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Differences in Growth and Wood Properties between Narrow and Normal Crowned Types of Norway Spruce Grown at Narrow Spacing in Southern Finland

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In recent years there has been increased interest in the so called narrow crowned Norway spruce ($Picea\ abies\ f.\ pendula$), which is a rare mutant of Norway spruce ($Picea\ abies\ (L.)$ Karsten), as a suitable wood raw material source for pulp and paper production. This is because it is less sensitive to competition than the normal crowned Norway spruce, and thus, could be more productive especially at dense spacing. In the above context, we investigated how the growth and yield (such as height, diameter, stem volume and ring width) in addition to wood density traits and fibre properties (such as wood density, fibre length and width, cell wall thickness and fibre coarseness) were affected in trees from 9 full-sib families representing narrow crowned Norway spruce grown at narrow spacing of 1 m \times 1 m in Southern Finland. For comparison, we used normal crowned Norway spruce trees from 6 breeding regions.

We found that, compared to growth and yield traits, wood density traits and fibre properties showed, on average, lower phenotypic variations. In addition, these variations were smaller for narrow crowned families than for normal crowned genetic entries. Narrow crowned families also showed, on average, higher growth and yield and fibre length, but lower wood density. Moreover, the phenotypic correlations between growth, yield, wood density traits and fibre properties, ranged, on average, from moderate (narrow crowned) to high (normal crowned). As a whole, the growth and wood properties of narrow crowned families were found to be less sensitive to tree competition than the normal crowned genetic entries used as a comparison.

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1 Introduction

The quantity of stem wood, in combination with its quality, affects the suitability of tree species and their genetic entries as a raw material for mechanical wood processing and pulp and paper production (Panshin and de Zeeuw 1980, Zobel and van Buijtenen 1989). For example, wood density affects the pulp yield, while variations in fibre length, fibre width and cell wall thickness are major determinants of the characteristics and quality of final paper products (Ekenstedt et al. 2003, Karlsson 2006). Even relatively small variations in the material properties of wood have an effect on both the industrial processes as well as on the properties of the final products. Faced with this concern, in recent years tree breeders have highlighted that wood quantity and quality should not be managed as independent factors in tree breeding (Karlsson and Rosval 1993, Zhang and Morgenstern 1995, Zhang et al. 1996, Rozenberg and Cahalan 1997).

As a matter of fact, the use of tree breeding to select genetic entries with desired wood quality properties is particularly attractive, since properties such as wood density and fibre morphology are usually moderately to highly inherited (Boyle et al. 1987, Zobel and van Buijtenen 1989, Hylen 1999). Furthermore, they show moderate genetic age-age correlations between juvenile and mature wood, indicating that tree selection could be successful even in reasonably young trees (Petty et al. 1990, Hannrup and Ekberg 1998, Hannrup et al. 1998, 2001). Additionally, some properties may have a significant relationship among them. For instance, wood density can be used as an indicator of fibre morphology, since it has a strong effect on the wood density (Zhang and Morgenstern 1995, Pot et al. 2002).

In Scandinavian countries, Norway spruce (*Picea abies* (L) Karsten) is one of the most important commercial tree species for the pulp and paper industry. In these conditions, the growth of individual trees and the formation of wood properties such as wood density and fibre characteristics are mainly affected by a relatively short growing season and fairly low summer temperatures (Leikola 1969, Peltola et al. 2002, Kilpeläinen et al. 2005, 2007). In these circum-

stances, the total stem wood production can be increased only by increasing either the rate of biomass production or the proportion of biomass allocated to the stem (Cannell 1978). In previous studies, the crown form has been found to be an important factor both in respect to the total biomass production of the individual trees and the allocation rate between tree components (Cannell et al. 1983, Ford 1985, Pulkkinen 1991a, 1991b, 1991c). Similarly, the crown structure has been found to affect the total stem wood production capacity of tree stands, i.e. small to medium crown sized trees would have higher stem wood production efficiencies per occupied ground area than similar sized trees with larger crowns (e.g. Assmann 1970, Jarvis et al. 1976, Cannell 1982, Kellomäki et al. 1985, Pukkala and Kuuluvainen 1987, Kuuluvainen 1991).

For the first time, a rare mutant of normal crowned Norway spruce (narrow crowned Picea abies f. pendula), was discovered in the 1950s in a small stand located in southern Finland (Saarnijoki 1954). This narrow crowned spruce has previously shown significantly higher share of stem wood biomass of total above ground biomass production than normal crowned Norway spruce (Pulkkinen 1991a, 1991c). In addition, needles' efficiencies (i.e. annual stem wood production per unit dry weight of needles) have been found to be higher in narrow crowned Norway spruce (Kuuluvainen 1988, Pulkkinen and Pöykkö 1990, Pulkkinen 1991a, 1991b). This may be explained by the fact that the total amount of branch wood is much higher in normal crowned Norway spruce and thus, requires much higher maintenance respiration than the narrow crowned spruce (Pulkkinen 1991c). On the other hand, narrow crowned Norway spruce is also characterized by very thin hanging branches and extremely narrow crown and this morphological structure may result in the lower shading of needles within crown than in normal crowned trees (Pulkkinen 1991a).

