The effects of thinning and fertilisation on wood and tracheid properties of Norway spruce (*Picea abies*) – the results of long-term experiments

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Academic dissertation

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ABSTRACT

The aim of this thesis was to study the basic relationships between thinning and fertilisation, tree growth rate and wood properties of Norway spruce (*Picea abies* (L.) Karst.) throughout a stand rotation.

The material consisted of a total of 109 trees from both long-term thinning (Heinola, 61°10'N, 26°01'E; Punkaharju, 61°49'N, 29°19'E) and fertilisation-thinning experiments (Parikkala, 61°36'N, 29°22'E; Suonenjoki, 62°45'N, 27°00'E) in Finland. Wood properties, i.e., radial increment, wood density, latewood proportion, tracheid length, cell wall thickness and lumen diameter, as well as relative lignin content, were measured in detail from the pith to the bark, as well as from the stem base towards the stem apex.

Intensive thinning and fertilisation treatments of Norway spruce stands increased (8%–64%) the radial increment of studied trees at breast height (1.3 m). At the same time, a faster growth rate slightly decreased average wood density (2%–7%), tracheid length (0%–9%) and cell wall thickness (1%–17%). The faster growth resulted in only small changes (0%–9%) in lumen diameter and relative lignin content (1%–2%; lignin content was 25.4%–26%). However, the random variation in wood properties was large both between and within trees and annual rings.

The results of this thesis indicate that the prevailing thinning and fertilisation treatments of Norway spruce stands in Fennoscandia may significantly enhance the radial increment of individual trees, and cause only small or no detrimental changes in wood and tracheid properties.

Keywords: forest management, growth rate, lignin content, tracheid cross-sectional dimensions, tracheid length, wood density

ACKNOWLEDGEMENTS

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by five research articles. In the review, the articles are referred to by Roman numerals. The articles are reprinted with kind permission of the publishers.

I   Jaakkola, T., Mäkinen, H. & Saranpää, P. 2005. Wood density in Norway spruce: changes with thinning intensity and tree age. Canadian Journal of Forest Research 35(7): 1767–1778. doi: 10.1139/X05-118.

II   Jaakkola, T., Mäkinen, H. & Saranpää, P. 2006. Wood density of Norway spruce: Responses to timing and intensity of first commercial thinning and fertilisation. Forest Ecology and Management 237(1–3): 513–521. doi: 10.1016/j.foreco.2006.09.083.

III   Jyske, T., Mäkinen, H. & Saranpää, P. 2008. Wood density within Norway spruce stems. Silva Fennica. (In press) http://www.metla.fi/silvafennica/

IV   Jaakkola, T., Mäkinen, H., Sarén, M.-P. & Saranpää, P. 2005. Does thinning intensity affect the tracheid dimensions of Norway spruce? Canadian Journal of Forest Research 35(11): 2685–2697. doi: 10.1139/X05-182.

V   Jaakkola, T., Mäkinen, H. & Saranpää, P. 2007. Effects of thinning and fertilisation on tracheid dimensions and lignin content of Norway spruce. Holzforschung 61(3): 301–310. doi: 10.1515/HF.2007.059.

Tuula Jyske (formerly Jaakkola) is fully responsible for the summary part of this doctoral thesis. She was responsible for all the data analyses in papers **I** and **IV**; partial design of the sample selection, part of the measurements, and all the data analyses in **II**, **III** and **V**, and she was the main author of all the papers.

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ABBREVIATIONS

Abbreviation	Unit	Scientific explanation
AR(1)		Autoregressive covariance structure
a.s.l.	m	Above sea level
AVI	$m^3ha^{-1}y^{-1}$	Annual volume increment
BA	m^2/ha	Stand basal area
BAI	cm^2	Basal-area increment of an annual ring, or earlywood or latewood
BH	m	Breast height (1.3 m)
CV		Coefficient of variation
DBH	cm	Diameter at breast height (1.3 m)
d.d.	degree days	Temperature sum
DW	mg	Total dry weight of wood
ED	$g\ cm^{-3}$	Earlywood density at 12% moisture content
F_0		Unfertilised control treatment
F_1		Fertilisation treatment with nitrogen dosage of 150 kg N ha^{-1}
F_2		Fertilisation treatment with nitrogen dosage of 300 kg N ha^{-1}
H_{100}	m	Dominant height at the age of 100 year
ha	10 000 m^2	Hectare
LD	$g\ cm^{-3}$	Latewood density at 12% moisture content
ld	µm	Tracheid lumen diameter in radial direction
LW%	%	Latewood proportion
MC	%	Moisture content
MOE	GPa	Modulus of elasticity
MOR	MPa	Modulus of rupture
NPK		Nitrogen (N), phosphorus oxide (P_2O_5), potassium oxide (K_2O)
OMT		*Oxalis-Myrtillus* forest site type, which corresponds to fertile sites typical for Norway spruce
RD	$g\ cm^{-3}$	Average wood density of individual annual rings at 12% moisture content, cf. WD
REML		Restricted maximum likelihood
TH	%	Relative tree height
RW	mm	Ring width
T_0		Delayed first commercial thinning
T_1		Normal first commercial thinning
T_2		Intensive first commercial thinning
TBA	cm^2	Tree basal area
TP		Transition point between earlywood and latewood within ring
WD	$g\ cm^{-3}$	Wood density at 12% moisture content, cf. RD
WS		Whole-stem
wt	µm	Double cell wall thickness of tracheid in radial direction (i.e., thickness of tangential cell wall)

1   INTRODUCTION

1.1   Motivation of the study

Norway spruce (*Picea abies* (L.) Karst.) is an evergreen coniferous tree species, native to the temperate and boreal regions of the Northern Hemisphere (Kramer and Green 1990). In Europe, Norway spruce grows naturally from Scandinavia to the Ural Mountains, and also in the mountains of central and southern Europe (Jalas and Suominen 1973).

Norway spruce has a major ecological and economic importance throughout northern Europe (Mather 1990). In Finland, 30% of the total growing stock volume comprises Norway spruce (Peltola and Ihalainen 2007). Norway spruce timber is mainly utilised in mechanical pulping, sawmilling, plywood and laminated veneer lumber (LVL) (Hakkila 1995, Ylitalo 2007).

Wood and tracheid properties determine the suitability of wood for a particular end-use. Wood properties result from the relative amounts of different cell types, as well as their properties (Chaffey 2000, Pereira et al. 2003). Wood formation is controlled both by environmental and genetic factors (e.g., Larson 1969, Olesen 1982, Megraw 1985, Lindström 1997, Savidge 2003). Silvicultural practices, such as thinning and fertilisation, can be used to modify the environmental factors controlling wood formation and properties. This thesis will study the basic relations between thinning and fertilisation, tree growth, and wood properties of Norway spruce grown in central and southern Finland during the entire stand rotation period.

1.2   Formation of wood

Wood (*secondary xylem*) is a secondary vascular tissue produced by *a vascular cambium* (herein referred to as *cambium*) (Philipson et al. 1971). Cambium is a lateral meristem derived from the *apical meristem* that induces primary (i.e., longitudinal) growth (Larson 1994). The cambial zone is located concentrically underneath the bark and consists of a thin layer of cells, i.e., cambial initials and undifferentiated derivatives arranged in radial files (Romberger et al. 1993, Larson 1994, Kitin et al. 2000). Wood production requires mitosis and cytokinesis in the cambium, and *xylogenesis*, a complex process of cellular development whereby thin-walled cambial cells mature into water-conducting tracheids with lignified secondary cell walls (Roberts and McCann 2000, Samuels et al. 2006).

The cambial cells differentiate inwardly into *secondary xylem* and outwardly into *secondary phloem* (Chaffey 1999). Vertically elongated *fusiform initials* give rise to axial (longitudinal) elongate elements of the xylem and phloem (Romberger et al. 1993). Approximately isodiametric *ray initials* divide to form ray parenchyma and ray tracheids that elongate radially (Romberger et al. 1993). In conifers, the ray initials are usually grouped together in short vertical rows, but the fusiform initials occur irregularly without any horizontal pattern (i.e., *nonstoried* cambium) (Mauseth 1998).

After cambial division, the derivative cells enter a zone of radial growth where they deposit *a primary cell wall* (P, Fig. 1) and expand mainly in radial diameter (Wilson 1963, Samuels et al. 2006). The expansion is driven by turgor pressure (Kozlowski et al. 1991, Taiz and Zeiger 1991) and is determined by cell wall plasticity (Mellerowicz 2006). Just before the cessation of the expansion, *a secondary cell wall* (S, Fig. 1) deposition begins on the
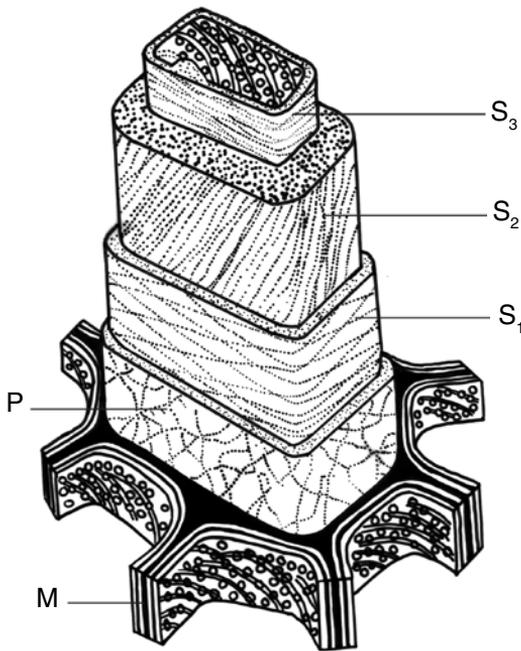
Figure 1. Schematic presentation of the cell wall layers of a tracheid. ML, middle lamella; P, primary cell wall; S_1, S_2 and S_3, layers of secondary cell wall. The picture is redrawn from Côté (1967).

inner surface of the primary wall (Abe et al. 1997). The differentiating cells then enter the zone of maturation, where secondary cell wall thickening is completed and lignification and protoplast autolysis occur (Wodzicki 1971, Samuels et al. 2006).

The successive steps of xylogenesis are driven by the expression of various genes (e.g., Fukuda 2004, Nieminen et al. 2004, Carslbecker and Helariutta 2005, Klein and Tibbits 2006, Tuskan et al. 2006). Xylogenesis is also controlled by a range of extrinsic (e.g., temperature, photoperiod and precipitation) and intrinsic (phytohormones) factors and their interactions (e.g., Eschrich and Blechschmidt-Schneider 1992, Plomion et al. 2001, Fukuda 2004, Carlsbecker and Helariutta 2005, Bishopp et al. 2006). The knowledge of the cellular, molecular and developmental mechanisms behind xylogenesis is still fragmentary (Plomion et al. 2001, Nieminen et al. 2004, Samuels et al. 2006).

Longitudinal tracheids (referred to as fibres in the pulping industry) comprise 94% of Norway spruce wood (Petrić and Šćukanec 1973, Siau 1984). Radially oriented ray tracheids and ray parenchyma cells comprise the rest of Norway spruce wood (Petrić and Sćukanec 1973).

Coniferous tracheids are mainly responsible for structural support and water conduction from roots to leaves (Romberger et al. 1993, Barnett 2004). Nearly all of the tracheids in coniferous sapwood conduct water (Pittermann et al. 2006). Ray tracheids conduct water and nutrients radially, while ray parenchyma cells store water and food (Romberg et al. 1993, Barnett 2004). The water flow between the axial tracheids, as well as between axial tracheids and radial ray cells, occurs through bordered and half-bordered (i.e., cross-field pitting) pit pairs, respectively (Siau 1984). This torus-margo pitting of conifers is hydraulically superior (Pittermann et al. 2005).

The within-stem variation in tracheid dimensions is predominantly caused by the maturation of the cambium (Olesen 1977, 1978, 1982; Lindström 1997, Sirviö and Kärenlampi

2001b). The cambium is subject to two types of maturation processes: 1) the maturation of the apical meristem at the time of cambium formation (cyclophysis), and 2) the changes taking place in the cambium after its formation (Olesen 1978, 1982). Cambial maturity is primarily determined by the number of cambial cell divisions (Philipson and Butterfield 1967, Sirviö and Kärenlampi 2001b, Mäkinen et al. 2002a). The ageing of xylem along the three major axes of the tree is shown in Figure 2.

The juvenile–mature wood pattern is a systematic change in the anatomy, chemistry and properties of wood from the pith outwards (Gartner 2005). Juvenile wood is produced near the pith by a young cambium, whereas mature wood is produced farther from the pith by more mature cambium (Fig. 2; Larson 1994, Kučera 1994). In Norway spruce, approximately the first 10 annual rings from the pith represent juvenile wood and the rings formed thereafter are mature wood (Danborg 1994, Saranpää 1994, Saranpää et al. 2000). In juvenile wood, tracheids are generally shorter with thinner cell walls, smaller lumen diameters, higher MFA, lower strength, increased longitudinal shrinkage, and a lower cellulose to lignin ratio than in mature wood (Olesen 1977, Romberger et al. 1993, Saranpää et al. 2000, Burdon et al. 2004).

Tracheid dimensions are under moderate to strong genetic control (Khalil 1985, Rozenberg and Cahalan 1997, Hannrup et al. 2001, Larson et al. 2001, Hannrup et al. 2004). The genetic control changes with tree age (Hannrup et al. 2004, Cameron et al. 2005). It is high in the juvenile wood, whereas in the mature wood the environmental factors have a more marked effect on wood formation and tracheid microstructure (Lindström 1997).
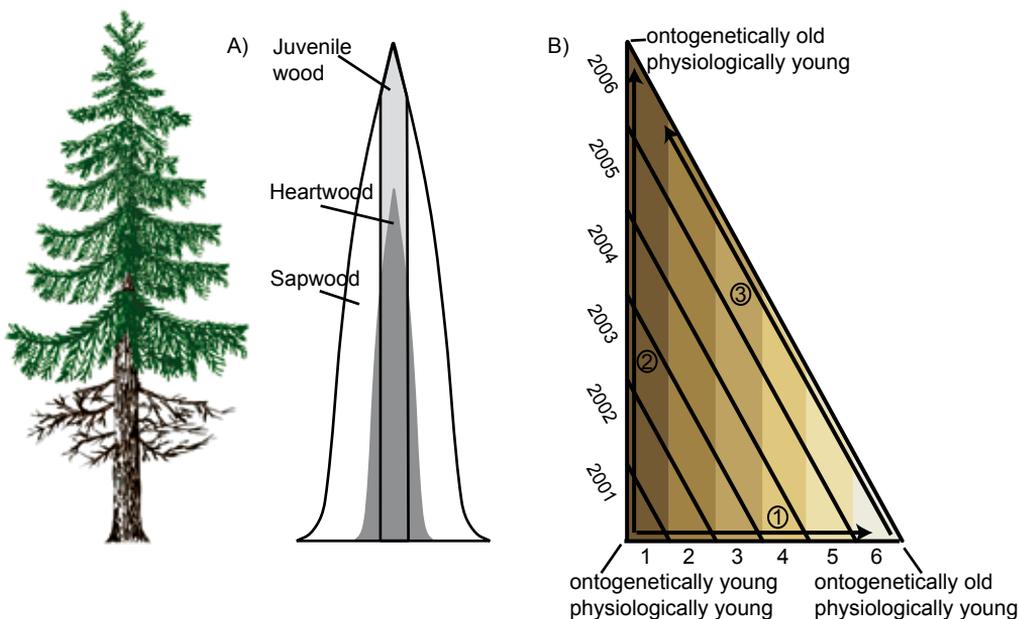
Figure 2. Juvenile wood, heartwood and sapwood in Norway spruce stem (A). Ageing of the xylem along the three major axes of the stem (B): radially from the pith to the bark (1), vertically from the stem base to the stem apex in a given annual ring from the pith (2), and concentrically around the given annual ring from the bark (3) (redrawn and modified from Duff and Nolan 1953, Schweingruber et al. 2006).

1.3 Cell wall chemistry

The Norway spruce stem wood consists of 48% α-cellulose, 21% hemicellulose and 29% lignin (Anttonen et al. 2002). The wood also contains small amounts of pectin, proteins (Westermark et al. 1986), and inorganic (Berglund et al. 1999) and extractive compounds (e.g., Sjöström 1993). Cellulose microfibrils form the structurally strong framework of the cell wall (Fengel 1969). This framework is embedded with matrix polymers – hemicelluloses and pectins – and encrusted with lignin.

Cellulose provides high tensile strength for the cell wall. Cellulose is a linear polymer chain of β-D-glucose molecules linked together by β-(1 – 4) glycosidic bonds (Saxena and Brown 2005). Two bonded glucose molecules form an anhydroglucose unit. The pair of units is called cellobiose, the repeating chemical entity of the cellulose polymer (Brown et al. 1996). Several chains of cellulose are linked by hydrogen bonding and Van der Waals forces to form microfibrils, which include both crystalline and amorphous cellulose (Cousins and Brown 1995). Microfibrils are further combined to larger fibrils and lamellae.

Hemicelluloses are heteropolysaccharides that comprise various types of sugar units (Sjöström 1993). They are usually amorphous, branched-chain polymers that form a link between cellulose and lignin (Page 1976). Hemicelluloses permeate water and thus provide flexibility and support in the cell wall. Galactoglucomannans and xylans are the main hemicelluloses in conifers (Pereira et al. 2003).

Lignin is a complex, aromatic polymer of phenylpropane units (Fengel 1976). In Norway spruce, lignin is mainly composed of guaiacylpropane units (G-lignin) derived from coniferyl alcohol, which is the main lignin precursor of conifers (Pereira et al. 2003). Lignin occurs both between and within the cell walls. Between the walls, it binds the adjacent cells together. Within the walls, lignin combines cellulose and hemicellulose and gives rigidity and compression strength to the cell (Pereira et al. 2003). Lignin is almost insoluble and hydrophobic. Thus, lignin reduces the permeability of cell walls and improves the water conduction efficiency of the tracheids (Romberger et al. 1993). Since lignin is difficult to degrade, it serves as a physical barrier against pathogens (Zabel and Morrell 1992). As expressed in chemical energy, lignin exceeds cellulose in a conifer stem (Savidge 2000a). Aromatic monomers in lignin have higher bond energies than aliphatic bonds in cellobiose, and thus a mass unit of lignin yields ca. 43% more heat from combustion energy than an equal mass unit of cellulose (Savidge 2000a).

1.4 Ultrastructure of cell walls

The cell wall of the coniferous tracheid is divided into an amorphous *middle lamella* (M), a thin primary wall and a multi-layered secondary wall comprised of a thin S_1 *layer*, a thick S_2 *layer*, and a thin S_3 *layer* (Fig. 1; Kerr and Bailey 1934). The layers differ in both chemical composition and microfibril orientation (Butterfield 2003, Pereira et al. 2003, Abe and Funada 2005).

Middle lamella is situated between the cells binding them together. During cell expansion, M is mainly based on pectins, but becomes highly lignified later. The middle lamella is difficult to distinguish from the primary cell wall. Thus, the M with the primary cell wall on both sides is referred to as a *compound middle lamella* (CM). The CM of the spruce tracheid contains ca. 60% lignin, 14% cellulose, and 27% hemicellulose (Fengel 1976). It is only 0.2–1.2 µm in width, and 20%–25% of the total lignin in wood is located in the CM. The primary cell wall

is the thinnest layer (0.1–0.2 μm; Timell 1965). It contains the loose network of microfibrils that have a varying microfibril angle (MFA), i.e., the angle between the cellulose microfibril orientation and the longitudinal axis of the cell (Timell 1965, Butterfield 2003, Barnett and Bonham 2004, Abe and Funada 2005).

The S_1 layer of the secondary cell wall is about 0.2–0.3 μm in width, with 3–4 lamellae (Klein and Tibbits 2006). The microfibrils in the S_1 layer form either an S- or Z-helix having an MFA of 50°–75° from the longitudinal axis of the cell (Walker 1993a, Abe and Funada 2005). The S_1 layer contains about 29% lignin, 36% cellulose, and 36% hemicellulose (Fengel 1976).

The dominating cell wall layer is the S_2 layer. It is 1–5μm in width, with up to 150 lamellae (Klein and Tibbits 2006). In the S_2 layer, microfibrils form the Z-helix and have an MFA of 10°–30° from the longitudinal axis of the cell (Walker 1993a, Abe and Funada 2005). The S_2 layer contains ca. 27% lignin, 58% cellulose, and 15% hemicellulose (Fengel 1976). Because the S_2 layer accounts for 80%–90% of the wood mass in the cell wall, over 70% of the total lignin in the wood is located in the S_2 layer (Sjöström 1993).

The S_3 layer is thin, only about 0.1 μm (Walker 1993a). It contains 27% lignin, 58% cellulose, and 15% hemicellulose (Fengel 1976). Microfibrils are oriented in the S-helix having an MFA of 60°–90° from the longitudinal axis of the cell (Panshin and de Zeeuw 1980, Walker 1993a).

1.5 Microstructure of Norway spruce tracheids

1.5.1 Tracheid length

Tracheid length varies both between and within Norway spruce trees (e.g., Dinwoodie 1961, Sirviö and Kärenlampi 2000, Mäkinen et al. 2002a). Within a tree, the average tracheid length normally varies from 1 to 5 mm (e.g., Helander 1933, Atmer and Thörnqvist 1982, Molteberg and Høibø 2006). Tracheid length is related to the radial and vertical location in the stem, as well as the growth rate of the tree (e.g., Sanio 1872, Bailey and Shepard 1915, Dinwoodie 1961).

