associated with a higher minimum wood density and higher latewood percentage for the slow growing trees. The maximum wood density decreased as the growth rate decreased, although the differences were not statistically significant. The smaller range of wood density values for the trees with the lowest growth rate was not reflected in the uniformity factor, which showed no consistent variation with growth rate. Instead, the uniformity factor increased with increasing shelterwood density, although not significantly (*table VII*).

When the effect of ring width on wood density was taken into account by calculating density level regressions, there were no significant differences between any of the shelterwood treatments or growth rate classes for annual rings 21–30 (data not shown). Therefore, a common density level regression was computed showing that an increase in annual ring width from 1 to 2 mm would result in an 18 % decrease in wood density, i.e. from 463 to 392 kg m^{-3}. A further increase in ring width from 2 to 3 mm causes an additional 12 % decrease in wood density, i.e. from 392 to 350 kg m^{-3} (*figure 2*).

Latewood percentage showed a strong correlation with mean wood density for annual rings 21–30 and, in a linear regression, it explained 84 % of the variation in wood density (*figure 3*). No significant differences were detected between the regressions for the different shelterwood treatments or growth rate classes (data not shown), and thus a common regression was computed which showed that an increase in

Table VII. Arithmetic mean values for wood density traits in annual rings 21–30 at breast height for the different shelterwood treatments and growth rate classes with one SE of the mean given within brackets.

	Shelterwood							
Growth rate class	Dense		Sparse		No		Average	
Annual ring width (mm)								
High	1.51	(0.1)	1.56	(0.1)	1.77	(0.2)	1.61 ^{A}	(0.1)
Intermediate	1.47	(0.1)	1.23	(0.1)	1.23	(0.1)	1.32 ^{B}	(0.1)
Low	1.11	(0.1)	0.91	(0.1)	1.02	(0.1)	1.02 ^{C}	(0.1)
Average	1.38 ^{a}	(0.1)	1.29 ^{a}	(0.1)	1.34 ^{a}	(0.1)	1.34	(0.1)
Arithmetic mean density (kg m^{-3})								
High	401	(19.6)	438	(12.4)	407	(19.4)	416 ^{A}	(10.1)
Intermediate	420	(14.2)	464	(24.8)	431	(14.3)	436 ^{AB}	(10.4)
Low	462	(33.3)	465	(16.3)	475	(12.3)	468 ^{B}	(12.7)
Average	425 ^{a}	(13.2)	453 ^{a}	(10.4)	437 ^{a}	(10.3)	438	(6.7)
Minimum density (kg m^{-3})								
High	165	(19.0)	164	(13.5)	117	(17.6)	150 ^{A}	(10.2)
Intermediate	153	(23.1)	158	(27.3)	179	(14.9)	163 ^{A}	(12.5)
Low	196	(23.5)	202	(16.9)	222	(14.0)	208 ^{B}	(10.6)
Average	170 ^{a}	(12.6)	171 ^{a}	(11.6)	173 ^{a}	(12.1)	171	(6.9)
Maximum density (kg m^{-3})								
High	1 013	(50.4)	987	(31.6)	1 044	(32.8)	1 014 ^{A}	(22.5)
Intermediate	988	(23.3)	1 025	(54.7)	1 017	(80.4)	1 009 ^{A}	(31.3)
Low	1 016	(61.4)	898	(38.5)	973	(33.4)	968 ^{A}	(27.5)
Average	1 005 ^{a}	(25.5)	977 ^{a}	(25.5)	1 011 ^{a}	(30.4)	999	(15.7)
Uniformity factor								
High	227	(29.6)	200	(15.9)	193	(18.0)	207 ^{A}	(12.7)
Intermediate	223	(15.2)	218	(52.3)	237	(32.6)	226 ^{A}	(19.0)
Low	206	(32.6)	248	(33.0)	199	(15.8)	215 ^{A}	(15.4)
Average	220 ^{a}	(14.6)	218 ^{a}	(19.8)	210 ^{a}	(13.5)	216	(9.1)
Latewood percent (%)								
High	18.2	(1.80)	22.7	(1.60)	19.1	(1.81)	20.0 ^{A}	(1.04)
Intermediate	19.0	(1.41)	23.0	(3.00)	20.1	(2.28)	20.5 ^{A}	(1.27)
Low	25.6	(4.16)	25.2	(2.31)	23.5	(1.81)	24.7 ^{B}	(1.65)
Average	20.6 ^{a}	(1.51)	23.4 ^{a}	(1.29)	20.9 ^{a}	(1.16)	21.6	(0.78)

Values followed by the same letter are not significantly different according to the Tukey test. Capital letters denote differences between growth rate classes, lower-case letters differences between shelterwood treatments.