Altogether, the narrow crowned spruce has been found to be less sensitive to stand density (competition) than the normal crowned one. Therefore, it is also expected to more efficiently use the occupied growing space and produce significantly more stem volume per hectare (and stem biomass) at narrow spacing compared to normal crowned Norway spruce (Pöykkö and Pulkkinen 1990,

Pulkkinen 1991a, 1991b). It has also been previously suggested that the narrow crowned Norway spruce may be grown in very dense stands even without any thinning and with short rotations (Pöykkö and Pulkkinen 1990, Pulkkinen 1991b). Therefore, it has increasingly been considered as a future option as a wood raw material source for pulp and paper production. On the other hand, the use of narrow crowned Norway spruce trees in practical forestry is difficult without vegetative propagation, since the inheritance of the crown type is based only on a few genes or gene groups, and thus, the progenies of open pollinated pendulous trees consist of only 18-50% pendulous seedlings (Lepistö 1985, Pulkkinen and Tigerstedt 1992).

In normal crowned Norway spruce, the growth rate of trees has typically been negatively related, especially, to wood density, but also to fibre length (Dutilleul et al. 1998, Hannrup et al. 2004, Jaakkola et al. 2005, 2007, Zubizarreta Gerendiain et al. 2007). However, currently no studies exist on the growth and yield with concurrent impacts on wood density and fibre properties of narrow crowned Norway spruce. In this context, we investigated how the growth and yield (such as height, diameter, stem volume, ring growth) in addition to wood density traits and fibre properties (such as wood density, fibre length and width, cell wall thickness and fibre coarseness) were

affected in trees from 9 full-sib families representing the narrow crowned Norway spruce grown at narrow spacing. For comparison, we used normal crowned Norway spruce from 6 southern Finnish breeding regions.

2 Material and Methods

2.1 Experimental Data

The experimental data used in this study was collected from a Norway spruce field trial established in 1991 in Loppi, southern Finland (60°38'N, 24°13'E, 115 m above sea level). The spacing of the trial was 1 m×1 m and it was located on agricultural soil with site fertility conditions typical for Norway spruce. The trial consists of 79 genetic entries replicated on 10 randomly arranged blocks, with two replications for each genetic entry per block (i.e. total of 20 sample trees for each genetic entry).

During the winter 2005–2006, personnel from Haapastensyrjä Breeding Station of the Finnish Forest Research Institute harvested 15 of these 79 different genetic entries. Nine of those were genetically narrow crowned Norway spruce (*Picea abies* f. *pendula*) full-sib families originating from controlled crosses between narrow

Table 1. Harvested Norway spruce narrow crown families (NC1–NC9) and normal crowned genetic entries (C10–C15) and the geographical origin and crown types of the mother trees (NC for narrow crowned, C for normal crowned).

Genetic entries	Origin	Sample trees	
NC1	E473 Mäntsälä (NC) × E236 Mynämäki (C)	5	
NC2	E473 Mäntsälä (NC) × E479 Mäntsälä (NC)	6	
NC3	E477 Mäntsälä (NC) × E473 Mäntsälä (NC)	5	
NC4	E477 Mäntsälä (NC) × K954 Pieksänmaa (C)	5	
NC5	E480 Mäntsälä (NC) × E1218 Muurame (C)	5	
NC6	E2507 Jäsmä (C) × E480 Mäntsälä (NC)	5	
NC7	K805 Pieksämäki (C) × E478 Mäntsälä (NC)	4	
NC8	K954 Pieksänmaa (C) × E480 Mäntsälä (NC)	4	
NC9	K956 Puolanka (C) × E480 Mäntsälä (NC)	6	
C10	Breeding region 1:Loppi Haapastensyrjä (C)	5	
C11	Breeding region 1:Loppi Jam (C)	5	
C12	Breeding region 1:Miehikkälä (Ć)	5	
C13	Breeding region 3: Pihtipudas (C)	5	
C14	Breeding region 2: Juva (C)	5	
C15	Breeding region 3: Lieksa (C)	5	

crowned spruces from Mäntsälä stand (60°40'N, 25°15'E) with the narrow crowned spruces from the same stand (NC2, NC3) or with normal crowned spruces (NC1, NC4-NC9) originating from southern or central Finland (latitudes 60°45'N-64°58'N). The additional six genetic entries (C10-C15) were normal crowned Norway spruces originating from seeds collected from commercial forest stands located in southern Finland (latitudes 60°40'N-63°22'N). In total, six randomly selected blocks out of the total 10 were selected for harvesting. The initial aim was to randomly collect one individual sample tree for each genetic entry and block, but due to survival problems the final number of harvested trees varied from 4 to 6 for each genetic entry, giving a total of 75 sample trees (Table 1).

At the time of harvesting, the height and diameter at 1.3 and 6 meters of each sample tree were measured, which were subsequently used to calculate the stem volume in each sample tree using the functions developed by Laasasenaho (1982) for Norway spruce. In addition, sample discs at a stem height of 1 m were taken from each sample tree for further laboratory analyses of intraring growth variables, wood density traits and fibre properties.

2.2 Laboratory Measurements

For intraring wood density analyses of the sample trees, small rectangular wood specimens of 5 mm×5 mm size (a radial segment from pith to bark) were cut from each sample disc with a twin-bladed circular saw. Thereafter, these wood specimens were kept for a few weeks under fixed environmental conditions before the measurements were carried out, so that they were stabilised to have a moisture content of 12% (air dry). Subsequently, they were scanned with an ITRAX X-ray microdensitometer (Cox Analytical Systems, Göteborg, Sweden), which works with an automatic collimator alignment at a geometrical resolution of 40 measurements per mm (Bergsten et al. 2001). In our work, the standard X-ray intensity (30 kV, 35 mA) for X-ray measurements was used. An exposure time of 20 ms was selected based on previous work by Kilpeläinen et al. (2005) and Peltola et al. (2007).

