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**BREEDING FOR WOOD QUALITY:
THE IMPACT OF CAMBIAL AGE ON THE GENETICS
OF WHITE SPRUCE WOOD TRAITS**

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Résumé

L'épinette blanche (*Picea glauca* [Moench] Voss) est l'une des essences les plus importantes pour l'industrie forestière au Canada et son bois est apprécié pour diverses utilisations. De nombreuses études nous permettent de prédire des pertes de la qualité du bois avec l'utilisation accrue d'arbres provenant de plantations et en raison d'une sélection génétique axée uniquement sur la croissance. L'amélioration génétique et la biologie moléculaire pourraient être appliquées pour sélectionner des arbres ayant un ensemble de propriétés plus désirables et ainsi neutraliser la perte de qualité du bois. L'objectif de cette thèse était de déterminer les paramètres génétiques essentiels à cette tâche, notamment, l'héritabilité et les corrélations des principales propriétés du bois chez l'épinette blanche. Dans la présente étude, des carottes de bois ont été récoltées de 375 arbres couvrant 25 familles issues de pollinisation libre et venant d'un test de provenance–descendances répété sur trois sites dans la province de Québec. Avec le système SilviScan^{MD} des profils de haute résolution ont été obtenus de la moelle à l'écorce pour différentes propriétés du bois liées à la force mécanique (par exemple, la densité du bois et la rigidité) et à l'anatomie des cellules (dont l'épaisseur de la paroi et le diamètre cellulaire). Des analyses statistiques ont indiqué un contrôle génétique modéré à élevé pour les propriétés du bois, surtout dans le bois initial. Les valeurs d'héritabilité étaient généralement plus basses dans les cernes près de la moelle et dans le bois final. Il n'y a que le contrôle génétique de l'angle des microfibrilles (AMF) qui ne variait pas significativement entre les cernes. La plupart des corrélations génétiques et phénotypiques entre différentes propriétés étaient basses près de la moelle mais augmentaient avec l'âge et se stabilisaient au niveau du bois de transition. Les fortes corrélations observées entre le bois juvénile et le bois de transition permettent d'anticiper une sélection précoce efficace à l'âge cambial de 8 à 10. Nos observations indiquent un très bon potentiel pour la sélection précoce de l'AMF autour de l'âge 4 ; mais l'AMF est un critère de sélection peu pratique en raison de son coût élevé. En plus, la sélection directe des propriétés mécaniques serait limitée par un contrôle génétique faible à modéré. Notre étude montre qu'une approche efficace pour maîtriser ce problème est l'amélioration indirecte de la rigidité en effectuant une sélection par indice incluant la densité du bois et la longueur des carottes. Il semble aussi difficile d'améliorer simultanément les propriétés mécaniques du bois et les propriétés anatomiques des fibres

liées à la fabrication des pâtes et papiers, en raison des corrélations fortement défavorables. Les résultats de cette thèse contribueront à rendre l'amélioration génétique des propriétés du bois plus accessible et plus efficace. Ils permettront à long terme de mieux valoriser les bois d'épinette blanche issus des plantations futures.

Abstract

White spruce (*Picea glauca* [Moench] Voss) is one of the most important tree species for the Canadian forest industry and its wood is highly valued for a variety of end uses. Research evidences allow us to predict that wood quality will decrease with the increasing use of plantation grown trees and with the selection for faster growth in tree improvement programs. Traditional breeding and modern molecular genetics may be deployed to select trees with more desirable wood properties and thus counter the problem. The objective of this thesis was to obtain requisite quantitative genetic parameter estimates, such as heritability and genetic correlations for white spruce wood traits. In this study, wood cores were collected from 375 trees originating from 25 open-pollinated families of a provenance-progeny test repeated on three sites in the province of Québec. Using the SilviScanTM system, high resolution pith to bark profiles were obtained for a number of different wood traits that are related to mechanics (e.g. wood density and stiffness) or cell anatomy (e.g. cell wall thickness and cell diameter). Statistical analyses revealed moderate to high genetic control, especially for earlywood traits. The heritability estimates were generally lower in the rings close to the pith and in the latewood. Only the heritability of microfibril angle (MFA) did not vary significantly in different rings. Most genotypic and phenotypic correlations between traits were low near the pith but became stronger as cambial age increased and levelled off close to transition wood rings. Good juvenile-transition wood correlations were observed, and early selection around cambial age 8 – 10 was found to be effective for most of the wood traits. Our observations indicated good potential for very early selection of MFA around age 4; however, MFA may not be a practical selection criterion in breeding programs due to its high evaluation costs. In addition, direct improvement of mechanical traits such as stiffness may be hampered by low to moderate genetic control. Our study shows that indirect improvement of stiffness through index selection on wood density and ring increment is one way to overcome this problem cost effectively for breeding. It also appears difficult to improve mechanical traits concurrently with pulp and paper related cell anatomy traits, due to strong adverse correlations. The results of this thesis will help to effectively include wood traits into tree breeding programs and to enable the production of high quality value added products from plantation grown white spruce wood in the future.

Avant-Propos

Inclusion d'articles

Cette thèse se divise en quatre chapitres. Après une introduction générale (chapitre I) deux chapitres (chapitres II et III) suivent sous forme de publications scientifiques. J'ai agi à titre de premier auteur dans chacune de ces publications. J'ai donc procédé à l'analyse et à la présentation des données ainsi qu'à la rédaction du texte. Différents co-auteurs ont participé aux publications conseillant et surveillant mes travaux ainsi qu'en participant à la correction de mes manuscrits. Notamment, il s'agit de John MacKay (directeur de la thèse, Université Laval), Jean Beaulieu (co-directeur, Centre de la fibre du bois, Service canadien des forêts) et Alain Cloutier (co-directeur, Université Laval). Pour le chapitre trois, il faut ajouter André Rainville du Ministère des Ressources naturelles et de la Faune du Québec.

Chapitre II :

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Chapter I – General Introduction

1.1 Introduction

For many years there has been an increasing interest all over the world to grow wood in short rotation plantations due to different reasons that amount to a growing demand for wood and wood products accompanied by a decrease of land available for silviculture. Pressure from the development of agriculture and urbanism but also new forest policies, for example in Quebec, and from more and more territory being set aside for conservation purposes have reduced the land available for forest management. In Canada, slow growth of the boreal forests leads furthermore to decreasing dimensions of the harvested trees and a need to exploit remote regions. To grow trees close to the processing industry under short rotations seems to be a promising solution, but it was shown that intensive management practices often generate loss of wood quality (Bendtsen 1978; Kennedy 1995). Yet, silvicultural treatments allow controlling wood variation and quality to some extent (Bowyer et al. 2007). There is also strong evidence that genetics offers a very significant potential for improvement of both: wood quality and yield in the near future.