In the cambial zone, the *periclinal* (i.e., parallel to the tangential plane of the stem), longitudinal divisions of fusiform initials produce tracheids in radial files, thus increasing the stem diameter (Romberger et al. 1993, Larson 1994). The tracheids are essentially the same length as the cambial initials, on average 3.3 mm in length (Bailey 1923), from which they are derived, since the elongation during tracheid differentiation and maturation is limited (Bailey 1920, Savidge 2003). In Bailey's studies (1920), Norway spruce tracheids were only 9% longer than the fusiform initials.

As the tree grows in diameter, the *pseudotransverse*, anticlinal (parallel to the radial plane of the stem surface) divisions of fusiform initials maintain the continuous circumferential growth of the cambium (Bailey 1923). Each anticlinal division generates two short initials. They elongate at their apices by intrusive growth and become as long as or longer than the original initials (Bailey 1923, Bannan 1968).

As the stem increases in diameter, the anticlinal activity of the cambium decreases, i.e., a larger tree needs a relatively smaller number of anticlinal divisions than a smaller tree in order to maintain the continuous growth of the cambium (Bailey 1923, Bannan 1950, Philipson and Butterfield 1967, Brändström 2001). Accordingly, tracheid length increases rapidly from the pith outwards, as reported by several authors (Helander 1933, Bisset et al. 1951, Dinwoodie

1961, Atmer and Thörnqvist 1982, Frimpong-Mensah 1987, Saranpää 1994, Lindström 1997, Herman et al. 1998a, Mäkinen et al. 2002a, Molteberg and Høibø 2006). The rate of increase levels off in mature wood, at about 20–50 mm from the pith (e.g., Philipson and Butterfield 1967, Fujiwara and Yang 2000, Mäkinen et al. 2002a). Also the variability in tracheid length increases from the pith outwards (Herman et al. 1998b).

Several authors have reported the negative relationship between ring width and tracheid length for many conifers (e.g., Lee and Smith 1916, Helander 1933, Frimpong-Mensah 1987, Dutilleul et al. 1998, Herman et al. 1998ab, Sirviö and Kärenlampi 2001a, Mäkinen et al. 2002a). A wide annual ring is possibly associated with the high rate of anticlinal divisions and is therefore correlated with shorter cambial initials and tracheids (Bisset et al. 1951, Bannan 1963, 1967). In the wide ring, the anticlinal divisions may also occur earlier in the growing season than in the narrow ring (Bannan 1963, 1965, 1967, 1968).

The average tracheid length in narrow rings exceeds that in a single wide ring having the same total width (Bannan 1965). This is probably due to the longer period of time involved in the production of several narrow rings compared to the single wide ring, i.e., the duration of cell elongation during the tracheid differentiation is longer in narrow rings (Bannan 1965).

Even if the constant ring width is maintained, the relative growth rate of stem circumference decreases with the increasing stem diameter. Fujiwara and Yang (2000) found a negative relationship between the circumferential growth rate and tracheid length for several conifers. When discussing the effect of growth rate on tracheid length, the circumferential growth rate or the distance from the pith should therefore be considered (Fujiwara and Yang 2000, Brändström 2001).

The axial variation of tracheid length in the stem is generally less than that in the radial direction. Tracheid length in a given annual ring from the pith first increases from the stem base towards the stem apex until the maximum tracheid length is reached at the relative height of about 30%–50% in the stem (Helander 1933, Dinwoodie 1961, Atmer and Thörnqvist 1982, Kučera 1994, Molteberg and Høibø 2006). Thereafter, the tracheid length decreases with the increasing height in the stem (Atmer and Thörnqvist 1982, Saranpää 1994). In juvenile wood, however, the axial variation in tracheid length is less apparent (Saranpää 1994).

Generally, the latewood tracheids are considered to be longer than earlywood tracheids (e.g., Helander 1933, Dinwoodie 1961, Kennedy 1966, Fujiwara and Yang 2000, Mäkinen et al. 2002a). According to Mork (1928), Kennedy (1966) and Mäkinen et al. (2002a), the latewood tracheids of Norway spruce were on average 11%–15% longer than earlywood tracheids. In a recent study, however, neither a significant difference between early- and latewood nor a systematic trend in tracheid length from early- to latewood in Norway spruce was found (Mäkinen et al. 2008). The within-ring variation in tracheid length is possibly related to fluctuations of favourable and unfavourable weather conditions during the growing season. The rate of pseudotransverse, anticlinal divisions and the amount of cell elongation during the tracheid differentiation most likely affect the variation pattern of tracheid length within annual rings (Bisset and Dadswell 1950, Bannan 1965, Mäkinen et al. 2008).

1.5.2 Cross-sectional dimensions of tracheids

The variation in cross-sectional (transverse) dimensions of Norway spruce tracheids, i.e., tracheid and/or lumen diameter and cell wall thickness, has been studied less than the variation in tracheid length (Atmer and Thörnqvist 1982, Tyrväinen 1995). Similar to tracheid length, the dimensions of Norway spruce tracheids vary both between and within stems and annual rings depending on the radial and axial position in the stem, and tree growth rate.

Cell wall thickness and the perimeter of single Norway spruce tracheids are the largest in the middle of the tracheid while the rate of change is greatest in the vicinity of the tracheid tip (Sirviö 2001). The coefficients of variation of cell wall thickness and perimeter in the tracheids are 0.1–0.3, and they are independent of cambium maturity and the mean value of the property in question (Sirviö 2001). Tracheids are also symmetrical relative to their middle point, and this symmetry is not affected by the maturation of the cambium (Sirviö 2001).

Generally, the tracheid diameter increases from the pith outwards, but the rate of increase declines in mature wood (Olesen 1977, Atmer and Thörnqvist 1982, Romberger et al. 1993, Kučera 1994, Saranpää et al. 2000, Mäkinen et al. 2002a, Burdon et al. 2004, Molteberg and Høibø 2006). Olesen (1977) found that the tangential tracheid diameter was about 15 μm near the pith and increased to about 30–40 μm in the outer sapwood. The thickness of cell wall also increases from the pith outwards, but the rate of increase levels off towards the cambium (e.g., Panshin and de Zeeuw 1980, Mäkinen et al. 2002a).

Tracheid and lumen diameter have been shown to be positively related to annual ring width (Ollinmaa 1959, Denne 1973, Atmer and Thörnqvist 1982, Saranpää et al. 2000, Mäkinen et al. 2002a, Lundgren 2004a) and the rate of shoot elongation (Denne 1973). In contrast, cell wall thickness usually decreases with increased ring width (Mäkinen et al. 2002a, Lundgren 2004a). Contradictory results have, however, been reported on the relationship between ring width and tracheid dimensions (Brix and Mitchell 1980, Koga et al. 1997, Bergqvist et al. 2000).

The axial variation in tracheid dimensions has not been widely studied and the results are contradictory. Tracheid diameter and cell wall thickness tend to decrease as height increases in the stem (Mork 1928, Atmer and Thörnqvist 1982, Mäkinen et al. 2002a). The differences in tracheid dimensions among the different stem heights are, however, small (Mäkinen et al. 2002a). Furthermore, the decreasing trend of the tracheid dimensions towards the stem apex is possibly related to the radial variation in these dimensions (Tyrväinen 1995).

The largest variation in the tracheid dimensions of Norway spruce occurs within an annual ring between early- and latewood. In the spring, the cambium produces large diameter, earlywood tracheids that have thin cell walls. Towards the end of the growing season, the cambium produces latewood tracheids of smaller diameter and thicker cell walls. The transition from earlywood to latewood is rather gradual in Norway spruce (Butterfield 1993). The increase in cell wall thickness from earlywood to latewood is due to the increasing thickness of the S_2 layer, and to a lesser degree, due to the increasing thickness of the S_1 and S_3 layers (Fengel and Stoll 1973).

Latewood tracheids provide more mechanical support while earlywood tracheids perform most of the water conduction. In Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), earlywood tracheids had 11 times the water conductivity of latewood tracheids and about 90% of the water flow occurred through the earlywood (Domec and Gartner 2002).

Within an annual ring, the variation in tracheid dimensions is larger in the radial direction than in the tangential direction (Ollinmaa 1959, Fengel 1969, Tyrväinen 1995). The radial tracheid diameter decreases from about 40 μm in earlywood to about 13 μm in latewood (Fengel 1969). The tangential tracheid diameter is about 33 μm in earlywood and 32 μm in latewood (Fengel 1969). The radial cell wall thickness is about 2–4 μm in earlywood and 4–6 μm in latewood (Ollinmaa 1959, Fengel 1969). The tangential cell wall thickness increases from about 3 μm in earlywood to about 5 μm in latewood (Ollinmaa 1959).

1.5.3 Environmental control of tracheid dimensions

The tracheid dimensions are a result of the combined effects of factors that 1) affect the rate of cell production from the cambium and 2) determine the time period during which each differentiating tracheid will spend in a particular zone of tracheid differentiation (Dodd and Fox 1990, Uggla et al. 2001).

The rate of cambial division is adjusted to the demands of water transport required by the live crown and the support of the increasing weight of the tree (Zimmermann 1983, Romberger et al. 1993, Barnett 2004). Environmental factors (e.g., precipitation, temperature, photoperiod, nutrients and CO_2) interact to control the activity of the crown, e.g., leaf growth and photosynthesis, thus adjusting transpiration, carbohydrate allocation, phytohormone gradients (e.g., indole-3-acetic acid [IAA]) and, eventually, wood formation accordingly (e.g., Roberts 1988ab, Luxmoore et al. 1995, Teskey et al. 1995, Larcher 2003, Iivonen et al. 2006).

The apical growth is integrated with the cambial growth rate by the basipetal flow of IAA from apical shoots to roots (e.g., Jacobs 1952, Brown 1970, Tuominen et al. 1997, Uggla et al. 1998, Savidge 2000b, Aloni 2001). The radial concentration gradient of IAA acts as a positional signal to the differentiating tracheids. It determines the width of the zones of tracheid differentiation. In other words, it controls the duration of cell division, expansion and secondary wall formation and ultimately the anatomical characteristics of the xylem and, in turn, technological features of the wood (Uggla et al. 1996, Tuominen et al. 1997, Uggla et al. 1998, Savidge 2000b, Sundberg et al. 2000, Mellerowicz et al. 2001, Butterfield 2003). The sucrose gradient and hormones other than IAA have also been shown to control cambial growth by interacting with IAA in a synergetic (e.g., gibberellins, cytokinins, brassinosteroids and ethylene) or inhibitory (abscisic acid) manner (Plomion et al. 2001, Bishopp et al. 2006). The decreasing concentration gradients of IAA down the stem have been proposed to explain the variations in cambial growth and tracheid differentiation along the stem (Larson 1969, Aloni and Zimmermann 1983, Aloni 2001). However, not all studies have supported this assumption (Dodd and Fox 1990, Little and Pharis 1995, Uggla et al. 1998).

Different physiological processes regulate the consequent zones of tracheid differentiation (e.g., Larson 1969, Brown 1970, Antonova and Stasova 1997). The different zones may also react differently to the effects of various environmental factors (Antonova and Stasova 1997, Uggla et al. 2001).

The transition from earlywood to latewood (Fig. 3) is a result of a slower rate of cambial cell division, a shorter duration of cell radial expansion, a longer duration of secondary wall thickening, and a decrease in the cellulose to lignin ratio (Wodzicki 1971, Dodd and Fox 1990, Klein and Tibbits 2006, Rossi et al. 2006). The initiation of latewood formation and the cessation of leader growth have been found to occur around the same time (Larson 1969). This suggests that the increase in secondary wall thickening occurs when the requirements of the major metabolic sinks within the crown have been met and photosynthates are transported primarily to the stem (Larson 1969). However, Renninger et al. (2006) demonstrated that in Douglas fir saplings growing in the Pacific Northwest, the cessation of leader growth is not a cause for latewood formation, but both phenomena are possibly correlated with the same environmental cues independently of one another.

Earlywood 1991   Latewood   Earlywood
                                                                                                      1991   1992
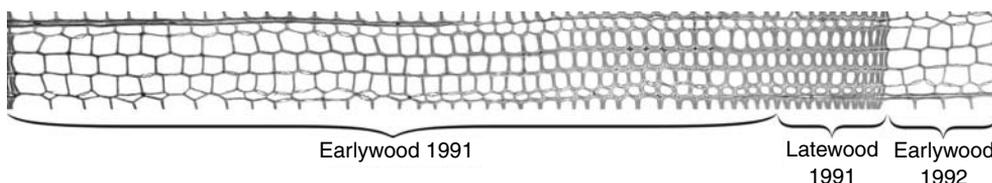
Figure 3. A cross-section of Norway spruce wood in a 57-year old stem in Punkaharju in south-eastern Finland, high magnification (x 400). Growth rings were formed in 1991 and 1992 (only the first cells formed in spring). Transition from earlywood to latewood is gradual and determined here according to Mork's definition (Mork 1928, Denne 1989).

For boreal and high-altitude conifer species, daily temperature and temperature sum are important factors affecting tracheid production (Leikola 1969, Antonova and Stasova 1993, 1997; Antonova et al. 1995, Vaganov et al. 1999, Mäkinen et al. 2000, 2003; Deslauriers et al. 2003, Schmitt et al. 2004, Deslauriers and Morin 2005). Cambial activity and radial growth begins in May and concludes in August in the boreal zone or in September or October in the southern high-altitude sites (Deslauriers et al. 2003, Mäkinen et al. 2003, Schmitt et al. 2004, Gričar et al. 2005, Rossi et al. 2006). Temperature controls the post-winter recovery of photosynthetic capacity, thus affecting the growing-season length (Bergh et al. 1998, Vaganov et al. 1999, Jarvis and Linder 2000, Suni et al. 2003). The prolongation of the growing season in response to elevated temperature (Peltola et al. 2002) has increased the radial growth of juvenile Scots pine (*Pinus sylvestris* L.) stems in Finland (Leikola 1969, Peltola et al. 2002, Kilpeläinen et al. 2003, 2005).

Antonova and Stasova (1997) showed that in central Siberia air temperature affected all the zones of cytogenesis (i.e., the formation, development and variation of cells) of larch (*Larix sibirica* Ledeb.), but the optimum temperatures varied between the different zones of cytogenesis. In Scots pine growing in central Siberia, temperature had the main influence on secondary wall formation while precipitation was the main factor affecting cambial divisions and cell expansion (Antonova and Stasova 1993). Cregg et al. (1988) found that in Oklahoma (south-central USA) higher temperatures increased the cambial growth of loblolly pine (*Pinus taeda*) early in the growing season, but limited the growth towards the end of the growing season.

Mäkinen et al. (2003) suggested that the fastest annual growth rate of Norway spruce in southern Finland was regulated by temperature: the most rapid xylem formation occurred during the first 10 days of July, corresponding to the highest temperatures measured during the year. However, Rossi et al. (2006) observed that the highest rate of cell production of the main conifer species of the Northern Hemisphere (genera *Picea*, *Pinus*, *Abies*, and *Larix* from high-altitude forests in Italy and boreal forest in Canada) did not occur during the warmest period of year, but around the time of maximum day length, i.e., summer solstice on the 21st of June. They proposed that maximum photoperiod acts as a growth constraint after which the rate of tree-ring formation decreases, thus allowing trees to safely complete the tracheid differentiation before winter (Gindl et al. 2000, Gričar et al. 2005, Rossi et al. 2006).

Consequently, photoperiod is related to the initiation of latewood formation (Creber and Chaloner 1984). Larson (1969) found that a shorter photoperiod stopped needle elongation and slowed down the rate of cambial divisions, and initiated the formation of latewood-type tracheids in young red pines (*Pinus resinosa*) in the northern temperate zone. Accordingly,

when red pines growing under long days were exposed to short days, they produced false rings with latewood type tracheids corresponding to the shorter photoperiod (Larson 1962).

Precipitation and water deficit also have an impact on the growing-season length, wood formation, and latewood transition (Larson 1969, Brix 1972, Cregg et al. 1988, Antonova and Stasova 1997, Horacek et al. 1999). Generally, water deficit has more influence on cell expansion than on cell division (Kozlowski et al. 1991). In the studies of Douglas fir in the Pacific Northwest, water deficit decreased the total amount of wood produced and resulted in latewood formation (Brix 1972). In northern Europe, however, precipitation has been shown to have less effect on radial growth of conifers than temperature (Henttonen 1984, Mäkinen et al. 2000).

1.6 Wood density of Norway spruce, its variation and determinants

1.6.1 Determination of wood density

Wood density is a measure of the mass of wood substance per given unit volume (Saranpää 2003). *Basic density* is determined as oven-dry (0% moisture content; MC) mass per unit volume of green wood (kg m^{-3}; g cm^{-3}) (Saranpää 2003). *Weight density* is also defined as mass per unit volume of wood, but both the mass and volume are measured at the same moisture content, e.g., at 12% MC (Saranpää 2003). *Specific gravity* is the ratio of the weight of the wood substance to the weight of an equal volume of water at 4°C (Saranpää 2003). Since the density of water is ca. 1 g cm^{-3}, the specific gravity of wood equals numerically its density (Saranpää 2003). Specific gravity is based on oven-dry mass. The volume can be measured at any MC but it must be specified (Saranpää 2003).

Wood structure and density are related to the support of the tree against gravity, wind, snow load, and other environmental forces (Hacke et al. 2001). In addition, the rate of water flow through a coniferous stem is sensitive to the variations in wood structure and density (Hacke et al. 2001, Roderick and Berry 2001). Pittermann et al. (2006) showed that in the species of *Pinaceae*, wood density and the ratio of tracheid cell wall thickness to lumen diameter were clearly associated with the protection of drought-induced embolism, indicating that mechanical strength is needed to withstand tracheid collapse by negative sap pressure. However, the increase in mechanical reinforcement is attained at the expense of reduced hydraulic efficiency (Pittermann et al. 2006).

Norway spruce wood is light or moderately light (Panshin and de Zeeuw 1980). In southern Finland, the mean basic density of Norway spruce wood is 380 ± 25 kg m^{-3} (e.g., Hakkila 1966, Hakkila and Uusvaara 1968, Hakkila 1979, Saranpää and Repola 2001, Saranpää 2003). The main determinants of wood density are genotype, tree age, and growth rate as controlled by the environment (e.g., Panshin and de Zeeuw 1980, Lindström 1996, Hylen 1997, Hannrup et al. 2004).

1.6.2 Radial variation in wood density

The radial variation in wood density of Norway spruce is well-known (Olesen 1977, Frimpong-Mensah 1987, Petty et al. 1990, Saranpää 1994, 2003). Close to the pith, wood density is high. After that, wood density decreases from the pith outwards until the minimum value is reached around rings 10–20. Thereafter in mature wood, wood density gradually increases outwards (Olesen 1977, Frimpong-Mensah 1987, Petty et al. 1990, Kučera 1994,

Saranpää 1994, 2003; Mäkinen et al. 2002b, Lundgren 2004b, Molteberg and Høibø 2006).
At the same time, latewood density slightly increases and earlywood density decreases from
the pith outwards (Olesen 1976, Mäkinen et al. 2002b). The radial trend in wood density from
the pith outwards is caused by the maturation of the cambium (e.g., Tyrväinen 1995, Zhang
1998, Kärenlampi and Riekkinen 2004, Koga and Zhang 2004).

Wood density is positively related to the latewood percentage (LW%) (e.g., Lindström
1997, Mäkinen et al. 2002b). In Norway spruce, LW% is low near the pith but increases
towards the bark. Hakkila (1968) found that the LW% was 20 in ring 20 from the pith, but
increased to 35 in ring 110 from the pith. This increase in LW% is due to a decreasing growth
rate from the pith outwards. With age, canopies become more closed and the lower bole of
the tree produces narrower rings (Larson 1969). Concurrently, the width of latewood remains
almost constant, thus increasing the LW% (Olesen 1976, 1977).

A negative relationship between wood density and radial growth rate has been reported
for many species of *Picea* (Zobel and van Buijtenen 1989). In Norway spruce, the negative
relationship between wood density and radial growth rate is strong (Olesen 1976, 1977; Petty
et al. 1990, Lindström 1996, Rozenberg and Cahalan 1997, Herman et al. 1998a, Pape 1999ab,
Mäkinen et al. 2002b, Saranpää 2003) but nonlinear (Olesen 1982, Saranpää 2003). Wimmer
and Downes (2003) showed that the negative relationship between wood density and the
radial growth rate of Norway spruce was indirect and diminished with a constant LW%.
Furthermore, they reported that the ring width–wood density relationship was highly variable
between years and climatic conditions. Higher late-season rainfall resulted in a more positive
relationship, whereas higher early-season rainfall produced a more negative relation.

In Norway spruce, a high variation in wood density occurs within annual growth rings,
shifting from ca. 300 kg m^{-3} in earlywood to ca. 600 kg m^{-3}–1000 kg m^{-3} in latewood (Olesen
1976, 1982; Zobel and van Buijtenen 1989, Mäkinen et al. 2002b, Decoux et al. 2004).
The transition from earlywood to latewood is rather gradual (Butterfield 1993), and the
distribution of intra-ring density is almost unimodal (i.e., distribution with one maximum)
(Ivković and Rozenberg 2004).

Intra-ring variation in wood density is mainly due to differences between thin-walled,
large earlywood tracheids and thick-walled, smaller latewood tracheids. The density of dry
cell wall material is nearly constant in softwoods (1.517 kg m^{-3}–1.529 kg m^{-3}; Kellogg and
Wangaard 1969, Skaar 1988). It increases only slightly from earlywood to latewood due to
the variation in the structure and chemical composition of the cell wall (Fengel and Stoll
1973, Decoux et al. 2004). Since Norway spruce wood is mainly composed of tracheids, its
density depends on the relative proportions of tracheid cell walls and tracheid cell lumens.
For Norway spruce, Mäkinen et al. (2002b) have shown a close relationship between wood
density, cell wall thickness and cell diameter. Correspondingly in Scots pine, Hannrup et al.
(2001) have reported a strong correlation between wood density and the lumen diameter of
earlywood.