Afterwards, the X-ray images were analysed with the Density software program (Bergsten et al. 2001) and excel macros, and parameters such as ring width (RW, mm), earlywood and latewood widths (EWW and LWW, mm), mean intraring wood density (WD, g/cm³), minimum and maximum wood densities (g/cm³) and earlywood and latewood densities (EWD and LWD, g/cm³) were determined based on intraring density profiles. In this analysis, the mean of the maximum and minimum intraring densities were used as the threshold for earlywood and latewood for each ring; the values above this threshold representing the latewood and the values below the earlywood.

For the intraring analysis of the fibre properties, matchstick-sized wood specimens (each representing two annual rings) were chipped away from the wood specimens used for X-ray analysis and were subsequently macerated in a boiling 1:1 (v/v) mixture of acetic acid and hydrogen peroxide. Afterwards, fibre length (FL, mm) and fibre width (FW, µm) were measured with a L&W Fiber Tester (AB Lorentzen & Wettre, Kista, Sweden) based on image analysis. In fibre measurements, the highly diluted suspension flows between two glass plates, which have very short distance between them and thus limits the possibility of the fibres moving in one direction, but allows them to move freely in the other two directions. Two-dimensional images enable the measurement of fibre length and deformations separately. The use of the L&W Fiber Tester with a novel measurement system makes it possible to determine a large number of fibres for each sample (i.e. up to ten thousands fibres).

Based on dry weight of the sample and total length of fibres measured in that sample, fibre coarseness (C, fibre mass per unit fibre length of sample, $\mu g/m$) was calculated (see Karlsson 2006). Similarly, an average of fibre wall thickness (FWT) per sample was defined based on fibre measurements as follows:

$$FWT = \frac{FW}{2} - \sqrt{\frac{FW^2}{4} - \frac{C}{\pi \times R}}$$
 (1)

where FW is the average fibre width (μm), C the average coarseness of the sample ($\mu g/m$), and R is the expected density of fibre wall (in our case 1.5 g/cm³).

2.3 Data Analyses

Based on the intraring measurements from pith to the stem surface, the weighted averages for overall wood density (WD), earlywood density (EWD), latewood density (LWD), fibre length (FL), fibre width (FW), fibre wall thickness (FWT) and coarseness (C) were calculated by weighting each value with its corresponding ring width. Mean widths of the annual ring (RW), earlywood (EWW) and latewood (LWW) were also determined for each sample tree for further statistical analyses. Thereafter, the phenotypic coefficient of variation (CV_p) for each genetic entry was calculated by normalising the standard deviation (σ) by the mean (μ) of the property for each genetic entry (i.e. $CV_p = \sigma \times 100/\mu$).

Statistical analyses were conducted using the SPSS statistical program package (SPSS for Windows, version 15.0, SPSS, Chicago, IL.). Analysis of variance was performed for the growth and yield (diameter, height, stem volume, EWW, LWW, RW), wood density traits (WD, EWD, LWD) and fibre properties (FL, FW, FWT, C) for the crown types and the genetic entries nested within the crown using the General Linear Model procedure. The model applied to test the differences was

$$Y_{iik} = \mu + C_i + GE_{i(i)} + e_{iik} \tag{2}$$

where Y_{ijk} is the value of the studied trait, μ is the general mean, C_i is the crown type fixed effect, $GE_{j(i)}$ is the random effect of the genetic entries within the crown type, and e_{ijk} is the residual effect. Furthermore, to find out in more detail the differences between genetic entries within crown type, a pair-wise analysis with Tukey's test (p < 0.05) was also applied.

Relationships between the different yield, growth, wood density traits and fibre properties were also studied using phenotypic correlations instead of genetic correlations, since all genetic entries were grown in the same environmental conditions. In this work, the phenotypic correlations (r_p) between properties were computed using the Pearson's correlation method (Eq. 3);

$$r_p = \sigma_{p1p2} / \sigma_{p1} \sigma_{p2} \tag{3}$$

where σ_{p1p2} is the phenotypic covariance between properties 1 and 2, while σ_{p1} and σ_{p2} are the phenotypic standard deviation for properties 1 and 2, respectively. Correlations significant at p < 0.05 level were identified by a bold colour.

3 Results

3.1 Phenotypic Variation in Different Traits

In regards to the measured yield traits of the narrow crowned families of Norway spruce, height showed, on average, the smallest phenotypic variation (H, 18%) followed by diameter (D, 20%), while stem volume showed remarkably larger phenotypic variation (V, 46%) (Table 2). As a comparison, in normal crowned spruce the phenotypic variation in the yield traits was, on average, about twice that of narrow crowned families. Among the narrow crowned families NC6, NC7 and NC9 had, on average, 8-11% higher height, 6-13% higher diameter and 23-35% higher stem volume compared to the average for narrow crowned ones. The lowest average height, diameter and stem volume for individual narrow crowned families were 88%, 82% and 65% of that average, respectively.

The average yield traits of narrow crowned families also differed significantly from the normal crowned genetic entries used in comparison (p < 0.05). The narrow crowned families had, on average, significantly higher height (34%), diameter (30%) and stem volume (66%) than the normal crowned genetic entries (Fig. 1). Moreover, among the individual genetic entries, narrow crowned families represented the largest values for the studied yield traits, while in general, the lowest ones were found in normal crowned genetic entries (Table 3). Within each crown type, there was no statistically significant difference in regard to the yield traits among the genetic entries, although relatively large phenotypic variation was observed (Table 2).