White spruce *Picea glauca* (Moench) Voss has a transcontinental range and is valued for its growth rate and wood quality in temperate regions of eastern Canada (Beaulieu 1994; Zhang and Koubaa 2008). It is a promising tree species for intensive management and breeding programs have been implemented in different provinces, primarily for enhanced growth. In Quebec, wood traits have begun to be included into selection criteria in order to maintain wood quality under improved growth (Beaulieu et al. 2009). Diverse research projects investigated the genetics of white spruce wood and growth traits in the past (e.g. Nienstaedt 1985; Corriveau et al. 1987; Beaulieu et al. 2006). Recently, research projects such as *Arborea* were focussing on the species' molecular genetics, with the aim to associate variability of commercially valuable traits to variation in DNA sequences (Bousquet et al. 2007). But still, there are several unanswered questions about basic genetic characteristics – such as genetic control of many white spruce wood traits that influence end product quality.

This thesis presents estimates for quantitative genetic parameters such as heritability, correlations between traits or the efficiency of early selection for a variety of wood traits that are related to wood anatomy, pulp quality and structural application of wood. A strong emphasis is put on the variability of wood properties as a function of cambial age. The findings are used to discuss selection strategies and at which age optimal response to selection can be expected with the aim to consider as many wood traits as possible in future tree improvement operations. Findings should thus help to maintain a high quality of wood and wood products in the long term.

This introductory chapter starts by providing a broad background overview on the principal wood traits and their impact on wood utilization (1.2 Wood and wood variation). Key to the topic of wood utilization and quality, the principal sources of wood variability and potential opportunities to control them are presented as well. Next, basic principles of quantitative genetics are presented in connection with the genetics of wood traits (1.3 Genetics of wood properties), before reviewing selection strategies and implications for breeding (1.4 Breeding for improved wood traits). The introduction ends with the thesis' objectives and hypotheses to be verified during the following main chapters.

1.2 Wood and wood variation

Trees are complex organisms whose ancestors arose some 380 million years ago in the middle Devonian (Willis and McElwain 2002) and the formation of wood evolved with them. In competition for light, trees form a lignified stem in order to position their crown with its vital organs for photosynthesis and reproduction high above the ground in advantage over other competitors. The woody trunk plays a key role in tree development and survival: it needs to withstand all mechanical forces arising from gravity or environmental influences such as wind load on the crown. Secondly, through its vascular tissues, it needs to ensure the transport of water and minerals to the live crown.

Within living memory, humans have selected and used the wood of the trunk and transformed it for example into tools, building material or simply fuel wood. Today, wood is very often utilized in applications demanding characteristics that are very different to

needs of the tree which shaped its structure. As a consequence, humans try to influence the properties of wood through silviculture, genetics and modern techniques of wood transformation that often decompose wood into particles and reassemble them afterwards. All these techniques allow producing large homogenous products suited to human needs and thus to overcome some restrictions due to the dimensions of the trunk and natural variation of wood.

1.2.1 Wood variation

Wood formation takes place at the cambium, a secondary meristem located immediately beneath the bark of the tree (Larson 1994). The **cambium** forms **phloem** or bast cells towards the exterior; but most cells are segregated towards the interior part of the stem and are called **xylem** or wood. Most xylem cells are submitted to a short differentiation phase and die within days after their formation (e.g. through terminal differentiation) in order to assume their tasks of water transport and trunk stabilization (Pallardy and Kozlowski 2008). Structure of the wood as well as cell morphology and chemical composition of the cell wall are determined within days or a few weeks and are not altered after cell death. Cambial activity and influences during the short differentiation phase are thus the ultimate reasons for wood variation (Zobel and van Buijtenen 1989).

Variation of wood properties represents a significant challenge for wood processing and utilization. Major differences of wood and wood formation are observed between species, but also inside a single tree between different ages or even within a single growth ring. The following paragraphs will elucidate those three main sources for wood variation. Variation of traits within a species' distribution will be discussed below (see section 1.3.1).

Taxonomy

In the course of evolution, a myriad tree species evolved that have very different ecological and morphological characteristics, and also bare differences in their wood. Botanically, there are two major categories of trees: **gymnosperms** which include conifers and **angiosperms** which include hardwoods. They are differentiated because of their reproductive structure: gymnosperms have no true flowers and their seeds are borne naked often subtended by a scale; whereas seeds and ovules of angiosperms are borne within

ovaries. Gymnosperms arose some 200 million years before the first angiosperms (Willis and McElwain 2002). Because of the early evolution, the wood of gymnosperms, including today's conifers, is relatively simple. It consists of vertical tracheids, horizontal ray cells and may contain specialized resin canals and associated cells. Tracheids take over both functions of water transport and mechanical support. They are arranged in radial files, giving a homogeneous structure to the wood. Tracheid tips are organized in an irregular pattern due to pseudo transverse anticlinal division of cambium initials. The overlapping of cell tips allows a rapid transport of water through pores of radial cell walls; but it also provides a high axial strength in timber (Barnett and Jeronimidis 2003).

The wood of angiosperms is more complex. Angiosperm trees separate functions of conduction and support between different cell types. Large diameter cells or vessel elements form conduits for long distance water transport. Fibres and, in some woods, also tracheids as well as fiber–tracheid ensure the support of the wood. The arrangement of these different cell types, along with axial parenchyma lead to a vast variety of anatomies in angiosperms. This pattern is further complicated by the presence of multiseriate rays that can be as large as 30 cells in some species such as *Quercus* spp. The variation and pattern of different cell types and their anatomy directly influence wood traits like density, strength or stiffness. Knowledge of variation is of great importance in determining the utility of hardwoods for a given product (Zobel and van Buijtenen 1989).

Juvenility and maturity

While wood variation between different species is the result of long-term evolution, within tree variation is mediated by the tree genes, it follows a pre-programmed developmental pattern that reacts to different environmental influences during the tree's life. The juvenile to mature changes in several wood properties may be observed by examining a transverse section across the stem of a tree which typically reveals substantial radial variation from the pith (located at the center of the stem) to the bark. Typical variation pattern in white spruce can be seen in the results section of chapter II (Fig. 2.1). Distinct patterns are found in hardwoods and softwoods, but they are more pronounced in softwoods (Zobel and Sprague 1998).

