Cell Wall Thickness and Tangential and Radial Cell Diameter of Fertilized and Irrigated Norway Spruce

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Two Norway spruce nutrient trials were used to evaluate the effects of fertilization and irrigation on transverse tracheid dimensions. Three different treatments and a control (C) were used; daily irrigation (I), daily liquid fertilization (IL) and an annual solid fertilization (F). The nutrient optimisation was based on foliage analysis and both liquid and solid fertilization essentially comprised the same amount of nutrients but the latter was applied annually in solid form. The cell measurements; cell wall thickness, radial and tangential cell widths, were obtained using image analysis (SilviScan at CSIRO, Melbourne, Australia). Mean annual cell wall thickness was decreased by fertilization (F and IL) on both sites whereas no effect of the irrigation on wall thickness could be detected. Radial cell width was increased by treatment at Flakaliden but at Asa the effect of irrigation and fertilization was reversed when the data structure i.e. development from pith and out and annual ring width was taken into account. Tangential cell width was not significantly affected by treatment at Flakaliden. At Asa fertilization caused a small increase on tangential cell width. Ring width was positively affected by treatment and is an important factor explaining the effects on primarily cell wall thickness and radial cell width.

Keywords cell wall thickness, tangential tracheid diameter, radial tracheid diameter, tracheid dimensions, nutrient optimisation, juvenile wood
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1 Introduction

The interest in exploring the potential of more intensively managed forests using techniques as the continuous application of fertilizers has increased in recent years in Sweden (Vollbrecht 1996). Trials for nutrient optimisation have been used to study the effects of fertilizers on dry matter production and growth rate for Norway spruce (Linder 1995). In northern Sweden application of liquid fertilizers was found to increase the volume production fourfold whereas the corresponding treatment in southern Sweden, doubled the volume production (Berg 1997).

An increase in growth rate can change wood properties. Norway spruce wood density is negatively correlated to ring width (e.g. Olesen 1976) as an increased growth rate causes an increase in earlywood content. Tracheid width of spruce has been found to be positively correlated with growth ring width and rate of xylem increment (Denne 1973). However cell wall thickness did not vary with shoot vigour (Denne 1973) in Sitka spruce and Stairs et al. (1966) found no relationship between growth rate and cell length, diameter or wall thickness in Norway spruce.

Application of fertilizers, in particular nitrogen, can cause formation of wood with lower density (Shepard et al. 1980) and shorter tracheids. Mäkinen et al. (2002) found that fertilized trees had shorter and wider fibres but the difference in fibre width diminished when examined with respect to distance from pith. An increase in growth rate due to fertilization is sometimes said to change wood properties more than a corresponding increase due to other operations such as thinning (Zobel and van Buijtenen 1989). The decrease in density is however generally outweighed by the larger increase in volume production. Increased water availability has been linked to formation of wider tracheids particularly in the radial direction (Vysotskaya and Vaganov 1989, Von Wilpert 1991). It has also been shown that trees grown on unfavourable sites have smaller cells (Bannan 1965a).

Density is a measure of the proportion of cell wall material in the wood and is hence dependent on the ratio of cell wall thickness and cell diameter. These properties can vary between wood samples of identical density, which is why assessments of properties at the cellular level are needed in order to properly classify the wood (Kibblewhite 1999). Fibre length is one of the most important and well-researched individual fibre properties. Density and fibre length are both positively correlated with tear strength (Fuglem et al. 2003). Fibre wall thickness in conjunction with fibre width influences fibre collapsibility during paper making. Thin-walled fibres collapse more easily and bond well together which affects tensile strength, light scattering and surface smoothness positively (Jang and Seth 1998).

Juvenile wood is a concern for utilisation, particularly for fastgrown trees where the relative amount of juvenile-like wood is greater if the same tree dimensions at harvest are compared. The juvenile wood is sometimes defined as a fixed number of annual rings from the pith outwards. For Norway spruce 10–15 years have been suggested (Saranpää 1994, 2000, Wilhelmsson et al. 2002). Juvenile wood properties (e.g. thinner cell walls and smaller cell dimensions) can be desirable for certain pulp and paper products but the presence of juvenile wood induces a greater variability in the raw material. In Norway spruce, wood properties like density are highly dependent on growth rate (i.e. annual ring width) (Zobel and van Buijtenen 1989, Olesen 1976) which implies that it can be possible to influence some wood properties by regulating growth at an early age which has been shown for density by Johansson (1993). For cell width it has been suggested that distance from pith rather than ring number from pith (cambial age) should be used to define the juvenile to mature wood development (Mäkinen 2002, Sirviö and Kärenlampi 2001, Olesen 1982). However it has also been stated that the elongation of the fusiform initial over a couple of narrow growth rings exceeds that of one big ring of same total width why the time factor is important (Bannan 1965b). The tangential cell width is almost the same as that of the fusiform initial (Bannan 1965a).

