

Radial Variation in the Anatomy of *Betula pendula* Wood from Different Growing Sites

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Abstract

Radial trend in several anatomical characteristics is a well known phenomenon in tree trunks, as the young cambium forms juvenile wood before maturing. This phenomenon is stronger in softwoods than in hardwoods, and thus investigated less in the hardwoods. Another factor that may cause variations in the wood anatomy is growth rate, as it differs between growing sites of different fertility. In this study several anatomical characteristics were compared between silver birch (*Betula pendula* Roth.) trees grown on different growing sites, of which two were fertile planted sites, and two less fertile naturally regenerated sites. Several of the measured characteristics had a radial trend, commonly increasing with cambial age, but decreasing in the case of number of rays per millimetre. However, radial diameter of earlywood fibres seemed to reach a stable size around 20-30 years of age, and thus it could be suitable for determining the maturation of silver birch wood. The clearest difference in wood anatomy between growing sites was that walls of both vessels and fibres were thicker in trees of natural than planted origin. In addition, the diameter of ray cells was clearly larger in naturally regenerated than in planted birches, although ray width was similar for all origins. The differences observed in cell wall thickness between growing sites most probably affect other properties of birch wood (e.g. density and colour) that are important in the mechanical use of birch timber.

Key words: Birch, diameter, fertility, fibre, growth rate, ray, vessel, wall thickness

Introduction

The radial variation in wood properties is well known in both hardwoods and softwoods. Wood properties change rapidly in the cambially youngest juvenile wood as the cambium ages, after which the change evens out; the properties are quite constant in the mature wood. In softwoods the variation is widely studied, because the properties of juvenile and mature wood differ from each other markedly, and the difference also has marked importance regarding the usage of timber (e.g. Zobel and van Buijtenen 1989, Zobel and Sprague 1998). The difference in properties between juvenile and mature wood is clearly smaller in hardwoods, and mainly density, ring width and fiber length has been studied in hardwoods in this respect (e.g. Bhat 1980, Bhat and Kärkkäinen 1980, Björklund and Ferm 1982, Luostarinen et al. 2009). Few studies concerning radial variation of other anatomical characteristics than fiber length in hardwoods exists, the characteristics studied including cell wall thickness, lumen diameter and ray width (e.g. Bhat 1980, Bhat and

Kärkkäinen 1980, Helińska-Raczowska and Fabisiak 1999).

Differences in anatomical characteristics have been observed to exist due to growth rate (Fujiwara and Yang 2000) and thus differences in radial wood anatomy may exist in trees of the same species growing on different sites. Silver birch (*Betula pendula* Roth) plantations have been commonly established on more fertile sites than natural stands, which emphasises faster growth of the planted trees. As a consequence they reach the harvestable size younger, and therefore they consist of larger proportion of juvenile wood at that time. Some properties, i.e. wood density, shrinkage (Möttönen and Luostarinen 2006) and colour (Luostarinen and Möttönen 2009) have been compared between naturally regenerated and planted birch trees with good results regarding the planted ones, but additional information is needed to make more comprehensive evaluations about the quality of timber of planted trees for the mechanical wood industry. Planted birch trees will play an increasingly important role in the Finnish forest industry in the 2010s, because

the oldest plantations will be mature for harvesting during this period.

One aim of this study was to investigate how selected anatomical characteristics of wood change when birch trees age, and the differences in these anatomical characteristics between trees grown on different growing sites. Another aim of this study was to compare the achieved results with earlier found density and colour results of planted and naturally regenerated birches to find out any possible linkage between these properties, important in the mechanical usage of birch timber, and anatomical properties. Thus the results can be taken into account in the cultivation of birch, because this information helps to evaluate the effect of fast growth on the juvenility and the quality of timber of the planted birch trees in the use.