The wood in the first 10 to 20 growth rings close to the pith is often referred to as juvenile or core wood. In conifers, it is of a poorer quality than the mature or outer wood that is formed by the cambium in older growth rings (Kennedy 1995). The **juvenile wood** is usually characterized by cells with thinner walls and a lower wood density in comparison to the **mature wood** (Jozsa and Middleton 1994). The angle between cell axis and cellulose microfibrils of the secondary cell wall (also called microfibril angle or MFA, Fig. 1.1) is large in the juvenile wood (e.g. Mansfield et al. 2009). Microfibril angle is closely related to wood mechanics. As a consequence wood stiffness (measured through the modulus of elasticity or MOE) and strength are lower in juvenile wood than in mature wood (Walker and Nakada 1999).



The term juvenile wood is somewhat misleading; traits within the juvenile wood zone are not uniform, but rapidly changing from the pith outwards. Following this rapid change there is a levelling off creating a transition zone, also called **transition wood**, leading to the mature wood zone where changes in wood properties are small (Zobel and van Buijtenen 1989). The conversion from juvenile wood to mature wood is gradual and normally occurs over several years (Zobel and Sprague 1998).

Fig. 1.1. Cellulose microfibrils in the secondary cell wall (S_2) of a tracheid. The angle between cell axis and the main microfibril direction is called microfibril angle (MFA). Photo credit: FPIInnovations-Paprican.

There have been different approaches to explain the formation of juvenile and mature wood. Several authors suggested that formation of juvenile wood was related to the year of formation of the cambial initial (Yang et al. 1986; Zobel and Talbert 1984) as it forms a somewhat cylindrical or conical zone in the center of the tree (Zobel and Sprague 1998). Yang et al. (1994) for example reported a strong correlation between the number of growth rings in juvenile wood and the age of the cambial initials. The arguments of these authors hint towards a fixed program and that the onset of mature wood formation would be triggered through genetics together with some environmental influence.

An entirely different view, but not necessarily conflicting to the previous ideas is Larson's concept of "crown wood" (Larson 1969; Sanwo 1987). Although questioned by some authors, it represents the widely accepted opinion today. Larson and other authors (Larson 1962; Sanwo 1987; Zahner 1963) associated the formation of juvenile wood to the proximity of green (live) branches, i.e. close to the physiological processes originating from the living crown. Herein, it is understood that hormones that are produced by apical meristems are transported basipetally, i.e. from the crown downwards to the vascular cambium in lower parts of the stem. Together with photosynthates, growth hormones, such as auxins, influence cambial activity and cell differentiation (Savidge 2001). Different authors reported that auxins stimulate cell enlargement (Aloni and Zimmermann 1983) and the formation of thin-walled tracheids (Wodzicki 2001 and references herein). The influence of hormones diminishes with distance from the apical meristems. In old trees, the cambium forms juvenile wood in the crown zone but within the same growth ring mature wood at the base of the stem. Likewise, Larson (1967) stated that "(...) there is a progressive lag in the appearance of mature wood upward the stem".

The exact physiology behind the formation of juvenile and mature wood does not seem to be completely understood (Zobel and Sprague 1998). However, the existence of juvenile wood presents a challenge for solid wood utilization. This is principally due to its weakness compared to mature wood which can make it inappropriate for structural applications (Zobel and Sprague 1998). Another significant drawback is the variation of wood traits from one ring to another, especially microfibril angle and density, which causes problems

in dimensional stability and warping during drying of solid wood products (Bowyer et al. 2007).