The objective of this study was to compare the development of the transverse cell dimensions from pith towards cambium between sites and treatments and to describe the radial development of radial and tangential cell width and cell wall thickness from Norway spruce grown with an optimal supply of nutrients and/or water.

2 Material and Methods

2.1 Data Collection and Measurements

Two Norway spruce (*Picea abies* (L.) Karst.) nutrient trials were used; Asa in the south of Sweden at lat. 57°08’ and Flakaliden in the north at lat. 64°07’. Asa was planted in 1975 with two-year-old seedlings of an unknown seed source. Flakaliden was planted in 1963 with four-year-old seedlings of local provenance. The nutrient and irrigation treatments commenced in 1987 at both

Table 1. Factors involved in the experiments.

Notation	Irrigation	Fertilization
C	–	–
F	–	Solid
I	Yes	–
IL	Yes	Liquid

sites. Three different treatments, and a control (C) were available; IL, F, I and C. IL was irrigation with added liquid nutrients applied daily during the growing season (Table 1). F was the same amount of nutrients as IL but applied in solid form annually in the beginning of the growing season. I was daily irrigation. Each treatment was applied to 4 plots per site. The compositions of fertilizers were determined by annually repeated foliage analysis per site and treatment, and consisted of both macro- and micronutrients. For further information about the procedures for nutrient optimisation see Linder (1995). At Asa, which is a good site (SI at H_{100} 34 m), the nutrient optimisation and irrigation (IL) more than doubled volume production approximately 10 years after the commencement of treatments. At Flakaliden, which is a poor site (SI at H_{100} 18 m), there was a four-fold increase in the corresponding volume production with the fertilization (F). For further information about growth in the trials see Bergh et al. (1999).

The plots were 50 × 50 m with approximately 10 m wide buffer zones. Buffer zones were treated in the same way as the core plots. Sample trees were randomly selected in the buffer zones from the two rows immediately adjacent to the plot to minimise edge effects. Increment cores were taken with a 12 mm borer at breast height (1.3 m) in the westerly direction. At Asa 5 trees per plot and in total 20 trees per treatment were sampled but two of the plots with solid fertilization and one of the control plots were discarded, leaving a total of 65 samples. At Flakaliden 2–3 trees per plot were sampled depending on the number of plots available for each treatment ensuring that the total number of samples per treatment would be 20. The irrigated plots were not sampled at Flakaliden as irrigation had no effect on volume production (Bergh et al. 1999); hence the total number of samples amounted to 60. After sampling the increment cores were immersed in ethanol to prevent fungal attacks and subsequent staining. After approximately 36 hours the samples were taken out of the ethanol and dried.

The samples were taken to CSIRO, Clayton Victoria, Australia, for sample preparation and measurements. The sample preparation was carried out using the methods described by Evans et al. (1995). Radial strips 2 mm × 6 mm where cut from pith to bark, extracted in acetone and conditioned at 20°C and 40% relative humidity. After this the transverse surface was polished by 600 to 1500 grit until cells were clearly distinguishable in transmitted light.

The samples were run in the SilviScan machine (described by Evans 1994) to obtain cross-sectional dimensions and density. The tangential and radial cell widths were measured on the cross-sections by image analysis and the density was measured by X-ray diffraction. In the SilviScan system cell wall thickness is assumed to be uniform around the cell and is calculated using the measured density and cell dimensions. Averages per annual ring were calculated for all variables and formed the basis for all analyses in this paper.

2.2 Data Analyses

Cell dimensions were plotted by calendar year in order to visually examine the effect of treatments. In order to properly analyse these effects the growth curve structure of the data i.e. the development from pith and out due to cambial maturation will have to be considered. A quadratic function form with distance from pith as the independent variable was found to be applicable. The variation in cell wall thickness and radial and tangential cell diameter was thus analysed using the following model:

$$Y_{ijkl} = \mu + \beta_0 d_k + \beta_1 d_k^2 + \beta_2 I_i + \beta_3 F_j + \beta_4 IF d_{ijk} + \beta_5 r_k + \beta_6 n_k + \varepsilon_{ijkl} \quad (1)$$

where Y_{ijkl} represents the dependent variable, μ is the overall mean, $\beta_0 - \beta_6$ are fixed effects for: d – distance from pith, I – irrigation, F – fertilization, r – ring width, n – cambial age (ring number counted from pith) and ε_{ijkl} is random error. The

Table 2. Models for fixed effects at Asa.

