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Influence of Cambial Age and Growth Conditions on Microfibril Angle in Young Norway Spruce *(Picea abies* [L.] Karst.)

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Keywords

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Summary

Microfibril angle (MfA) of the trachcid cell wall of conifers influences the performance and properties of forest products. For instance a high MfA has been found detrimental for solid wood properties. Although it is assumed that there is a correlation between MfA and the growth conditions a tree experiences. there are few studies on how growth conditions influence MfA.
In this study mean MfA of the cell walls was determined for 646 early wood samples, from pith and outwards, of *Picea abies* trees using automated double gaussian curve fitting of the 002 arcs generated by X-Ray diffraction and recorded using a area detector. The determinations of mean MfA were based on appr. 500-2000 tracheids per wood sample. It was indicated that a determination of mean MfA would require less than 3 minutes, if the curve fitting program is included already at the time of data acquisition. In an attempt to model the dependency of MfA on factors related to wood formation, the age effect was Found most descriptive and a simple model based on 1/cambial age gave an $r^2 = 0.69$. Only a slightly higher correlation ($r^2 = 0.73$) was reached when additional variables significant at $p \leq 0.001$ were used, although they, together with the age effect, supported the assumption that growth conditions affect MfA. The study suggests that to concentrate and minimize the volume of wood with high MfA, in an individual tree, juvenile growth suppression in combination with an extended rotation period should be used.

Introduction

MfA in tracheid cell walls and its influence on forest products

The tracheid cell wall consists of three secondary layers S1, S2 and S3, each composed of microfibrils i.e. cellulose crystalline fibrils embedded in hemicellulose and lignin. A distinct orientation between the cell axis and the fibrils has been found for each layer, where the S1- and S3-layers have high fibril angle, while the fibrils in the predominant S2-layer are more aligned with the cell axis (Mark 1967; Fujita and Harada 1991; Saka 1993). MfA has been found to influence shrinkage of wood (Harris and Meylan 1965; Meylan 1968; Barrett *et al.* 1972; Boyd 1983; Watanabe and Notimoto 1994; Ying *et al.* 1994; Persson 1997). and the mechanical properties of wood (Schniewind 1966; Cave 1968; Meylan 1968; Mark and Gillis 1973; Megraw 1985; Bendtsen and Senft 1986; Cave and Walker 1994; Persson 1997). In addition, differences in paper properties such as stretch, stiffness, and strength have in part been ascribed to MfA (Watson and Dadswell 1964; Kellogg et al. 1975; Armstrong *et al.* 1977; Page *et al.* 1977; Megraw 1985).

The function of MfA *in a living conifer tree*

During formation of a tracheid's primary wall microfibrils form a loosely connected web that allows cell expansion and elongation. When surface growth of the primary wall eventually ceases, which marks the onset of secondary wall growth, microfibrils start to deposit in lamellae that have a certain angle to the longitudinal cell axis (Fujita and Harada 1991; Kataoka *et al.* 1992; Romberger *et al.* 1993; Fosket 1994; Mauseth 1996). Several theories on cell wall growth regulation of MfA have been proposed (Roelofsen 1959; Chafe 1978; Preston 1982; Boyd 1985a). At the macro level, it has been shown that MfA varies with cambial age, growth rate, and height within the stem of a conifer tree (Erickson and Arima 1974; Kyrkjeeide 1990; Donaldson 1992; Pedini 1992; Cave and Walker 1994). In addition, MfA seems to be under genetic control (Donaldson 1993; Hirikawa and Fujisawa 1995). In later years, it has been argued that lignin swelling inbetween microfibrils (Münch 1938; Boyd 1973a, 1985b) and cellulose crystallisation (Bamber 1979) interact to produce compressive and tensile stresses (Archer 1987; Kubler 1987; Fournier *et al.* 1990; Nilsson 1993; Okuyama *et al.* 1994; Yamamoto *et al.* 1995). Such growth stresses are believed to assist the tree in reorienting if it becomes bent from a vertical position (Westing 1965; Boyd 1973a, 1973b, 1985a; Timell 1986; Kyrkjeeide and Thömqvist 1993; Mattheck and Kubler 1995). MfA is also said to affect tree stiffness, e.g. high MfA in the first growth rings from pith will ensure great flexibility of a young seedling while high stiffness in the mature outer wood of an older tree is achived through a lower MfA (Timell 1986: Niklas 1992). It is therefore suggested that MfA is indicative of the shifting demands that a conifer tree experiences throughout its various life phases. and that the MfA of tracheids is a responsive function to vascular cambium activity, turgor pressure. and mechanical strains on the tree stem (Wilson and Archer 1979; Timell 1986; Niklas 1992; Okuyama *et al.* 1995; Mattheck and Kubler 1995).