Material and methods

The wood samples were taken from birch boards (30 mm × 70 mm × 1200 mm) that belonged to a study in which colour changes of sawn birch timber during drying was studied (Luostarinen and Möttönen 2009). Fifteen silver birch (*Betula pendula* Roth) trees were taken for the experiments from each of the selected growing sites, located in North Karelia, eastern Finland: 1) naturally regenerated medium-fertility MT (*Myrtillus*-type) site, 2) naturally regenerated low-fertility VT (*Vaccinium*-type) site, 3) a typical planted forest regeneration area of high fertility OMT (*Oxalis-Myrtillus*-type), and 4) an abandoned agricultural field afforested by planting, all four on mineral soil. The sites will later be referred to in this paper as MT, VT, OMT and field, respectively. On the naturally regenerated sites the age of the harvested trees was 70-80 years while on the planted sites, which represented the oldest planted birch trees in North Karelia, the age was 33 years. Only healthy planted trees with sound (according to visual inspection) wood were accepted as sample trees; this was determined from the cross-cut ends of logs after felling. In naturally regenerated trees the darkened wood around the pith, which virtually always develops in mature birch trees, was not used for the study. Thus the cambially youngest wood used in this study was 20-30 years for the naturally regenerated birches; other cambial age classes (CACs) for them were 30-40 and 60-80 years and for the planted birches 0-10 and 10-20 years, in addition to 20-30 years. Thus comparison between naturally regenerated and planted birches was made for the CAC 20-30 years, and averages for anatomical characteristics were counted for CACs, but not for growing sites as between growing sites the mean age of the studied wood was different.

The wood samples were stored in a freezer (-20°C) in plastic bags until crosscuts were prepared. For the microtomy, the samples were softened in 4 % ethylenediamine for 4 days, after which they were rinsed in tap water 3 times for 2 hours to make it easier to complete the crosscuts (Carlquist 1982). Crosscuts were then stained with safranin-alcian blue (Fagerstedt et al. 1996) and mounted with DePex. Each characteristic (see Table 1) was measured ten times from each sample, the average of these measurements being the result for one sample, using Image-Pro software. From the cells their whole diameter (lumen + 2 x wall) was measured, from fibres and vessels both in radial and tangential direction. Measured cell wall thicknesses represented the thickness of one wall. Ray number was counted for a distance of one millimetre (mm) in a tangential direction. Ray width was measured in micrometers (µm) and in cell numbers in earlywood and latewood, and average tangential diameter of ray cells was calculated by dividing the metric ray width by the ray width as cell numbers. As birch is a diffuse porous species, latewood is not pronounced in it. Instead, there are 3-4 cell layers at the end of each annual ring in which the cells are clearly flattened when compared with the cells of earlier part of a ring. Those 3-4 layers were classified as latewood, and the zone without flattening of cells was classified as earlywood.

The results were analysed with the General Linear Model (GLM) multivariate procedure of the SPSS statistical software. GLM is a typical variance analysis that compares the means of different groups, assuming that the results are normally distributed and the variances of groups do not differ significantly from each other. GLM comparisons were made for each anatomical characteristic between growing sites within a CAC, between CACs within a growing site, and between CACs when the results of growing sites were combined. The characteristics tested between earlywood and latewood were the width of rays, radial diameter of fibres and tangential diameter of ray cells; these comparisons were made with Kruskal-Wallis test. Kruskal-Wallis test is nonparametric, used in the cases that GLM could not be used.

Results

A radial trend was observed within each growing site for most of the measured characteristics (Figures 1, 2, 3, 4, and 5). The size of most of the characteristics increased with increasing cambial age, with several significant differences (Figures 1, 2, 3 and 4). However, the number of rays decreased (Figure 5). The trends were emphasised when the results for the CACs were calculated for combined growing sites (Table 1).