Effect	I	F	Cell wall thickness Estimate	s.e.	Radial cell width Estimate	s.e.	Tangential cell width Estimate	s.e.	Ring width Estimate	s.e.
Int.			2.24	0.0720	22.3	0.464	20.8	0.299	4.76	0.291
I	0		–0.122	0.0723	–0.648	0.329	0.0164	0.207	0.553	0.231
I	1		0	.	0	.	0	.	0	.
F		0	–0.233	0.0792	–1.928	0.384	–0.820	0.231	–0.727	0.257
F		1	0	.	0	.	0	.	0	.
d			–1.02E-3	3.33E-3	0.0548	0.0228	0.136	0.0146	0.131	0.0149
d^2			–2E-5	3.7E-5	–4.5E-4	2.47E-4	–1.18E-3	1.43E-4	–1.03E-3	1.67E-4
IFd	0	0	0.0238	5.10E-3	0.0794	0.0134	0.0315	9.11E-3	1.56E-4	0.0106
IFd	0	1	3.15E-3	5.00E-3	0.0273	0.0125	0.0192	8.97E-3	–0.0295	9.81E-3
IFd	1	0	0.0230	4.51E-3	0.0629	0.0116	0.0184	7.80E-3	0.0101	9.15E-3
IFd	1	1	0	.	0	.	0	.	0	.
IFd^2	0	0	–2.0E-4	6.5E-5	–	–	–		–	–
IFd^2	0	1	–2E-5	7.0E-5	–	–	–		–	–
IFd^2	1	0	–2.2E-4	5.5E-5	–	–	–		–	–
IFd^2	1	1	0	.	–	–	–		–	–
r			–0.0592	6.10E-3	0.799	0.0470	0.0936	0.0315	–	–
n			–	–	0.379	0.0527	0.199	0.0361	–0.421	0.0354

Parameters for the *intercept*, *d* and d^2 are to be adjusted according to parameter estimates associated with *I* and *F*.

mixed procedure in SAS statistical program package, was used for the analysis (SAS OnlineDoc 2000). A repeated measures analysis of variance was used (*k* repeated measures per sample) and the growth curve part of the model (*d* and d^2) were included as random components. The covariance matrix was assumed to be unstructured. *I* and *F* were treated as dummies representing the presence of irrigation and fertilization and assuming the value 1 or 0 depending on whether the sample came from a treated plot or not and whether the ring had formed prior to or after 1987, the first year of treatment, or not. At Flakaliden where the I treatment was not sampled, the *I* and *F* dummies were not used. Instead data were analysed as three classes (C, F and IL) according to treatment (*T*). In order to avoid discrepancies in the data which may occur close to the pith, rings closer to the pith than 2 rings were excluded from the statistical analysis. Effects that were far from being significant ($p > 0.10$) were not included in the final models except for the effects of treatment which were always included.

In order to make comparisons between the two sites and in order to study the effect of treatment and geographical site on juvenile wood development the controls from both sites were plotted by ring number from pith and distance from pith. The radial development of juvenile wood was furthermore studied by plotting the different treatments from the same site by distance from pith. The development of tangential cell diameter in relation to ring number from pith and distance from pith were also plotted for the Flakaliden experiment to facilitate comparisons of the juvenile wood core between treatments.

3 Results

The general statistical model taking into account the inherent structure of the data over distance from pith was initially targeted at cell width development but its basic form was found to be an appropriate model for all variables studied (Tables 2 and 3 with associated variance components in Table 4).

The graphical studies of the cell properties against calendar year enabled a visual analysis of the effect of treatment. At Asa both irrigation and fertilization had an effect on ring width whereas the F and IL treatments caused almost identical growth ring patterns at Flakaliden (Fig. 1). The cross-section area (Fig. 1) is a cumulative expression of the ring width and shows that the differences between the control and the fertilized trees in area, is accentuated further out from the

Table 3. Models for fixed effects at Flakaliden.