Determination of MfA

Direct determination of the MfA of individual tracheids can be done by optical and scanning electron microscopy methods (Manwiller 1966; El-Hosseiny and Page 1973; Leney 1981; Senft and Bendtsen 1985; Kyrkjeeide 1990; Donaldson 1991; Abe *et al.* 1992; Huang 1995). However, these methods are very time consuming, and relatively few tracheids are taken to represent the average MfA (Prud'homme and Noah 1975; Stuart and Evans 1995). In order to determine the mean fibril orientation of a large number of tracheids, X-ray diffraction has been used (Cave 1966; Meylan 1967; Tripp and Conrad 1972; Lofty *et al.* 1973; Preston 1974; Prud'homme and Noah 1975; Yamamoto *et al.* 1993; Stuart and Evans 1995; Evans *et al.* 1996; Sahberg *et al.* 1997; Cave 1997) The X-ray method is based on the principle that the pattern of diffracted X-rays is determined by the arrangement of crystalline elements in the irradiated sample. On a typical X-ray fiber diffraction experiment a cellulose fiber or group of fibers is irradiated perpendicular to the fiber length by a narrow, monochromatic X-ray beam, and at a distance behind the fiber(s) the diffraction pattern is recorded on film or other electronic recording device (Fig. 1). The diffractogram pattern in this type of fiber diagram consists of interrupted arcs on a set of concentric circles. These arcs can be indexed as corresponding to the spacings of crystalline planes within the cellulose crystalline fibrils that comprise the windings of the cellulose fiber. Because the cellulose crystals are aligned within the fibril windings, the 002 reflection arising from the crystalline planes lying parallel to the fiber axis is spread out in the azimuthal arc. Tracing the intensity of the 002 reflection around the azimuthal angle, ψ, gives a curve like (Fig.2). The width of the 002 reflection spread out on the azimuthal represents fibril orientation of, primarily, the S2 layer of the tracheid cell wall. This width, T, can be evaluated by manually drawing the tangent to the 002 arc at its inflection points (Cave 1966; Meylan 1967; Preston 1974; Boyd 1977) (see Fig. 2). An automated method to determine T has been developed using double Gaussian curvefitting of the 002 arc (Stuart and Evans 1995). The T value can thereafter be used in the calculation of MfA (Cave 1966; Yamamoto *et al.* 1993).

Objectives

The aim of this study is to see how varying growth conditions influence mean MfA development of young Norway spruce *(Picea abies* [L.] Karst) trees. This was formalized into the three following objectives: To use Stuart and Evans' (1995) method to calculate mean MfA on earlywood of Norway spruce. To evaluate machine precision and human factor variability when determining mean MfA of Norway spruce using X-ray diffraction. To provide a regression of the development of mean MfA on growth conditions over time.

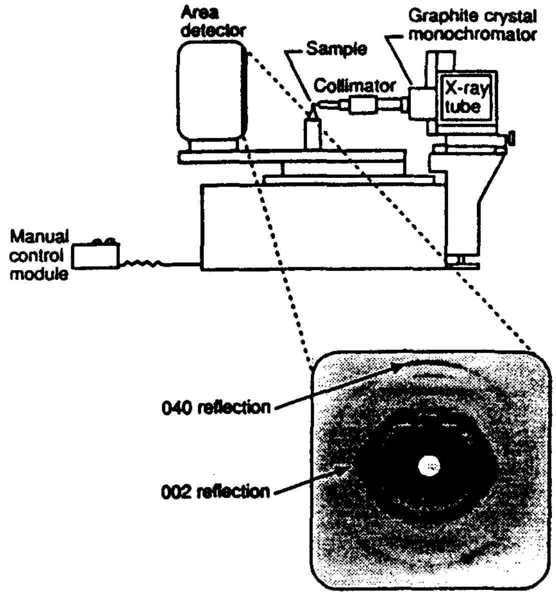

Fig. 1. General principle of obtaining an X-ray diffraction pattern.