Bouriaud et al. (2005) found that earlywood density was relatively independent of the
radial growth rate and climatic conditions. In contrast, latewood density was dependent on
growth rate and climate, e.g., temperature and water availability (Bouriaud et al. 2005). The
increasing density from earlywood to latewood was related to increasing temperature, solar
radiation and water depletion towards the end of the growing season (Bouriaud et al. 2005).

The average ring density and its components – early- and latewood density and LW%
– are under genetic control (Hannrup et al. 2001, 2004; Raiskila et al. 2006), that changes
with tree age (Lewark 1982, Rozenberg and Cahalan 1997, Hannrup et al. 2004). In Norway
spruce, heritability for wood density was found to decrease with increasing cambial age

(Lewark 1982). In radiata pine (*Pinus radiata*), genetic control of wood density was strong at an early cambial age (rings 2 and 3), dropped to zero within the transition from juvenile to mature wood (rings 6–8), and varied thereafter from low to moderate (Zamudio et al. 2002).

1.6.3 Vertical variation in wood density

In Norway spruce, the vertical variation of wood density from the stem base to the stem apex in a given ring number from the pith is low to moderate (Saranpää 2003). Some authors have reported a slight decrease in wood density of cross-sectional discs from the stem base to about 30%–50% of tree height, and then a steady increase towards the stem apex (Hakkila 1966, Frimbong-Mensah 1987, Petty et al. 1990, Repola 2006). Others have found that wood density cross-sectional discs slightly increases from the stem base to about 50% of tree height, above which wood density decreases towards the stem apex (Hakkila and Uusvaara 1968, Olesen 1982, Johansson 1993). The diversity of the results may be due to different sampling practices and sample sizes (Heger 1974, Molteberg and Høibø 2006). Different silvicultural practices may also affect the axial variation in wood density.

1.7 Wood and tracheid properties in relation to wood utilisation

1.7.1 End-uses of Norway spruce wood

In Finland, the total consumption of Norway spruce wood was 28 Mill. m³ in 2006 (Ylitalo 2007). About 50% of this was used in sawmilling, 8% in plywood and LVL manufacturing, and 42% in pulp and paper industries (Ylitalo 2007). In the pulp industries, the majority (71%) of the Norway spruce wood was used in mechanical pulping, while semi-chemical (0.6%) and chemical (29%) processes used less spruce wood (Ylitalo 2007). The different end-uses of wood depend on different wood and tracheid properties.

1.7.2 Sawn goods

In wood-products manufacturing, the strength, stiffness, appearance, dimensional stability and treatability of timber are of primary importance (e.g., Kliger et al. 1995, Zhang 1997, Macdonald and Hubert 2002, Gartner 2005). These characteristics, with respect to wood and tracheid properties, are related to wood density, MFA, spiral grain angle (i.e., the alignment of tracheids relative to the axial direction of the stem; Kozlowski and Winget 1963; Gjerdrum et al. 2002), juvenile wood, reaction wood (i.e., compression wood in conifers), and growth stresses (Macdonald and Hubert 2002).

Wood density is the most widely-used indicator of wood quality for different end-uses. The mechanical strength and stiffness properties of solid wood, described by the modulus of rupture (MOR) and the modulus of elasticity (MOE), respectively, are positively correlated with wood density (e.g., Verkasalo 1992, Zhang 1995, Saranpää and Repola 2001, Raiskila et al. 2006). The swelling and shrinking behaviour of timber is also related to wood density, but not as directly as the strength properties (Saranpää 2003). Variation in wood density affects the end-use potential: non-uniform wood is preferred for decorative products, whereas uniform wood is favoured in the pulp industry (Tyrväinen 1995) and veneer and panel board manufacturing (Koubaa et al. 2002).

MFA has a negative impact on timber stiffness and dimensional stability (Cave 1968, Zhang 1997, Gindl 2002, Macdonald and Hubert 2002). Grain angle is also negatively related to timber strength and stiffness, as well as the dimensional stability of timber (Harris 1989, Kliger et al. 1995, Pape 1999c, Macdonald and Hubert 2002, Warensjö 2003).

Since juvenile wood is characterised by higher MFA, higher spiral grain angle and higher variation in tracheid properties than mature sapwood, a high proportion of juvenile wood reduces the strength, stiffness and dimensional stability of timber (Macdonald and Hubert 2002, Gartner 2005). Juvenile wood may also contain a high amount of compression wood since a small tree is susceptible to environmental forces, e.g., wind, that causes the formation of compression wood (Zobel and Sprague 1998).

Compression wood forms on the lower side of a leaning conifer stem and under branches (Westing 1965). A rapid growth rate may also result in compression wood formation throughout the stem (Walker 1993b). Compression wood is characterised by shorter tracheids, thicker and more rounded cell walls, higher MFA, higher lignin content, and darker colour than normal wood (Ollinmaa 1959, Timell 1986). The presence of compression wood decreases radial and longitudinal shrinkage, but increases tangential shrinkage, thus causing drying distortion in sawn timber (Timell 1986, Kliger et al. 1995, Perstorper et al. 2001). According to Gindl (2002), the dominant influence of MFA leads to decreased tensile strength of timber. Conversely, MFA causes no reduction in the compression strength of timber because of the reinforcing action of increased lignin content and altered lignin composition in Norway spruce compression wood (Gindl 2002).

Growth stresses may also cause deformations in timber, e.g., check, shake or crack (Dinwoodie 1966, Savidge 2003). Growth stresses exist in all three major axes of a standing tree (Dinwoodie 1966). The stresses are most probably caused by the shortening of the tracheids after their formation (Dinwoodie 1966).

1.7.3 Pulp and paper

Among Fennoscandian and North American conifers, Norway spruce is one of the most favoured species for pulping, especially for mechanical pulping, due to its light colour, low extractive content, low wood density, and long and slender tracheids (Tyrväinen 1995, Varhimo and Tuovinen 1999, Da Silva Perez and Fauchon 2003).

In the pulp and paper industry, wood density is used to indicate the yield of pulp per unit volume, and energy consumption in pulping (Varhimo and Tuovinen 1999). Wood density is also related to potential paper properties since it is related to cell wall thickness, and indirectly to tracheid length (Uprichard and Walker 1993).

Tracheid dimensions and their ability to bond to each other affect the physical and optical properties of pulp and paper (e.g., Jackson 1988, Kärenlampi et al. 1996, Corson 2002, Fuglem et al. 2003). Tracheid length is correlated with the degree of fibre-bonding and is thus proportional to the tear strength of paper (Jackson 1988, Young 1994, Da Silva Perez and Fauchon 2003). Fuglem et al. (2003) reported that Norway spruce wood with long tracheids and high density (i.e., sapwood) produced thermomechanical pulps (TMP) with the highest strength, but the lowest optical properties. In contrast, wood with short tracheids and low density (i.e., juvenile wood) produced pulps with the lowest strength, but the best optical properties (Fuglem et al. 2003). Short tracheids (e.g., in juvenile or compression wood) are associated with a high MFA that lowers the tensile strength of the tracheid. Thus, short tracheids result in low tensile and tear strength of pulp and paper (Kellogg and Thykeson 1975).

Cell wall thickness is the main factor affecting tracheid conformability, i.e., flexibility and collapsibility, which determines the bonding ability of tracheids (Paavilainen 1993). Thin-walled tracheids of low-density wood (i.e., earlywood tracheids) are flexible, collapse easily and have a good bonding potential, contributing positively to the sheet density and tensile strength of pulp and paper (Paavilainen 1993). On the contrary, thick-walled tracheids of high-density wood (i.e., latewood tracheids or compression wood tracheids) are rigid and have low collapsibility. They provide tear strength, breaking length (i.e., the length of a strip of paper of uniform width beyond which it would break by its own weight if suspended from one end; m), the bulk and absorbance properties for pulp and paper (Da Silva Perez and Fauchon 2003). Thick-walled tracheids require more energy in refining than thin-walled ones (Tyrväinen 1995, Da Silva Perez and Fauchon 2003). In addition, thick-walled tracheids fracture easily in refining, leading to shortened fibres and lower tear strength (Da Silva Perez and Fauchon 2003). Furthermore, high latewood percentage may cause surface instability and poor sheet structure (Tyrväinen 1995, Da Silva Perez and Fauchon 2003).

Lignin is responsible for poor brightness stability (i.e., yellowing) of pulp and paper (Wallis and Wearne 1981). Fast-growing Norway spruce has thin cell walls, meaning that a large proportion of the cell wall is formed by the middle lamella, and thus the wood has a higher lignin content (Saranpää et al. 2000). It has also been shown that earlywood tracheids have higher lignin content and lower cellulose content than latewood tracheids (Fukazawa and Imagawa 1981, Gindl 2001, Bertaud and Holmbom 2004).

Mechanical pulps contain almost all the wood components, including lignin, since wood logs or chips are separated into individual tracheids by using steam and mechanical power (Sjöström 1993, Tyrväinen 1995). Lignin-containing pulps are used for short-life products, e.g., newsprint, magazine and fine papers (Aarne 2006). In chemical pulping, on the contrary, the ultimate goal is to produce lignin-free tracheids (Da Silva Perez and Fauchon 2003). Tracheid separation is obtained through delignification of the middle lamella with chemicals, e.g., sodium hydroxide and sodium sulphide in Kraft pulping (Sjöström 1993). Due to the removal of lignin, chemical pulps have better optical and physical properties than mechanical pulps, but the pulp yield is lower (Da Silva Perez and Fauchon 2003). A high lignin content in wood reduces the chemical pulp yield and increases the need for environmentally-harmful bleaching chemicals and energy (Tyrväinen 1995, Chen et al. 2001, Pereira et al. 2003).

1.8 Forest management

1.8.1 Thinning

Thinning reduces stand density and, thus, competition among the remaining trees for growing space, mineral nutrients, soil water and solar radiation (Larson 1969, Savill et al. 1997, Larson et al. 2001). Thinning does not usually increase the total yield per unit area, but it increases tree growth rate, crown development, and the yield of log-sized timber (Vuokila 1981, Zeide 2001, Mäkinen and Isomäki 2004ab). The profitability of thinning depends on the amount and value of thinning removal, the harvesting costs, and the timing and intensity of the thinning (Huuskonen and Hynynen 2006).

Thinning intensities increased during the 1960s in response to the mechanisation of harvesting operations. Currently in Finland, tending of young stands is recommended and one to three successive thinnings should be carried out during the stand rotation which often exceeds 80 years (Tapio 2006). The number of commercial thinnings depends on the tree

species, site fertility, geographical location, altitude, and the goal of forest management (Tapio 2006).

In 2006, the total area subject to fellings was 619 000 ha, of which the commercial thinnings amounted to 71% (Juntunen and Herrala-Ylinen 2007). Nevertheless, neglected or delayed tending and delayed first commercial thinning are problems that may result in decreased timber supply. The reason for neglect or delay is probably the low profitability due to small stem size and high harvesting costs (cf. Huuskonen and Hynynen 2006). To increase the profitability of the first thinning, the trend in forestry has been towards larger removals. However, heavy thinnings may decrease the total volume increment per unit area. Late timing of first thinning has been shown to increase the thinning removal and revenue, assuming that early tending of the stand was carried out (Huuskonen and Ahtikoski 2005, Huuskonen and Hynynen 2006).

1.8.2 Fertilisation

Low availability of nitrogen (N) usually limits the growth of boreal forests on mineral soils (Viro 1972, Tamm 1991). Nitrogen fertilisation either alone or together with phosphorus (P) has proved to be the added nutrients that have the greatest impact on tree growth (Kukkola and Saramäki 1983, Ingerslev et al. 2001, Nilsen 2001, Saarsalmi and Mälkönen 2001, Saarsalmi et al. 2006). Increased atmospheric deposition of N has also increased the availability of N in forest soils (Matson et al. 2002).

In Finland, the introduction of state subsidies in the 1960s increased the area of forest fertilisation (Saarsalmi and Mälkönen 2001). In the late 1980s, the area of forest fertilisation decreased because of diminishing subsidies and increasing awareness of nutrient leaching (Saarsalmi and Mälkönen 2001, Ingerslev et al. 2001). Currently in Finland, the area of fertilised forests equals 26 000 ha yr^{-1} (Juntunen and Herrala-Ylinen 2007). N-fertilisation is recommended for Norway spruce stands on mineral sites of moderate fertility and good soil water conditions where the main growth-limiting factor is the availability of N (Kukkola and Saramäki 1983, Tapio 2006). Moreover, fertilisation should be carried out at the latter part of the stand rotation, ensuring that the N addition does not increase the branchiness of the butt log, but increases the yield of high quality wood before final harvesting (Saramäki and Silander 1982, Tapio 2006). Besides N application, a balanced nutrient status is important for wood production (Möttönen et al. 2003). Low boron (B) availability has caused growth disturbances in many areas in eastern and northern Finland (Hynönen et al. 1999, Saarsalmi and Mälkönen 2001, Saarsalmi and Tamminen 2005). Vitality fertilisation is recommended for the stands suffering from nutrient imbalance (Saarsalmi and Tamminen 2005).

1.8.3 The effects of thinning and fertilisation on wood density and tracheid properties

To maintain a high level of timber supply, increase incomes and reduce harvesting costs, the trend in silviculture has been towards more intensive forest management (i.e., intensive thinnings and repeated fertilisations) with shorter rotations. Increasing the growth rate of the trees may, however, result in changes in wood properties.

The overall effects of thinning and fertilisation on radial growth rate and wood density of Norway spruce are fairly well known (e.g., Klem 1972, Saikku 1975b, Kukkola and Saramäki 1983, Barbour et al. 1992, Lindström 1996, Eriksson and Karlsson 1997, Herman et al. 1998a, Mäkinen et al. 2002b). In general, a faster growth rate due to thinning or N addition has been suggested to decrease wood density (e.g., Petty et al. 1990, Herman et

al. 1998a, Mäkinen et al. 2002b). This decline is due to increased production of earlywood relative to that of latewood (Hakkila 1966, Smith 1980, Zhang et al. 1996, Mäkinen et al. 2002b). In addition, an increased growth rate has been suggested to decrease the density of earlywood and latewood (e.g., Zhang et al. 1996, Borders et al. 2004, Alteyrac et al. 2005, Mäkinen et al. 2002b).

A faster growth rate caused by intensive thinning or fertilisation may change tracheid properties – enlarge cell lumen diameter, and decrease tracheid length and cell wall thickness (Helander 1933, Dinwoodie 1961, Herman et al. 1998a, Mäkinen et al. 2002a, Lundgren 2004a). In addition, lignin content has been suggested to increase with increased growth rate (Brolin et al. 1995, Anttonen et al. 2002).

However, many of the existing studies on radial growth rate and wood properties have been based on temporary sample plots and information on previous management history is lacking. Permanent sample plots could possibly provide more reliable information on the long-term effects of environmental factors and management practices on wood properties. Moreover, detailed research on the long-term effects of intensive thinning and/or fertilisation regimes on wood density and tracheid properties of Norway spruce is still scarce under Nordic conditions.

2   THE AIMS OF THE THESIS

The aim of this thesis was to study the relationship between silvicultural treatments, i.e., thinning and fertilisation, tree growth rate, and wood and tracheid properties of Norway spruce throughout the entire stand rotation. The hypotheses were that the long-term thinning and/or N-fertilisation would affect the radial growth rate of the trees, and the changes in growth rate would be reflected in wood and tracheid properties. The stand development of the utilised experiments (two long-term thinning and two long-term fertilisation-thinning experiments in southern and central Finland) has already been recorded for ca. 30 years since the phase of the first commercial thinning. This made it possible to study in detail the wood properties of the sample trees from the pith to the cambium, and at different heights in the stems during the entire rotation period at a stand level. The specific objectives of the thesis were:

- to study the long-term effects of the intensity and timing of thinning and/or N-fertilisation on annual radial increment, latewood percentage, and wood density (i.e., mean ring density, early- and latewood density; **I**, **II**), as well as to study in detail the intra-ring and inter-ring variation in wood density from the pith to the cambium, and at the different heights of Norway spruce stems (**III**), and

- to study the long-term effects of the intensity and timing of thinning and/or N-fertilisation on tracheid properties (i.e., tracheid length, cell wall thickness, lumen diameter and cell wall proportion; **IV**, **V**) and lignin content (**V**) from the pith to the cambium, and at the different heights of Norway spruce stems (lignin studied only at the height of 1.3 m).

3 MATERIALS AND METHODS

3.1 Experimental design and sampling

3.1.1 Thinning experiments in Heinola and Punkaharju

The sample trees (**I** and **IV**) were harvested from two thinning experiments in south-eastern Finland. The experiments were established in Heinola (He; 61°10′N, 26°01′E) in 1970 and in Punkaharju (Pu; 61°49′N, 29°19′E) in 1964 by the Finnish Forest Research Institute (Fig. 4). The experiments were even-aged, pure, or almost pure Norway spruce stands planted with seeds of local origin in 1917 (He) and 1938 (Pu). The experiments were on mineral sites classified as *Oxalis–Myrtillus* (OMT) forest site type (Cajander 1909), corresponding to fertile sites typical for Norway spruce. For other stands' properties, see **I** and **IV**.

To study the effects of thinning intensity on radial increment, wood density (**I**) and tracheid dimensions (**IV**), three plots of different thinning intensity from both experiments were chosen: normal thinning intensity recommended for forestry practice in the 1970s, low thinning intensity with a stand denser than normal, and high thinning intensity with a stand sparser than normal. The thinning intensities were defined based on the stand basal area (BA) remaining after thinning. The plots of normal and high thinning intensity were thinned from below (i.e., the suppressed or damaged trees were removed first), twice in Heinola and three times in Punkaharju. In Punkaharju, the plot of low thinning intensity was also lightly thinned 15 years after establishment. In contrast in Heinola, no thinning operations were carried out at the plot of low thinning intensity. The development of the BA as plotted against dominant tree height is shown in Figs. 5A and 5B.

Both in Heinola and Punkaharju, 12 trees were felled in autumn 2001. The cumulative basal area distribution on each plot was divided into three classes, each class having the same basal area: small, intermediate, and large trees. Because the spread of stem size increased with increasing stand density, the number of sample trees was also increased with increasing stand density. One sample tree on each plot was randomly chosen from each size class. On the plots of normal and low thinning intensity, one additional sample tree was chosen from the size class of the largest trees. On the plot of low thinning intensity, one sample tree was also chosen from the size class of intermediate trees. Thus, the total number of sample trees was 3, 4 and 5 for the plots of high, normal and low thinning intensity, respectively. From each tree, 30 cm thick sample discs were cut at breast height (BH; 1.3 m) and at a height of 12 m, avoiding whorls and defects.

3.1.2 Fertilisation-thinning experiments in Parikkala and Suonenjoki

The sample trees (**II**, **III** and **V**) were harvested from two fertilisation-thinning experiments in south-eastern and central Finland. The experiments were established by the Finnish Forest Research Institute in Parikkala (Pa; 61°36′N, 29°22′E) in 1977 and in Suonenjoki (Su; 62°45′N, 27°00′E) in 1978 (Fig. 4). The stands were even-aged and almost entirely Norway spruce. They were planted with seeds of local origin in 1939 (Pa) and in 1925 (Su). The experiments were on mineral soil classified as OMT forest site type (Cajander 1909). For other stands' properties, see **II**, **III** and **V**.
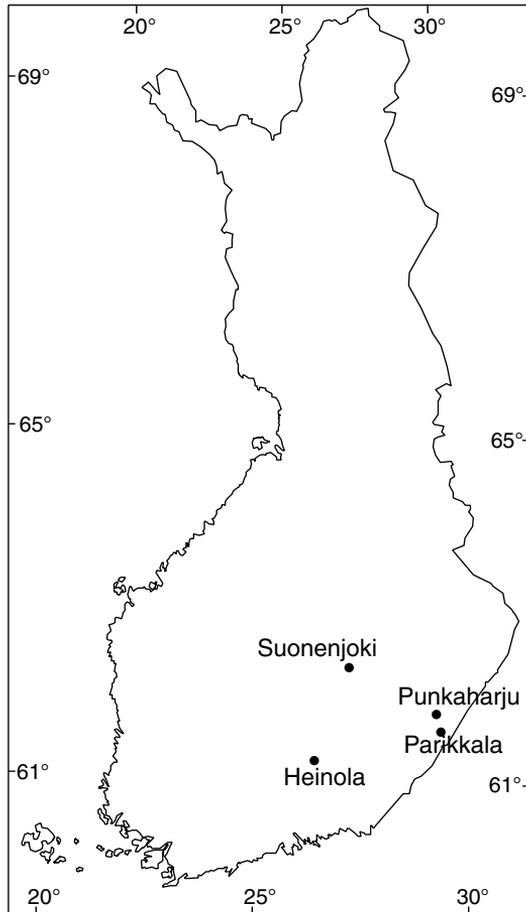
Figure 4. The location of thinning and fertilisation-thinning experiments in Finland.

Both experiments comprised three fertilisation and thinning treatments of varying intensity and timing in a randomised block design, giving rise to nine different combinations in both experiments. Fertilisation treatments were: unfertilised (F_0); 150 kg nitrogen (N), 75 kg phosphorus oxide (P_2O_5) and 75 kg potassium oxide (K_2O) per ha (F_1); and 300 kg (N), 150 kg (P_2O_5) and 150 kg (K_2O) per ha (F_2). On the fertilised plots, NPK fertiliser was applied every five years. Thinning treatments based on the number of stems ha^{-1} were: delayed first thinning, i.e., 60% of the original number of stems removed 15 years after establishment (T_0); normal thinning with ca. 30% of the original number of stems removed when the treatment was established, and ca. 30% of the original number of stems 10 years after establishment (T_1), and intensive first thinning with 60% of the original number of stems removed at the establishment of treatment (T_2). The plots were thinned from below. The development of the BA as plotted against dominant tree height is shown in Figs. 5C and 5D.