In the case of growth traits, ring width showed, in narrow crowned families, the lowest phenotypic variation (RW, 17%), followed by the earlywood width (EWW, 18%) and latewood width (LWW, 24%) (Table 2). In comparison, the phenotypic

Table 2. Analysis of variance (F-value and associated propability ¹) for crown type and genetic entries nested within crown type, in addition to phenotypic coefficient of variation within each crown type for yield (diameter, height, stem volume), growth (earlywood with (EWW), latewood width (LWW), ring width (RW)), density traits (earlywood density (EWD), latewood density (LWD), wood density (WD)), and fibre properties (fibre length (FL), fibre width (FW), fibre wall thickness (FWT), coarseness (C)).

Genetic entry F-ratio	within crown P-value	Coefficient of v Narrow crown	ariation within:
F-ratio	P-value	Morrowy arossyn	
		ranow crown	Normal crown
1.31	0.23	20.2	42.4
1.41	0.18	17.7	33.2
1.68	0.09	45.9	81.5
1.23	0.28	18.3	45.1
2.54	0.01	24.3	27.6
1.68	0.09	17.2	36.9
1.46	0.16	7.8	11.7
0.92	0.54	5.5	4.9
1.09	0.38	7.6	1.6
2.03	0.03	8.5	16.9
1.38	0.19	4.2	7.3
0.94	0.52	5.2	7.4
1.20	0.31	7.4	8.2
	1.41 1.68 1.23 2.54 1.68 1.46 0.92 1.09 2.03 1.38 0.94	1.41 0.18 1.68 0.09 1.23 0.28 2.54 0.01 1.68 0.09 1.46 0.16 0.92 0.54 1.09 0.38 2.03 0.03 1.38 0.19 0.94 0.52	1.41 0.18 17.7 1.68 0.09 45.9 1.23 0.28 18.3 2.54 0.01 24.3 1.68 0.09 17.2 1.46 0.16 7.8 0.92 0.54 5.5 1.09 0.38 7.6 2.03 0.03 8.5 1.38 0.19 4.2 0.94 0.52 5.2

¹Significance of F-ratio with p < 0.05 is given in bold

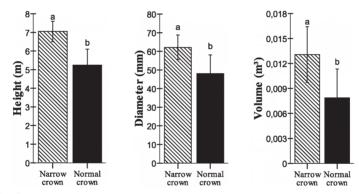


Fig. 1. Mean tree diameter, height and volume, with their standard desviation observed over the narrow and normal crowned genetic entries. Different letters above the bars indicate differences among two groups (p < 0.05).

variations observed in normal crowned genetic entries were, approximately, double those for narrow crowned ones regarding EWW and RW, but nearly equal for LWW. Among the families within the narrow crowned ones, NC5, NC7 and NC9 showed substantially larger EWW (4–17%), LWW (6–32%) and RW (6–15%) compared to the other narrow crowned families, while the lowest average EWW, LWW and RW were 84–85% of that average (Table 3). The analysis of variance also showed that the narrow crowned families had, on average, significantly larger EWW (37% higher) and RW (30% higher) than the normal

crowned genetic entries (p<0.05), but not LWW (only 11% higher) (Table 2). In addition, within each crown type there was statistically significant differences for LWW between genetic entries. Among all the individual genetic entries, narrow crowned families represented in general the largest values for the studied growth traits, whereas the lowest ones were found in normal crowned genetic entries (Table 3).

Compared to the growth and yield traits of narrow crowned families, significantly less phenotypic variation was observed in wood density traits. Moreover, LWD showed the smallest phe-

Table 3. Mean values with standard deviation and phenotypic coefficient of variation (CV_p) for yield traits (tree diameter, volume and height) and growth traits (earlywood width (EWW), latewood width (LWW) and ring width (RW)) for the different narrow crowned (NC1–NC9) and normal crowned (C10–C15) genetic entries.