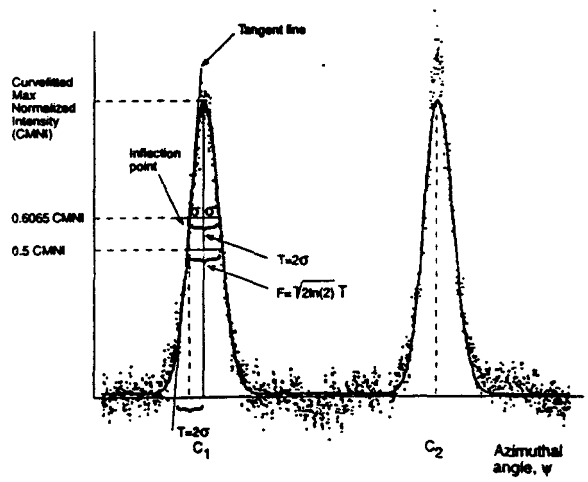

Fig. 2. Curvefitting of the X-ray diffraction intensity to use as a measurement of T.

Material and Methods

Plant material

The material, 54 Norway spruce trees planted as three-year old seedlings from the same seed source in 1957 and clearfelled in 1989, is described in three earlier studies (Lindström 1996a, 1996b, 1997). Briefly, the material represents 3 suppressed, 3 intermediate, and 3 dominant trees grown in 6 parcels of different site quality attained through fertilization, at the same geographical location (Tamm *et al.* 1974; Mead and Tamm 1988). Stern discs were taken out at breast height (1.3m) on each tree. In this study. those growth variables found to have a significant influence on wood structure development in two earlier studies (Lindström l996b, 1997) are investigated for their influence on MfA development.

Growth variables

Cambial age was recorded for each of the 646 growth rings. Daily variations in temperature and precipitation were recorded at a meteorological station of the Swedish Meteorological and Hydrological institute (SMHI), located in Falun approximately 40km southwest of the trial during 1961-1992 From 1986-1992, weather data were recorded at a meteorological station located in Vintjärn, approximately 10km south of the trial. Weather data from both locations were used to calculate an adjustment coefficient of the Falun data from 1961-1985. This adjustment coefficient was used to calculate the average temperature in Celsius for Jun-Aug at Vintjärn 1966-1989. Total precipitation in mm during Jun-Aug was recorded and adjusted similar to the temperature data from 1966-1989. Ring widths of the growth rings used as material for sample preparation were determined to the nearest 0.01 mm, using methods described by Kucera (1994). The site quality of each of the six parcels was regulated by the level of fertilization: unfertilized, moderately fertilized (N1P1), and heavily fertilized (N3P2) (Mead and Tamm 1988). Site quality was defined and measured in each parcel as total stem volume production per hectare, $m^3sk\ ha^{-1}$ (Eriksson 1976; Aronsson and Tamm 1991) (Table 1). The numbers of seedlings in 1966 within each parcel were recalculated to numbers of seedlings per hectare and used as a measurement of initial stand density. (Table 1). 3 suppressed, 3 intermediate, and 3 dominant trees were sampled based on relative diameter within each parcel and given a numerical code as a sign of tree class; 1 = suppressed, 2 = intermediate, 3 = dominant (Table 1). All parcels were subjected to thinning in 1982; in addition. four of the six stands were thinned in 1988. Only the thinning procedure of 1982 was included in the model because 1989 was the last vegetation period before clearfelling, which gave the thinning for 1988a very limited tree growth response (Aronsson and Tamm 1994) Thus, in the SAS model. the variable 0 was used before 1982 and 1 after 1982.