Effect	T	Cell wall thickness Estimate	s.e.	Radial cell width Estimate	s.e.	Tangential cell width Estimate	s.e.	Ring width Estimate	s.e.
Int.		2.07	0.0288	21.4	0.182	20.3	0.125	0.172	0.129
T	C	–0.0975	0.0483	–0.462	0.250	–0.179	0.153	0.916	0.177
T	F	0.0696	0.0420	–0.738	0.242	–0.253	0.154	0.641	0.172
T	IL	0	.	0	.	0	.	0	.
d		1.84E-3	3.19E-3	0.190	0.0245	0.0958	0.0166	0.278	0.0128
d^2		–4E-5	4.4E-5	–1.26E-3	2.25E-4	–7.5E-4	1.53E-4	–2.55E-3	1.59E-4
Td	C	0.0164	5.04E-3	–	–	–	–	–0.0725	8.54E-3
Td	F	–7.27E-3	4.20E-3	–	–	–	–	–0.0309	7.18E-3
Td	IL	0	.	–	–	–	–	0	.
Td^2	C	–1.4E-4	8.1E-5	–	–	–	–	–	–
Td^2	F	8.3E-5	5.9E-5	–	–	–	–	–	–
Td^2	IL	0	.	–	–	–	–	–	–
r		–0.0299	6.31E-3	0.521	0.0438	0.187	0.0322	–	–
n				0.237	0.0359	0.212	0.0255	–0.183	0.0231

Parameters for the *intercept*, *d* and d^2 are to be adjusted according to parameter estimates associated with *T*.

Table 4. Covariance parameter estimates.

Parameter	Cell wall thickness	Radial cell width	Tangential cell width	Ring width
Asa				
d	4.2E-4	6.83E-3	2.53E-3	2.04E-3
d^2	6.57E-9	1.47E-6	3.594E-7	4.86E-7
Flakaliden				
d	9.9E-5	6.79E-3	1.55E-3	1.19E-3
d^2	2.10E-8	1.06E-6	2.99E-7	7.56E-7

pith. The growth layers formed in e.g. 2000 may have the same width for the treated and untreated trees due to increased competition for the more densely stocked F and IL stands but represent more wood for fertilized trees.

Fertilization decreased mean cell wall thickness (Fig. 2) at both sites. Fig. 2 also suggests that the addition of irrigation did not have an effect on wall thickness. This agreed with the analysis of variance (Tables 5 and 6). The analysis of variance also shows that there was a strong effect of ring width for both Asa and Flakaliden but that the development from pith and out explained a significant part of the variation. The interaction factors were significant which means that treatment affects both lean and shape of the model.

There were significant treatment effects on radial cell width and at Asa both fertilization and irrigation were found significant (Tables 5 and 6). The treatment effects were however weak compared with the effects of ring width. The increased ring width was however also an effect of treatment. At Flakaliden the effect of fertilization was distinct when looking at the calendar year plot (Fig. 3) but when other factors, primarily ring width, were taken into account the remaining positive effect was small. The effect of fertilization at Asa was less apparent (Fig. 3) and when distance from pith was the independent variable, C and I showed larger radial cell width compared with their fertilized counterparts which explains the significant effects in the analysis of variance (Table 5) and the larger parameter estimate of *d* for C and I (Table 2).

The tangential cell width showed a stronger dependence on distance from pith than the radial cell width, and the effect of ring width was weaker (Fig. 4, Tables 5 and 6). At Flakaliden there was no effect of treatment on tangential width which may be due to the stronger effect of ring width and ring number from pith. There was no effect of irrigation at Asa but the trees from the I treat-

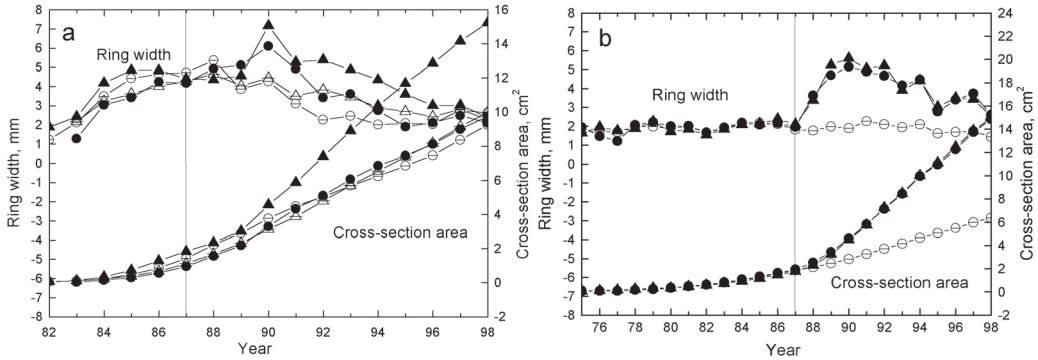

Fig. 1. Ring width and cross-sectional area of sample trees at Asa (a) and Flakaliden (b), mean values per year. ○ = C, control, △ = I, irrigation, ● = F, solid fertilization and ▲ = IL, liquid fertilization.