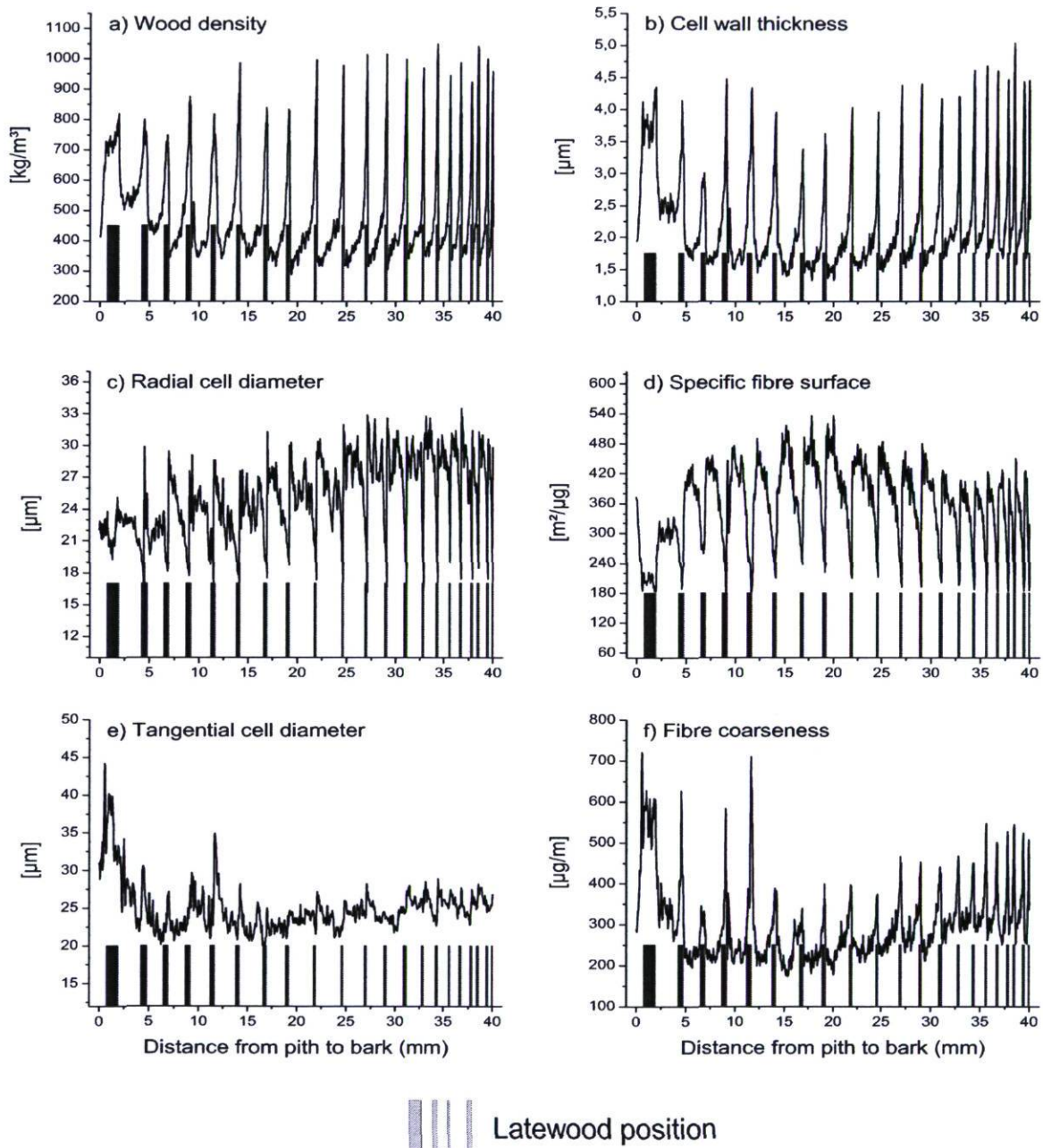
Seasonality

In the temperate and boreal regions, the periodical change of photoperiod and temperature throughout a year leads to another important source of variation in wood properties: the difference between **earlywood** and **latewood**. In the beginning of a growth season, the cambium forms earlywood which is characterized by large and thin-walled cells optimized to conduct water in order to satisfy the demand of re-emerging crown foliage. Latewood is formed towards the end of the growing season and after cessation of active primary growth of the stem leader(s) at the top of the tree (Kennedy 1971; Larson 1969).

Especially in conifers, the latewood contains small cells with thick walls that ensure mechanical stability of the trunk. One layer of earlywood and latewood together form a growth ring; whereas the change from earlywood to latewood is gradual in species like spruce, it can be abrupt in other species and traits like cell size or density can thus change very significantly from one cell to another (Pallardy and Kozlowski 2008). In any case, the change from latewood to next year's earlywood is very abrupt due to cambial dormancy during winter. In wood from sub-tropical or tropical climates, the ring structure can be totally missing or is due to reasons such as drought or some other, irregular growth stresses (Schweingruber 2007).

The variation of cell anatomy and density is demonstrated in Fig. 1.2. Variation between earlywood and latewood is major for some wood traits; Megraw (1985) stated that "the greatest variability in specific gravity occurs within each annual ring." These rapid changes in cell size and density between earlywood and latewood bands have consequences for wood transformation: such wood is difficult to machine to a smooth condition or to peel on a veneer lathe (Bowyer et al. 2007). Uniformity of wood is desirable for solid wood products and also for fibre manufacture to permit even processing of all wood components.

Fig. 1.2. Seasonal changes of wood traits in a white spruce increment core: Wood density, cell wall thickness, cell diameter, fibre coarseness, and specific fibre surface; measures were taken in 25 μm increments.



1.2.2 Wood utilization

Wood variation was described to have a major influence on wood transformation and its suitability for different applications. And yet, the expressions “suitability” or “wood quality” are somewhat arbitrary and always need to be linked to a specific purpose of wood

utilization. Like many conifers, spruce wood has a variety of end uses that require different wood and fibre properties. The following paragraphs address the main fields of utilization of spruce wood and mention the wood traits of interest.

Structural applications

Spruces and especially white and black spruce in Eastern Canada are highly valued for lumber and their end uses are highly versatile. Dimensional lumber and boards present the main products manufactured in various sizes and grades. They are used for structural purposes in construction for example as trusses, framing, roofing or sub-flooring (Zhang and Koubaa 2008). Spruce wood is also used for general millwork and a variety of other uses such as interior finishing, edge joists or boxes. The use of spruce for engineered wood products is experiencing an increasing importance. Glue laminated timber (glulam) is one of them, which presents a structural building material manufactured by gluing together individual pieces of lumber (Zhang and Koubaa 2008).

The main properties that influence the suitability of wood for structural applications are bending **strength** and **stiffness**. Strength is the ability of a material to carry an applied force whereas stiffness is a measure of resistance to deformation. In this research project we focussed on stiffness, also called modulus of elasticity (MOE). It is an important measure because it determines the amount a joist, in a floor or a roof, for example will deflect under load and thus how solid the construction will appear (Bowyer et al. 2007). Overall, mechanical properties of white spruce are inferior to red spruce, black spruce and especially jack pine and Douglas-fir wood (Zhang and Koubaa 2008).

Wood density is often considered as a key trait and a determining factor for wood quality (Zobel and Van Buijtenen 1989). Besides density, mechanical wood traits are essentially influenced by MFA (Fig. 1.1). Thereby MFA can explain up to 70% of the variation of MOE (Alteyrac et al. 2006a; Cave and Walker 1994; Walker and Butterfield 1996).

A major concern for structural applications of wood is the low density and comparably high MFA in wood from fast grown plantations (Bendtsen 1978; Kennedy 1995). The wood contains a significant amount of *weak* juvenile wood; and additionally, economic interests motivated optimization of plantation increment in the past, although wood quality traits are

largely negatively correlated to growth (Zobel and Van Buijtenen 1989, Gapare et al. 2009). Similar results were reported by Beaulieu et al. (2006) in a study on bending properties of white spruce lumber from young fast growing plantations: as a consequence, most of the tested pieces did not meet current design requirements. Thus, traits such as MFA, density and traits with a direct influence on density (ring width, latewood proportion and earlywood proportion) need to be controlled by silviculture and genetics in order to produce valuable lumber.

Pulp and paper

Spruces are suited for all types of pulps including chemical, stone ground and a variety of mechanical pulps (Zhang and Koubaa 2008 and references herein). Currently only tree tops, some lower quality logs and especially sawmill residues are used to produce pulp from spruce in Canada. Rarely entire spruce plantations are dedicated to pulp production.

The pulps are used whether pure or in mixtures to produce a variety of products such as coated paper, newsprint, facial tissue and also paperboard. The variety of applications demands very different paper properties: paper for printing for example needs smooth surfaces and high opacity; packing paper such as paper bags need high tear and burst indices. These properties are principally affected by **cell anatomical dimensions** of the wood, such as tracheid length, cell diameter, cell wall thickness and coarseness (Dinwoodie 1965; Zhu et al. 2008).