The cumulative basal area distribution on each plot was divided into five classes (tree size-classes 1–5; tree size-class 1: the smallest trees, …, tree size-class 5: the largest trees), each having the same BA. One sample tree was randomly chosen per plot and size class. In Parikkala, 45 sample trees were felled in autumn 2003. In Suonenjoki, 40 sample trees were felled in spring 2003. From each tree, one sample disc (30 cm thick) was sawn at BH, avoiding whorls and defects. From the trees on plots F_0T_0, F_0T_1, F_0T_2, F_1T_0, F_1T_1, and F_1T_2,
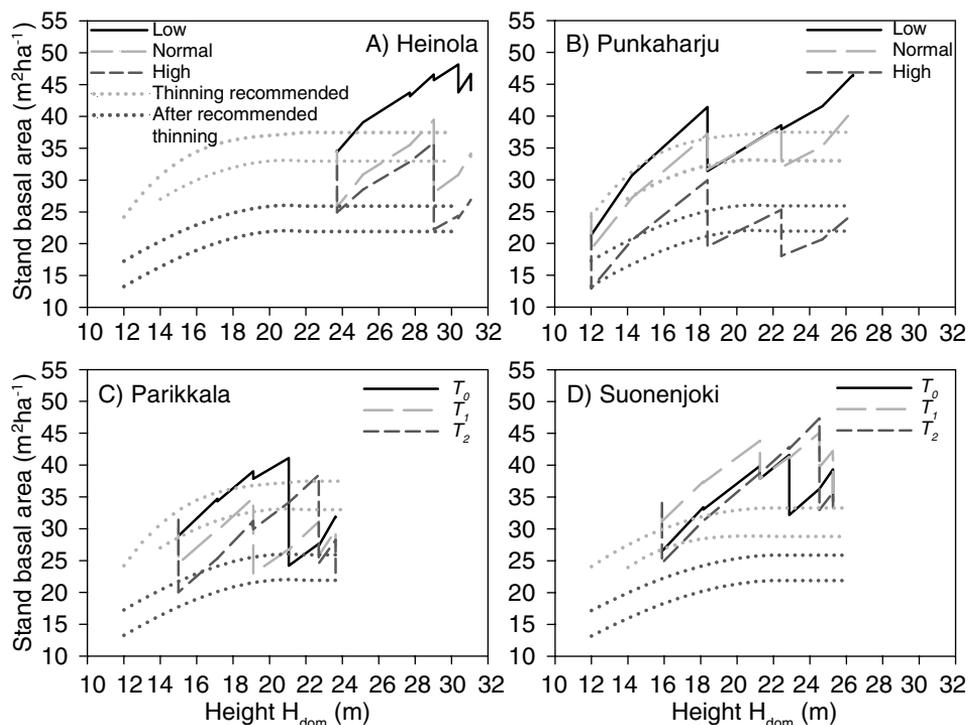
Figure 5. Stand basal area (BA) related to the dominant height of the stand in Heinola (A, 1970–1998) and Punkaharju (B, 1964–1999) in low, normal and high thinning intensity (for the stand basal areas after thinning operations, see **I**), and in Parikkala (C, 1977–2002) and Suonenjoki (D, 1978–2003) in fertilisation-thinning treatments. In C and D, the values for T_0, T_1, and T_2 are the means for thinning treatments in combination with all the different levels of fertilisation intensity (e.g., T_0 is the average of T_0F_0, T_0F_1 and T_0F_2; T_0, delayed first thinning, i.e., 60% of the original number of stems removed 15 years after treatment onset; T_1, normal first thinning, i.e., 30% of the original number of stems removed at treatment onset, and 30% of the original number of stems ten years after treatment onset; T_2, intensive first thinning, i.e., 60% of the original number of stems removed at treatment onset; F_0, unfertilised; F_1, 150 kg N ha^{-1}; and F_2, 300 kg N ha^{-1}). Grey dotted lines indicate the currently suggested timing and intensity of thinning operations and black dotted lines show the suggested BA after thinning for the stands with annual temperature sum of > 1200 d.d. (in Heinola, Punkaharju and Parikkala) and 1000–1200 d.d. (in Suonenjoki) (Tapio 2006).

additional sample discs were sawn at 4-metre intervals above BH (i.e., 5 m, 9 m, etc.) until the stem diameter was < 16 cm, and thereafter at 3-metre intervals until the stem diameter was < 8 cm.

In addition to the tree size-classes described above, sample trees in each plot were grouped into 'small' and 'large' trees according to the median basal area of sample trees (TBA; as calculated for all sample trees together) at the time of treatment onset (i.e., TBA > median: 'large' tree, TBA < median: 'small' tree) in order to more accurately describe the treatment effects on wood properties of different tree size-classes.

3.2 The structural analyses of wood and tracheid properties

3.2.1 Radial increment and wood density

Wood density (weight density, 12% moisture content, g cm^{-3}) and annual radial increment (ring width, mm) (**I–V**) were measured using X-ray densitometry. From the sampled discs, 8 cm thick wedges were sawn along the south radius. The wedges were air-dried for 6 months, and samples (5 mm wide and thick) were sawn. Resins were not extracted due to the low extractive concentration (ca. 1%) in Norway spruce. The moisture content of the samples was adjusted to 12% at 20°C and 65% relative humidity for ca. 3 weeks. The samples were then placed on a film and X-rayed for 5 min, 16 kV, 20 mA, at a distance of 2.5 m (Saikku, 1975a). Films were scanned (25.4 μm pixel^{-1}, 256 grey levels) and a continuous wood-density profile for each sample was measured using WinDENDRO™ software (Regent Instruments Inc., Québec, Québec, Canada). The measured grey levels were converted to wood density with a standard plastic step wedge of known physical and optical density. For each annual ring or disc, the mean density values (RD, ring density; ED, earlywood density; LD, latewood density) were determined. In addition, the widths of annual ring, early- and latewood, and latewood percentage (LW%) were determined. The widths of annual ring, early- and latewood were converted into basal-area increments (BAI, cm^2, **I–II**) with the assumption of circular stem cross-section. A transition point (TP) between early- and latewood was defined separately for each annual ring:

$$TP = MAX - [(MAX - MIN) \times 0.3] \qquad\qquad (1)$$

In Eq. 1, MAX and MIN are the maximum and minimum densities of the ring. When examined visually, the factor 0.3 was found to have the best fit to the captured images.

3.2.2 Tracheid length

For tracheid length measurements (**IV–V**), wedges (3 cm thick and wide) were sawn along the south radius of the sampled discs. Earlywood zones of every fifth annual ring from the bark to the pith were split into match-size sticks and macerated in a solution of glacial acetic acid and hydrogen peroxide (1:1, v/v) at +60 °C over one to two nights (Franklin 1945). A suspension of washed tracheids was deposited on microscope slides. The lengths of 50 unbroken tracheids per annual ring were measured by image analysis (Image-Pro Plus, Media Cybernetics, USA) from the images captured with a camera (**IV:** Cohu 4912, Cohu Inc., Poway, USA; **V:** SPOT Insight B/W, Diagnostic Instruments, Inc., Burroughs, USA) attached to a light microscope (Olympus BH-2, Olympus Optical Co., LTD., Japan). The size of a pixel was 10.64 μm (**IV**) and 4.48 μm (**V**).

3.2.3 Cross-sectional dimensions of tracheids

For the measurements of cell wall thickness and lumen diameter (**IV–V**), wedges (3 cm × 3 cm) were sawn from the southern half of the sampled discs. Small samples (1 cm^{-3}) were boiled in water in a microwave oven for 1–4 min, then frozen and cut into transverse sections (16 μm thick) at −16°C by cryo-microtome (Leitz 1516, Leica Microsystems, Wetzlar, Germany). The sections were stained with a 1%-solution of safranin, rinsed with water, dehydrated in an ascending alcohol series, rinsed with xylene, and mounted in Canada balsam.

Digital images were taken from the annual rings with a camera (**IV:** SPOT Insight B/W, Diagnostic Instruments, Inc., Burroughs, USA; **V**: CCD digital camera, Media Cybernetics, Inc., Maryland, USA) attached to a light microscope (Olympus BX-60 microscope, Olympus Optical Co., LTD., Japan). The size of the pixel was 0.182 μm (**IV**) and 0.115 μm (**V**). To cover the whole annual ring from early- to latewood, successive overlapping images were taken and joined. The cell walls and lumens were identified by a threshold method (Otsu 1979). The cell wall thickness (i.e., double cell wall thickness) and lumen diameter were measured in radial direction along three cell rows in each annual ring. The transition point between early- and latewood was determined according to Mork's definition: a cell belongs to the latewood when its double cell wall thickness is equal to or greater than half of the lumen diameter as measured in radial direction (Mork 1928, Denne 1989).

3.3   Determination of lignin content

The FTIR (Fourier transform infrared spectroscopy) -based estimation method was used to predict the total lignin concentration of the sampled discs (**V**). Wedges were sawn along the north radius of the sampled discs, and further split into small samples. Potassium bromide (KBr) pellets (Ø13 mm, 3.0–3.4 mg wood powder with 299.9–300.1 mg KBr) of dried, milled and sieved (hole size 0.125 mm) wood samples were prepared. From the pellets, the FTIR spectra (FTIR-spectrometer: Perkin Elmer System 2000, MIRTGS detector, resolution of 4 cm^{-1}) were recorded and normalised by the line subtraction method. The baseline passing through the intensity values at wave numbers 4000, 1929, 835 and 500 was subtracted from the spectrum, and the maximum intensity value was set to 1.5.

The total relative concentration of lignin (Klason lignin and acid soluble lignin) of wood dry mass (WD) was predicted by the principal component regression (PCR) model devised for predicting the lignin content of Norway spruce wood (Raiskila et al. 2007). The 4 PCs calculated from the spectral range of 1850–500 cm^{-1} were used as independent variables of the model while the total lignin concentration was a dependent variable. The model selection criteria included an adequate fit in the estimation data ($R^2 = 0.74$; root mean squared error of lignin content in the estimation data, RMSE = 0.61%) and a good prediction performance in the test data ($R^2 = 0.90$; root mean squared prediction error in the test data, RMSPE = 0.53%) (Raiskila et al. 2007). The model was based on three different Norway spruce cutting clones (12 trees), from three different sites in Finland. The model estimation data comprised 18 samples from 9 trees, and the model test data consisted of 6 samples from 3 trees for which the relative concentration of Klason and acid soluble lignin was determined by the Klason method (KCL 1982, Dence 1992).

3.4   Statistical analyses

The statistical significance of treatment effects was analysed with mixed models (Linear mixed models in SPSS; PROC MIXED in SAS) including both fixed and random effects. The differences between treatment means were analysed by Bonferroni's pairwise comparisons (**I**, **IV**) or Tukey's post hoc tests (**II**, **V**). The statistical analyses were obtained by the SPSS (**I, IV**; versions 12.0.1 and 14.0, SPSS, Inc., Chicago, IL, USA) and the SAS software (**II–III, V**; version 9.1, SAS Institute Inc., Cary, NC, USA).

In **I** and **IV**, the wood and tracheid properties of Norway spruce (i.e., mean annual, early- and latewood increment; latewood percentage; mean ring, early- and latewood density; tracheid length; cell wall thickness of early- and latewood; lumen diameter of early- and latewood) were tested for the effects of thinning intensity, the year of ring formation and their interaction. In **I**, a covariate was employed in the model in order to remove the initial differences between trees. In **IV**, the tracheid properties were also tested for the random effect of distance from the pith, i.e., the effect of tree size.

In **II** and **V**, wood and tracheid properties (i.e., mean annual, early- and latewood increment; latewood percentage; mean ring, early- and latewood density; tracheid length; cell wall thickness of early- and latewood; lumen diameter of early- and latewood; relative total lignin content) were tested for the effects of thinning and fertilisation, the year of ring formation, the relative height in the stem, the distance from the pith, i.e., the effect of tree size (only in **V**), and their interactions. The covariates were applied in the models to remove the initial differences between trees prior to the treatment onset.

In **III**, the variation in wood density was analysed independent of the effect of growth rate (i.e., annual ring width was used as a covariate). The high resolution data on wood density was tested for several random factors: tree, relative height in the stem, cambial age (i.e., ring number from the pith), and the ontogenic age of annual rings (i.e., the difference between the calendar years of ring formation and tree birth date).

The data of **I–V** had a hierarchical structure (e.g., individual tracheids within annual rings, discs, trees, plots and sites), i.e., the individual measurements from the same batch were correlated. This correlation was taken into account by employing the nested data structure in the mixed models (**I–V**). In the mixed models, the parameters are allowed to vary randomly around the fixed population mean from one individual to another. In addition, the successive observations from each tree were dependent, i.e., there was autocorrelation within trees (**I–II**, **V**). To model this autocorrelation, a first-order autoregressive covariance structure (AR(1)) was applied in the statistical analyses in **I–II**, and **V**. The restricted maximum likelihood estimation (REML) was applied in all the analyses (**I–V**). When necessary, the data were transformed in order to fulfil the assumptions of valid statistical analysis.

4   RESULTS

4.1   Radial increment and proportion of latewood

All the results presented throughout this results section are based on the estimated marginal means at BH predicted by the statistical models in **I–V** (except in Figs. 6, 8 and 9, where the original values are presented). In the models (except in Eq. 3 in **I** as wood density from Punkaharju was analysed, and Eqs. 2 and 3 in **IV**), a covariate was used to remove the initial differences in wood properties between the different thinning and fertilisation treatments pre-existing the treatment onset.

In the thinning experiments in Heinola and Punkaharju, normal and high thinning intensity significantly increased (24%–64%) the basal area increment (BAI) of the sample trees as compared to low thinning intensity (Table 1, Fig. 6; **I**). At the same time, in normal and high thinning intensity, the proportion of latewood was slightly lower (9%–33%) than in low thinning intensity (Table 1, Fig. 6; **I**).

In the fertilisation-thinning experiments in Parikkala and Suonenjoki, fertilisation (F_1 and F_2) significantly increased the BAI of sample trees by ca. 40% as compared to unfertilised control (F_0) (Table 2, Fig. 6; **II**). In normal thinning (T_1) and intensive first thinning (T_2), the BAI of sample trees at BH was 8% and 29% higher, respectively, than in delayed first thinning (T_0) (Table 2, Fig. 6; **II**). In Parikkala and Suonenjoki, only small differences (1%–14%) were found in the proportion of latewood between different fertilisation and thinning treatments (Table 2, Fig. 6; **II**).

Fertilisation and thinning had an effect on the BAI in all tree-size classes (despite size-class 3, Fig. 2A in **II**) that were formed on the basis of the basal area distribution on each plot at the time of sampling, as well as in the groups of 'small' and 'large' trees based on the median TBA of sample trees at the time of treatment onset (Fig. 7A).

4.2 Wood density

4.2.1 The effects of thinning and fertilisation on wood density

In both Heinola and Punkaharju, the differences in the mean ring density (RD), earlywood density (ED) and latewood density (LD) of the sample trees between the thinning intensities were not statistically significant (Table 1; **I**). In normal and high thinning intensity, the RD and ED were slightly (up to 5%) lower than in low thinning intensity (Table 1, Fig. 6). In contrast, the LD was slightly higher (3%–8%) in normal and high thinning intensity than in low thinning intensity (Table 1).

In Parikkala and Suonenjoki, fertilisation (F_1 and F_2) decreased the RD and ED of sample trees by 6%–9% compared to unfertilised control (F_0; Table 2, Fig. 6; **II**). Moreover in fertilised plots (F_1 and F_2), the LD of the sample trees was slightly lower (1%–3%) than in unfertilised control plots (F_0; Table 2, Fig. 6; **II**). Between the thinning treatments, however, the differences in RD, ED and LD were small (2%–4%) and not statistically significant (Table 2, Fig. 6; **II**). The effects of fertilisation and thinning treatments on growth rate and wood density were similar in direction, and the relatively largest increase in growth and the greatest reduction in wood density were obtained by the combined effects of fertilisation (F_1) and intensive first thinning (T_2).

The effects of fertilisation and thinning on RD, ED and LD were similar in the groups of 'small' and 'large' trees formed using the TBA distribution of sample trees at the time of treatment onset (Fig. 7). While studied between five tree-size classes used in **II**, the effects of fertilisation and thinning on RD and ED were relatively largest in the classes of the smallest and largest trees (size-classes 1 and 5; Fig. 2 in **II**). For LD, the effects of fertilisation and thinning were variable among the size-classes (Fig. 2 in **II**).

4.2.2 Within-stem variation in wood density

In all the experiments, the general trend for mean ring density in mature wood was an increase towards the bark (**I**–**III**). However, wood density was highly variable between annual rings. The variation among rings explained up to 27% of the total variation in wood density (**III**). Between different heights in the stem, wood density varied only slightly (**I** and **III**). The largest variation (up to 80%) in wood density was within annual rings (**III**). The difference in wood density between early- and latewood increased from the pith to the bark (**III**). Both

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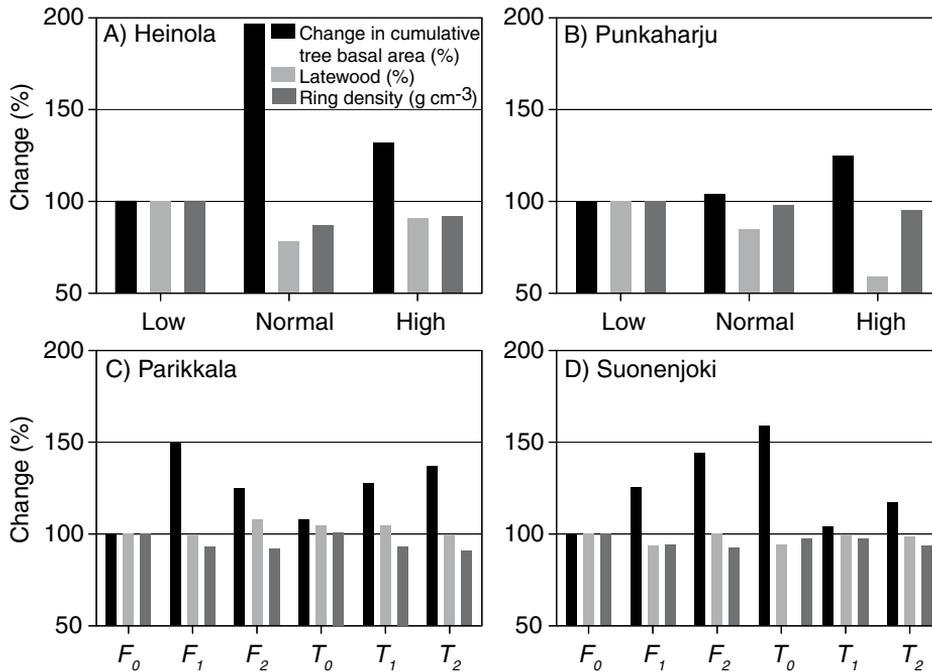
Figure 6. Percent change in tree basal area (TBA at tree harvesting relative to that prior treatment; note that the treatment period differs between A, B, C and D), and the proportion of latewood and ring density at breast height of the sample trees in normal and high thinning intensity as compared to low thinning intensity in Heinola (A) and Punkaharju (B); and in fertilised plots (F_1 and F_2) and thinning treatments (T_0, T_1 and T_2) as compared to unfertilised plots (F_0) in Parikkala (C) and Suonenjoki (D). The values for the proportion of latewood and ring density are means for the whole treatment period (A, 1970–2001; B, 1964–2001; C, 1978–2002; D, 1979–2001). In A and B, the means are weighted by tree size-class (see **I**). For an explanation of treatments, see Fig. 5.

latewood density and the proportion of latewood increased from the pith outwards, while earlywood density increased only slightly (**III**). Therefore, an increase in the mean wood density of annual ring from the pith to the bark is due to an increasing amount and density of latewood.
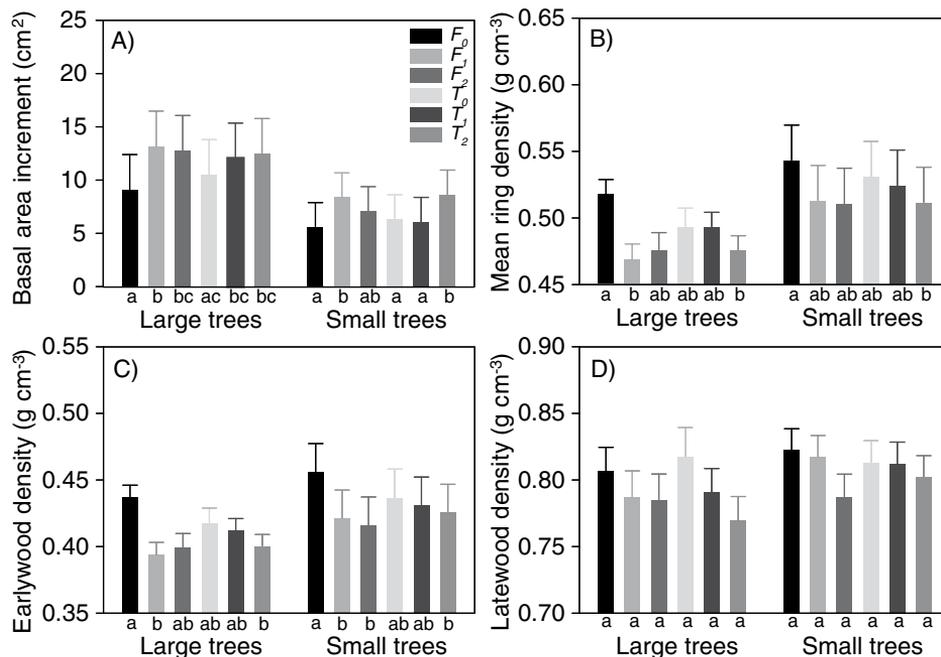
Figure 7. Radial increment (A), ring density (B), earlywood (C) and latewood density (D) of the sample trees at breast height in the groups of small and large trees in fertilisation and thinning treatments in Parikkala (1978–2002) and Suonenjoki (1979–2001). The values are the estimated marginal means of the statistical analyses (Eqs. 3 and 4 in **II**). The number of trees per size group and treatment is 1–4. The same letter below the bars indicates non-significant ($p > 0.05$) differences between the means. For an explanation of treatments, see

4.3 Tracheid properties

4.3.1 Tracheid length

After the treatment onset in Heinola and Punkaharju, high thinning intensity resulted in 9% and 4% shorter tracheids, respectively, as compared with low thinning intensity (Table 1, Fig. 8; **IV**). In Parikkala and Suonenjoki, only small (0%–6%) differences in tracheid length were found between the different combinations of fertilisation and thinning treatments as calculated over the whole treatment period (Fig. 8; **V**). When examined as a function of calendar year, the effects of fertilisation and thinning on tracheid length varied according to treatment combination, and the interaction effect between fertilisation and thinning was statistically almost significant at the significance level of 95% ($p = 0.06$, Table 2).