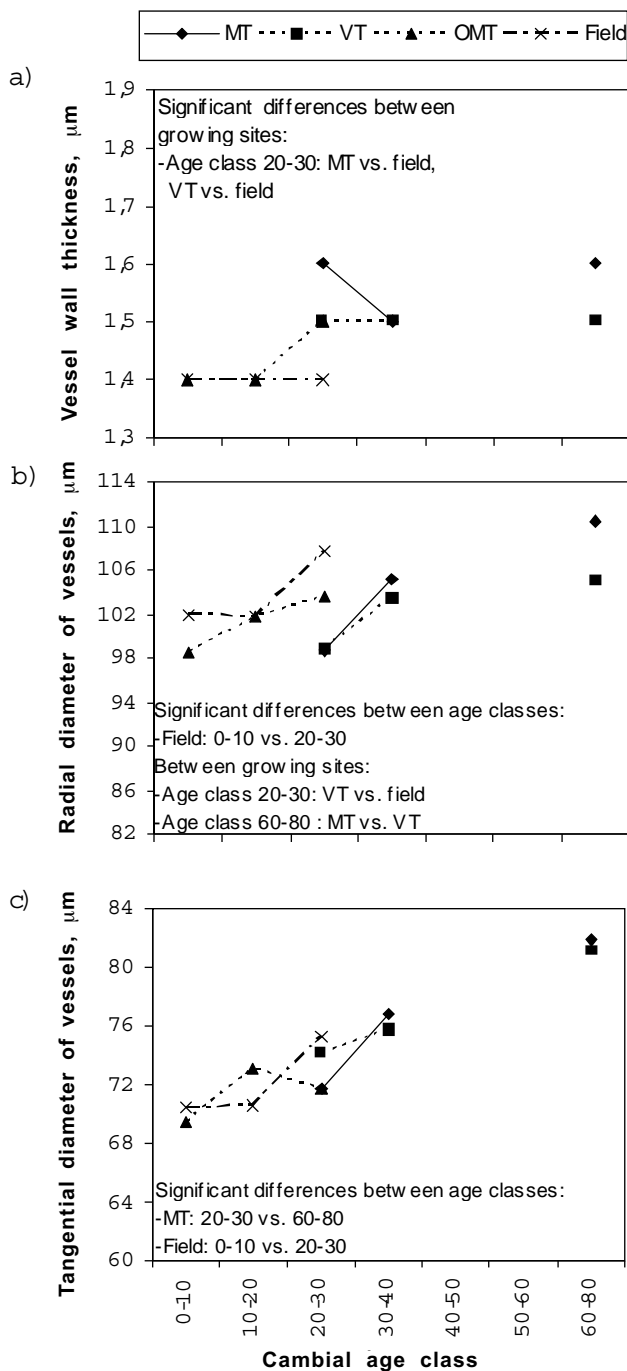


Figure 1. a) Wall thickness, b) radial diameter, and c) tangential diameter of vessels by cambial age classes and growing sites

Observed significant differences between CACs included both diameters and wall thickness of vessels, tangential diameter and wall thickness of fibres in both earlywood and latewood, and width of rays (µm) and tangential diameter of ray cells in both earlywood and latewood, as well as ray number per distance of one millimetre (Table 1). In addition, the increase in the

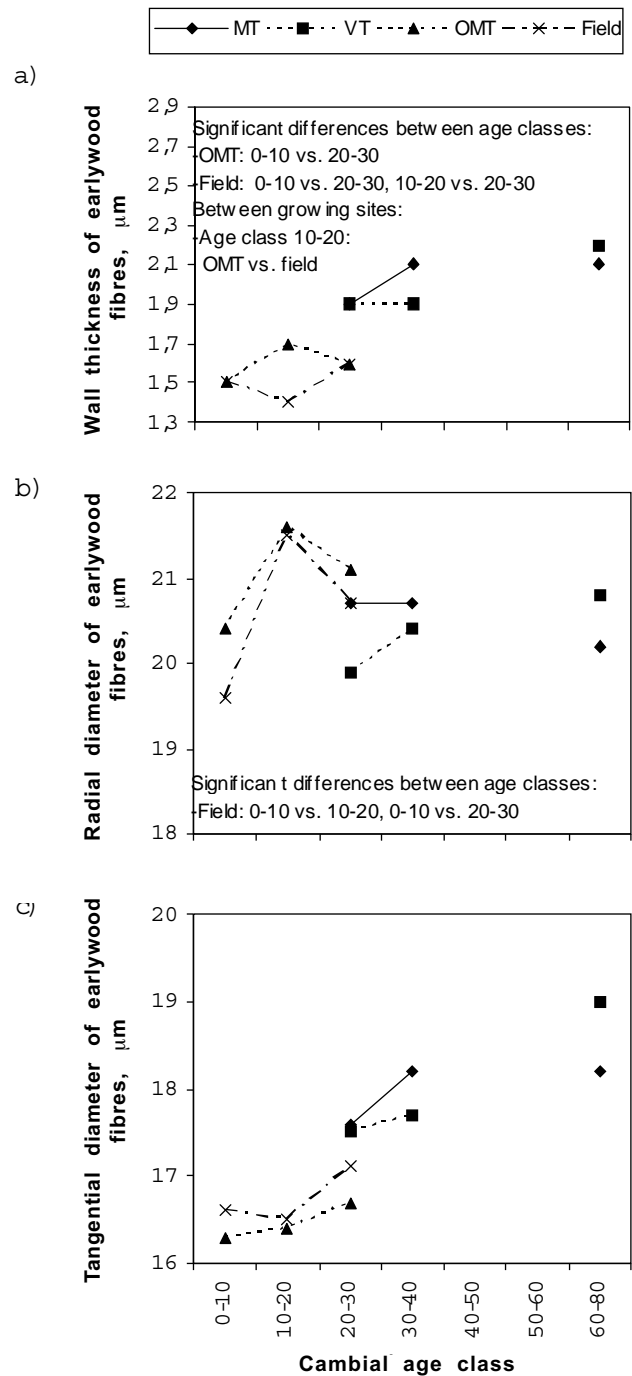


Figure 2. a) Wall thickness, b) radial diameter, and c) tangential diameter of earlywood fibres by cambial age classes and growing sites