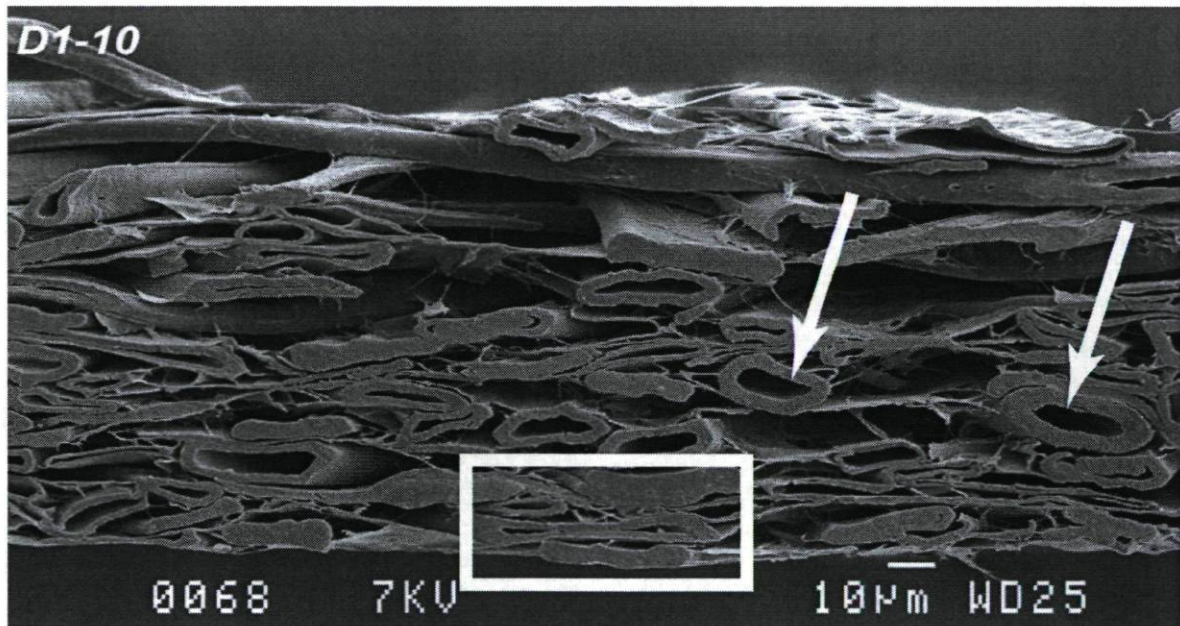
Thin-walled fibres with large lumen diameter collapse ribbon-like and provide good bounding between fibres (Fig. 1.3), thus increasing burst and tensile strength. Coarse fibres with thick walls do not easily collapse and do not contribute to inter-fibre bounding in the same way, but positively influence paper strength such as tear and breaking length (Smook 2002). White spruce pulps are characterized by well balanced strength properties, good color and high brightness. They also profit from low resin content as well as long and strong fibres (Zhang and Koubaa 2008).

The presence of juvenile wood can be problematic for pulp and paper production as it alters pulp and paper qualities. Lower density negatively affects pulp recovery, and low cell wall thickness and coarseness reduce strength. However, Duchesne and Zhang (2004) concluded

that white spruce wood from fast grown plantations appears appropriate for higher quality bounded paper grades where good surface smoothness and printability are required.

The above considerations show that fibre anatomy traits such as diameter, cell wall thickness and coarseness need to be monitored when wood quality is altered through silviculture or genetics. Such monitoring would enable the industry to offer a wide variety of pulp and paper grades also in the future.

Fig. 1.3. Cross-section of a paper sheet. Large diameter fibres collapsed ribbon-like (white square) and provide optimal inter-fibre bounding. Rigid latewood fibres in contrast keep their shape (white arrows). Electron microscopy photograph by FPInnovations – Paprican Division.



Emerging and novel products

In the recent years, some new products have evolved that are more or less related to the pulp or chemical forest industry. One of the current buzzwords is **biofuel** which includes the direct combustion or the processing of lignocelluloses into ethanol, and potentially into other higher value liquid fuels (Ragauskas et al. 2006; Pu et al. 2007). Using wood as an energy source becomes an interesting alternative in the quest to replace fossil energy carriers and to reduce carbon emissions. However, the economics of using wood as an

energy source and producing ethanol, for example, represent an unresolved issue that is closely linked to the cost of petroleum (Chambost and Stuart 2007).

The idea to produce ethanol by hydrolysis of wood and subsequent fermentation of sugars is not new; however, it comes with some major challenges, one of them is the high energy demand. Pimentel and Patzek (2005) reported that production of wood based ethanol needs almost 60% more fossil energy than standard fuel-produced ethanol. This is mostly due to the need of hydrolytic pre-treatments of wood in order to give microorganisms and enzymes access to carbohydrates; also the recovery of 8% ethanol from the broth with 92% water is very energy demanding. Different pre-treatments have been studied to improve accessibility (Pu et al. 2008), and some authors suggested integration of biofuels into pulp manufacture: extraction of wood chips prior to Kraft pulping could provide a constant hemicellulose stream for biofuel production (Ragauskas et al. 2006), taking advantage from the existing infrastructure and resource supply of pulp mills. A case study of the Forest Products Association of Canada highlights the economical and social advantage of the integration of bioenergy and bioproducts into traditional industry operations also in Canada (Anonymous 2010).

Future pulp and paper mills seem to offer a variety of possibilities for biofuel and biochemical production. Waste fibre sludges could be used for ethanol production (Sjöde et al. 2007); various gaseous or oleaginous chemical products could be extracted from spent and black liquor by **gasification** or **pyrolysis** (Pu et al. 2008): The ideas are manifold and declining competition of cheap petroleum based products promises an increasing importance of forest biorefinery in the near future.

It remains difficult to identify beneficial wood traits for the variety of these different products. However, a high hemicellulose content of some hardwoods and a few conifers such as white spruce definitely benefits fermentation and thus ethanol production (Ragauskas et al. 2006). The increasing demand for biofuels and biochemicals is expected to put additional pressure on the wood market. The establishment of fast growing plantations especially, mainly of hardwoods using intensive silviculture techniques, could represent a solution for providing the fibre sources to future bio-integrated industries.

A very recent development in forestry is **nanotechnology**. It provides a means for developing or improving forestry products creating lighter, stronger and multifunctional materials. Nano-fibrils from ligno-cellulose as well as cellulose nano-crystals form very important classes of nano-materials. Nanocrystalline cellulose (NCC) can increase resistance and strength of materials it is added to. It can alter surface of materials like paper, changing its permeability, strength and optical properties (McCrank 2009). Some current research projects are aiming to include NCC molecules into surface coatings for reinforcement and higher durability (Bernard Riedl, Laval University, personal communication).