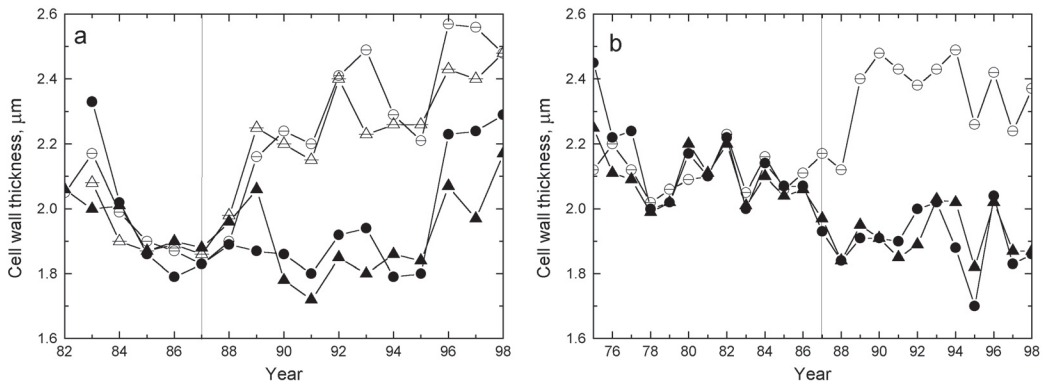

Fig. 2. Cell wall thickness at Asa (a) and Flakaliden (b), mean values per year. ○ = C, control, △ = I, irrigation, ● = F, solid fertilization and ▲ = IL, liquid fertilization.

Table 5. Analysis of variance, type III tests of fixed effects at Asa.

Effect	Cell wall thickness F	Cell wall thickness p	Radial cell width F	Radial cell width p	Tangential cell width F	Tangential cell width p	Ring width F	Ring width p
I	2.86	0.0912	3.88	0.0493	0.01	0.9368	5.75	0.0167
F	8.68	0.0033	26.58	< 0.0001	12.58	0.0004	8.00	0.0048
d	27.46	< 0.0001	20.75	0.0740	122.86	< 0.0001	86.21	< 0.0001
d^2	19.18	< 0.0001	3.30	< 0.0001	67.77	< 0.0001	37.65	< 0.0001
IFd	10.76	< 0.0001	14.10	< 0.0001	4.34	0.0048	4.17	0.0061
IFd^2	6.08	0.0004	–	–	–	–	–	–
r	94.20	< 0.0001	288.55	< 0.0001	8.83	0.0031	–	–
n	–	–	51.78	< 0.0001	30.40	< 0.0001	140.92	< 0.0001

ment did have smaller tangential width than the control for a number of years when looking at the calendar year plot (Fig. 4). If the model is applied only to rings formed after the onset of treatments (1987) I and IL have smaller least square means than F and C at Asa both for tangential and radial cell width. At Flakaliden however IL has larger least square mean estimate than F for both cell width measures.

The trees at Asa start to produce mature wood in terms of larger radial and tangential cell diameters earlier than the trees at Flakaliden when

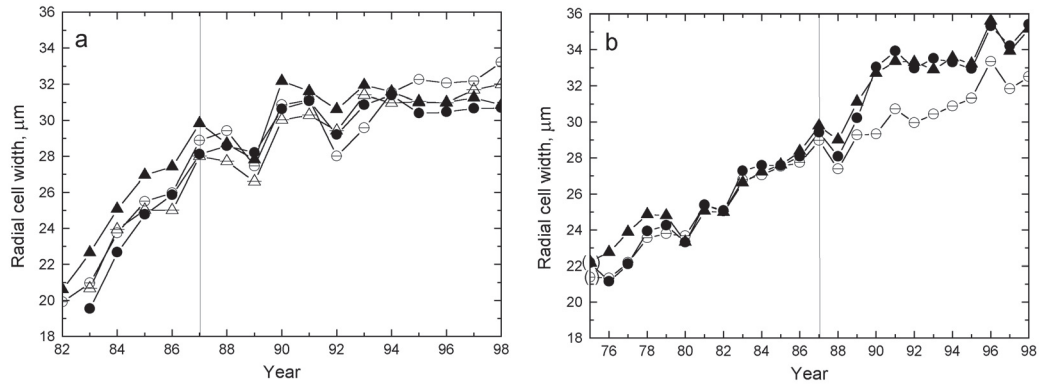

Fig. 3. Radial cell width at Asa (a) and Flakaliden (b), mean values per year. ○ = C, control, △ = I, irrigation, ● = F, solid fertilization and ▲ = IL, liquid fertilization.