Sample preparation

In this study, early wood samples were taken from cores that had been air-dried for more than 2 years, thereby minimizing MfA variation caused by varying moisture content (Boyd 1977). A Carl Zeiss stereoscope and a razor blade were used to split the core sections into 646 early wood samples representing every second growth ring outward from the pith (2,4,6,8,..,n). The stereoscope allowed for distinguishing individual tracheids, and thus the boundaries between the early- and late wood zones

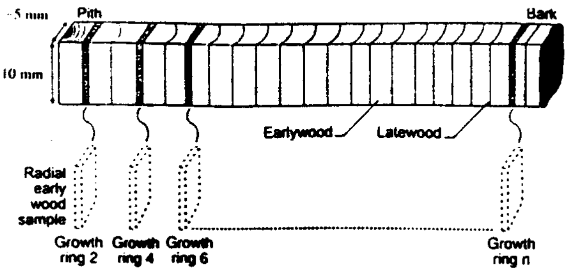

Fig. 3. Earlywood sample sectioning, from pith outwards.

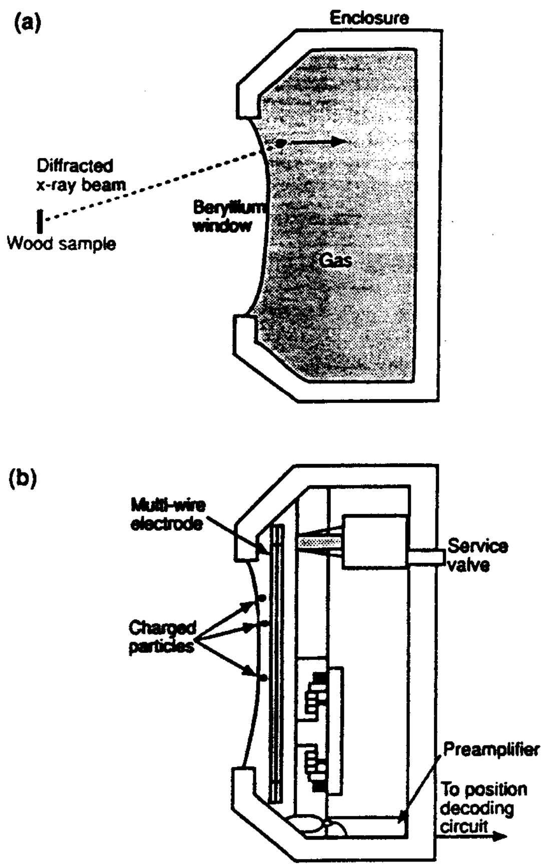

Fig. 4. Principle of the two dimensional area detector.

Table 1. Stand characteristics of each parcel

Parcel	Treatment[a]	Site quality ($m^3sk\ ha^{-1}$)[b]	Initial stand density (Number of seedlings ha^{-1})	Average diameter[c] suppressed tree class (mm)	Average diameter[c] intermediate tree class (mm)	Average diameter[c] dominant tree class (mm)
P34	Unfertilized	39.5	2525	59	84	114
P51	Unfertilized	87.2	1750	71	126	177
P10	N1P1	218.8	3025	114	153	178
P36	N1P1	249.5	2775	100	160	195
P18	N3P2	321.3	2625	131	200	244
P41	N3P2	227.5	2625	130	184	213

[a] Unfertilized, N1P1, and N3P2 corresponds with three levels of fertilization: none, intermediate, and heavy (Mead and Tamm 1988). [b]$m^3sk\ ha^{-1}$ is total bole volume above stump height per hectar (Eriksson 1976). [c]Based on diameter close to breastheight (1.3m) outside bark, at the time of clearcutting.