Research in Canada on forestry related nanotechnology is led by the Canadian Forest Service and FPInnovations. Efforts are concentrated on the production of NCC, to develop applications with a special attention to forest products processes and to elaborate chemistry applications, including fire resistance of building materials or surface impregnation (McCrank 2009). Applications of nanotechnology seem very versatile and its development is expected to influence the forestry sector in the following years. Furthermore, the production of nano-particles and their application will most likely alter the demand and the quality requirements of wood resources in the near future.

1.2.3 Manipulation of wood properties

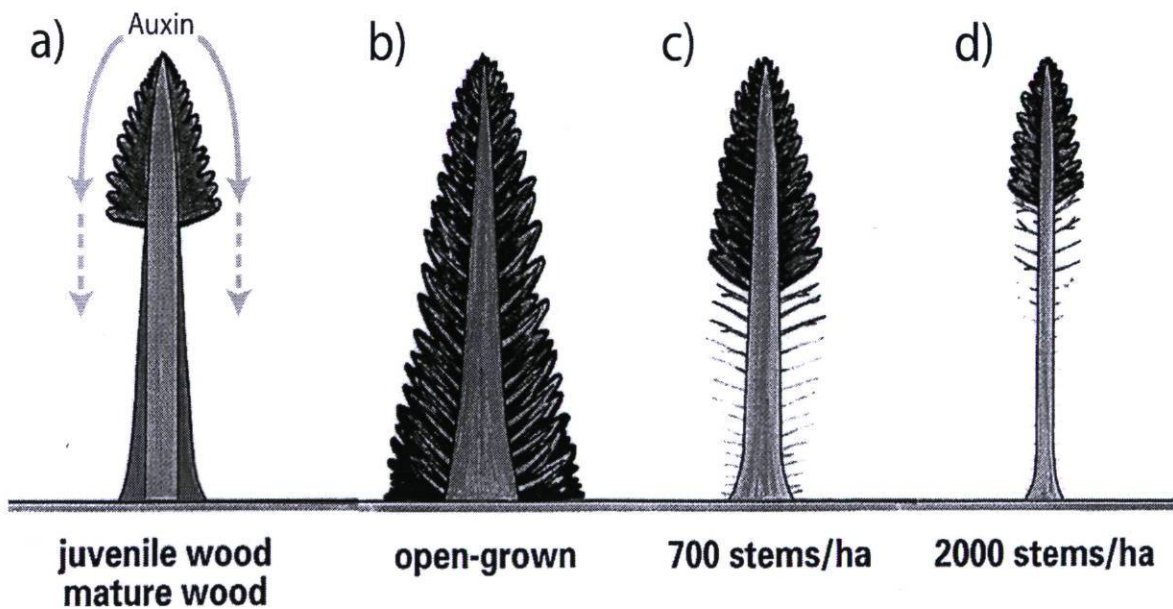
Foresters can alter wood properties through genetics or silvicultural treatments in order to produce high quality wood for a variety of end uses. Even if reasonable improvement of wood quality can be expected through genetics, the best results are achieved by a combination of genetics and optimized silvicultural treatments (Zobel and Talbert 1984). The following paragraphs give an overview of silvicultural management techniques and their influence on wood quality.

Silviculture influences the growth rate of trees and especially juvenile wood content. Planting distance is thereby crucial, as widely spaced trees will grow more quickly, profiting from a large photosynthetic crown, than narrow spaced trees (Fig. 1.4). But large spacing also promotes large knots, stem taper and a high percentage of juvenile wood

which penalizes the production of quality wood for structural applications (Bendtsen 1978; Bowyer et al. 2007). Foresters have thus to make certain choices between wood quality and growth resulting in a higher yield of merchantable wood.

Fertilization or irrigation enhance tree growth, but are mostly unfavourable for wood quality. Both have been reported to abruptly increase cell size and lower density and strength (Zobel van Buijtenen 1989; Lundgren 2004). In turn these changes negatively influence, wood uniformity, which can also represent a general problem of too intense silvicultural treatments. Bowyer et al. (2007) are stating that “silvicultural treatments should (...) be prescribed with uniformity as well as density of wood in mind.”

Fig. 1.4. Stand density, crown form and their influence on stem form and juvenile wood. (a) Auxins provoke juvenile wood formation close to the living crown. (b) to (d) stand density influences crown form und thus taper and juvenile wood content in the stem. Adapted from Josza and Middleton (1994).



1.3 Genetics of wood properties

The field of genetics offers perhaps the greatest potential for improvement of wood yield and quality in the future (Bowyer et al. 2007). However, because of the relative complexity of variation in wood properties, as discussed above, achieving actual improvement of wood traits requires a significant effort of genetic research to be done in order to describe the variation, the genetic control and to estimate the gain that could be achieved.

Forest genetics research has a long history dating back to the 17th century in Europe and also Japan (Zobel and Talbert 1984 and references herein). But genetic research on wood properties only developed since the 1950ies when the forest industry started to establish large programs of applied genetics. There are some early studies on wood anatomy traits such as tracheid length and cell dimensions (Goggans 1964), spiral grain and chemical composition as reviewed by Zobel (1961). But the main scientific interest has been in wood density (specific gravity) and density components such as latewood–earlywood proportion and also ring width.

Zobel and Jett (1995) wrote that “genetic studies have been done for many different species; some have been excellent and well designed (...)” but many also baring “a lack of understanding about the importance of sampling”. This problem was linked to the cost and tedious methods used for wood property determinations.

Recently, quantitative genetic analyses of coniferous wood properties have focussed more and more on fast growing and economically important species such as radiata and loblolly pine (Dungey et al. 2006; Kumar 2004; Myszewski et al. 2004; Roth et al. 2007). Most of these studies were aimed at physical and mechanical properties that include wood density, stiffness or microfibril angle. Only a few genetic studies looked at anatomical cell features like cellular dimensions, wall thickness or fibre coarseness that are important for the pulp and paper industry (Ivkovich et al. 2002b; Jones et al. 2005). Some studies also look at chemical composition of wood (Sykes et al. 2005; Sykes et al. 2006). Overall, there are fewer quantitative genetic studies on conifers other than pines. Some recent genetic studies have been published on spruces such as Norway spruce (e.g. Hannrup et al. 2004; Rozenberg et al. 2001), but they were still concentrating on growth traits and wood density.

No complex study covers the estimation of genetic parameters of mechanical properties and chemical composition of white spruce wood.