When examined as a function of distance from the pith (i.e., tree size was taken into account), the effects of fertilisation and thinning on tracheid length were not statistically significant (Table 2).

Figure 8. Tracheid length in low and high thinning intensity in (A) Heinola (He) and Punkaharju (Pu), and in fertilisation-thinning treatments in (B) Parikkala and (C) Suonenjoki. Each point represents the mean tracheid length of an individual annual ring of an individual tree as a function of distance from the pith. For an explanation of treatments, see Fig. 5.

Figure 9. Double cell wall thickness of earlywood in low and high thinning intensity in (A) Heinola (He) and Punkaharju (Pu), and in fertilisation-thinning treatments in (B) Parikkala and (C) Suonenjoki. Each point represents the mean cell wall thickness of an individual annual ring of an individual tree as a function of distance from the pith. For an explanation of treatments, see Fig. 5.

4.3.2 Cell wall thickness and lumen diameter

Cell wall thickness and lumen diameter were highly variable between and within annual rings and trees both before and after the treatment onset in all the experiments. However in all the experiments, the proportion of cell wall within an annual ring slightly (2%–9%) decreased with increasing thinning and fertilisation intensity (Tables 1 and 2).

In Heinola and Punkaharju, high thinning intensity resulted in 3%–12% thinner cell walls of early- and latewood tracheids than low thinning intensity (Table 1, Fig. 9; **IV**). For lumen diameter, only small changes (1%–3%) due to increasing thinning intensity were found (Table 1; **IV**).

In Parikkala and Suonenjoki, only small differences in cell wall thickness (1%–17%; Fig. 9) and lumen diameter (0%–9%) were found among different fertilisation-thinning treatments (Table 2; **V**). As studied in the relation to calendar year, fertilised trees had 7% thinner cell walls of earlywood tracheids than unfertilised trees (Table 2; **V**). Fertilisation and thinning also had a significant interaction effect on the cell wall thickness of latewood when studied as a function of calendar year (Table 2; **V**). When examined as a function of distance from the pith (i.e., tree size was considered), fertilisation and thinning had no statistically significant ($p < 0.05$) effect on tracheid dimensions (Tables 1 and 2, Fig. 9; **IV** and **V**).

4.4   Lignin content

In Parikkala and Suonenjoki, the predicted relative total lignin content was 23.4%–29.6% (± 0.8%) of DW. Over the entire study period, normal first thinning (T_1) and intensive first thinning (T_2) had slightly higher (2%) lignin content than delayed first thinning (T_0) (26.0% and 25.9% vs. 25.4%; Table 2; **V**). In fertilisation levels F_1 and F_2, the amount of lignin was 1% and 2% higher, respectively, than in unfertilised control (F_0) (25.8% and 26.0% vs. 25.4%; Table 2; **V**).

Table 1. Summary of all the variables studied at breast height (BH; 1.3 m) and at the height of 12 m in the sample trees in thinning experiments in Heinola (He) and Punkaharju (Pu). The *p* values for the main effect of thinning obtained in the statistical analyses in **I** (Eq. 3) and **IV** (Eqs. 2 and 3).

Exp.	Variable	Thinning effect (p)		Change compared with low thinning intensity (%)					
				Normal thinning intensity		High thinning intensity			
		BH	12 m	BH	12 m	BH			12 m
He	Increment total	**0.01**	**0.02**	+64	+53	+42			+69
	Increment early	**0.01**	**0.02**	+67	+54	+44			+70
	Increment late	**0.01**	**0.03**	+76	+73	+40			+65
	Latewood %	0.37	0.35	−17	−16	−9			−6
	Density ring	0.68	0.48	−4	−4	−4			−0.1
	Density early	0.67	0.91	−4	−1	−5			+1
	Density late	0.38	0.71	+6	+3	+3			+4
		Eq.2[a]	Eq.3[b]				Eq.2[a]	Eq.3[b]	
	Tracheid length	**0.01**	**0.01**	–	–	–	−9	−9	–
	wt early	0.63	0.62	–	–	–	−8	−8	–
	wt late	0.28	0.28	–	–	–	−11	−12	–
	ld early	0.61	0.58	–	–	–	−3	−3	–
	ld late	0.60	0.69	–	–	–	−3	−3	–
	Cell wall %	0.63	0.63	–	–	–	−9	−9	–
Pu	Increment total	0.09	0.06	+24	+65	+59			+101
	Increment early	0.06	0.07	+30	+64	+72			+100
	Increment late	0.77	**0.03**	+4	+63	+13			+91
	Latewood %	**0.01**	0.58	−18	−7	−33			−6
	Density ring	0.81	1.00	−2	+0.2	−3			−0.3
	Density early	0.90	0.99	−2	+0.6	−2			−0.3
	Density late	0.20	0.73	+6	+2	+8			+2
		Eq.2[a]	Eq.3[b]				Eq.2[a]	Eq.3[b]	
	Tracheid length	0.51	0.51	–	–	–	−4	−4	–
	wt early	0.80	0.77	–	–	–	−3	−4	–
	wt late	**0.00**	0.08	–	–	–	−11	−12	–
	ld early	0.82	0.84	–	–	–	−1	−1	–
	ld late	0.79	0.72	–	–	–	+1	+3	–
	Cell wall %	0.36	0.36	–	–	–	−8	−8	–

–, not measured; [a] Tracheid dimensions analysed as a function of calendar year (Eq. 2 in **IV**); [b] Tracheid dimensions analysed as a function of distance from the pith (Eq. 3 in **IV**). wt, thickness of double cell wall; ld, lumen diameter; Cell wall %, relative amount of cell wall within an annual ring.

Table 2. Summary of all the variables studied at breast height (BH; 1.3 m) and at the whole-stem level (WS) in the sample trees in fertilisation-thinning experiments in Parikkala and Suonenjoki (combined data). The p values for the main effects of thinning (Th) and fertilisation (Fe), as well as their interaction (Th × Fe) obtained in the statistical analyses **II** (Eqs. 3 and 5) and **V** (Eqs. 1 and 2).

Variable	Effect (p)						Change compared with T_0 (%)				Change compared with F_0 (%)			
	Th		Fe		Th × Fe		T_1		T_2		F_1		$F_2{}^{[a]}$	
	BH	WS	BH	WS	BH	WS	BH	WS	BH	WS	BH	WS	BH	WS
Increment $_{total}$	**0.03**	0.08	**0.00**	**0.00**	0.34	0.38	+8	+3	+29	+16	+41	+34	+38	+38
Increment $_{early}$	**0.02**	0.25	**0.00**	**0.00**	0.28	0.45	+7	+3	+30	+17	+45	+47	+38	+47
Increment $_{late}$	0.10	**0.01**	**0.01**	**0.00**	0.43	0.16	+10	+3	+25	+18	+26	+19	+40	+19
Latewood %	0.81	0.72	0.27	**0.00**	0.19	0.86	–2	+2	–3	–1	–5	–14	+4	–14
Density $_{ring}$	0.21	0.45	**0.00**	**0.00**	0.68	0.94	–2	–0.3	–4	–2	–6	–8	–7	–8
Density $_{early}$	0.37	0.61	**0.00**	**0.00**	0.93	0.93	–2	–1	–4	–2	–8	–7	–9	–7
Density $_{late}$	0.15	0.74	0.10	0.04	0.52	0.77	–2	–1	–3	–2	–1	–1	–3	–3
Eq.	Eq. 1A[b]	Eq. 2[d]	Eq. 1A[b]	Eq. 2[d]	Eq. 1A[b]	Eq. 1B[c]	Eq. 1A[e]		Eq. 1A[b]	Eq. 1B[c] 2[d]	Eq. 1A[b]	Eq. 1B[c]	Eq. 2[d]	Eq. 1A[e]
Tracheid $_{length}$	0.55	–	0.28	–	0.06	0.47	–	–	+1	–1	–2	+0.1	–	–
wt $_{early}$	0.34	0.99	**0.05**	0.99	0.75	0.16	–	–	–3	–1	–7	–12	–	–
wt $_{late}$	**0.05**	0.99	0.65	0.99	**0.01**	0.89	–	–	–7	–10	–1	+1	–	–
ld $_{early}$	0.48	0.98	0.86	0.98	0.52	0.73	–	–	–2	–6	+0.4	+2	–	–
ld $_{late}$	0.98	0.99	0.98	0.99	0.17	0.23	–	–	+0.2	+4	–0.1	+1	–	–
Cell wall %	0.54	–	0.79	–	0.78	0.67	–	–	–5	–3	–2	–4	–	–
Lignin %	0.08	–	0.09	–	0.91	–	+2	–	+2	–	+1	–	–	+2

–, not measured; T_0, delayed first thinning; T_1, normal first thinning; T_2, intensive first thinning; F_0, unfertilised; F_1, 150 kg N ha^{-1}; F_2, 300 kg N ha^{-1}; wt, thickness of double cell wall; ld, lumen diameter; Cell wall %, relative amount of cell wall within an annual ring; Lignin %, total relative concentration of lignin of wood dry mass; [a] Variables in F_2 were only measured at BH; [b] Tracheid dimensions and lignin content analysed as a function of distance from the pith (Eq. 1B in **V**); [c] Tracheid dimensions analysed as a function of calendar year (Eq. 1A in **V**); [d] Tracheid dimensions above BH were only measured from four trees grown in F_0T_0 (two trees) and F_1T_2 (two trees) (Eq. 2 in **V**; tracheid dimensions among trees within plot and site analysed for stem height); [e] Lignin content analysed as a function of sample number from the pith (Eq. 1A in **V**).

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5   DISCUSSION AND CONCLUSIONS

5.1 Fertilisation and thinning operations and their impacts on tree growth rate and wood properties

5.1.1 Wood density

In thinning experiments (Heinola and Punkaharju), the radial growth rate of the sample trees at BH was considerably increased (up to 64%) by normal and high thinning intensity compared to low thinning intensity (**I** and **IV**) as calculated over the entire study periods, i.e., 32 and 38 years in Heinola and Punkaharju, respectively. At the same time, normal and high thinning intensity caused a small reduction (2%–4%) in mean ring density compared to low thinning intensity. Also in fertilisation-thinning experiments (Parikkala and Suonenjoki) as averaged over the entire study period (i.e., 24 years), fertilisation (F_1 [150 kg N/ha/5 yrs] and F_2 [300 kg N/ha/5 yrs]; in **II** and **V**) significantly (ca. 40%) increased the annual radial increment of the sample trees compared to the unfertilised plots (F_0), while the ring density on fertilised plots decreased by 7%. In normal and intensive first thinning, the radial growth rate of the sample trees was also higher (by up to 29%) than in delayed first thinning, whereas the reduction in ring density was 2%–4% (**II** and **V**). The increased growth rate affected wood density in a similar manner irrespective of the treatment, i.e., thinning or fertilisation, promoting individual tree growth.

The higher growth rate following long-term thinning and/or N addition in this study was of a similar magnitude as the growth increase reported in many previous studies on various conifer species (Tamm 1991, Gustavsen and Lipas 1975, Kukkola and Saramäki 1983, Valinger et al. 2000, Mäkinen et al. 2002a, Nyakuengama et al. 2002, Kostiainen et al. 2004, Lundgren 2004ab, Mäkinen and Isomäki 2004ab, Brockley 2005). Correspondingly, our results on wood density agree well with the previous findings; many authors have found a relatively small decrease in wood density after a considerable increase in radial growth rate due to thinning and fertilisation of spruce and pine stands (e.g., Klem 1972, Wolcott et al. 1987, Petty et al. 1990, Valinger et al. 2000, Mäkinen et al. 2002b, Mörling 2002, Lundgren 2004b). For instance, Saikku (1975b) found a 26% increase in volume increment with 4% decrease in wood density during the five-year post-fertilisation period in Norway spruce stands (age of the stands varied between 10 and > 95 years). Similarly for 56-year old Scots pine, Mörling (2002) found no significant change in wood density after a 14% and 40% increase in mean ring width during the 12-year period after thinning and fertilisation, respectively. For 34-year old Scots pine, Peltola et al. (2007) reported that heavy thinning (post-thinning stand density < 1000 stems ha^{-1}) resulted in 9%–20% higher radial growth rate, but only 0%–4% lower wood density as compared to moderate thinning (post-thinning stand density 1000–2000 stems ha^{-1}) during a 12-year post-thinning period.

In the nutrient optimisation trials of Norway spruce in Sweden, Mäkinen et al. (2002b) and Lundgren (2004b) demonstrated the potential growth increase and the resultant decrease in wood density of 40-year old Norway spruce during the 12-year period of treatment. They found a reduction of ca. 20% in wood density following a higher increase (100%–200%) in radial increment after nutrient addition. However, the nutrient additions applied in commercial forestry, like those used in this thesis, increase tree growth rate and decrease wood quality considerably less (Mäkinen et al. 2002a).

The results of this thesis are based on long-term data (study periods of 24–38 years in different thinning and fertilisation experiments) while many of the above-mentioned, previously reported results on growth rate and wood density had been based on shorter-term data. Thus, the results obtained in this thesis may be considered as more representative in terms of the effects of repeated thinning and fertilisation on growth rate and concurrent changes in wood properties throughout the stand rotation.

In thinning experiments in Heinola and Punkaharju, the decrease in wood density was due to increased production of earlywood relative to the proportion of latewood (cf., Hakkila 1966, Smith 1980, Zhang et al. 1996, Mäkinen et al. 2002b). In contrast in fertilisation-thinning experiments in Parikkala and Suonenjoki, only small differences in the proportion of latewood were found among different fertilisation and thinning treatments. The decrease in ring density following thinning and/or fertilisation was mainly due to a decrease in earlywood density. Also latewood density was slightly decreased with increasing treatment intensity, but the differences among the treatments were not significant. The decrease both in early- and latewood density after increased tree growth rate has been reported in some previous studies on conifers (e.g., Zhang et al. 1996, Borders et al. 2004, Alteyrac et al. 2005, Mäkinen et al. 2002b).

Wood density is closely linked to many mechanical wood properties, e.g., strength and stiffness. Saranpää and Repola (2001) reported that the MOR of mature Norway spruce grown in monocultures and mixed stands in Finland, Sweden and Norway increased linearly with increasing wood density and decreased with increasing ring width. The MOE was also dependent on wood density, but the relationship was weaker than in the case of MOR (Saranpää and Repola 2001). In their study, the average weight density of wood was 462 kg m^{-3}, the MOR 82.3 MPa and the MOE 12.6 GPa (Saranpää and Repola 2001). In this study, the average ring density (i.e., weight density) of wood varied from 481 kg m^{-3} to 569 kg m^{-3} between the treatments (i.e., low, normal and high thinning intensity in Heinola and Punkaharju, and F_0, F_1, F_2, T_0, T_1 and T_2 in Parikkala and Suonenjoki) as calculated over the whole study periods, indicating that the strength properties of this material were most likely within the range of values reported for spruce (Kliger et al. 1995, Zhang 1995, Saranpää and Repola 2001, Raiskila et al. 2006). However, growth rate may have a larger impact on mechanical properties than on wood density (Zhang 1995). Therefore, the effect of growth rate on mechanical properties cannot be entirely evaluated through the relationship between wood density and growth rate (Kliger et al. 1995, Zhang 1995). Moreover, wood density alone is not always a good indicator of mechanical properties of timber; the end-use potential of timber is also dependent on the integration of other factors, such as knots, grain angle, microfibril angle, as well as the proportion of juvenile wood (Perstorper et al. 2001, Macdonald and Hubert 2002).

5.1.2 Tracheid properties

Both in thinning experiments (Heinola and Punkaharju, **IV**) and fertilisation-thinning experiments (Parikkala and Suonenjoki, **V**), the differences in tracheid length, cell wall thickness and lumen diameter were small (0%–17%) between different thinning and fertilisation treatments. A faster growth rate due to intensive thinning and/or N addition slightly decreased tracheid length (Fig. 8) and cell wall thickness (Fig. 9), and somewhat changed lumen diameter. The proportion of the cell wall within an annual ring was slightly (2%–9%) lower in faster-growing trees than in slower-growing ones. The effects of higher growth rate on tracheid properties were of a similar magnitude irrespective of the treatment,

i.e., thinning or fertilisation, accelerating tree growth. In fertilisation-thinning experiments, the effects of fertilisation and thinning on tracheid properties varied among the treatment combinations.

In many previous studies, the faster growth rate of conifers has resulted in the formation of shorter tracheids with a larger diameter and a wider lumen, but thinner cell walls (e.g., Helander 1933, Denne 1973, Herman et al. 1998a, Sirviö and Kärenlampi 2001ab, Mäkinen et al. 2002a, Lundgren 2004a). Herman et al. (1998a) reported that the tracheid length of Norway spruce decreased by 2.5% when ring width increased by 56% after heavy thinning. According to Mäkinen et al. (2002a), Norway spruce tracheids were 17% shorter when ring width was tripled after nutrient optimisation. For the same Norway spruce stems, Mäkinen et al. (2002a) found a 12% increase in tracheid diameter while the cell walls were thinner and lumens wider. However, the differences in tracheid dimensions diminished when examined as a function of distance from the pith instead of calendar year (Mäkinen et al. 2002a).

Some contradictory results on the relationship between radial growth rate and tracheid dimensions in Norway spruce have also been reported. Bergqvist et al. (2000) found that the tracheid length of Norway spruce growing under birch shelterwood decreased with decreasing growth rate, and was shortest for suppressed trees. According to Zobel and van Buijtenen (1989), tracheid length is correlated with shoot length, with suppressed trees having shorter shoots and tracheids than dominant trees. Brix and Mitchell (1980) found for Douglas fir that cell wall thickness of earlywood increased due to the faster growth rate after thinning. In the same study, fertilisation and combined fertilisation-thinning treatments decreased the cell wall thickness of latewood (Brix and Mitchell 1980). In the studies of Kilpeläinen et al. (2003, 2005), elevated temperature (2–6 °C > ambient) increased the tracheid length of juvenile Scots pine trees by 5%–15% while the radial growth rate increased by 19%–47% as compared to control trees.

The development of wood properties is a complex process that is controlled by multiple factors – genetics, environment, maturation processes, and the size and the status of the tree in a stand (e.g., Bowyer et al. 2007). Both in thinning and fertilisation-thinning experiments, tracheid dimensions were strongly related to the distance from the pith, i.e., the radial and vertical variation in tracheid properties was controlled by cambial maturation as trees grew in diameter (Olesen 1978, Mitchell and Denne 1997, Sirviö and Kärenlampi 2001b, Mäkinen et al. 2002a). In this thesis, the differences in tracheid dimensions found between the trees from different thinning and fertilisation treatments were smaller than the inherent variation in tracheid dimensions from the pith outwards within individual stems. For instance, the average tracheid length varied from 3.4 mm to 4.3 mm between the different treatments as calculated over the entire study periods. Within the stem, the average tracheid length of Norway spruce normally increases from 1 to 5 mm from the pith towards the cambium (e.g., Helander 1933, Atmer and Thörnqvist 1982, Molteberg and Høibø 2006). Thus, the magnitude of changes in tracheid length between slow- and fast-growing trees of this thesis was within the range of changes between juvenile and mature wood. In addition, there was a large random variation in tracheid dimensions both between and within annual rings and trees. The effects of forest management practices on wood and tracheid properties are intricate and difficult to interpret in northern long-rotation forestry. Therefore, long-term studies, as in this thesis, provide more reliable information on the effects of repeated thinning and fertilisation treatments over the entire rotation.

Even though tracheid length and tracheid cross-sectional dimensions, i.e., tracheid width and cell wall thickness, have a decisive role in pulping and papermaking, it is difficult to quantify the effect of a single tracheid property on pulping since different tracheid properties may

counteract each other (Tyrväinen 1995, Lundgren 2003). For instance, in thermomechanical pulping, long fibres give high tear strength but low printability and poorer paper formation (i.e., physical characteristics of paper, e.g., the consistency in thickness and the squareness of the sheet, determined by the structure and orientation of fibres during the paper formation process), whereas short fibres result in good paper smoothness and opacity, but low tear strength (Tyrväinen 1995). In addition, mechanical and chemical pulping processes have different requirements for raw material quality (Paavilainen 1993, Tyrväinen 1995).