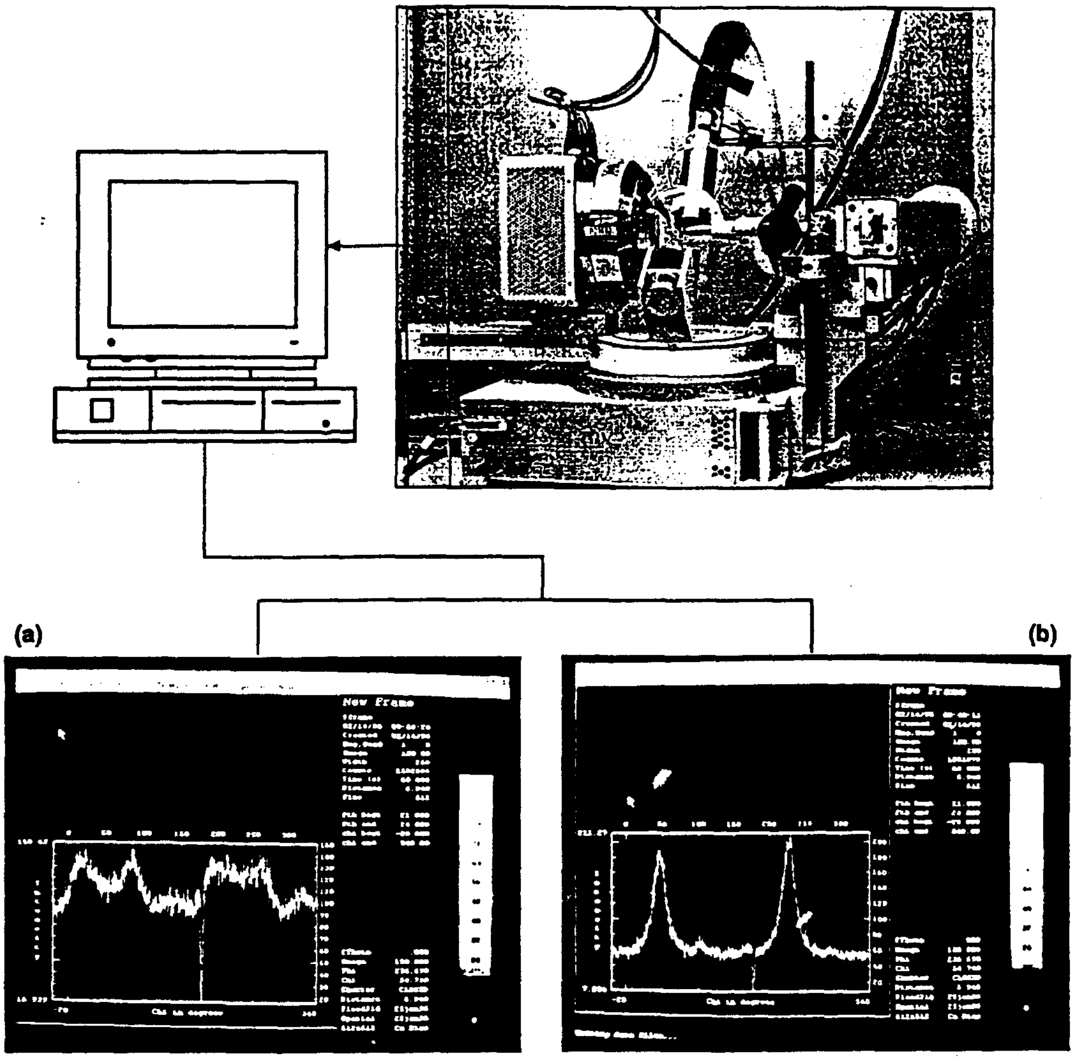

Fig. 5. Plots of intensity over azimuthal angle, as they appear on the PC monitor for two of the determined wood samples, taken from a tree, representing growth ring 2 (a) and 22 (b).

(Mork 1928; Denne 1989) To permit faster early wood sample preparation, the following 3 criteria were used: Sample thickness should be up to of the total growth ring width. Resin ducts were used as a sign of the transition zone into late wood formation. Close to pith, where growth rings are very curved. sample size was limited to avoid inclusion of latewood. Following these criteria gave early wood samples of approx. 10mm height. 5mm width, and appr. 0.5-2.5mm thickness (Fig.3).