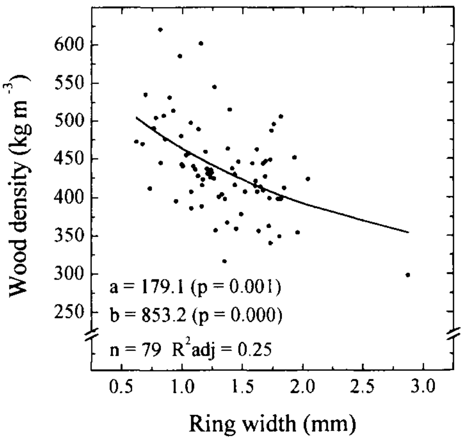

Figure 2. Density level at breast height for annual rings 21–30 in the Norway spruce understorey and estimates for the regression $Y = a + b{\cdot}RW'$, where Y is wood density and RW' is transformed ring width.

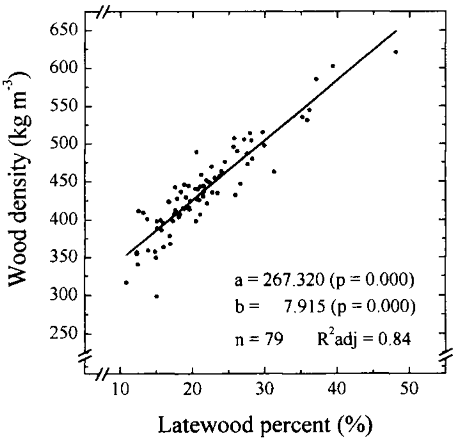

Figure 3. Regression of density on latewood percentage at breast height for annual rings 21–30 in the Norway spruce understorey and estimates for the regression $Y = a + b{\cdot}LW$, where Y is wood density and LW is latewood percentage.

the proportion of latewood from 20 to 40 % corresponded to an increase in wood density from 426 to 584 kg m^{-3}, i.e. by 37 %.

4. DISCUSSION

Measuring wood density with micro-densitometry equipment usually generates large amounts of data. The normal way to present this data is to calculate mean values for individual annual rings, as in *figure 1*. However, in statistical evaluation using ANOVA or regression, it is important to consider that values from individual annual rings within the same tree will most likely be correlated, and thus one of the basic restrictions on the data in such analyses will be violated [53]. Therefore, tree mean values were used as observations in all statistical evaluations. Based on the analysis of the residual plots, this model was deemed appropriate. Likewise, the juvenile–mature wood boundary could only be assessed manually rather than by statistical methods such as regression analysis, due to the risk of data being correlated.

Wood density was measured on samples without extraction, which might be important when comparing trees with different growth rates. Stairs et al. [49] reported a higher content of extractives in slow grown Norway spruce compared to fast grown trees. However, the amount of extractives is generally low in Norway spruce, i.e. below or around 2 % [23, 49]; and Nylinder and Hägglund [37] found no significant correlation between content of extractives and wood density in Norway spruce.