Pulpwood assortments, e.g., wood from first thinnings, from final cuttings, and sawmill chips, can differ greatly in end-product quality (Tyrväinen 1995, Persson et al. 2003). Wood from first thinnings with a high proportion of juvenile wood has been shown to give pulp of good optical properties but lower tear strength and higher energy consumption (Persson et al. 2003). Sawmill chips give higher tear strength and require less energy, but result in inferior optical properties (Persson et al. 2003).

5.1.3 Lignin content

Lignin content was slightly (1%–2%) higher for fertilised (F_1 and F_2) than for unfertilised (F_0) trees (25.8% and 26.0% vs. 25.4% DW, respectively). After normal (T_1) and intensive first thinning (T_2), the lignin content of the sample trees was 2% higher than in delayed first thinning (T_0) (26.0% and 25.9% vs. 25.4% DW, respectively).

Our results on lignin content are in accordance with earlier results. In nutrient-optimisation trials in Sweden, the lignin content was slightly higher (7%) after a considerable increase (100%–200%) in the radial growth rate (Anttonen et. al 2002). Accordingly, the 23% increase in the radial growth rate following nutrient optimisation was accompanied by a small (2%) increase in the lignin content (Kostiainen et al. 2004). In contrast in the long-term fertilisation experiments in southern (Heinola) and northern (Kemijärvi) Finland, the growth increase was not as high as in nutrient optimisation and no increase in lignin content was found (Kaakinen et al. 2007).

Since the lignin content is higher in the middle lamella than in the secondary cell wall, the increased lignin content after rapid growth rate may be due to decreased cell wall thickness (Berlyn and Mark 1965, Fengel and Wegener 1989, Gindl 2001). The increased proportion of earlywood compared to that of latewood may also result in increased lignin content since earlywood tracheids have higher lignin and lower cellulose content than latewood tracheids (Fukazawa and Imagawa 1981, Gindl 2001, Bertaud and Holmbom 2004).

In general, high lignin content is undesirable for pulping processes since it increases the demand for chemicals and energy and decreases the pulp yield. A small variation in lignin content (25.4%−26.0% of DW) found in this study among different fertilisation and thinning treatments is most likely of minor importance for pulping. Furthermore, the concurrent growth gains after thinning/N addition more than compensate for the small increase in lignin content.

5.2 Aspects of long-term thinning and fertilisation experiments

The material of this study was collected from two long-term thinning and two long-term fertilisation-thinning experiments established by the Finnish Forest Research Institute in the 1960s and 1970s. Most previous studies on radial growth rate and wood properties have been based on shorter-term sample plots without information on previous management

history. Longer-term, permanent sample plots can provide more accurate information on the long-term effects of environmental factors and management practices on wood properties. In this study, the stand development and forest management operations have already been recorded for over 30 years, and the stands are approaching maturity. This made it possible to investigate the tree growth rate and wood and tracheid properties throughout the whole stand rotation period.

All the data utilised in this thesis was collected from southern and central Finland. Thus, the material covered the most important geographical regions with respect to wood production in Finland. However, it is difficult to generalise the findings of this thesis to the trees grown under different environmental conditions (cf. Peltola et al. 2002). The results should not be applied in northern Finland. Moreover, the results of this thesis are not applicable to peatland since all the material was collected from stands on mineral soil. Furthermore, only one level of site fertility, classified as *Oxalis-Myrtillus* forest site type, was included.

The thinning experiments (Heinola and Punkaharju; **I**, **IV**) were originally planned to study the effects of heavy and seldom-repeated thinnings on growth and yield (Vuokila 1983). However, the thinning intensity in forest practice has considerably increased in recent decades. The highest thinning intensity used in this study equals the intensity of thinning operations currently carried out in Finland (Tapio 2006; Fig. 5). In fertilisation-thinning experiments (Parikkala and Suonenjoki; **II**, **III**, **V**), the original idea was to study the effects of timing and intensity of first commercial thinning and fertilisation on growth and yield throughout the stand rotation. At the time of treatment onset in the 1970s, the intensive first thinning (T_2) was considered extremely intensive. According to the current recommendations for practical forestry, the T_2-treatment is regarded as relatively intensive even nowadays (Tapio 2006; Fig. 5C).

Although the thinning experiments in Heinola and Punkaharju followed the same original idea, the stand age and the timing of the treatment onset differed between them. In Heinola at the onset of the thinning experiment (1970), the stand had already passed the phase of the first commercial thinning. In contrast in Punkaharju at the onset of the experiment (1964), the stand was at the stage of first thinning. Therefore in the analysis, Heinola and Punkaharju were regarded as independent experiments instead of treating them as parallel. The number of sample trees per treatment was thus small (5, 4 and 3 trees in low, normal and high thinning intensity in both experiments).

The fertilisation-thinning experiments in Parikkala and Suonenjoki had been established in consecutive years (in 1977 and 1978, respectively) and they both comprised nine treatment combinations. The plots with similar treatment combinations in Parikkala and Suonenjoki were treated as parallel plots, and thus the number of sample trees in each treatment level (i.e., 30 trees in F_0, F_1, T_1, T_2, and 25 trees in T_0 and F_2) was larger. In Suonenjoki, plot F_2T_0 was not included since it had been completely damaged by wind. This may have caused a small bias in determining the effects of fertilisation (F_2) and delayed first thinning (T_0) on wood and tracheid properties.

Regarding the population sizes used in conventional studies of forest growth and yield, it is clear that the number of sampled trees in this thesis (altogether 109 trees) is relatively small. However, no other detailed data exists on the long-term effects of fertilisation and thinning on wood and tracheid properties of Norway spruce in Finland. Moreover, all the material from different experiments in this thesis was measured with identical methods. The resolution of the analysis was high, i.e., measurements were carried out at the level of individual rings and tracheids, making it possible to study the radial and vertical variation of wood and tracheid properties within the stem.

The impact of thinning and fertilisation on wood formation and tracheid properties depends on the status of the tree in a stand. Many previous studies have reported a higher absolute, but lower relative growth rate for the dominant and co-dominant trees compared to suppressed and intermediate ones (e.g., Pape 1999b, Mäkinen and Isomäki 2004ab, Peltola et al. 2007). For Scots pine, Peltola et al. (2007) found that trees from different crown classes differed in their growth rate and wood density, and these differences were related to thinning intensity. As compared to moderate thinning intensity, intensive thinning increased the radial growth of the larger trees by 9%, while the growth of the smaller trees increased by 20% (Peltola et al. 2007). The relatively higher growth rate in smaller trees was accompanied by a 3.8% decrease in mean wood density, while the corresponding decrease in larger trees was 0.5% (Peltola et al. 2007). These decreases in wood density were comparable to those detected in this thesis following intensive thinning.

In this thesis, thinning and fertilisation affected the radial growth rate and wood density in all tree size-classes in Parikkala and Suonenjoki (except size-class 3 in the case of radial growth), while the relative effects of thinning and fertilisation on growth rate and wood density were largest in the smallest trees. However, in this thesis, the sampling of the trees from different tree size-classes in the different thinning intensities was carried out based on the cumulative stand basal area at the end of the treatment period. Due to repeated thinnings, the available range of tree sizes in the plots of different thinning intensities varied at the end of treatment. That is, thinning intensity directed the sampling: the higher the thinning intensity, the larger the trees available for sampling within each tree size-class. This selection process may have contributed to the detected differences in growth rate and wood properties between different thinning treatments (cf. Pape 1999a). On the other hand, the use of a tree-wise covariate (the mean value of the measured variable in the wood formed prior to the treatment onset) should have reduced the effect of the selection process on the measured variables. Moreover, the effects of fertilisation on growth rate and wood properties were detected based on all the plots including the same intensity of fertilisation, i.e., the effect of fertilisation level F_1 is averaged over the plots of all different thinning intensities (i.e., F_1T_0, F_1T_1 and F_1T_2). Furthermore, the objective of this thesis was to study the differences between the trees left in the stand at the time of final felling. Considering this, the sampled trees are representative of the different tree size-classes in different thinning treatments at the time of final felling.

Other factors altering the impact of thinning and fertilisation on wood formation are, e.g., the intensity, timing and type of silvicultural treatment, site fertility, crown closure, the genetic origin of the tree, and the position in the stem. In this study, some of these factors could not be thoroughly taken into account. Thus, further studies are still needed in order to more completely understand the variation in wood and tracheid properties. Incorporating climatic variables (i.e., the annual and monthly variation in temperature and precipitation) in future studies could possibly diminish the large residual variation found among individual trees and annual rings.

5.3 Conclusions and future prospects

The demand for wood, both as a raw material of the forest industry and as a source of energy, is growing (Finnish Forest Industries Federation 2006, Finnish Government 2007). More intensive forest management and shorter rotations have been suggested to ensure the timber supply in future.

In this thesis, it was shown that the prevailing thinning and fertilisation treatments of Norway spruce stands in Finland considerably increased the radial growth rate of the trees, but resulted in only minor changes in wood density, tracheid properties and lignin content. The magnitude of the effects of faster growth rate on wood and tracheid properties was similar irrespective of the treatment, i.e., thinning or fertilisation, promoting tree growth. The data of this thesis were obtained from long-term experiments over the entire stand rotation; the results thus support the findings of earlier shorter-term studies indicating that increased growth rate of Norway spruce causes only minor changes in wood density and tracheid properties.

However, the treatments in this thesis were not extremely intensive. More information is thus required in order to quantify the effects of more intensive forest management on tree growth rate and wood quality with respect to different wood end-uses. For instance, trees being grown for sawn timber and pulpwood may have different threshold growth rates after which the advantages of increased growth rate no longer offset the disadvantages related to the modified wood properties. The impacts of intensive thinning and fertilisation on properties other than those studied in this study, e.g., stem form, branchiness, as well as the uniformity of the wood, should be evaluated against the wood end-use potential.

Not only the intensity, but also the timing of forestry practices has a major influence on wood properties. One serious problem related to faster growth rate and shorter rotations is the higher proportion of juvenile wood in the stem (e.g., Bowyer et al. 2007). The difference in wood properties between juvenile and mature wood, i.e., change from the pith towards the bark, is the main source of variation within the stem (e.g., Saranpää 1994); this was also shown in this thesis. Juvenile wood adversely affects especially the strength properties of solid wood products (e.g., Passialis and Kiriazakos 2004). Intensive silvicultural treatments may also result in an increased amount of compression wood, especially in the juvenile core (Timell 1986). Thinning and fertilisation should therefore be carried out after the completion of the juvenile period. Intensive thinning and fertilisation have also less impact on older stands than on younger stands (Saranpää 2003).

Under Nordic conditions, other problems than the share of juvenile wood are also related to faster growth rate and intensive management practices. For instance, silvicultural issues associated with e.g., windfalls (also in this thesis, one plot with intensive first thinning was damaged by the wind) and snow damage, and quality questions such as (micro) checking of sawn timber as a result of wider annual rings are of at least equal importance.

In addition to environmental control, genetics plays a major role in determining wood and tracheid properties. In this thesis, wood density and tracheid properties were highly variable among individual trees indicating high between-tree genetic variation. Since most wood properties have high heritability values, considerable improvement of both yield and quality of wood may be attained by the means of tree breeding in the future (e.g., Bowyer et al. 2007). The engineering of superior trees by the means of modern biotechnology, i.e., genetically modified trees (Chen et al. 2001, Corson 2002), is, however, a hot political issue.

The potential wood production and growth rate of Norway spruce trees in the temperate and boreal climate is shown to be considerably higher than the current yields (Bergh et al. 2005). It has also been suggested that the production of log-sized stems as fast as possible with high thinning intensities and repeated fertilisations would be the most profitable silvicultural regime on relatively fertile sites. The profitability of different forestry practices depends, however, on timber prices, costs of silvicultural practices, and the applied discount rate. The profitability of different silvicultural regimes in relation to their effects on wood quantity and quality depends also on the future needs in the wood-conversion chain.

REFERENCES

Aarne, M. 2006. Forest industries. In: Peltola, A. (ed.). The Finnish statistical yearbook of forestry 2006. The Finnish Forest Research Institute, Helsinki. p. 289–308.

Abe, H. & Funada, R. 2005. Review – The orientation of cellulose microfibrils in the cell walls of tracheids in conifers. A model based on observations by field emission-scanning electron microscopy. IAWA J. 26(2): 161–174.

—, Funada, R., Ohtani, J & Fukazawa, K. 1997. Changes in the arrangement of cellulose microfibrils associated with the cessation of cell expansion in tracheids. Trees 11: 328–332.

Aloni, R.A. 2001. Intrinsic regulation of cambial growth. J. Plant Growth Regul. 20: 52–77.

— & Zimmermann, M.H. 1983. The control of vessel size and density along the plant axis – a new hypothesis. Differentation 24: 203–208.

Alteyrac, J., Zhang, S.Y., Cloutier, A. & Ruel, J.-C. 2005. Influence of stand density on ring width and wood density at different sampling heights in black spruce (*Picea mariana* (MILL.) B.S.P.). Wood Fiber Sci. 37(1): 83–94.

Antonova, G.F. & Stasova, V.V. 1993. Effects of environmental factors on wood formation in Scots pine stems. Trees 7: 214–219.

— & Stasova, V.V. 1997. Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. Trees 11: 462–468.

—, Cherkashin, V.P., Stasova, V.V. & Varaksina, T.N. 1995. Daily dynamics in xylem cell radial growth of Scots pine (*Pinus sylvestris* L.). Trees 10: 24–30.

Anttonen, S., Manninen, A.-M., Saranpää, P., Kainulainen, P., Linder, S. & Vapaavuori, E. 2002. Effects of long-term nutrient optimisation on stem wood chemistry in *Picea abies*. Trees 16: 386–394.

Atmer, B. & Thörnqvist, T. 1982. The properties of tracheids in spruce (*Picea abies* Karst.) and pine (*Pinus sylvestris* L.). The Swedish university of agricultural sciences, department of forest products. Reports No. 134. 59 p. (in Swedish with English summary).

Bailey, I.W. 1920. The cambium and its derivative tissues. II. Size variations of cambial initials in gymnosperms and angiosperms. Am. J. Bot. 7(9): 355–367.

— 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium. Am. J. Bot. 10(9): 499–509.

— & Shepard, H.B. 1915. Sanio's laws for the variation in size of coniferous tracheids. Bot. Gaz. 60(1): 66–71.

Bannan, M.W. 1950. The frequency of anticlinal divisions in fusiform cambial cells of *Chamaecyparis*. Am. J. Bot. 37: 511–519.

— 1963. Cambial behavior with reference to cell length and ring width in *Picea*. Can. J. Bot. 41: 811–822.

— 1965. The rate of elongation of fusiform initials in the cambium of *Pinaceae*. Can. J. Bot. 43: 429–435.

— 1967. Sequential changes in rate of anticlinal division, cambial cell length, and ring width in the growth of coniferous trees. Can. J. Bot. 45: 1359–1369.

— 1968. Anticlinal divisions and the organization of conifer cambium. Bot. Caz. 129(2): 107–113.

Barbour, R.J., Bailey, R.E. & Cook, J.A. 1992. Evaluation of relative density, diameter growth, and stem form in a red spruce (*Picea rubens*) stand 15 years after precommercial thinning. Can. J. For. Res. 22: 229–238.

Barnett, J.R. 2004. Xylem physiology. In: Burley, J., Evans, J. & Youngquist, J.A. (eds.). Encyclopedia of Forest Sciences. Elsevier Academic Press, Oxford, San Diego, California. p. 1583–1590.

— & Bonham, V.A. 2004. Cellulose microfibril angle in the cell wall of wood fibres. Biol. Rev. 79(2): 461–472.

Bergh, J., McMurtrie, R.E. & Linder, S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. For. Ecol. Manage. 110: 127–139.

—, Linder, S. & Bergström, J. 2005. Potential production of Norway spruce in Sweden. For. Ecol. Manage. 204(1): 1–10.

Berglund, A., Brelied, H., Rindby, A. & Engström, P. 1999. Spatial distribution of metal ions in spruce wood by synchrotron radiation microbeam X-ray florescence analysis. Holzforschung 53(5): 474–480.

Bergqvist, G., Bergsten, U. & Ahlqvist, B. 2000. Fibre properties of Norway spruce of different growth rates grown under birch shelterwoods of two densities. Can. J. For. Res. 30: 487–494.

Berlyn, G.P. & Mark, R.E. 1965. Lignin distribution in wood cell walls. For. Prod. J. 15: 140–141.

Bertaud, F. & Holmbom, B. 2004. Chemical composition of earlywood and latewood in Norway spruce heartwood, sapwood and transition wood. Wood Sci. Technol. 38: 245–256.

Bishopp, A., Mähönen, P. & Helariutta, Y. 2006. Signs of change: hormone receptors that regulate plant development. Development 133: 1857–1869.

Bisset, I.J.W. & Dadswell, H.E. 1950. The variation in cell length within one growth ring of certain angiosperms and gymnosperms. Australian Forestry 14: 17–29.

—, Dadswell, H.E. & Wardrop, A.B. 1951. Factors influencing tracheid length in conifer stems. Australian Forestry 15(1): 17–30.

Borders, B.E., Will, R.E., Markewitz, D., Clark, A., Hendrick, R., Teskey, R.O. & Zhang, Y. 2004. Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia. For. Ecol. Manage. 192: 21–37.

Bouriaud, O., Leban, J.-M., Bert, D. & Deleuze, C. 2005. Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Phys. 25(6): 651–660.

Bowyer, J., Shmulsky, R. & Haygreen, J.G. 2007. Forest products and wood science: an introduction. Blackwell Publishing Ltd., Oxford, UK. 558 p.

Brändström, J. 2001. Micro- and ultrastructural aspects of Norway spruce tracheids: a review. IAWA J. 22(4): 333–353.

Brix, H. 1972. Nitrogen fertilization and water effects on photosynthesis and earlywood-latewood production in Douglas fir. Can. J. For. Res. 2(4): 467–478.

— & Mitchell, A.K. 1980. Effects of thinning and nitrogen fertilization on xylem development in Douglas-fir. Can. J. For. Res. 10: 121–128.

Brockley, R.P. 2005. Effects of post-thinning density and fertilization on the growth and development of young lodgepole pine. Can. J. For. Res. 35: 1952–1964.

Brolin, A., Norén, A. & Ståhl, E.G. 1995. Wood and pulp characteristics of juvenile Norway spruce: A comparison between a forest and an agricultural stand. Tappi 78: 203–214.

Brown, C.L. 1970. Physiology of wood formation in conifers. Wood Sci. 3: 8–22.

Brown R.M., Saxena, I.M. & Kudlicka, K. 1996. Cellulose biosynthesis in higher plants. Trends in plant science 1(5): 149–156.

Burdon, R.D., Kibblewhite, R.P., Walker, J.C.F., Megraw, R.A., Evans, R. & Cown, D.J. 2004.

Juvenile versus mature wood: a new concept, orthogonal to corewood versus outerwood, with special reference to *Pinus radiata* and *P. taeda*. Forest Science 50(4): 399–415.

Butterfield, B.G. 1993. The structure of wood: an overview. In: Walker, J.C.F. Primary wood processing. Principles and practise. Chapman & Hall, London-Glasgow-New York-Tokyo-Melbourne-Madras. p. 1–22.

— 2003. Wood anatomy in relation to wood quality. In: Barnett, J.R. & Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing Ltd, Oxford, UK. p. 30–52.

Cajander, A.K.J. 1909. Ueber Waldtypen. Simelii Arfvingars Boktryckeriaktiebolag, Helsingfors, Finland. (in German). 175 p.

Cameron, A.D., Lee, S.J., Livingston, A.K. & Petty, J.A. 2005. Influence of selective breeding on the development of juvenile wood in Sitka spruce. Can. J. For. Res. 35: 2951–2960.

Carlsbecker, A. & Helariutta Y. 2005. Phloem and xylem specification: pieces of the puzzle emerge. Curr. Opin. Plant Biol. 8: 512–517.

Cave, I.D. 1968. Anisotropic elasticity of the plant cell wall. Wood Sci. Technol. 2: 268–278.

Chaffey, N. 1999. Cambium: old challenges – new opportunities. Trees 13: 138–151.

— 2000. Cytoskeleton, cell walls and cambium: new insights into secondary xylem differentiation. In: Savidge, R.A., Barnett, J.R. & Napier, R. (eds.). Cell and molecular biology of wood formation. BIOS Scientific publishers Ltd, Oxford, UK. p. 31–42.

Chen, C., Baucher, M., Christensen, J.H. & Boerjan, W. 2001. Biotechnology in trees: towards improved paper pulping by lignin engineering. Euphytica 118: 185–195.

Corson, S.R. 2002. Fibre — redefining the boundaries. Paperi ja Puu – Paper and Timber 84: 20–25.

Côté, W.A. Jr. 1967. Wood ultrastructure: An atlas of electron micrographs. University of Washington Press, Seattle. 62 p.

Cousins, S.K. & Brown, R.M. 1995. Cellulose I microfibril assembly: computational molecular mechanics energy analysis favours bonding by van der Waals forces as the initial step in crystallization. Polymer 36: 3885–3888.

Creber, G.T. & Chaloner, W.G. 1984. Influence of environmental factors on the wood structure of living and fossil trees. Bot. Rev. 50(4): 357–447.

Cregg, B.M., Dougherty, P.M. & Hennessey, T.C. 1988. Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. Can. J. For. Res. 18(7): 851–858.

Da Silva Perez, D. & Fauchon, T. 2003. Wood quality for pulp and paper. In: Barnett, J.R. & Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing Ltd, Oxford, UK. p. 157–186.

Danborg, F. 1994. Density variation and demarcation of the juvenile wood in Norway spruce. Danish Forest and Landscape Research Institute, Forskningserien Nr. 10: 1–78.