radial diameter of earlywood fibres levelled off between CACs 10-20 and 20-30 in planted trees.

Some differences were observed between growing sites within a CAC (Figures 1, 2, 3, 4, and 5). The differences observed in vessels and fibres were more often between a planted origin and a naturally regenerated origin (in CAC 20-30) than between the two planted

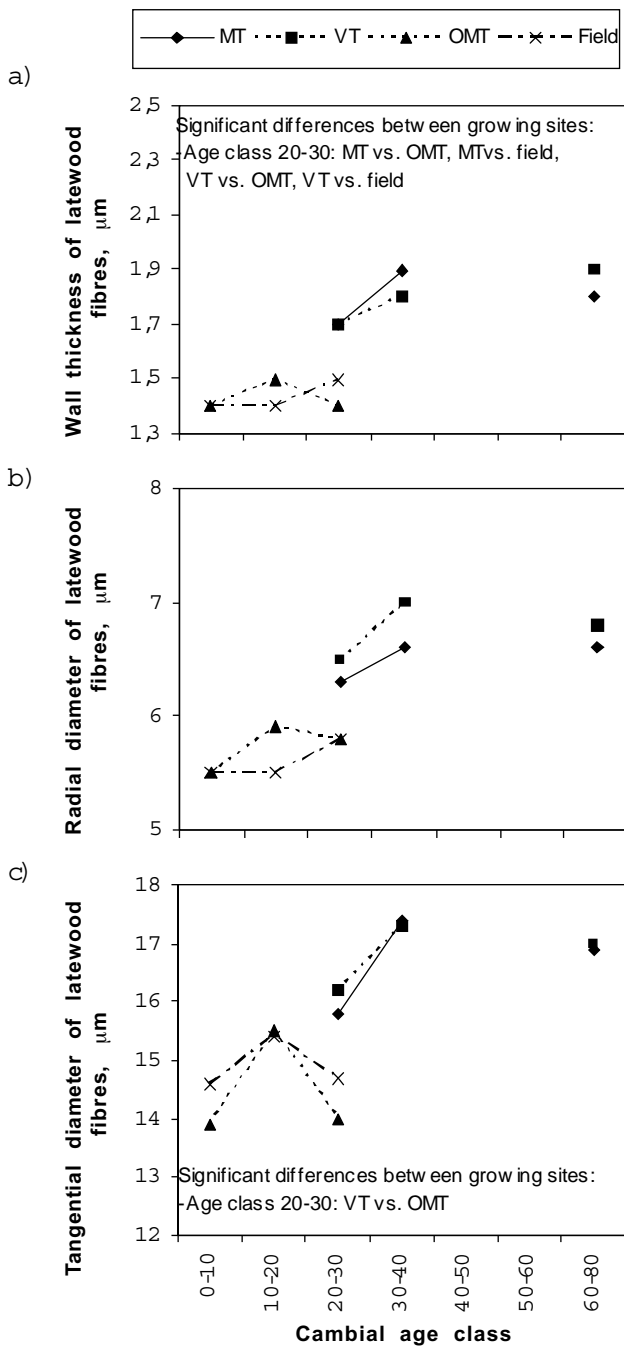


Figure 3. a) Wall thickness, b) radial diameter, and c) tangential diameter of latewood fibres by cambial age classes and growing sites

origins or the two naturally regenerated origins (Figures 1, 2 and 3): wall thickness both in fibres and vessels was larger in the wood of the naturally regenerated trees than in that of the planted trees, and radial diameter of vessels was larger in the planted than in the naturally regenerated birches, while tangential diameter of latewood fibres was larger in the naturally regenerated than the

planted birches. However, radial diameter of the fibres was similar between origins (Figures 1, 2 and 3). Earlywood fibres were wider than latewood fibres; also the fibre walls were thicker in the earlywood; with fibre wall thickness increasing radially more in the earlywood than in the latewood (Table 1). Regarding the rays, their width was similar in the naturally regenerated and in planted birches, both when compared the metric widths and those determined according to cell number (Figure 4). The tangential diameter of the ray cells, particularly in the earlywood, was clearly larger in the wood of the naturally regenerated than in that of the planted birches.