1.3.1 Wood trait evaluation

The challenge in improvement for wood traits is to precisely evaluate them on many, often thousands of trees in a quick and cost-efficient way. Some of the techniques currently used for wood trait determination in breeding imply modern, automated systems. One of these is the **SilviScan** system that allows fully automated image analysis, X-ray densitometry, and X-ray diffractometry on wood cores. This system allows to estimate about a dozen of wood traits related to cell anatomy and wood mechanics (see appendix 1 for details and references). Several years ago methods using **spectroscopy** have been developed to predict wood traits of a large number of samples in a cost-efficient way. Successful predictions of chemical composition of wood (Kelley et al. 2004; Jones et al. 2006) as well as physical wood properties (Xu et al. 2011; Schimleck et al. 2003; Schimleck et al. 2004) have been achieved using near-infrared (NIR) spectroscopy. More rarely infrared (IR) or Raman spectroscopy (Ona et al. 1997; Ona et al. 1998) have been used to predict wood traits. The application of spectroscopic methods in tree improvement comes with challenges. They imply the construction of a statistical model based on a calibration sample set for which both spectral information and the trait of interest needs to be known. The model can then be used on samples, with unknown properties, but needs to be regularly validated with new samples, especially those that might be outside of the range encountered in samples used to develop the model initially. Model validation is a key to ensuring the precision of the spectroscopic models which is crucial for selection in a breeding context.

The main focus in wood quality assessment for breeding has been on wood density as it is believed to be correlated to many end-use wood traits. Classically it is evaluated by X-ray densitometry on wood cores or disc-sections; besides density, information on ring width as well as earlywood and latewood characteristics and proportions can be available with this method. Other in-field methods for density evaluation are the **Pylodyn** pin penetration and the **Resistograph**. Pylodyns have been used for rapid, non-destructive assessment of wood density in breeding programs (Raymond and MacDonald 1998 and references herein). The

Resistograph (Rinn et al. 1996) is a tool that relies on drill resistance; its efficacy in selection for tree improvement was discussed by Isik and Li (2003).

Recently, devices have been developed for the quick evaluation of wood stiffness or strength, which are highly important traits for the mechanical utilisations of wood. A series of different acoustic tools has been developed that rely on sonic resonance or sound velocity. The velocity of sound in wood is closely related to stiffness and also to some extent to microfibril angle and to wood density. Acoustic tools appear to be very promising for application in selection in breeding; several quantitative genetic studies have already been published that use acoustic devices (Kumar et al. 2002; Kumar 2004; El-Kassaby 2011).

1.3.2 Genetic and phenotypic variability

Almost all traits that have been studied in trees are continuous or quantitative characteristics that are more or less normally distributed in a population. Unlike qualitative traits, quantitative traits are assumed to be linked to multiple genes or loci with small additive effect; they do not follow classical Mendelian inheritance patterns (Zobel and Talbert 1984; Falconer and Mackay 1996). The investigation of genetic and phenotypic variability is one of the first steps in genetic research on a species or a species' subpopulation. Genetic variation is due to variation in alleles of genes and occurs within or between populations. It is ultimately created through mutation and then driven by forces such as meiotic recombination, natural selection, genetic drift or gene flow. Genetic variation is the basis for natural selection or man-made breeding programs. It is thus important to investigate if a trait has enough variation and potential for improvement by selection prior introducing it into a breeding program.

Due to evolutionary selection over hundreds of millions of years, we can today find significant variation between segments of a species that may grow in very different environments (Zoble and Jett 1995). These segments are called populations, provenances or geographic sources. Numerous studies have described the variation between provenances of different species and different wood traits. Outcomes show that variation is sometimes linked to climatic and geographic gradients along longitude, latitude and elevation. But patterns observed for wood traits seem less evident than for growth and adaptive traits,

which are under strong environmental influence. Zobel and van Buijtenen (1989) give an overview of provenance variation in the most important coniferous species, including spruce. For example, wood from Norway spruce shows patterns from the north to the south of the species' natural range with northern and high altitude sources having less dense wood (Zobel and van Buijtenen 1989 and references herein); but relationships are weak and intra-provenance variation is more important than inter-provenance variation (Nepveu 1984; Worrall 1975). Similarly, an important tree-to-tree variation in specific gravity was found in black spruce from New Brunswick (Zhang and Morgenstern 1995), but no geographic gradient could be reported for Newfoundland progenies (Hall 1984). Studies linking variability of wood traits to geographic variation of a specie's entire natural distribution seem to be lacking for black and other North American spruces.

Research on the genetics of white spruce began in the 1950ies and many studies have shown an important variation of growth and adaptive characteristics (Corriveau and Boudoux 1971; Dhir 1976; Li et al. 1993; Li et al. 1997). Some other studies aimed to obtain better knowledge on the genetic variation of wood characteristics such as wood density (Corriveau et al. 1991; Taylor et al. 1982), fibre length (Beaulieu 2003; Wang and Micko 1984) and decay resistance (Yu et al. 2003). Table 1.1 gives a general impression of mean values as well as the phenotypic variation of wood stiffness and gravity in several Canadian tree species.

Table 1.1. Specific gravity and MOE of Canadian woods (data from Jessome 1977).

Species	Origin of material tested	Specific Gravity (basic)		MOE (static bending)*	
		Mean	CV %	Mean [GPa]	CV %
White spruce	NB, QC, MB, SK, AB	0.35	(10.2)	9.9	(18.6)
Black spruce	NB, QC, MB, SK	0.41	(9.4)	10.4	(22.3)
Lodgepole pine	BC, AB	0.40	(8.8)	10.9	(14.3)
Jack pine	NB, ON, MB, SK	0.42	(8.8)	10.2	(19.8)
Douglas-fir	BC	0.45	(11.4)	13.5	(17.7)

* conditioned to 12% humidity

Large variation of specific gravity was reported for white spruce sources from all over Canada by Holst (1960), ranging from 0.31 for the Lake Edwards (Quebec) provenance to contrasting 0.47 for the Kananaskis (Alberta) provenance. However, a similar picture to the above cited black spruce and Norway spruce is drawn when only Quebec provenances are considered: Beaulieu and Corriveau (1985) found very significant tree-to-tree variation while differences between provenances only account for 10% of the total variation. Authors reported a variation of provenance means from 0.33 to 0.37 (basic specific gravity) where samples were varying between 0.28 and 0.42. Latitude has a little and statistically insignificant influence on wood density (Corriveau et al. 1987). Correlations between wood density and longitude as well as elevation were negligible. Due to their findings, these authors estimated that there is a good potential for improvement of density of eastern white spruce, especially when best individuals from high density provenances would be selected.