A somewhat unexpected finding was the lack of a detectable juvenile wood zone irrespective of shelterwood treatment. Juvenile wood is produced in the inner annual rings closest to the pith, and exhibits pronounced systematical variations with increasing ring number for most wood properties [46]. Depending on the criteria for definition, the juvenile wood zone usually continues for 5 to 20 annual rings from the pith, and its rapid ring-to-ring variations will override any variations due to, for instance, silvicultural treatment [4]. This was one reason for choosing annual rings of cambial age 21–30 years for the statistical evaluation. The failure to establish a juvenile–mature wood boundary was due to the absence of the characteristic density dip in juvenile wood (i.e. very high wood density closest to the pith followed by rapidly decreasing density for a number of annual rings, again followed by a rising density) that had been found in other investigations [5, 8, 21, 24, 36]. However, investigations on wood density in Norway spruce have normally studied widely-spaced trees growing on fertile sites in a relatively favourable climate, and thus they show fairly high growth rates. In an investigation of unevenly aged Norway spruce forests with suppressed juvenile growth showing a mean ring width of 1.64 mm, Eikenes et al. [11] reported that it was not possible to separate juvenile and mature wood based on wood density or annual ring width. When examining wood properties in naturally regenerated Norway spruce growing on a fertile site but with severely suppressed juvenile growth due to an initial stand density of 76 000 stems ha^{-1}, Johansson [18] found no juvenile dip in the radial density variation. It could therefore be argued that the pronounced ring-to-ring variations generally used to define juvenile wood are only useful given trees with high juvenile growth rates. It is important to consider that all trees in this investigation were severely suppressed until establishment of the field trial in 1973–1975. At that time the trees averaged 10 years of age at breast height. The lack of a detectable juvenile wood zone, even in trees growing without shelter, is therefore considered to be mainly a result of the low overall growth rate which in turn might be due to the harsh climate, as demonstrated by the short growing season, low temperature sum and relatively low soil fertility and/or the suppressed growth for the first 10 years.

Mean wood density for annual rings 21–30 increased as growth rate decreased, and was highest for the slow growing trees.

This pattern is supported by the findings of Johansson [17] and Mazet et al. [31]. With growth rate taken into account, there were no statistically significant differences in wood density in contrast to results reported by Kärkkäinen [20], who found that suppressed Norway spruce trees had a lower wood density and dominant trees a higher wood density than would have been predicted based on growth rate alone. The variation in wood density at a given ring width was very large between individual trees, resulting in a low R^2 for the regression. As argued by Ståhl and Karlmats [48], there is probably no causal relationship between ring width and wood density, but they are both related to annual weather conditions. This could explain why the pronounced increase in annual ring width for the Norway spruce after the release cutting in the no shelterwood treatment was not coupled to a similar decrease in wood density.

A lower growth rate resulted in an increased minimum wood density and decreased maximum wood density, although only changes in minimum density were statistically significant. Minimum density also increased with decreasing shelterwood density, although differences were small and not significant. The smaller range of wood density values for the trees with low growth rate was not accompanied by an increase in uniformity factor, so the two were apparently not correlated. Instead, the uniformity factor increased with increasing shelterwood density. Although not statistically significant, these results indicate that it might be possible to use shelterwoods as a means of producing a more homogeneous wood with respect to wood density.

Mean wood density in annual rings 21–30 was highest for trees growing under the sparse shelterwood and lowest for the trees growing under the dense shelterwood, although differences were small and not significant. This somewhat unexpected finding might be explained by the fact that, although of almost exactly the same cambial age, the annual rings included in the statistical analysis were formed during different years in the different shelterwood treatments.

Latewood percentage showed a pronounced influence on mean wood density for annual rings 21–30, explaining 84 % of the variation in density. This is in accordance with the findings of de Kort et al. [9], Lassen and Okkonen [27] and Lindström [29]. According to theories regarding hormonal regulation of wood formation, latewood is produced after apical growth cessation until the end of the growing season [52] and can be seen as an effect of the within-season growth rhythm, i.e. apical versus cambial growth. Wood density is negatively correlated with the dates of cambial growth initiation and latewood transition, and positively correlated with the date of cambial growth cessation [51]. However, the shelterwood densities compared in this investigation did not affect growth rhythm in the understorey trees; at least, the wood density traits tested did not reveal any such influence.

5. CONCLUSIONS

Considerable differences in wood density between trees with different growth rates were found, which gives the forester an argument for tree selection in the logging operation. If a residual stand with high mean wood density is desired, trees with high growth rates should be harvested early in thinning operations. On the other hand, if high wood density in the trees harvested during the thinning operation is more important, then trees with low growth rates should be harvested. The choice of silvicultural system, Norway spruce growing under shelter versus Norway spruce growing without shelter, seems to be less important than growth rate when managing stands for high wood density, at least for the shelterwood densities tested and at the low overall growth rates demonstrated in this investigation. It would be an exception if the shelterwood system resulted in a larger proportion of trees with low growth rates, something not considered in this investigation. However, when small fluctuations in annual ring width are desired, the shelterwood system provides an efficient tool of management. The results also indicate that Norway spruce growing under shelter produce a more homogeneous wood with regard to wood density, and that wood uniformity increases with increasing shelterwood density.

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