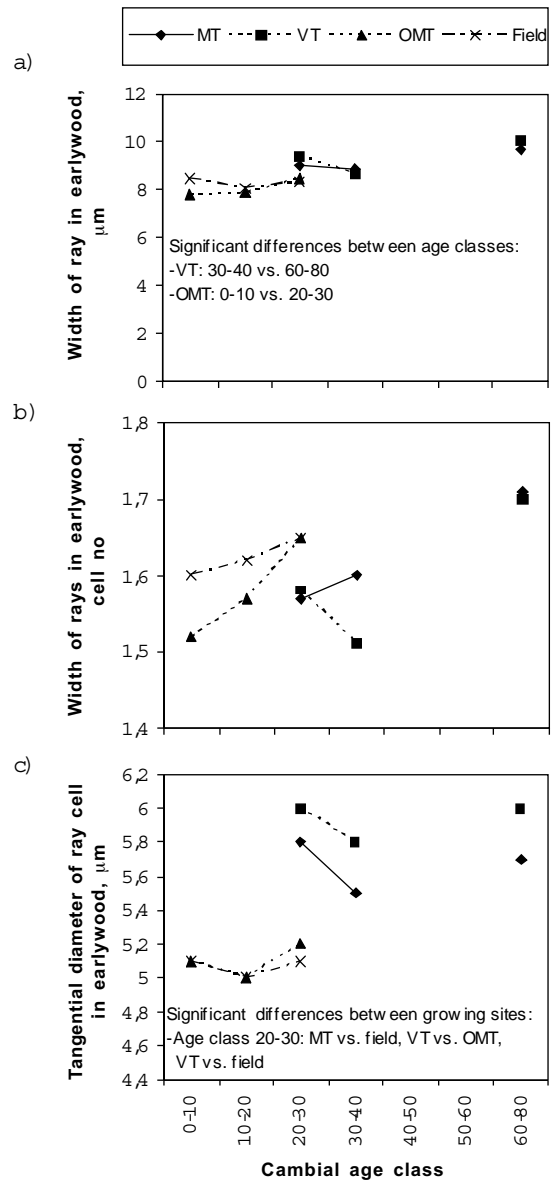


Figure 4. Width of rays as a) micrometres and b) cell number, and c) tangential diameter of ray cells in earlywood, and width of rays as d) micrometres and e) cell number, and f) tangential diameter of ray cells in latewood by cambial age classes and growing sites

Table 1. Averages (x) and standard errors of the mean (SE) of measured anatomical characteristics by cambial age classes (CAC's)