X-ray measurements

A Siemens X-ray scattering system, including a Kristalloflex® 710D X-ray generator equipped with a 3.0kW sealed X-ray tube. a two-dimensional Siemens HI-STAR Area detector system and Siemens General Area Detector Diffraction Software (GADDS) version 3.310 for Windows NT. was used in the X-ray measurements. Each wood sample was mounted on the goniometer head with a sample clip holder, holding the wood sample perpendicular to the incident X-ray beam. which passed through in the radial direction near the center of the sample. The experimental conditions were: CuKa (λ = 1.54 Å). 40kV, 20mA, 0.5 mm aperture of incident beam collimator. 60 or 120 seconds exposure time, dependent on sample thickness. The diffracted X-ray beams pass through a beryllium window of the area detector. which holds xenon gas under appr. 4 bar pressure. individual xenon atoms in the enclosure are ionized by incident X-rays. producing a shower of charged particles each time an X-ray passes through the gas. Charged particles are then electrically attracted to a multi wire electrode assembly in the detector. This generates electrical signals indicative of the original xy position of the original X-ray (Fig. 4). The intensity of the complete diffractogram was recorded digitally on a personal computer, where the GADDS program was used to integrate intensity over azimuthal angle with a 0.1 ° resolution of the diffractogram's two 002 arcs (Fig. 5). For every early wood sample (n = 646) a data tile. approx. 44-45kB in size was generated including an intensity value (y-value) and a corresponding azimuthal angle (x-value), to be used in the calculations of MfA. In the altempt to estimate measurement precision with the X-ray scattering system, an early wood sample prepared from growth ring 14, representing an intermediate tree, was subjected to 24 subsequent irradiations and data acquisitions at identical sample position. In addition, the combined effect of machine precision

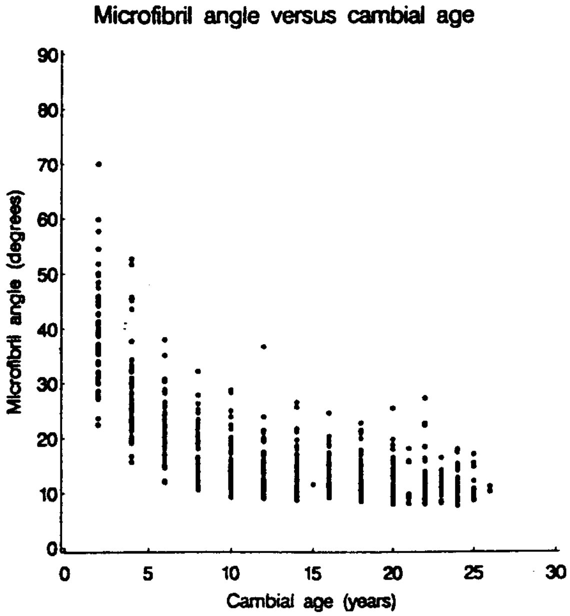

Fig. 6. MfA development.

and human factor standard deviation was estimated by using early wood samples of growth rings 2, 6, 10, 14, 18, and 22 from the same tree. Every sample was removed and remounted for 12 subsequent irradiations with corresponding data aquisition.

Calculation of T *by curvefitting*

Following the methods to calculate T (Cave 1966) as an indicator of MfA, Pakkaari and Serimma (1984) used curve fitting to calculate T. This method was developed by Stuart and Evans (1995). who noted that an individual xy datafile containing intensity and corresponding azimuthal angle. could be fit to a double Gaussian curve, using the equation,

$$y = B + I\left[\exp\left(\frac{-4\ln(2)(x-C_1)^2}{F^2}\right) + \exp\left(\frac{-4\ln(2)(x-C_2)^2}{F^2}\right)\right] \quad (1)$$

where B is the constant background, C_1 and C_2 are the means of the two Gaussians, and F is the full width at half maximum of I (Fig.2). The inflection points of the Gaussians are given by

$$C_i \pm \left(\frac{F}{2\sqrt{2\ln 2}}\right) = C_i \pm \sigma \quad (2)$$

where σ is the standard deviation of the Gaussians. It can be shown that the tangent line to the Gaussian at the $x = C_1 - \sigma$ inflection point intersects the background line at $x = C_1 - 2\sigma$ (Fig.2).