Genetic entries	Diameter (mm) Mean±sd CV		Volume (m ³) Mean±sd CV _I	EWW (mm) Mean±sd CV _p	LWW (mm) Mean±sd CV _p	RW (mm) Mean±sd CV _p	
NC1	61.0±4.8 7.9	6.90±0.36 5.2	0.0116±0.002 16.7	2.17±0.21 9.9	0.58±0.09 15.3	2.75±0.25 9.0	
NC2	54.5±16.4 30.1	6.20±1.52 24.6	0.0096±0.005 49.6	1.91±0.51 26.8	0.65±0.11 17.2	2.56±0.58 22.8	
NC3	61.2±3.4 5.6	6.84±0.62 9.1	0.0114±0.002 16.7	2.06±0.28 13.6	0.58±0.08 13.4	2.64±0.27 10.1	
NC4	60.8±14.3 23.5	7.05±1.26 17.8	0.0126±0.006 49.2	1.97±0.25 12.8	0.62±0.17 27.3	2.59±0.38 14.7	
NC5	64.2±10.1 15.7	6.67±0.56 8.3	0.0128±0.005 35.8	2.23±0.38 16.9	0.73±0.20 26.7	2.96±0.57 19.2	
NC6	66.0±13.9 21.1	7.63±0.87 11.4	0.0161±0.007 44.1	2.21±0.36 16.4	0.60±0.08 14.0	2.81±0.43 15.3	
NC7	70.0±17.3 24.7	7.66±1.35 17.6	0.0177±0.011 61.7	2.33±0.38 16.4	0.86±0.33 38.7	3.19±0.53 16.7	
NC8	50.8±13.5 26.6	6.63±0.99 14.9	0.0085±0.005 62.0	1.81±0.44 24.3	0.55±0.06 11.9	2.35±0.44 18.5	
NC9	70.7±8.5 12.0	7.84±0.59 7.5	0.0176±0.005 29.0	2.49±0.36 14.4	0.69±0.06 8.4	3.18±0.36 11.4	
C10	43.6±16.9 38.7	5.20±1.94 37.2	0.0062±0.005 75.3	1.29±0.57 43.9	0.58±0.13 22.0	1.87±0.63 33.7	
C11	60.8±24.8 40.8	6.38±1.91 30.0	0.0134±0.009 67.2	1.89±0.80 42.0	0.70±0.11 15.7	2.59±0.87 33.4	
C12	38.5±27.2 70.7	4.19±2.13 50.9	0.0057±0.007 115.4	1.44±0.86 59.2	0.43±0.10 24.5	1.87±0.95 50.6	
C13	37.3±14.6 39.2	4.31±1.42 33.2	0.0039±0.003 76.3	1.20±0.53 43.8	0.49±0.11 21.6	1.69±0.52 30.9	
C14	58.7±17.7 30.1	5.82±0.74 12.7	0.0105±0.006 60.7	1.98±0.87 43.8	0.73±0.15 21.2	2.71±0.85 31.4	
C15	49.4±14.4 29.2	5.55±1.65 29.8	0.0076±0.005 69.1	1.55±0.50 32.4	0.58±0.17 30.0	2.14±0.64 29.7	

notypic variation (6%), followed by WD and EWD (8%) (Table 2). In comparison, the phenotypic variation was observed to be appreciably smaller in normal crowned genetic entries especially for WD (2%), but also to some degree for LWD (5%). Among the narrow crowned families, the highest wood densities were observed in NC2 for EWD and WD (7% higher than the average of narrow crowned families) and in NC4 for LWD (4% higher). The lowest averages observed for EWD, LWD and WD for individual narrow crowned families were 94–95% of that average.

The results from the analysis of variance regarding the wood density traits showed that average wood density and earlywood density differed significantly between the narrow crowned and normal crowned genetic entries (p<0.05), unlike latewood density (Table 2). The normal crowned genetic entries had on average 6% higher EWD and 8% higher WD compared to narrow crowned families (Fig. 2). As a consequence, normal crowned ones also showed, among all the compared genetic entries, the highest EWD, LWD and WD; while in general, the lowest ones were found in narrow crowned families (Table 4).

Among the measured fibre traits of narrow crowned families, fibre length showed, on average,

the highest phenotypic variation (9%), followed by coarseness (7%), fibre wall thickness (5%) and fibre width (4%). The phenotypic variation followed, in the normal crowned genetic entries, the same patterns as those of narrow crowned families, but they were in general larger, ranging from 7 to 17%. Among the narrow crowned families, NC6 had the longest fibres (9% longer than average for narrow crowned families), highest FWT (3% higher) and largest C (6% higher), while NC5 had slightly wider fibres (3% higher). The lowest averages observed for FL, FW, FWT and C were 93, 98, 97 and 92% of that average for individual narrow crowned families, respectively.

In regard to average fibre properties, and similar to the growth and yield and wood density traits, the narrow crowned families differed on average significantly from normal crowned genetic entries used for comparison (p<0.05) (Table 2). The narrow crowned families had, on average, 11% longer and 7% wider fibres, but also 4% thicker cell walls and 10% higher coarseness than the normal crowned genetic entries (Fig. 3). Accordingly, among all the individual genetic entries, narrow crowned families represented the largest values for the studied fibre properties, whereas in general, the lowest ones were found in normal

Table 4. Mean values with standard deviation and phenotypic coefficient of variation (CV_p) for
earlywood density (EWD), latewood density (LWD) and mean wood density (WD) for the
different narrow crowned (NC1-NC9) and normal crowned (C10-C15) genetic entries.

Genetic	EWD (g/ci	m ³)	LWD (g/	cm ³)	WD (g/ci	WD (g/cm ³)			
entries	Mean±sd	CV_p	Mean±sd	CV_p	Mean±sd	CV_p			
NC1	0.31±0.02	7.7	0.52±0.03	5.5	0.35±0.03	7.9			
NC2	0.35 ± 0.02	4.8	0.56 ± 0.02	3.3	0.40 ± 0.02	5.7			
NC3	0.33 ± 0.02	6.8	0.55 ± 0.04	7.7	0.38 ± 0.03	7.5			
NC4	0.33 ± 0.01	4.4	0.57 ± 0.04	7.5	0.38 ± 0.02	4.1			
NC5	0.33 ± 0.01	3.8	0.55 ± 0.03	6.0	0.39 ± 0.01	3.6			
NC6	0.32 ± 0.02	7.1	0.54 ± 0.02	3.8	0.37 ± 0.02	5.9			
NC7	0.33 ± 0.06	18.6	0.56 ± 0.03	5.8	0.38 ± 0.06	16.4			
NC8	0.33 ± 0.02	7.4	0.55 ± 0.03	5.7	0.38 ± 0.02	6.4			
NC9	0.32 ± 0.01	3.4	0.54 ± 0.02	3.2	0.37 ± 0.01	3.9			
C10	0.34 ± 0.03	7.3	0.56 ± 0.04	6.3	0.41 ± 0.03	8.0			
C11	0.36 ± 0.06	17.7	0.56 ± 0.02	4.1	0.42 ± 0.05	13.0			
C12	0.37 ± 0.05	12.9	0.56 ± 0.00	0.7	0.42 ± 0.05	12.2			
C13	0.37 ± 0.03	8.5	0.58 ± 0.02	4.1	0.43 ± 0.05	10.8			
C14	0.31 ± 0.02	7.0	0.56 ± 0.03	4.9	0.38 ± 0.04	10.9			
C15	0.34 ± 0.02	6.2	0.54 ± 0.04	7.2	0.39 ± 0.03	8.0			