Cell type	Anatomical characteristics	0-10			10-20			20-30			30-40			60-80		
		x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Vessels	Radial diameter of cells (µm)	100.2 A	1.2	96	101.8 A	3.1	21	103.9 B	0.9	156	104.3 B	3.9	17	107.6 B	1.4	48
	Tangential diameter of cells (µm)	69.9 A	0.8	96	71.4 AB	2.6	21	73.2 B	0.7	156	76.3 C	2.6	17	81.4 C	1.3	48
	Thickness of wall (µm)	1.4 A	0.01	96	1.4 AB	0.02	21	1.5 B	0.01	156	1.5 C	0.04	17	1.6 C	0.03	48
Fibres	Radial diameter of cells in earlywood (µm)	20.2 a	0.2	96	21.5 a	0.4	21	20.7 a	0.2	156	20.5 a	0.5	17	20.5 a	0.3	48
	Tangential diameter of cells in earlywood (µm)	16.4 Ab	0.2	96	16.4 A	0.4	21	17.0 Ab	0.2	156	18.0 B	0.5	17	18.6 Bb	0.3	48
	Thickness of wall in earlywood (µm)	1.5 Ac	0.02	96	1.5 AB	0.07	21	1.7 Bc	0.03	156	2.0 C	0.2	17	2.1 Cc	0.08	48
	Radial diameter of cells in latewood (µm)	5.5 a	0.07	96	5.6 a	0.2	21	6.0 a	0.07	156	6.8 a	0.2	17	6.7 a	0.2	48
	Tangential diameter of cells in latewood (µm)	14.3 Ab	0.2	96	15.4 A	0.6	21	14.8 Ab	0.2	156	17.4 B	0.5	17	17.0 Bb	0.3	48
	Thickness of wall in latewood (µm)	1.4 Ac	0.02	96	1.4 AB	0.06	21	1.5 Bc	0.02	156	1.8 C	0.07	17	1.8 Cc	0.06	48
	Number/mm, measured tangentially	11.9 A	0.2	96	11.6 A	0.5	21	11.2 A	0.2	156	10.4 B	0.4	17	10.5 B	0.4	48
Rays	Width in latewood (µm)	16.1 Aa	0.3	96	17.0 a	0.8	21	16.4 Aa	0.3	156	17.2 a	0.8	17	18.4 Ba	0.4	48
	Width in earlywood (µm)	7.9 Aa	0.1	96	8.1 ABa	0.2	21	8.6 Ba	0.1	156	8.8 a	0.4	17	9.9 Ca	0.2	48
	Width in latewood (as cell number)	1.7 b	0.003	96	1.7 b	0.06	21	1.7 b	0.02	156	1.7 b	0.06	17	1.6 b	0.03	48
	Width in earlywood (as cell number)	1.6 b	0.03	96	1.6 b	0.04	21	1.6 b	0.02	156	1.6 b	0.04	17	1.7 b	0.03	48
	Tangential diameter of ray cell in latewood (µm)	9.3 Ac	0.1	96	9.8 A	0.3	21	9.6 Ac	0.1	156	10.4 B	0.3	17	11.2 Bb	0.2	48
	Tangential diameter of ray cell in earlywood (µm)	5.1 ABc	0.05	96	5.0 A	0.05	21	5.3 Bc	0.06	156	5.6 C	0.2	17	5.8 Cb	0.09	48

CAC's 0-10 and 10-20 includes only planted origins, CAC 20-30 includes both planted and natural origins, and CAC's 30-40 and 60-80 only natural origins. N – number of boards from which samples were taken. Different capital letters in a row indicates statistically significant difference. Same lower case letter in same characteristics of earlywood and latewood indicate statistically significant difference between earlywood and latewood. If no letter is written, the CAC does not differ significantly from any other CAC or the wood types do not differ from each other regarding the characteristics.

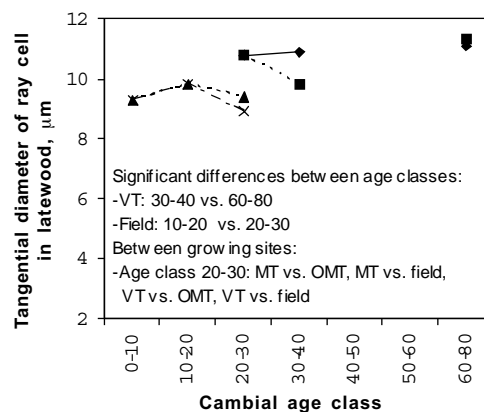
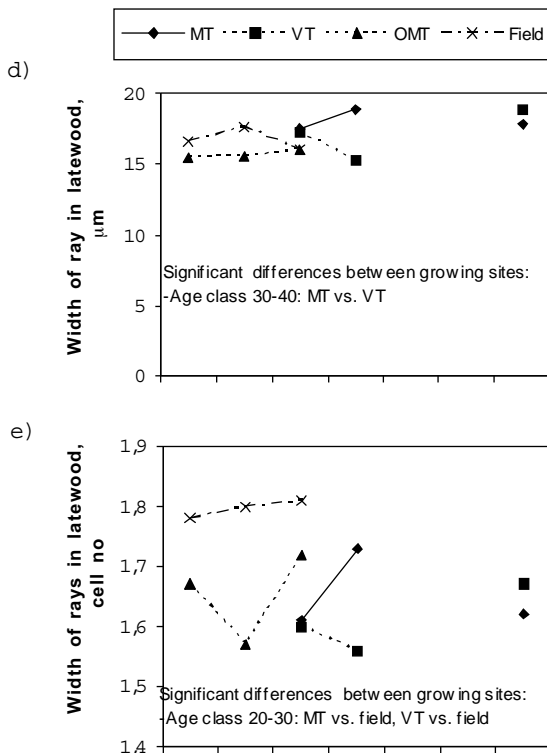


Figure 4. (Continuation)