Thus T is taken to equal $2\sigma = 2\left(\frac{F}{2\sqrt{2\ln(2)}}\right)$ which is equal to the full width

of the curve at approx. 0.6065 of maximum curve height. F, the full width of the curve at half maximum curve height, can be related to T as $F = \sqrt{21n(2)}T = 1.1774T$ (Fig. 2). The value T was calculated using a peak fit program developed by Dr. Steve Verrill. A' public domain version of this program can be obtained by contacting Dr. Verrill at steve@ws10.fpl.fs.fed.us.

Calculation of MfA

To calculate a value for MfA, both Meylan's (1967) linear relationship,

$$\text{Mfa} = 0.6T \quad (3)$$

and the polynomial relationship of Yamamoto *et al.* (1993).

$$\text{Mfa} = 1.575 \times 10^{-3}T^3 - 1.431 \times 10^{-1}T^2 + 4.693T - 36.19 \quad (4)$$

were used.

Statistical interpretation

The calculated value of MfA was used in the statistical analysis of the influence of growth condition variables,

$$Y = \sum_{i=0}^{n} b_i x_i + \varepsilon_i \quad (5)$$

where Y = MfA, and x_i = growth condition variables.

Version 6.09 of the SAS package (SAS Institute, 1994) was used to fit (5) to the data. The untransformed values were used in the statistical calculations of machine precision and human factor error.

Results

Calculation of MfA

In this study the polynomial relationship of Yamamoto *et al.* (1993) produced unrealistic values of MfA (400° < = MfA) when the T values were derived from some samples of the second growth rings (approx. 95°-105°). This suggests that

Table 2. MfA dependence on growth variables[a]

Regression equation		r^2	b_{i-n}	sb_{i-n}	x_{i-n}
(1 a)	(MfA)	0.69	9.643772***	0.306053	Intercept
			63.193414***	1.677941	1 / *Cambial age*
(1 b)	(MfA)	0.73	48.343796***	1.100280	Intercept
			0.693407***	0.095908	*Cambial age*
			−19.570391***	0.865067	Log *(Cambial age)*
			5.955801***	0.922171	1 / *Growth ring width*
			0.124931***	0.021307	*Growth ring width* * Cambial age
			−0.0000001***	0.00000000	*Initial stand density* * *(Site quality)*^{2} * *Tree class* 1

*, **, and ***, indicate p ≤ 0.05, p ≤ 0.01, and p ≤ 0.001, respectively (SAS Institute 1994). $^a m^3sk\ ha^{-1}$ is total bole volume above stump height produced per hectar.

Table 3. Variability, when measuring T, due to the combined effect of machine precision and human factor variability

Sample	Cambial age (i)	Mean (x)*	Standard deviation (σ)*	Coefficient of variation (%)*
a	2	89.3	4.16	4.66
b	6	43.4	2.09	4.81
c	10	17.4	0.39	2.27
d	14	16.5	0.50	3.03
e	18	16.9	0.31	1.81
f	22	14.2	0.33	2.31

*** Based on that sample a-f, with cambial age *i*, was removed and remounted for 12 subsequent irradiations with corresponding data acquisition.**

even if equation (4) is more accurate than equation (3) when 0° < = T < = 55° (Yamamoto *et al.* 1993). outside this range equation (3) should be used. Therefore, values derived by equation (3) are used in this study. In the statistical evaluation of the dependence of MfA on growth conditions with equation (5) the main factor affecting development was found to be cambial age (Fig. 6). Besides the dominant main effect, cambial age, several interaction effects of growth ring width, cambial age, site quality, initial stand density, and tree class could be seen. Correlation, statistical significance, and values of for the model are in Table 2.

Machine precision and human factor variability

The mean T of the 24 subsequent measurements of the early wood sample prepared from a growth ring with cambial age 14 was 17.3°. The standard deviation of these measurements was 0.159. This yields a coefficient of variation estimate of 0.9%. The combined effect of machine precision and human factor standard deviation was estimated by using early wood samples of growth rings 2, 6, 10, 14, 18, and 22 from the same tree (Table 3).