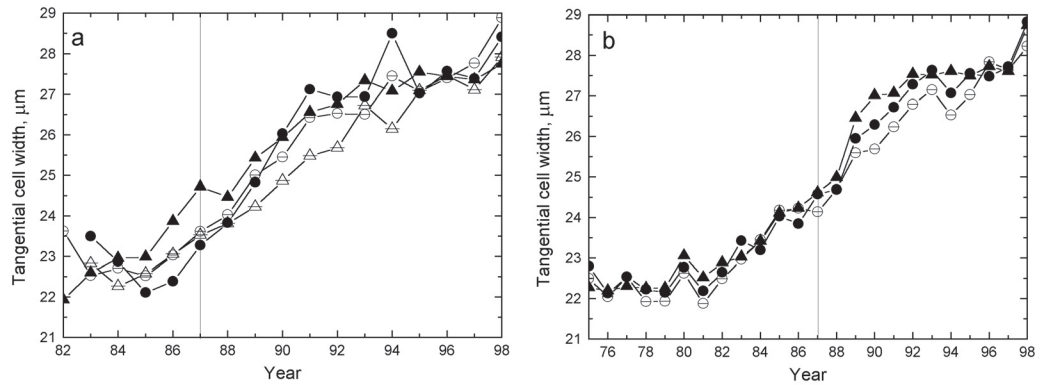

Fig. 4. Tangential cell width at Asa (a) and Flakaliden (b), mean values per year. ○ = C, control, △ = I, irrigation, ● = F, solid fertilization and ▲ = IL, liquid fertilization.

Table 6. Analysis of variance, type III tests of fixed effects at Flakaliden.

Effect	Cell wall thickness F	p	Radial cell width F	p	Tangential cell width F	p	Ring width F	p
T	5.99	0.0026	4.76.	0.0088	1.44	0.2366	14.41	< 0.0001
d	5.58	0.0216	59.94	< 0.0001	33.26	< 0.0001	341.79	< 0.0001
d^2	3.75	0.0579	31.46	< 0.0001	23.98	< 0.0001	256.52	< 0.0001
Td	11.19	< 0.0001	–	–	–	–	36.49	< 0.0001
Td^2	3.90	0.0205	–	–	–	–	–	–
r	22.54	< 0.0001	141.46	< 0.0001	33.74	< 0.0001	–	–
n	–	–	43.44	< 0.0001	68.63	< 0.0001	62.59	< 0.0001

cambial age is the independent variable. However when cell diameters were plotted by distance from pith the curves were almost identical (Fig. 5 and Fig. 6). This pattern could not be detected for cell wall thickness (not shown). When the development from juvenile to mature wood in different treatments was compared the same trend emerged; distance from pith gave a better discrimination than cambial age i.e. ring number from pith (Fig. 7).

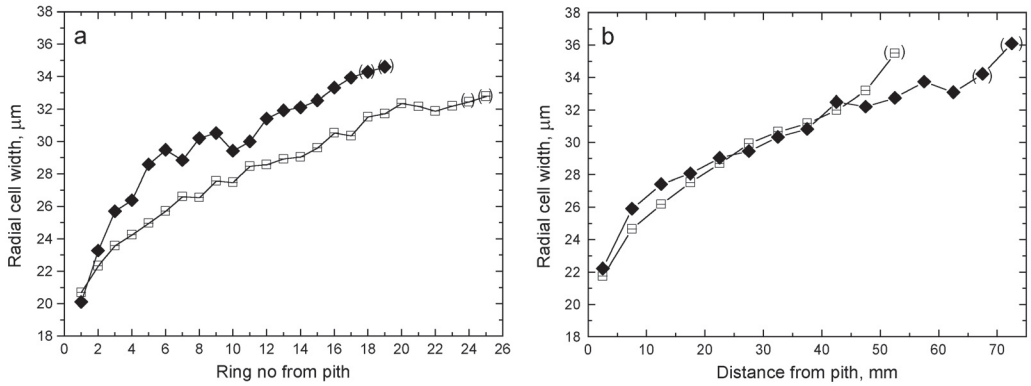

Fig. 5. Radial cell width by ring number from pith (a) and distance from pith (b), for the control trees from Asa (◆) and Flakaliden (□). Data points represented by less than 5 entries are inside brackets.