Discussion and conclusions

Several of the studied anatomical characteristics had, as it was expected, a radial trend in silver birch wood, which could be seen within a growing site, both in planted and in naturally regenerated birch trees, or

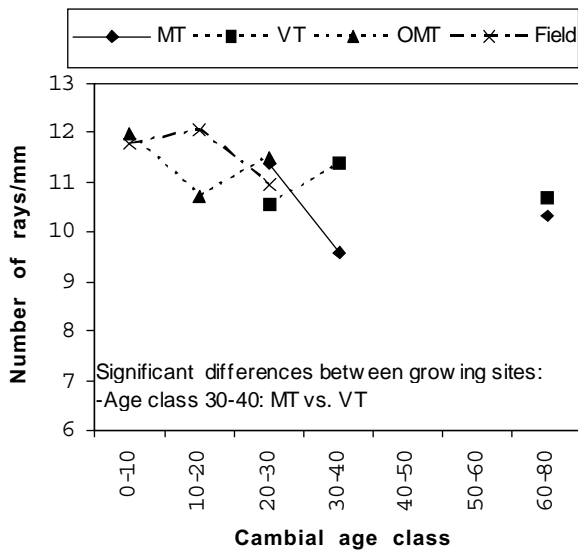


Figure 5. Number of rays in distance of one millimetre, measured tangentially by cambial age classes and growing

in combined material of all the studied trees. The trend was seen particularly in vessel dimensions, which increased from CAC 0-10 to CAC 60-80 without clear levelling off. Thus vessel diameter is not a good indicator for determining maturation age of silver birch wood, although in hybrid poplar (*Populus x euramericana* (Dode) Guinier), which is also diffuse-porous (Peszlen 1994), and in some ring-porous tree species (Helińska-Raczkowska 1994, Helińska-Raczkowska and Fabisiak 1999, Tsuchiya and Furukawa 2009) vessel size can be used for indicating it. However, the maturation age indicated by vessel size is higher than that defined by the fibre length. When compared to the dimensions measured earlier for silver birch vessels (Bhat and Kärkkäinen 1980), the dimensions were larger in this study, both in naturally regenerated and in planted trees, which is most probably caused by genetic and site differences between studied trees. In addition, walls of vessels were thicker and the radial diameter of them smaller in the naturally regenerated than in the planted birches in this study, which, as well, may be caused by both genetic and site factors. The differences in wall thickness and diameter of vessels between the planted and naturally regenerated birches may partly explain the smaller density of the wood observed in the planted birch trees (Möttönen and Luostarinen 2006).

In addition to vessel size, the size of fibres increased radially in the trunks. In this study the differences between CACs were best observed for radial diameter and thickness of wall of earlywood fibres. In planted birches, the increase in the radial diameter of earlywood fibres, levelled off between CACs 10-20 and

20-30. Thus radial diameter of earlywood fibres can be an indicator of maturation, even though fibre length and microfibril angle has been observed to indicate an earlier maturation of the silver birch wood, as they reach the maximum at ca. 15th growth ring from the pith (Bonham and Barnett 2001). Similar trends to those found in this study were also observed in hybrid poplar regarding the diameter and wall thickness of fibres (Peszlen 1994), while in *Eucalyptus globulus* Labill. fibre wall thickness did not differ significantly from pith to bark (Ramirez et al. 2009). The fibre diameters measured in this study corresponded to the birch fibre diameters measured by Bhat (1980), while the fibre wall thickness was clearly smaller than in Bhat's (1980) study or the values reported by Wagenführ (1996). The larger fibre wall thickness in the earlywood than in the latewood, which increased more with age, as well, emphasises the importance of the earlywood for the density of birch wood even though its lumens were larger than in the latewood. The fibre wall thickness differed most between planted and naturally regenerated birches, with it being smaller in the planted trees. This may be due to differences in ethylene synthesis, the increase in which stimulated the thickening of the walls in the study of Ingemarsson et al. (1991). Increasing amounts of ethylene is often connected to stress factors (Devlin and Witham 1983), which may be more abundant in older trees (Christmann and Frenzel 1997) and thus in less fertile natural sites in the case of this study. In addition, on the better sites the earlier maturation age of the wood causes smaller cells in the mature wood (Peszlen 1994, Bhat et al. 2001), signs of which could also be observed in fibre characteristics of planted birches in this study. Furthermore, planted birches, which annual rings are wider (Luostarinen and Möttönen 2009), have proportionally more earlywood fibres that are large in size, than naturally regenerated birches. Simultaneously thinner cell walls induce smaller amount of lignified cell wall material per volume unit in planted birches, which may have an impact on the colour of the wood, which is lighter in the planted birches (Luostarinen and Möttönen 2009). In addition, as a result of their larger proportion the size and wall thickness of the fibres affect, more than those of the vessels, the density of wood, that has been observed to be lower in the thinner-walled planted birches (Möttönen and Luostarinen 2006).