Discussion

Accuracy and time consumption of MfA measurements

The machine precision seems to be satisfactory as the coefficient of variation here was found to be less than 1%. The combined effect of machine precision and human factor variability was higher close to pith than the one found in growth rings further out from pith indicating that sample positioning will be important close to pith. This result could be due to the fact that growth rings are more curved close to pith, and many contain local compression wood, meaning that more wood variation will be found, making sample positioning more crucial. Nevertheless, combining the effect of human factor and machine precision variability based on these measurements yield a coefficient of variation of less than 5%, a result that indicate that the method is accurate. However, it was found that double Gaussian curvefitting was difficult on data arising from samples prepared from growth ring number 2. Similar results were obtained by Stuart and Evans (1995). Evans (1996). At a recent workshop on microfibril angle (Anon. 1997) several researchers claimed that as long as there is a good tit on the width of the diffractions, which there is in this study, the derived T values will become accurate. As a method, X-ray diffraction with an area detector, will save much time when obtaining MfA compared with microscopy techniques. In this study the direct data acquisition of an individual sample was close to the values obtained by Stuart and Evans (1995) (ie. approx. 3 minutes). Additional time is required for curvefitting and calculation of MfA. However, this second step is automated. which implies that no extra time would be necessary if the curvefitting program was included already at the time of data acquisition. The method is probably also more reliable, as each sample provides averages based on approx. 500-2000 tracheids. compared with maybe 3-10 observed tracheids per wood sample when microscopy methods are used.

Found relationship between MfA and growth conditions

It has been assumed that the changing MfA has a functional purpose in conifer tree growth. For instance, it is argued that MfA indicates an adaption of the cell wall ultrastructure to genetic and growth factors that together create a tree stem that is able to withstand mechanical strain (Wilson and Archer 1979; Boyd 1985a; Niklas 1992). MfA can here be seen as a composite function of an age dependent genetic pattern (long term influence), a gradual age dependent shift in growth conditions (long term influence), and a yearly variation in growth conditions (short term influence). It can be assumed that the age dependent decrease in MfA found in this study indicates a functional shift from the flexibility of a young shoot/stem to the greater rigidity of an older tree stem. It is also possible that high MfA found in the first growth rings might reflect a formation of compression wood that quickly will reorient an offset shoot or young stem to a vertical position (Boyd and Foster 1974; Timell 1986; Okuyama *et al.* 1994). In the statistical evaluation it was found that the inversed value of cambial age explained about 70% of the variation in MfA. When factors related to growth conditions were added to the model. through stepwise regression, only a slightly higher correlation was seen. This result has to be seen in the perspective that there are difficulties to separate causative factors. in terms of genetics and growth conditions. That is. cambial age of the growth rings will mirror both the gradual shift in growth physiology caused by environmental changes and a predetermined genetic component. Based on this study it can only be said that cambial age of a growth ring seem to be a major determinant of MfA in *Picea abies.*

Possibilities to control MfA through silviculture

To avoid undesirable effects caused by large MfA on forest products, it would be beneficial to use a silvicultural strategy to produce wood with small MfA. Based on the results from this study, where an age dependent relationship was seen. such a silvicultural strategy would include a limitation of juvenile diameter growth. This type of silviculture would reduce the volume of wood that has high MfA, in addition to other undesirable juvenile characteristics produced in growth rings near pith of a conifer tree (Kyrkjeeide 1990; Kennedy 1995). In addition. a reduction of juvenile tree growth rate will most likely increase the ratio between saw-log volume to pulpwood volume, a factor of importance as wood in the form of sawlogs has a higher value than pulp Wood.

Conclusions

It was possible, after a slight modification, to apply the method to determine MfA described by Stuart and Evans (1995). Coefficient of variability due to the combined effects of machine variability and human factor variability is taken to be approximately 5%. MfA was found inversely correlated with cambial age for Norway spruce (*Picea abies* [L.] Karst.). Other variables that mirror growth conditions were also found significant, although they did not add much to the model accuracy. So, to avoid the undesired effects associated with large MfA, juvenile diameter growth of Norway spruce should be restricted.

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