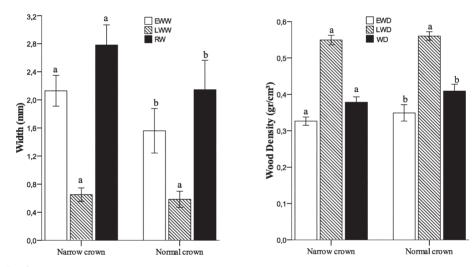


Fig. 2. Mean earlywood width (EWW), latewood width (LWW), ring width (RW), earlywood density (EWD), latewood density (LWD) and wood density (WD) with their standard deviations observed over the narrow and normal crowned genotypic entries. Different letters above the bars indicate differences among two groups (p < 0.05).

crowned genetic entries (Table 5). Statistically significant differences were also found among the genetic entries within the crown types only in regard to the fibre length.

Altogether, significantly higher growth and yield was observed in narrow crowned families than in normal crowned genetic entries, as was

also the case in regard to the fibre properties, but the opposite for wood density traits. However, both within narrow crowned families and normal crowned genetic entries relatively large differences could be found in these traits as could be seen in Fig. 4.

Table 5. Mean values with standard deviation and phenotypic coefficient of variation (CV_p) for fibre length (FL), fibre width (FW), fibre wall thickness (FWT) and coarseness (C) for the different narrow crowned (NC1-NC9) and normal crowned (C10-C15) genetic entries.

Genetic	FL (mr	n)	FW (μm)	FWT (µ	m)	C (µg/m)	C (µg/m)		
entries	Mean±sd	CV_p	Mean±sd	CV_p	Mean±sd	CV_p	Mean±sd	CV_p		
NC1	1.61±0.12	7.6	26.35±1.06	4.0	1.14±0.06	5.2	135.7±11.1	8.2		
NC2	1.52 ± 0.15	9.6	25.57±1.45	5.7	1.15±0.07	6.0	132.3±13.0	9.8		
NC3	1.58 ± 0.12	7.8	25.72±0.78	3.0	1.12±0.08	7.1	130.4±12.7	9.7		
NC4	1.49 ± 0.10	6.5	24.56±0.64	2.6	1.11±0.05	4.6	123.0 ± 6.2	5.1		
NC5	1.66 ± 0.12	7.3	26.48±0.83	3.2	1.16±0.05	4.6	138.2±10.5	7.6		
NC6	1.75 ± 0.15	8.4	26.40±1.43	5.4	1.18±0.06	5.1	140.9±14.4	10.2		
NC7	1.58 ± 0.12	7.5	26.28±0.99	3.8	1.15±0.05	4.1	135.9±10.5	7.7		
NC8	1.53 ± 0.10	6.6	25.16±0.42	1.7	1.16±0.09	7.5	130.9±9.9	7.5		
NC9	1.69 ± 0.10	5.7	25.86±0.59	2.3	1.13±0.04	3.3	132.2±6.3	4.8		
C10	1.47±0.26	17.9	23.85±1.53	6.4	1.07±0.06	5.6	115.7±13.8	11.9		
C11	1.69 ± 0.23	13.5	25.72±2.26	8.8	1.16±0.05	4.0	134.5±16.7	12.4		
C12	1.32 ± 0.38	28.7	23.42±2.82	12.0	1.05±0.15	14.1	112.1±27.1	24.2		
C13	1.36 ± 0.12	9.1	24.09±0.93	3.9	1.13±0.05	4.7	122.8±10.0	8.1		
C14	1.51±0.11	7.1	24.44±0.73	3.0	1.12±0.04	3.4	122.8±3.3	2.7		
C15	1.34 ± 0.15	11.0	23.82±1.26	5.3	1.08 ± 0.08	7.4	116.3±14.3	12.3		

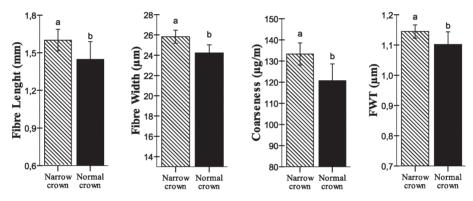


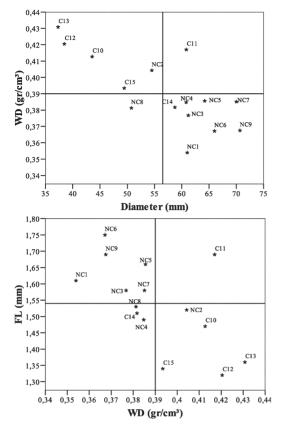
Fig. 3. Mean fibre length (FL), fibre with (FW), fibre wall thickness (FWT) and coarseness (C) with their standard deviation observed over the narrow and normal crowned genotypic entries. Different letters above the bars indicate differences among two groups (p < 0.05).