The rays were unexpectedly narrow in the trees of this study when compared with the results of Bhat and Kärkkäinen (1980) for both methods of measuring (μm , cell number). However, they were inside the limit values mentioned by Wagenführ (1996). Several differences were observed in the ray characteristics between the CACs and between the growing sites. Tangential diam-

eter of the ray cells as well as the width of rays (μm) increased with cambial age in some cases. Additionally, in ring-porous *Acanthopanax sciadophylloides* Franch. & Sav. the average ray width is strongly influenced by the cambial age (Tsuchiya and Furukawa 2007). Furthermore, the ray number/mm decreased slightly with age, which is in accordance with the results of Bhat and Kärkkäinen (1980), who, however, found that the ray numbers were clearly higher, and that the rays' radial decrease was larger than in this study. Instead, no clear differences in the ray width were observed between sites in this study, while for poplar the ray area was larger the better the growing site was (Peszlén 1994). Between sites the clearest difference was for the tangential diameter of the ray cells both in the earlywood and latewood, where these cells were wider in the naturally regenerated than in the planted birches. A reason for this may be genetic as well as a different response of plant's physiology to sites of different fertility. The hormone ethylene has been observed to increase the size of individual ray cells as well as ray width (Yamamoto et al. 1987).

In this study it is not possible to compare the radial trends between the planted and naturally regenerated sites because of the different ages of the trees. However, in CAC 20-30 several cell dimensions differed between the planted and naturally regenerated birch trees: some of them were larger, and some smaller in the planted trees. Radial diameter of the earlywood fibres reached a stable size around 20 years of age in the planted trees, which may mean that this characteristic indicates maturation of the wood. From the point of view of the mechanical use of wood, the most important difference between woods of planted and naturally regenerated trees is in the cell wall thickness, because cell wall thickness most probably affects both the colour and the density of the wood.

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РАДИАЛЬНЫЕ ВАРИАЦИИ В АНАТОМИИ ДРЕВЕСИНЫ БЕРЁЗЫ ПОВИСЛОЙ (*BETULA PENDULA*), ВЫРАЩЕННОЙ В РАЗЛИЧНЫХ МЕСТАХ

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Резюме

Радиальные тенденции, проявляющиеся в разных анатомических характеристиках – это хорошо известное явление для стволов деревьев, где ранний камбий образует молодую древесину перед созреванием. Это явление сильнее проявляется в анатомическом строении древесины хвойных пород, чем древесины лиственных пород и по этой причине оно менее изучено в отношении последней. Скорость роста является фактором, который может вызывать вариации в анатомии древесины, поскольку она изменяется в зависимости от плодородности места произрастания. Целью исследования было сравнение различных анатомических характеристик деревьев берёзы повислой (*Betula pendula* Roth.) выращенной в разных местах, два из которых относились к лесопосадкам, а два других были менее плодородными местами естественного возобновления. Различные измеренные характеристики имели радиальную тенденцию, усиливающуюся с возрастом камбия, но уменьшающуюся с числом лучей на миллиметр. Однако, как оказалось, радиальный диаметр волокон ранней древесины способен достигать стабильного размера приблизительно в возрасте 20 лет для посадок и 30 лет при естественном возобновлении деревьев. Вследствие вышеуказанной разницы, радиальный диаметр волокон ранней древесины может быть использован для определения зрелости деревьев берёзы. У деревьев, выросших в естественных условиях, клеточные стенки сосудов и волокон были значительно толще, чем у деревьев в посадках. В дополнение, диаметр лучевых клеток был значительно больше у деревьев, выросших в условиях естественного возобновления, хотя ширина луча была одинаковой во всех случаях. Наиболее вероятно, что обнаруженная разница в толщине клеточной стенки деревьев берёзы, выращенных в разных местах, влияет и на другие свойства (например, плотность и цвет) важные для механического использования пиломатериалов из берёзы.

Ключевые слова: Берёза, диаметр, плодородность, волокно, скорость роста, луч, сосуд, толщина клеточной стенки