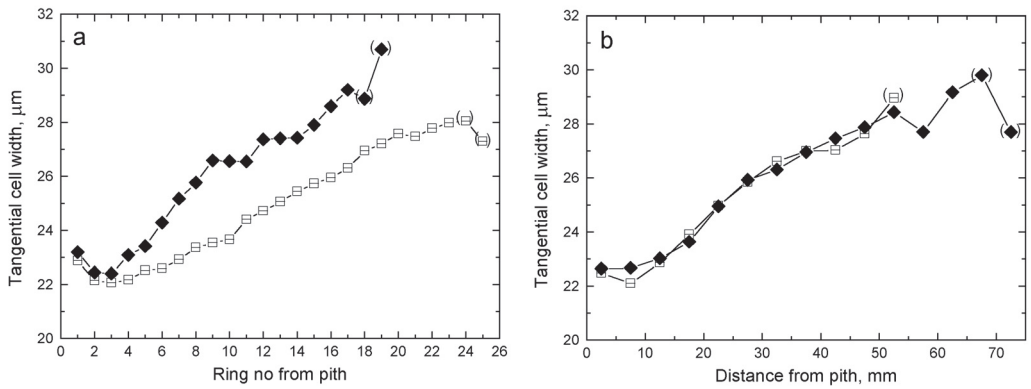

Fig. 6. Tangential cell width by ring number from pith (a) and distance from pith (b), for the control trees from Asa (◆) and Flakaliden (□). Data points represented by less than 5 entries are inside brackets.

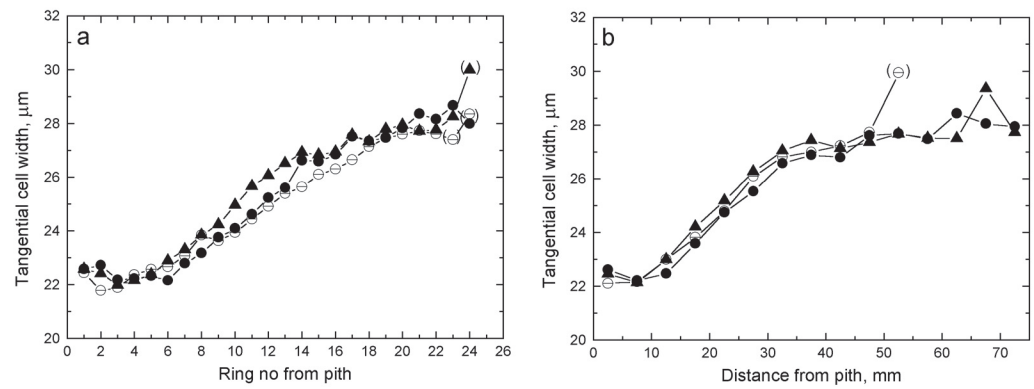

Fig. 7. Tangential cell width by ring number from pith (a) and distance from pith (b), for Flakaliden. ○ = C, control, ● = F, solid fertilization and ▲ = IL, liquid fertilization. Data points represented by less than 5 entries are inside brackets.

4 Discussion

The main effect of irrigation and fertilization : a reduced average cell wall thickness, was expected. It was also expected that the effects of treatment would act via higher growth rates which in turn affects mean cell properties (Mäkinen et al. 2002). In this material it was mainly cell wall thickness and radial cell width that were affected. Tangential cell widths were less affected by growth rate and treatment at both sites. This is in line with results on fertilized Douglas-fir where fertilization has been shown to have no effect on the tangential cell width but some effect on radial cell width of the early wood (Brix and Mitchell 1980).

A positive relationship between irrigation, or high water availability, and cell size has been reported (Olesen 1982, Bannan 1965b). The results from Flakaliden supported this relationship but at Asa there were indications of a contrasting effect as I and IL had smaller cell widths than C and F. As there is an effect of irrigation on volume production at Asa, whereas the Flakaliden site is not moisture deficient, this pattern is somewhat surprising as Bannan (1964) found that the largest tangential cell widths came from the sites with the widest annual rings. Tangential cell width distributions of Scots pine, however, displayed a small shift towards lower values for moist sites compared with moderatley moist sites (Vysotskaya and Vaganov 1989). An excess of water can inhibit water uptake and cause moisture stress and reduction of cell expansion in plants (Kozlowski et al. 1991 and Kramer and Kozlowski 1960). At Asa the irrigation is however carefully monitored and held near field capacity. Irrigation is discontinued at rainfall and the site is situated on a slope so overwatering should not occur.