3.2 Phenotypic Correlations between Different Traits

The phenotypic correlations observed among different yield traits (diameter, height and volume) were, on average, very high and positive (p<0.05) for the narrow crowned families (Table 6). The correlations observed among the different growth traits, but also with different yield traits, were similarly positive, but ranged from moderate to high (p<0.05). The narrow crowned families did not differ in this respect from normal crowned

genetic entries used as a comparison (Table 6).

Similarly, the phenotypic correlations observed between the wood density traits (EWD, LWD and WD) were positive for the narrow crowned families varying from very high (e.g. between WD and EWD) to moderate (e.g. between LWD and WD/EWD) (p<0.05). Moreover, WD and EWD showed a negative, but weak correlation with all yield and growth traits, excluding the correlation with LWW (latter one being positive, p<0.05). LWD also showed very weak and negative correlations with all growth and yield traits (only



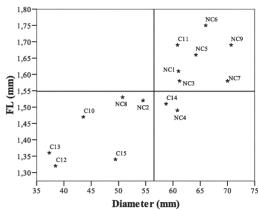


Fig. 4. Relationships between tree diameter and mean wood density (WD) (left side), tree diameter and fibre length (FL) (right side) and WD and FL (bottom) over all 15 genetic entries. The lines represent the average values over all the genetic entries for each trait.

with stem volume p < 0.05). When comparing the phenotypic correlations between wood density traits and growth and yield traits in narrow crowned families and normal crowned genetic entries, some differences could be observed. For example, the correlations between EWD/WD and the yield traits were generally stronger in normal crowned genetic entries. In addition, the correlation between EWD and LWW was positive for narrow crowned families, but negative for normal crowned genetic entries (p < 0.05) (Table 6).

Concerning the fibre properties, the phenotypic correlations observed between all the considered properties (FL, FW, C and FWT) were on average in narrow crowned families positive and strong (p<0.05) (Table 6). In addition, FL and FW showed moderate positive correlation (p<0.05) with growth traits and EWW, while FWT and C did not follow any general pattern in relation to growth and yields traits. In comparison, the correlations observed for normal crown genetic

entries were, between different fibre properties, also mainly positive, ranging from moderate to high depending on the fibre properties (p<0.05). Additionally FL, FW and C showed low to moderate negative correlation with WD in normal crown genetic entries (p<0.05), unlike in narrow crowned families, where these correlations did not follow any clear pattern (being in general very weak and non significant). Thus, considerable differences were found between narrow crowned families and normal crowned genetic entries in regards to fibre properties.

Table 6. Phenotypic correlations (r_p) between mean diameter at breast height (D), height (H), stem volume (V), earlywood with (EWW), latewood width (LWW), ring width (RW), earlywood density (EWD), latewood density (LWD), wood density (WD), fibre length (FL), fibre width (FW), fibre wall thickness (FWT) and coarseness (C), for narrow crowned (lower left) and normal crowned (upper right) genetic entries. (Correlations in bold are statistically significant at 0.05 levels).

		Upper right values for normal crowned genetic entries												
		D	Н	V	EWW	LWW	RW	EWD	LWD	WD	FL	FW	FWT	C
lies	D		0.93	0.96	0.93	0.60	0.95	-0.71	0.06	-0.73	0.72	0.81	0.58	0.74
ami	Н	0.85		0.88	0.79	0.68	0.84	-0.65	0.14	-0.60	0.77	0.81	0.66	0.78
g p	V	0.95	0.85		0.92	0.59	0.94	-0.61	0.00	-0.65	0.70	0.77	0.48	0.67
crowned families	EWW	0.91	0.78	0.86		0.46	0.98	-0.68	-0.03	-0.78	0.62	0.73	0.43	0.61
CLO	LWW	0.43	0.34	0.42	0.41		0.61	-0.37	0.09	-0.18	0.65	0.64	0.57	0.64
narrow	RW	0.88	0.75	0.84	0.95	0.67		-0.68	-0.01	-0.73	0.68	0.78	0.50	0.67
nar	EWD	-0.33	-0.37	-0.33	-0.26	0.30	-0.11		0.29	0.92	-0.55	-0.51	-0.32	-0.43
for	LWD	-0.25	-0.28	-0.29	-0.28	-0.14	-0.27	0.64		0.41	-0.03	0.14	0.29	0.22
nes	WD	-0.40	-0.43	-0.38	-0.39	0.32	-0.21	0.97	0.69		-0.50	-0.49	-0.25	-0.38
values	FL	0.38	0.34	0.38	0.32	-0.03	0.25	-0.1	0.11	-0.12		0.80	0.74	0.81
left	FW	0.48	0.35	0.40	0.44	0.08	0.39	-0.08	0.07	-0.13	0.74		0.84	0.97
	FWT	-0.06	-0.06	-0.02	-0.12	-0.23	-0.17	0.17	0.33	0.17	0.65	0.57		0.95
Below	C	0.22	0.16	0.21	0.17	-0.1	0.11	0.06	0.23	0.04	0.78	0.87	0.90	

4 Discussion and Conclusions

The growth and yield traits showed in narrow crowned Norway spruce families significantly higher phenotypic variations compared to the wood density traits and fibre properties. Moreover, the phenotypic variations observed in this work were, regardless of the wood property, generally significantly smaller for narrow crowned families than for normal crowned genetic entries (excluding WD and LWD). On the other hand, this could be expected, since the normal crowned genetic entries used in comparison were representing breeding regions instead of families. In general, our findings are in agreement, for example, with corresponding previous studies on Norway spruce and black spruce (Picea mariana), in which remarkably lower phenotypic variability was found for wood density traits and fibre properties (such as fibre length), compared to the growth and yield traits (e.g. Zhang and Morgenstern 1995, Hannrup et al. 2004, Zubizarreta Gerendiain et al. 2007, 2008).