Decoux, V., Varcin, E. & Leban, J.-M. 2004. Relationships between the intra-ring wood density assessed by X-ray densitometry and optical anatomical measurements in conifers. Consequences for the cell wall apparent density determination. Ann. For. Sci. 61: 251–262.

Dence, C.W. 1992. The determination of lignin. In: Lin, S.Y. & Dence, C.W. (eds.). Methods in lignin chemistry. Springer-Verlag, Heidelberg. p. 33–61.

Denne, M.P. 1973. Tracheid dimensions in relation to shoot vigour in *Picea*. Forestry 46(2): 117–124.

— 1989. Definition of latewood according to Mork (1928). IAWA Bull. New Ser. 10: 59–

48

62.

Deslauriers, A. & Morin, H. 2005. Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees 19: 402–408.

—, Morin, H., Urbinati, C. & Carrer, M. 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). Trees 17: 477–484.

Dinwoodie, J.M. 1961. Tracheid and fibre length in timber. A review of literature. Forestry 34:125–144.

— 1966. Growth stresses in timber – A review of literature. Forestry 39(2): 162–170.

Dodd, R.S. & Fox, P. 1990. Kinetics of tracheid differentiation in Douglas-fir. Ann. Bot. 65: 649–657.

Domec, J-L. & Gartner, B.L. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? J. Exp. Bot. 53(379): 2369–2379.

Duff, G.H. & Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa* Ait. Can. J. Bot. 13: 471–513.

Dutilleul, P., Herman, M. & Avella-Shaw, T. 1998. Growth rate effects on correlations among ring width, wood density, and mean tracheid length in Norway spruce (*Picea abies*). Can. J. For. Res. 28: 56–68.

Eriksson, H. & Karlsson, K. 1997. Effects of different thinning and fertilization regimes on the development of Scots pine (*Pinus sylvestris* (L.)) and Norway spruce (*Picea abies* (L.) Karst.) stands in long-term silvicultural trials in Sweden. Report 42. Swedish University of Agricultural Sciences, Department of Forest Yield Research. 135 p.

Eschrich, W. & Blechschmidt-Schneider, S. 1992. Extrinsic and intrinsic influences on tree growth – anatomical analysis of spruce branches. Trees 6: 179–185.

Fengel, D. 1969. The ultrastructure of cellulose from wood. Part I: Wood as the basic material for the isolation of cellulose. Wood Sci. Technol. 3: 203–217.

— 1976. Structure of native celluose. Chemische und elektronenmikroskopische Untersuchungen an schonend isolierten Nadelholzlignin. Holzforschung 30: 1–6. (in German with English summary).

— & Stoll, M. 1973. On the variation of the cell cross area, the thickness of the cell wall and of the wall layers of sprucewood tracheids within an annual ring. Holzforschung 27(1): 1–7. (in German with English summary).

— & Wegener, G. 1989. Wood: Chemistry, Ultrastructure, Reactions. Walter de Gruyter, New York. 613 p.

Finnish Forest Industries Federation. 2006. Finnish Forest Industries Yearbook 2006. [Online publication]. Available from: http://www.metsateollisuus.fi/files/julkaisut/pdf/32023_Metsateollisuus_vk_GB.pdf. [Cited 20 April 2007].

Finnish Government. 2007. Government Programme 2007, Prime Minister Matti Vanhanen's second Cabinet, published 19 April 2007. [Online publication]. Available from: http://www.valtioneuvosto.fi/hallitus/hallitusohjelma/pdf/ Paeaeministeri_Matti_Vanhasen_II_hallitusohjelma_A4_verkko.pdf. [Cited 20 April 2007].

Franklin, G.L. 1945. Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. Nature (London) 155: 51.

Frimpong-Mensah, K. 1987. Fibre length and basic density variation in the wood of Norway spruce (*Picea abies* L Karst) from northern Norway. Communications of the Norwegian Forest Research Institute 40.1: 1–25.

Fuglem, G., Sabourin, M. & Lundqvist, S.O. 2003. Influence of spruce wood properties

on thermomechanical pulping – pilot scale results. In: Proceedings of International Mechanical Pulping Conference, Quebec City, 2–5 June, 2003. p. 75–82.

Fujiwara, S. & Yang, K.C. 2000. The relationship between cell length and ring width and circumferential growth rate in five Canadian species. IAWA J. 21(3): 335–345.

Fukazawa, K. & Imagawa, H. 1981. Quantitative analysis of lignin using an UV microscopic image analyser. Variation within one growth increment. Wood Sci. Technol. 15: 45–55.

Fukuda, H. 2004. Signals that control plant vascular cell differentiation. Nat. Rev. Mol. Cell Biol. 5: 379–391.

Gartner, B.L. 2005. Assessing wood characteristics and wood quality in intensively managed plantations. J. For. March: 75–77.

Gindl, W. 2001. The effect of varying latewood proportion on the radial distribution of lignin content in a pine stem. Holzforschung 55: 455–458.

— 2002. Comparing mechanical properties of normal and compression wood in Norway spruce: The role of lignin in compression parallel to the grain. Holzforschung 56: 395–401.

—, Grabner, M. & Wimmer, R. 2000. The influence of temperature on latewood lignin content in treeline Norway spruce compared with maximum density and ring width. Trees 14: 409–414.

Gjerdrum, P., Säll, H. & Storø, H.M. 2002. Spiral grain in Norway spruce: constant change rate in grain angle in Scandinavian sawlogs. Forestry 75(2): 163–170.

Gričar, J., Čufar, K., Oven, P. & Schmitt, U. 2005. Differentiation of terminal latewood tracheids in silver fir trees during autumn. Ann. Bot. 95: 959–965.

Gustavsen, H.G. & Lipas, E. 1975. Effect of nitrogen dosage on fertilizer response. Folia For. 246. 20 p. (in Finnish with English summary).

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457–461.

Hakkila, P. 1966. Investigations on basic density of Finnish pine, spruce and birch wood. Commun. Inst. For. Fenn. 61(5): 1–98.

— 1968. Geographical variation of some properties of pine and spruce pulpwood in Finland. Commun. Inst. For. Fenn. 66(8): 1–59.

— 1979. Wood density survey and dry weight tables for pine, spruce and birch stems in Finland. The Finnish Forest Research Institute, Research Papers. 96(3): 1–59.

— 1995. Procurement of timber for the Finnish industries. The Finnish Forest Research Institute, Research Papers 557. 73 p.

— & Uusvaara, O. 1968. On the basic density of plantation-grown Norway spruce. Commun. Inst. For. Fenn. 66(6): 1–22.

Hannrup, B., Danell, Ö., Ekberg, I. & Moëll, M. 2001. Relationships between wood density and tracheid dimensions in *Pinus sylvestris* L. Wood Fiber Sci. 33(2): 173–181.

—, Cahalan, C., Chantre, G., Grabner, M., Karlsson, B., Le Bayon, I., Jones, G.L., Müller, U., Pereira, H., Rodrigues, J.C., Rosner, S., Rozenberg, P., Wilhelmsson, L. & Wimmer, R. 2004. Genetic parameters of growth and wood quality traits in *Picea abies*. Scand. J. For. Res. 19: 14–29.

Harris, J.M. 1989. Spiral grain and wave phenomena in wood formation. Springer-Verlag, Berlin-Heidelberg-New York. 214 p.

Heger, L. 1974. Longitudinal variation of specific gravity in stems of black spruce, balsam fir, and lodgepole pine. Can. J. For. Res. 4(3): 321–326.

Helander, A.B. 1933. Variations in tracheid length of pine and spruce. Foundation for forest

research of Finland. No. 14. 75 p. (in Finnish with English summary).

Henttonen, H. 1984. The dependence of annual ring indices on some climatic factors. Acta For. Fenn., Monograph No. 186. 38 p.

Herman, M., Dutilleul, P. & Avella-Shaw, T. 1998a. Growth rate effects on temporal trajectories of ring width, wood density, and mean tracheid length in Norway spruce (*Picea abies* (L.) Karst.). Wood Fiber Sci. 30(1): 6–17.

—, Dutilleul, P. & Avella-Shaw, T. 1998b. Intra-ring and inter-ring variations of tracheid length in fast-grown versus slow-grown Norway spruce (*Picea abies*). IAWA J. 19(1): 3–23.

Horacek, P., Slezingerova, J. & Gandelova, L. 1999. Effects of environment on the xylogenesis of Norway spruce (*Picea abies* (L.) Karst.). In: Wimmer, R. & Vetter, R.E. (eds.). Tree-ring analysis: biological, methodological and environmental aspects. CABI Publishing, Wallingford. p. 33–53.

Huuskonen, S. & Ahtikoski, A. 2005. Ensiharvennuksen ajoituksen ja voimakkuuden vaikutus kuivahkon kankaan männiköiden tuotokseen ja tuottoon. The effect of the timing and intensity of the first thinning on the wood yield and economic yield of a pine stand on a fairly dry forest site type. Metsätieteen aikakauskirja 2: 99–115. (in Finnish).

— & Hynynen, J. 2006. Timing and intensity of precommercial thinning and their effects on the first commercial thinning in Scots pine stands. Silva Fenn. 40(4): 645–662.

Hylen, G. 1997. Genetic variation of wood density and its relationship with growth traits in young Norway spruce. Silvae Genet. 46: 55–60.

Hynönen, T., Korhonen, K.T. & Tammilehto, E. 1999. Kuusen kasvuhäiriöt Pohjois-Savon kangasmetsissä. Growth disturbances in the heath forests of eastern Finland. Metsätieteen aikakauskirja 3: 577–581. (in Finnish).

Iivonen, S., Kaakinen, S., Jolkkonen, A., Vapaavuori, E. & Linder, S. 2006. Influence of long-term nutrient optimization on biomass, carbon, and nitrogen acquisition and allocation in Norway spruce. Can. J. For. Res. 36(6): 1563–1571.

Ingerslev, M., Mälkönen, E., Nilsen, P., Nohrstedt, H.-Ö., Óskarsson, H. & Raulund-Rasmussen, K. 2001. Main findings and future challenges in forest nutritional research and management in the Nordic countries. Scand. J. For. Res. 16: 488–501.

Ivković, M. & Rozenberg, P. 2004. A method for describing and modelling of within-ring wood density distribution in clones of three coniferous species. Ann. For. Sci. 61: 759–769.

Jackson, F. 1988. Fibre length measurement and its application to paper machine operation. Appita, 41(3): 212–216.

Jacobs, W.P. 1952. The role of auxin in differentiation of xylem around a wound. Am. J. Bot. 39(5): 301–309.

Jalas, J. & Suominen, J. (eds.). 1973. Atlas Florae Europaeae: Distribution of vascular plants in Europe. Vol. 2. Gymnospermae (*Pinaceae* to *Ephedraceae*). Committee for mapping the flora of Europe, Societas Biologica Fennica Vanamo, Helsinki. 40 p.

Jarvis, P. & Linder, S. 2000. Constraints to growth of boreal forests. Nature 405: 904–905.

Johansson, K. 1993. Influence of initial spacing and tree class on the basic density of *Picea abies*. Scand. J. For. Res. 8(1): 18–27.

Juntunen, M.-L. & Herrala-Ylinen, H. 2007. Silviculture. In: Peltola, A. (ed.). The Finnish statistical yearbook of forestry 2007. The Finnish Forest Research Institute, Helsinki. p. 103–150.

Kaakinen, S., Saranpää, P. & Vapaavuori, E. 2007. Effects of growth differences due to geographic location and N-fertilisation on wood chemistry of Norway spruce. Trees

21(2): 131–139.

Kärenlampi, P.P. & Riekkinen, M. 2004. Maturity and growth rate effects on Scots pine basic density. Wood Sci. Technol. 38: 465–473.

—, Suur-Hamari, H., Rantanen, R. & Hämäläinen, T. 1996. Management of softwood kraft pulp quality by wood raw material classification. University of Helsinki, Department of forest resource management publication no. 13. 80 p. (in Finnish with English summary).

KCL. 1982. Massan ja puun kokonaisligniinipitoisuus. Total lignin content of wood and pulp. KCL, Espoo, Finland. 115b. 3 p. (in Finnish).

Kellogg, R.M. & Wangaard, F.F. 1969. Variation in the cell-wall density of wood. Wood Fiber Sci 1: 180–204.

— & Thykeson, E. 1975. Predicting kraft mill paper strength from fiber properties. Tappi 58(4): 131–135.

Kennedy, R.W. 1966. Intra-increment variation and heritability of specific gravity, parallel-to-grain tensile strength, stiffness, and tracheid length, in clonal Norway spruce. Tappi 49: 292–296.

Kerr, T. & Bailey, I.W. 1934. The cambium and its derivative tissues. No. X. Structure, optical properties and chemical composition of the so-called middle lamella. J. Arnold Arbor. 15: 327–349.

Khalil, M.A.K. 1985. Genetics of wood characters of black spruce (*Picea mariana* (Mill.) B.S.P.) in Newfoundland, Canada. Silvae Genet. 34(6): 221–230.

Kilpeläinen, A., Peltola, H., Ryyppö, A. & Kellomäki, S. 2005. Scots pine responses to elevated temperature and carbon dioxide concentration: growth and wood properties. Tree Phys. 25: 75–83.

—, Peltola, H., Ryyppö, A., Sauvala, K., Laitinen, K. & Kellomäki, S. 2003. Wood properties of Scots pine (*Pinus sylvestris*) grown at elevated temperature and carbon dioxide concentration. Tree Phys. 23: 889–897.

Kitin, P., Funada, R., Sano, Y. & Ohtani, J. 2000. Analysis by confocal microscopy of the structure of cambium in the hardwood *Kalopanax pictus*. Annals Botany 86: 1109–1117.

Klein, A.S. & Tibbits, J. 2006. Cellulose synthase genes in conifers: what we know and what we need to learn. In: Hayashi, T. (ed.). The science and lore of the plant cell wall. Biosynthesis, structure, & function. BrownWalker Press, Boca Raton, Florida. p. 276–284.

Klem, G.S. 1972. The influence of fertilization of spruce (*Picea abies* (L.) Karst.) on summerwood percent, specific gravity and extractive content. Reports of the Norwegian Forest Research Institute 122: 283–324.

Kliger, I.R., Perstorper, M., Johansson, G. & Pellicane, P.J. 1995. Quality of timber products from Norway spruce. Part 3. Influence of spatial position and growth characteristics on bending stiffness and strength. Wood Sci. Technol. 29: 397–410.

Koga, S. & Zhang, S.Y. 2004. Inter-tree and intra-tree variations in ring width and wood density components in balsam fir (*Abies balsamea*). Wood Sci. Technol. 38(2): 149–162.

—, Oda, K., Tsutsumi, J. & Fujimoto, T. 1997. Effect of thinning on the wood structure in annual growth rings of Japanese larch (*Larix leptolepis*). IAWA J. 18(3): 281–290.

Kostiainen, K., Kaakinen, S., Saranpää, P., Sigurdsson, B.D., Linder, S. & Vapaavuori, E. 2004. Effect of elevated [CO_2] on stem wood properties of mature Norway spruce grown at different soil nutrient availability. Global Change Biol. 10: 1526–1538.

Koubaa, A., Zhang, S.Y.T. & Makni, S. 2002. Defining the transition from earlywood to latewood in black spruce based on intra-ring wood density profiles from X-ray

densitometry. Ann. For. Sci. 59: 511–518.

Kozlowski, T.T. & Winget, C.H. 1963. Patterns of water movement in forest trees. Bot. Caz. 124(4): 301–311.

Kozlowski, T.T., Kramer, P.J. & Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, California. 657 p.

Kramer, K.U. & Green, P.S. 1990. (eds.). Pteridophytes and gymnosperms. Vol I. In: Kubitzki, K. (ed.). The families and genera of vascular plants. Springer-Verlag, Berlin-Heidelberg-New York. 404 p.

Kučera, B. 1994. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood Fiber Sci. 26(1): 152–167.

Kukkola, M. & Saramäki, J. 1983. Growth response in repeatedly fertilized pine and spruce stands on mineral soils. Commun. Inst. For. Fenn. 114. 55 p.

Larcher, W. 2003. Physiological plant ecology. Ecophysiology and stress physiology of functional groups. 4th ed. Springer, Berlin-Heidelberg-New York-Hong Kong-London-Milan-Paris-Tokyo. 513 p.

Larson, P.R. 1962. The indirect effect of photoperiod on tracheid diameter in *Pinus resinosa*. Am. J. Bot. 49: 132–137.

— 1969. Wood formation and the concept of the wood quality. Bull. Yale Sch. For. 74: 1–54.

— 1994. The vascular cambium. Development and structure. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg-New York. 725 p.

—, Kretschmann, D.E., Clark A. III & Isebrands, J.G. 2001. Formation and properties of juvenile wood in southern pines: a synopsis. Gen. Tech. Rep. FPL-GTR-129. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, Wisconsin. 42 p.

Lee, H.N. & Smith, E.M. 1916. Douglas fir fibre, with special reference to length. For. Quart 14: 671–695.

Leikola, M. 1969. The influence of environmental factors on the diameter growth of forest trees. Auxanometric study. Acta For. Fenn. 92: 24–30.

Lewark, S. 1982. Studies of wood characteristics of young Norway spruce (*Picea abies*) from clonal experiments. Forstarchiv. 53(1): 14–21. (in German with English summary).

Lindström, H. 1996. Basic density in Norway spruce. Part I. A literature review. Wood Fiber Sci. 28: 15–27.

— 1997. Wood variation in young Norway spruce (*Picea abies* (L.) Karst.) created by differences in growth conditions. PhD thesis. Swedish university of agricultural sciences, Department of forest-industry-market-studies, Uppsala, Sweden. 34 p.

Little, C.H.A. & Pharis, R.P. 1995. Hormonal control of radial and longitudinal growth in the tree stem. In: Gartner, B.L. (ed.). Plant stems: Physiology and functional morphology. Academic Press, San Diego, California. p. 281–319.

Lundgren, C. 2003. Wood and fibre properties of fertilized Norway spruce. PhD thesis. Swedish university of agricultural sciences, Department of forest products and markets, Uppsala, Sweden. 33 p.

Lundgren, C. 2004a. Cell wall thickness and tangential and radial cell diameter of fertilized and irrigated Norway spruce. Silva Fenn. 38(1): 95–106.

— 2004b. Microfibril angle and density patterns of fertilized and irrigated Norway spruce. Silva Fenn. 38(1): 107–117.

Luxmoore, R.J., Oren, R., Sheriff, D.W. & Thomas, R.B. 1995. Source-sink-storage relationships of conifers. In: Smith, W.K. & Hinckley, T.M. (eds.). Resource physiology

of conifers. Acquisition, allocation, and utilization. Academic Press, San Diego-New York-Boston-London-Sydney-Tokyo-Toronto. p. 179–216.

Macdonald, R. & Hubert, J. 2002. A review of the effects of silviculture on timber quality of Sitka spruce. Forestry 75(2): 107–138.

Mäkinen, H. & Isomäki, A. 2004a. Thinning intensity and growth of Norway spruce stands in Finland. Forestry 77(4): 349–364.

— & Isomäki, A. 2004b. Thinning intensity and growth of Scots pine stands in Finland. For. Ecol. Manage. 201: 311–325.

—, Nöjd, P. & Mielikäinen, K. 2000. Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland to the Arctic timberline. Can. J. For. Res. 30: 769–777.

—, Saranpää, P. & Linder, S. 2002a. Effect of growth rate on fibre characteristics in Norway spruce (*Picea abies* (L.) Karst.). Holzforschung 56: 449–460.

—, Saranpää, P. & Linder, S. 2002b. Wood-density variation of Norway spruce in relation to nutrient optimization and fibre dimensions. Can. J. For. Res. 32: 185–194.

—, Nöjd, P. & Saranpää, P. 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. Tree Phys. 23: 959–968.

—, Jyske, T. & Saranpää, P. 2008. Variation of tracheid length within annual rings of Scots pine and Norway spruce. Holzforschung 62: 123–128.

Mather, A.S. 1990. Global forest resources. Timber Press, Portland, Oregon. 341 p.

Matson, P., Lohse, K.A. & Hall, S.J. 2002. The globalization of nitrogen deposition: consequences for terrestrial ecosystems. Ambio 31(2): 113–119.

Mauseth, J.D. 1998. Botany. An introduction to plant biology. Jones and Bartlett Publishers, Sudbury, Massachusetts, 1998. 794 p.

Megraw, R.A. 1985. Wood quality factors in loblolly pine. The influence of tree age, position in tree, and cultural practise on wood specific gravity, fiber length, and fibril angle. TAPPI Press, Atlanta, Georgia. 88 p.

Mellerowicz, E.J. 2006. Xylem cell expansion – lesson from poplar. In: Hayashi, T. (ed.). The science and lore of the plant cell wall. Biosynthesis, structure, & function. BrownWalker Press, Boca Raton, Florida. p. 267–275.

—, Baucher, M., Sundberg, B. & Boerjan, W. 2001. Unravelling cell wall formation in a woody dicot stem. Plant Mol. Biol. 47: 239–274.

Mitchell, M.D. & Denne, M.P. 1997. Variation in density of *Picea sitchensis* in relation to within-tree trends in tracheid diameter and wall thickness. Forestry 70: 47–60.

Molteberg, D. & Høibø, O. 2006. Development and variation of wood density, kraft pulp yield and fibre dimensions in young Norway spruce (*Picea abies*). Wood Sci. Technol. 40: 173–189.

Mork, E. 1928. Die Qualität des Fichtenholzes unter besonderer Rücksichtnahme auf Schleif- und Papierholz. Papier-fabrikant 26: 741–747. (in German).

Mörling, T. 2002. Evaluation of annual ring width and ring density development following fertilisation and thinning of Scots pine. Ann. For. Sci. 59: 29–40.