The change in the radial and tangential cell width with cambial age and distance from pith is in line with e.g. findings for Sitka spruce in Wales (Mitchell and Denne 1997). In spite of the great range in latitude between the two trials in this material (57° to 64°), the curves for tracheid width were almost identical when plotted against distance from pith, which supports earlier findings that number of cells produced can be a better measure of cambial maturation than age in years is (Mäkinen et al. 2002, Sirviö and Kärenlampi 2001, Olesen 1982).

Fibre lengths were not included in the present study. At Flakaliden however, lengths for control and the liquid fertilization have been analysed by Mäkinen et al. (2002) who showed that fertilization caused formation of shorter fibres. The analyses presented in this paper are exclusively based on annual ring means of the different variables and does not consider the effect of varying proportions between latewood and earlywood. This great source of variation within annual rings is always an issue for evaluation of material with varying ring widths. As latewood is characterised by thicker cell walls and smaller radial lumen diameters (Mork 1928) average cell wall thickness and radial cell diameter are dependent on latewood proportion. Tangential cell diameter is less affected. There are however advantages of not separating wood types within the ring; it gives a clear picture of the effects of treatment on the wood and there are no improprieties induced by using particular definitions to separate wood on a more or less continuous scale. This is especially true when performing the operation on fertilized wood which may be more homogeneous within the annual ring and display a more gradual development from early- to latewood (Polge 1969, Klem 1972).

The sampling of the trees used in this study was performed in the buffer zones. This type of sampling for wood properties is not uncommon (see e.g. Pape 1999) as the desire often is to keep the core plots as untouched as possible not to induce hazards for future research. The trees sampled in this study come from the two inner buffer rows which is well within half the buffers width of 10 m and edge effects should not have affected the overall results.

The cross-sectional areas of the sample trees (Fig. 1) displayed obvious differences between the control and some of the treatments. At Asa there was however little effect on the cross-sectional areas of the solid fertilization (F) compared with the control in spite of large differences in annual ring width for a number of years after commencement of treatment. This was not in line with more comprehensive diameter and volume measurements at Asa published by Bergh et al. (1999) so the F trees sampled in this study were slightly smaller than they should be. This unrepresentative

sample was a random effect of the smaller sample size for the F trees as only 9 F trees were used compared with the target and initially sampled 20 trees (two F plots were discarded as described in the Material and Methods section).

The development of tangential cell width close to the pith was different from studies on Norway spruce grown in Denmark (Olesen 1977). In Olesen's study the increase in tangential width is steep right from the very beginning whereas in this material there appeared to be a plateau or even a small decrease during the first years (Fig. 6). A possible explanation could be the difficulties to penetrate the pith correctly with the increment borer, which is also why there are fewer samples for the innermost rings (around 10). The wood samples are longitudinally aligned according to grain at the cambial end and the grain angle is known to be very low for the innermost rings and to reach a maximum around ring number 4 from the pith (Säll 2002). This could cause a bias as tracheids further from the cambium are more likely to be measured at an angle which would exaggerate their tangential widths. This does however not explain the distinct decrease for the first two rings. Another possibility is that the image analysis software had swapped tangential and radial widths which could happen if the tangential alignment is difficult due to curvature near the pith. The image analysis process was however manually supervised and this effect was not noted. The measurements close to the pith are of little importance as they represent very little wood and the wood structure near the pith can differ in many other aspects as well and were not used in the statistical analysis.

Treatments have begun towards the end of the juvenile wood phase. Depending on silvicultural regime and end use the mature wood would account for a larger value and importance than the juvenile wood. The effect of growth rate on cell width manifested itself through a faster increase in cell diameter with the maturing cambium for fastgrowing trees so that the size of the juvenile wood core defined by cell diameter was more or less constant between treatments and sites (Fig. 5–7).

The effect on wood properties should be regarded in relation to the volume affected. The total practical effect on average wood properties per tree and stand will be dependent on silvicultural regimes. At the studied breast height cross section, the cumulative area for the treated trees at Flakaliden grew to more than twice that of the control (Fig. 1). However, given the trend of decreasing differences at breast height when stands are closing, the effect on harvested volume will be smaller than during the studied years. These trials have never been thinned.

Fertilization did have a large, mainly growth-rate related effect on cell wall thickness and also some effect on radial cell width. The effects seems to be greater at the poorer Flakaliden site in the north which also has responded more to the treatments in terms of growth rate. The nutrient optimisation regimes used in these trials are very intensive. Commercial fertilization is likely to produce wood with thinner cell walls and somewhat larger cells but the magnitude of changes in wood properties are likely to be well within the limits set by this material.

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