In this work, narrow crowned families grown at narrow spacing also showed, on average, significantly higher growth and yield (e.g. 35% higher height, 30% higher diameter and 66% higher stem volume) and longer and wider fibres (11%)

longer FL and 7% higher FW), but lower wood density (8% lower WD) compared to normal crowned genetic entries. However, if referring to stem biomass production, the difference between the narrow and normal crowned trees would be to some degree less compared to the purely stem volume due to differences in average wood density.

The phenotypic correlations observed between growth, yield and fibre properties were generally positive, and ranging from moderate (fibre length and width) in narrow crowned families to relatively high in normal crowned genetic entries (all fibre properties). The phenotypic correlations were also negative and much lower between the growth and yield and wood density traits in narrow crowned families. Thus, the growth rate of trees seemed to affect, on average, less the wood properties in narrow crowned spruce than in the normal crowned one. As a result of our findings, we could also conclude that the selection based on one trait could simultaneously be expected to affect, to some degree, other traits. This is the case especially in the normal crowned genetic entries used for comparison with the narrow crowned families. In our investigation, we studied the relationships between different yield, growth, wood density traits and fibre properties in terms of

phenotypic correlations instead of genetic correlations, since all genetic entries were grown in the same environmental conditions. In addition, phenotypic correlations have also earlier been found to be generally comparable with genetic ones, especially if presented as an average over all the genotypes (Haapanen and Pöykkö 1993, Zhang and Morgenstern 1995). On the other hand, the phenotypic correlations are usually higher than the genetic correlations, thus, our correlations could be expected to, in some degree, overestimate the latter ones.

Similar to our work, in many previous studies an increase in growth rate of Norway spruce trees has induced, on average, lower wood density and wider fibres, however, contrary to our findings also shorter fibres (e.g. Dutilleul et al. 1998, Herman et al. 1998, Mäkinen et al. 2002). On the other hand, Zubizarreta Gerendiain et al. (2007, 2008) also found, in normal crowned Norway spruce (clones) grown in Southern Finland (at spacing of 2.0 m×2.5 m), that the relationship between growth and yield and average wood density and fibre properties of trees varied significantly between clones.

Altogether, we found that the narrow crowned families seemed to be, on average, less sensitive to competition than the normal crowned genetic entries grown at narrow spacing (of 1m×1m), which could be seen in terms of higher individual growth rate of trees. Thus, they could utilise the occupied growing space, on average, more efficiently than normal crowned genetic entries at narrow spacing as was previously suggested by Pulkkinen (1991a, 1991b, 1991c). There was also found within the narrow crowned crown type superior individual families, which could produce more stem volume per hectare (and stem biomass) at narrow spacing compared to the normal crowned genetic entries. In our study, unexpectedly large variations were also observed in growth, yield and wood properties in narrow crowned families despite the fact that they originated from a small stand located in southern Finland. Furthermore, this study also demonstrated that in normal crowned Norway spruce, any increase in the total stem wood production (per hectare) would occur at the cost of individual tree growth when grown at narrow spacing.

In this work, we also found that the total pro-

duction of stem wood per hectare (10000 trees/ ha in our work) would be superior in narrow crowned Norway spruce families (total average stem volume of 131 m³/ha) compared to that of normal crowned Norway spruce (average of 79 m³/ha). Additionally, in our trial, the normal crowned Norway spruces were surrounded by narrow crowned trees, meaning that they had more space to grow compared to a corresponding spacing for a stand consisting of pure normal crowned Norway spruce. Thus, our results would also slightly overestimate stem wood production potential of normal crowned Norway spruce at narrow spacing. According to Pulkkinen and Pöykko (1990), the maximum stand density for normal and narrow crowned Norway spruces such as used in our work could be about 3400 and 10300 trees/ha, respectively. This means that the corresponding maximum production of dry stem biomass could be about 12 Mg/ha and 28 Mg/ha.

Contradictory to our findings at narrow spacing, the average above ground dry biomass and stem diameter (about 18–19 years old open pollinated trees) have been earlier found to be on average significantly smaller in narrow crowned families (i.e. dry biomass about 18–31% smaller and diameter about half) compared to normal crowned genetic entries when grown at spacing of 2 m×2 m (see Pöykkö and Pulkkinen 1990, Pulkkinen 1991c). Thus, in this sense narrow crowned Norway spruce can not compete with normal crowned ones in typical spacing (about 2.5 m×2.0 m) used in practical forestry for Norway spruce.

On the whole, the material used in this work represented young trees (trial established in 1991) grown at very narrow spacing. Therefore, in the future, corresponding material from experiments with a range of different spacing and genetic entries would be needed in order to obtain a clearer picture on the possible differences in growth and yield traits, wood density and fibre properties of narrow and normal crowned genetic entries grown under different environmental conditions. We should also have in mind that compared to the typical spacing used in practical forestry in Norway spruce, the stand density of the experimental site was very high, approximately 10000 trees/ha, which would mean, in practice, very high regeneration costs (especially with cloned

seedlings). It would, therefore, be important to study which kind of spacing would be ideal for different genetic entries to provide desired biomass quantity and quality of stem wood in a cost-efficient way.

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