Möttönen, M., Lehto, T., Aphalo, P.J., Kukkola, M. & Mälkönen, E. 2003. Response of mature stands of Norway spruce (*Picea abies*) to boron fertilization. For. Ecol. Manage. 180: 401–412.

Nieminen, K.M., Kauppinen, L. & Helariutta Y. 2004. A weed for wood? Arabidopsis as a genetic model for xylem development. Plant Physiol. 135: 653–659.

Nilsen, P. 2001. Fertilization experiments on forest mineral soils: a review of the Norwegian results. Scand. J. For. Res. 16: 541–554.

Nyakuengama, J.G., Downes, G. & Ng, J. 2002. Growth and wood density responses to later-age fertilizer application in *Pinus radiata*. IAWA J. 23(4): 431–448.

Olesen, P.O. 1976. The interrelation between basic density and ring width of Norway spruce. Det forstlige forsøksvaesen i Danmark 34(4): 339–359.

— 1977. The variation of the basic density level and tracheid width within the juvenile and mature wood of Norway spruce. For. Tree Improv. 12: 1–21.

— 1978. On cyclophysis and topophysis. Silvae Genet. 27: 173–178.

— 1982. The effect of cyclophysis on tracheid width and basic density in Norway spruce. For. Tree Improv. 15: 1–80.

Ollinmaa, P.J. 1959. Study on reaction wood. Acta For. Fenn. 72: 1–54. (in Finnish with English summary).

Otsu, N. 1979. A threshold selection method from grey-level histograms. IEEE Trans. Syst. Man Cybernet. SMC-9: 62–66.

Paavilainen, L. 1993. Conformability – flexibility and collapsibility – of sulphate pulp fibres. Paperi ja Puu – Paper and Timber 75: 689–702.

Page, D.H. 1976. A note on the cell-wall structue of softwood tracheids. Wood Fiber Sci. 7(4): 246–248.

Panshin, A.J. & de Zeeuw, C. 1980. Textbook of wood technology. 4th ed. McGraw-Hill Book Company, New York. 722 p.

Pape, R. 1999a. Effects of thinning regime on the wood properties and stem quality of *Picea abies*. Scand. J. For. Res. 14: 38–50.

— 1999b. Influence of thinning and tree diameter class on the development of basic density and annual ring width in *Picea abies*. Scand. J. For. Res. 14: 27–37.

— 1999c. Influence of thinning on spiral grain in Norway spruce grown on highly productive sites in northern Sweden. Silva Fennica 33(1): 3–12.

Passialis, C. & Kiriazakos, A. 2004. Juvenile and mature wood properties of naturally-grown fir trees. Eur. Jour. For. Res. 62(6): 476–478.

Peltola, A. & Ihalainen, A. 2007. Forest resources. In: Peltola, A. (ed.). The Finnish statistical yearbook of forestry 2007. The Finnish Forest Research Institute, Helsinki. p. 33–74.

—, Kilpeläinen, A. & Kellomäki, S. 2002. Diameter growth of Scots pine (*Pinus sylvestris*) trees grown at elevated temperature and carbon dioxide concentration under boreal conditions. Tree Phys. 22: 963–972.

—, Kilpeläinen, A., Sauvala, K., Räisänen, T. & Ikonen, V.-P. 2007. Effects of early thinning regime and tree status on the radial growth and wood density of Scots pine. Silva Fennica 41(3): 489–505.

Pereira, H., Graça, J. & Rodrigues, J. 2003. Wood chemistry in relation to quality. In: Barnett, J.R. & Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing Ltd, Oxford, UK. p. 53–86.

Persson, E., Engstrand, P., Karlsson, L., Nilsson, F. & Wahlgren, M. 2003. Utilization of the natural variation in wood properties – a comparison between pilot plant and mill scale trials. In: Proceedings of International Mechanical Pulping Conference, Quebec City, 2–5 June, 2003. p. 83–90.

Perstorper, M., Johansson, M., Kliger, R. & Johansson, G. 2001. Distortion of Norway spruce timber. Part 1. Variation of relevant wood properties. Holz Roh-Werkst. 59: 94–103.

Petrić, B. & Šćukanec, V. 1973. Volume percentage of the tissues in wood of conifers grown in Yugoslavia. IAWA Bull. 2: 3–7.

Petty, J.A., Macmillan, D.C. & Steward, C.M. 1990. Variation of density and growth ring width in stems of Sitka and Norway spruce. Forestry 63(1): 39–49.

Philipson, W.R. & Butterfield, B.G. 1967. A theory on the causes of size variation in wood elements. Phytomorphology 17: 155–159.

—, Ward, J.M. & Butterfield, B.G. 1971. The vascular cambium. Its development and activity. Chapman & Hall Ltd, London. 182 p.

Pittermann, J., Sperry, J.S., Hacke, U.G., Wheeler, J.K. & Sikkema, E.H. 2005. Torus-margo pits help conifers compete with angiosperms. Science 310: 1924.

—, Sperry, J.S., Wheeler, J.K., Hacke, U.G. & Sikkema, E.H. 2006. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. Plant, Cell and Environment 29: 1618–1628.

Plomion, C., Leprovost, G. & Stokes, A. 2001. Woof formation in trees. Plant Physiol. 127: 1513–1523.

Raiskila, S., Saranpää, P., Fagerstedt, K., Laakso, T., Löija, M., Mahlberg, R., Paajanen, L. & Ritschkoff, A-C. 2006. Growth rate and wood properties of Norway spruce cutting clones on different sites. Silva Fenn. 40(2): 247–256.

—, Pulkkinen, M., Laakso, T., Fagerstedt, K., Löija, M., Mahlberg, R., Paajanen, L., Ritschkoff, A-C. & Saranpää, P. 2007. FTIR spectroscopic prediction of Klason and acid soluble lignin variation in Norway spruce cutting clones. Silva Fenn. 41(2): 351–371.

Renninger, H.J., Gartner, B.L. & Grotta, A.T. 2006. No correlation between latewood formation and leader growth in Douglas-fir saplings. IAWA J. 27(2): 183–191.

Repola, J. 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. Silva Fenn. 40(4): 673–685.

Roberts, K. & McCann, M. 2000. Xylogenesis: the birth of a corpse. Curr. Opin. Plant Biol. 3: 517–522.

Roberts, L.W. 1988a. Hormonal aspects of vascular differentiation. In: Roberts., L.W., Gahan, P.B. & Aloni, R. (eds.). Vascular differentiation and plant growth regulators. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg-New York-London-Paris-Tokyo. p. 22–38.

— 1988b. Physical factors, hormones, and differentiation. In: Roberts., L.W., Gahan, P.B. & Aloni, R. (eds.). Vascular differentiation and plant growth regulators. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg-New York-London-Paris-Tokyo. p. 89–105.

Roderick, M.L. & Berry, S.L. 2001. Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. New Phytol. 149: 473–485.

Romberger, J.A., Hejnowicz, Z. & Hill, J.F. 1993. Plant structure: Function and development. Springer-Verlag, Berlin-Heidelberg-New York. 524 p.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R. & Borghetti, M. 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol. 170: 301–130.

Rozenberg, P. & Cahalan, C. 1997. Spruce and wood quality: Genetic aspects (A review). Silvae Genet. 46(5): 270–279.

Saarsalmi, A. & Mälkönen, E. 2001. Forest fertilization research in Finland: a literature review. Scand. J. For. Res. 16: 514–535.

— & Tamminen, P. 2005. Boron, phosphorus and nitrogen fertilization in Norway spruce stands suffering from growth disturbances. Silva Fenn. 39(3): 351–364.

—, Kukkola, M., Moilanen, M. & Arola, M. 2006. Long-term effects of ash and N fertilization on stand growth, tree nutrient status and soil chemistry in a Scots pine stand. For. Ecol. Manage. 235: 116–128.

56

Saikku, O. 1975a. The effect of fertilization on the basic density of Scots pine (*Pinus sylvestris* L.). A densitometric study on the X-ray chart curves of the wood. Commun. Inst. For. Fenn. 85: 1–49.

— 1975b. The effect of nitrogen fertilization on the basic density of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies*) and common birch (*Betula verrucosa*). Commun. Inst. For. Fenn. 85(5): 1–24. (in Finnish with English summary).

Samuels, A.L., Kaneda, M. & Rensing, K.H. 2006. The cell biology of wood formation: from cambial divisions to mature secondary xylem. Can. J. Bot. 84: 631–639.

Sanio, K. 1872. Ueber die grösse der holzzellen bei der gemeinen kiefer (*Pinus sylvestris*). Jahrbuch Wissenschaftligen Bot. 8: 401–420. (in German).

Saramäki, J. & Silander, P. 1982. The effect of fertilization and thinning on the crown of pines. Metsäntutkimuslaitoksen tiedonantoja 52. 42 p. (in Finnish with English summary).

Saranpää, P. 1994. Basic density, longitudinal shrinkage and tracheid length of juvenile wood of *Picea abies*. Scand. J. For. Res. 9: 68–74.

— 2003. Wood density and growth. In: Barnett, J.R., Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing Ltd., Oxford, UK. p. 87–117.

— & Repola, J. 2001. Strength of Norway spruce from both mixed stands and monocultures. Finnish Forest Research Institute, Research Papers 822: 33–39.

—, Pesonen, E., Sarén, M., Anderson, S., Siiriä, S., Serimaa, R. & Paakkari, T. 2000. Variation of the properties of tracheids in Norway spruce (*Picea abies* (L.) Karst.). In: Savidge, R.A., Barnett, J.R. & Napier R. (eds.). Cell and molecular biology of wood formation. BIOS Scientific Publishers Limited, Oxford. p. 337–345.

Savidge, R.A. 2000a. Biochemistry of seasonal cambial growth and wood formation – an overview of the challenges. In: Savidge, R.A., Barnett, J.R. & Napier, R. (eds.). Cell and molecular biology of wood formation. BIOS Scientific publishers Ltd, Oxford, UK. p. 1–30.

— 2000b. Intrinsic regulation of cambial growth. J. Plant. Growth Regul. 20: 52–77.

— 2003. Tree growth and wood quality. In: Barnett, J.R. & Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing Ltd, Oxford, UK. p. 1–29.

Savill, P., Evans, J., Auclair, D. & Falck J. 1997. Plantation silviculture in Europe. Oxford University Press, Oxford-New York-Tokyo. 297 p.

Saxena, I.M. & Brown R.M. 2005. Cellulose biosynthesis: current views and evolving concepts. Ann. Bot. 96: 9–21.

Schmitt, U., Jalkanen, R. & Eckstein, D. 2004. Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest in Finland. Silva Fenn. 38(2): 167–178.

Schweingruber, F.H., Börner, A. & Schulze, E-D. 2006. Atlas of woody plants stems: evolution, structure, and environmental modifications. Springer, Berlin-Heidelberg. 229 p.

Siau, J.F. 1984. Transport processes in wood. Springer-Verlag, Berlin-Heidelberg-New York. 245 p.

Sirviö, J. 2001. Variation of cross-sectional properties within single Norway spruce tracheids. Wood Fiber Sci. 33(1): 16–25.

— & Kärenlampi, P. 2000. Two scales of variation in Norway spruce tracheid properties. Wood Fiber Sci. 32(3): 311–331.

— & Kärenlampi, P. 2001a. Fiber property models for Norway spruce trees and logs. Paperi ja Puu – Paper and Timber 83(6): 474–481.

— & Kärenlampi, P. 2001b. The effects of maturity and growth rate on the properties of spruce wood tracheids. Wood Sci. Technol. 35(6): 541–554.

Sjöström, E. 1993. Wood chemistry. Fundamentals and applications. 2nd ed. Academic Press Inc, Sand Diego-New York-Boston. 293 p.

Skaar, C. 1988. Wood-water relations. Springer-Verlag. Berlin-Heidelberg-New York. 283 p.

Smith, J.H.G. 1980. Influences of spacing on radial growth and percentage latewood of Douglas-fir, western hemlock, and western red cedar. Can. J. For. Res. 10: 169–175.

Sundberg, B., Uggla, C. & Tuominen, H. 2000. Cambial growth and auxin gradients. In: Savidge, R.A., Barnett, J.R. & Napier, R. (eds.). Cell and molecular biology of wood formation. BIOS Scientific publishers Ltd, Oxford, UK. p. 169–188.

Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P., Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., Huttula, T., Laurila, T. Aurela, M., Grelle, A., Lindroth, A., Arneth A., Shibistova, O. & Lloyd, J. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. Glob. Chang. Biol. 9: 1410–1426.

Taiz, L. & Zeiger, E. 1991. Plant physiology. The Benjamin/Cumming Publishing Company, Inc., Redwood City, California. 565 p.

Tamm, C.O. 1991. Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability. Ecol. Stud. 81. Springer-Verlag, Berlin. 115 p.

Tapio. 2006. Hyvän metsänhoidon suositukset. Recommendations for good silviculture. Libris Oy, Helsinki. 100 p. (in Finnish).

Teskey, R.O., Sheriff, D.W., Hollinger, D.Y. & Thomas, R.B. 1995. External and internal factors regulating photosynthesis. In: Smith, W.K. & Hinckley, T.M. (eds.). Resource physiology of conifers. Acquisition, allocation, and utilization. Academic Press, San Diego-New York-Boston-London-Sydney-Tokyo-Toronto. p. 105–140.

Timell, T.E. 1965. Wood and bark polysaccharides. In: Côté, W.A. Jr. (ed.). Cellular ultrastructure of woody plants. Syracuse University Press, Syracuse, New York. p. 127–156.

— 1986. Compression wood in gymnosperms. Vol. 1–3. Springer-Verlag, Berlin-Heidelberg-New York-Tokyo. 2150 p.

Tuominen, H., Puech, L., Fink, S. & Sundberg, B. 1997. A radial concentration gradient of indole-3-acetic acid is related to secondary xylem development in hybrid aspen. Plant Physiol. 115: 577–585.

Tuskan, G.A., DiFazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., Putnam, N., Ralph, S., Rombauts, S., Salamov, A., Schein, J., Sterck, L., Aerts, A., Bhalerao, R.R., Bhalerao, R.P., Blaudez, D., Boerjan, W., Brun, A., Brunner, A., Busov, V., Campbell, M., Carlson, J., Chalot, M., Chapman, J., Chen, G.-L., Cooper, D., Coutinho, P.M., Couturier, J., Covert, S., Cronk, Q., Cunningham, R., Davis, J., Degroeve, S., Déjardin, C., de Pamphilis, C., Detter, J., Dirks, B., Dubchak, I., Duplessis, S., Ehlting, J., Ellis, B., Gendler, K., Goodstein, D., Gribskov, M., Grimwood, J., Groover, A., Gunter, L., Hamberger, B., Heinze, B., Helariutta, Y., Henrissat, B., Holligan, D., Holt, R., Huang, W., Islam-Faridi, N., Jones, S., Jones-Rhoades, M., Jorgensen, R., Joshi, C., Kangasjärvi, J., Karlsson, J., Kelleher, C., Kirkpatrick, R., Kirst, M., Kohler, A., Kalluri, U., Larimer, F., Leebens-Mack, J., Leplé, J.-C., Locascio, P., Lou, Y., Lucas, S., Martin, F., Montanini, B., Napoli, C., Nelson, D.R., Nelson, C., Nieminen, K., Nilsson, O., Pereda, V., Peter, G., Philippe, R., Pilate, G., Poliakov, A., Razumovskaya, J., Richardson, P., Rinaldi, C., Ritland, K., Rouzé, P., Ryaboy, D., Schmutz, J., Schrader, J., Segerman, B., Shin, H., Siddiqui, A., Sterky, F., Terry, A., Tsai, C.-J., Uberbacher, E., Unneberg, P., Vahala, J., Wall, K., Wessler, S., Yang, G., Yin, T., Douglas, C., Marra, M., Sandberg, G., Van de Peer, Y. & Rokhsar, D. 2006. The genome of black cottonwood, *Populus trichocarpa*

(Torr. & Gray). Science 313: 1596–1604.

Tyrväinen, J. 1995. Wood and fibre properties of Norway spruce and its suitability for thermomechanical pulping. Acta For. Fenn., Monograph No. 249. 155 p.

Uggla, C., Mellerowicz, E.J. & Sundberg, B. 1998. Indole-3-acetic acid controls cambial growth in Scots pine by positional signaling. Plant. Physiol. 117: 113–121.

—, Moritz, T., Sandberg, G. & Sundberg, B. 1996. Auxin as a positional signal in pattern formation in plants. Proc. Natl. Acad. Sci. USA 93: 9282–9286.

—, Magel, M., Moritz, T. & Sundberg, B. 2001. Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in Scots pine. Plant Physiol. 125: 2029–2039.

Uprichard, J.M. & Walker, J.C.F. 1993. Pulp and paper manufacture. In: Walker, J.C.F. (ed.). Primary wood processing. Principles and practise. Chapman & Hall, London-Glasgow-New York-Tokyo-Melbourne-Madras. p. 481–534.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H. & Silkin, P.P. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400: 149–151.

Valinger, E., Elfving, B. & Mörling, T. 2000. Twelve-year growth response of Scots pine to thinning and nitrogen fertilisation. For. Ecol. Manage. 134: 45–53.

Varhimo, A. & Tuovinen, O. 1999. Raw materials. In: Sundholm, J. (ed.). Paper making science and technology. Book 5: Mechanical pulping. Fapet, Helsinki. 427 p.

Verkasalo, E. 1992. Relationships of the modulus of elasticity and the structure of Finnish Scots pine wood. Silva Fenn. 26(3): 155–168.

Viro, P.J. 1972. Die Walddüngung auf finnischen Mineralböden. Folia For. 138. 19 p. (in German).

Vuokila, Y. 1981. The response of young Scots pine stands to the first commercial thinning. Folia For. 468. 13 p.

— 1983. The past and future of Finnish growth and yield study. Finnish Forest Research Institute Research Paper 89. (In Finnish). 103 p.

Walker, J.C.F. 1993a. Basic wood chemistry and cell wall ultrastructure. In: Walker, J.C.F. (ed.). Primary wood processing. Principles and practise. Chapman & Hall, London-Glasgow-New York-Tokyo-Melbourne-Madras. p. 23–67.

— 1993b. Characteristics of stemwood and their manipulation. In: Walker, J.C.F. (ed.). Primary wood processing. Principles and practise. Chapman & Hall, London-Glasgow-New York-Tokyo-Melbourne-Madras. p. 153–196.

Wallis, A.F.A. & Wearne, R.H. 1981. Hydroxyethylation of lignin in mechanical pulps. Appita 36(3): 192–196.

Warensjö, M. 2003. Compression wood in Scots pine and Norway spruce – distribution in relation to external geometry and the impact on dimensional stability in sawn wood. PhD thesis. Swedish university of agricultural sciences, Department of forest products and markets, Uppsala, Sweden. 36 p.

Westermark, U., Hardel, H.L. & Iversen, T. 1986. The content of protein and pectin in the lignified middle lamella primary wall from spruce fibers. Holzforschung 40(2): 65–68.

Westing, A.H. 1965. Formation and function of compression wood in gymnosperms. Bot. Rev. 31(3): 381–480.

Wilson, B.F. 1963. Increase in cell wall surface area during enlargement of cambial derivates in *Abies concolor*. Amer. J. Bot. 50(1): 95–102.

Wimmer, R. & Downes, G.M. 2003. Temporal variation of the ring width-wood density relationship in Norway spruce grown under two levels of anthropogenic disturbance.

IAWA J. 24(1): 53–61.

Wodzicki, T.J. 1971. Mechanism of xylem differentiation in *Pinus sylvestris* L. J. Exp. Bot. 22: 670–687.

Wolcott, M.P., Shepard, R.K. & Shottafer, J.E. 1987. Age and thinning effects on wood properties of red spruce (*Picea rubens* Sarg.). Maine Life Sci. Agric. Exp. Stn. Tech. Bull. 127. 17 p.

Ylitalo, E. 2007. Wood consumption. In: Peltola, A. (ed.). The Finnish statistical yearbook of forestry 2007. The Finnish Forest Research Institute, Helsinki. p. 247–276.

Young, R.A. 1994. Comparison of the properties of chemical cellulose pulps. Cellulose 1: 107–130.

Zabel, R.A. & Morrell, J.J. 1992. Wood microbiology. Decay and its prevention. Academic Press, Inc., San Diego, California. 476 p.

Zamudio, F., Baettyg, R., Vergara, A., Guerra, F. & Rozenberg, P. 2002. Genetic trends in wood density and radial growth with cambial age in a radiate pine progeny test. Ann. For. Sci. 59: 541–549.

Zeide, B. 2001. Thinning and growth: a full turnaround. J. For. 99: 20–25.

Zhang, S.Y. 1995. Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. Wood Sci. Technol. 29: 451–465.

— 1997. Wood quality: Its definition, impact, and implications for value-added timber management and end uses. Part I: Its definition and impact. In: Zhang, S.Y., Gosselin, R. & Chauret, G. (ed.). Timber management toward wood quality and end-product value. Proceedings of the CTIA / IUFRO International wood quality workshop, August 18–22, 1997, Quebec City, Canada. p. 17–39.

— 1998. Effect of age on the variation, correlations and inheritance of selected wood characteristics in black spruce (*Picea mariana*). Wood Sci. Technol. 32: 197–204.

—, Simpson, D. & Morgenstern, E.K. 1996. Variation in the relationship of wood density with growth in 40 black spruce (*Picea mariana*) families grown in New Brunswick. Wood Fiber Sci. 28(1): 91–99.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg-New York-Tokyo. 143 p.

Zobel, B.J. & Sprague, J.R. 1998. Juvenile wood in forest trees. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg. 363 p.

— & van Buijtenen, J.P. 1989. Wood variation – its causes and control. Springer-Verlag, Berlin-Heidelberg-New York. 363 p.