A few other studies also investigated genetic variation of transformation of white spruce wood; but no or little differences in veneer production, machining properties or drying treatments could be attributed to different genetic provenances (Beaulieu et al. 2002; Hernandez et al. 2001; Zhang et al. 2004). A genetic improvement of transformation properties seems to be unattainable. Despite these reports, there is a lack of knowledge on genetic variation, genetic control and possibilities of improvement of spruce wood traits such as stiffness and strength that are aligned applications of white spruce wood.

When studying genetic and phenotypic variability, one observes that populations, provenances or progenies may perform differently when they are moved away from their site of origin natural stand. This is related to different environmental influences and a different interaction between the tree genotypes and the environment in different locations. To fully understand the effect of provenance variation, it is useful to acquire a clear understanding of environmental and genetic control of wood traits.

1.3.3 Genetic control

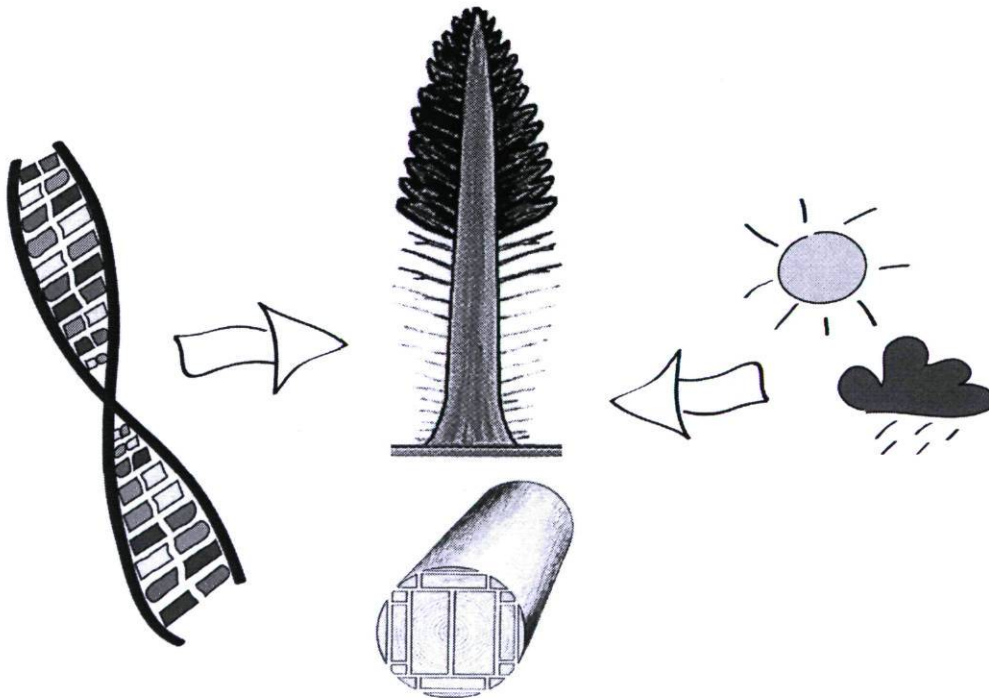
The estimation of genetic control is a key analysis in quantitative genetics. The amount of genetic control in a trait represents an important piece of information for geneticists as only genetic effects can be influenced through breeding and be transferred from one generation

to another regardless of environmental effects. To better understand the importance of genetic influence, one needs to recall some of the fundamental concepts in quantitative genetics: one of those is the assumption that every observed **phenotype is the combination of genetic and environmental effects** as well as their interaction (Fig. 1.5).

$$[1.1] \quad P = G + E + G \times E \quad \text{with } G \text{ split up into} \quad G = A + D + I$$

with P being the phenotype, G the Genotype and E the environmental effect. The genetic effect herein can be broken up into additive (A) and non-additive effects, latter are due to deviation from simple additive contribution of alleles to a phenotype. The non-additive part contains effects due to interactions between different alleles from the same gene or also called dominance effects (D) as well as effects due to interactions between different genes, also called epistasis (I) (Nanson 2004).

Fig. 1.5. Influences on the phenotype: a basic concept in quantitative genetics.



$$\text{Phenotype} = \text{Genotype} + \text{Environment} + G \times E \text{ Interaction}$$

To quantify the amount of genetic control of a trait geneticists use a measure called heritability:

$$[1.2] \quad H^2 = \frac{G}{P} \text{ in a broad sense or } h^2 = \frac{A}{P} \text{ in a narrow sense}$$

It consists of the ratio of genotype and phenotype or, in other words, the ratio of genetic variance and the total phenotypic variance. It is useful to distinguish between **broad** and **narrow sense heritability**. Broad sense heritability implies that all genetic effects are considered in the numerator, whereas only additive effects are considered in **narrow sense heritability**. Additive effects, which typically account for the largest part of genetic effects, can be estimated more easily through sib-analysis whereas analysis of total genetic effects mostly rely on extensive clonal testing (see next page for description of a clonal test).

Genetic control of wood traits is generally moderate to high (Zobel and Jett 1995). This means that observed phenotypes are good indicators of the genotype, which is favorable for tree improvement. There are numerous studies providing heritability estimates for wood density and some cellular components for hard pines and Douglas-fir. The *Picea* genus has been less extensively studied. Moderate individual heritability estimates (0.47) were reported for wood specific gravity of interior spruce by Yanchuk and Kiss (1993). Very similar results were found by Corriveau et al. (1991) for relative density of eastern white spruce provenances. In *Picea abies*, Mothe (1983) found provenance differences in heritability between $h^2=0.40$ and $h^2=0.60$. These estimates are in the same range as most reported values for other important conifer species such as hard pines and Douglas-fir (Zobel and Van Buijtenen 1989).

Studies of heritability of wood traits other than density are rare in spruce. Ivkovich et al. (2002a, b) published the only complete study in which they investigated heritability of cell anatomy components, density and MFA in selected growth rings of interior spruce (*Picea engelmannii* x *Picea glauca*). Some of the estimates were variable between different progenies but also between different growth rings. Their results and earlier findings by different authors (e.g. Gwinyai Nyakuengama et al. 1997; Hannrup and Ekberg 1998; Hylen 1999) indicate that heritability is not stable from one growth ring to another. But

detailed information related to this issue is lacking for spruces and especially for eastern progenies of white spruce, although genetic control and trends of control need to be known as precisely as possible for a given population when breeding for wood quality is considered.

Genotype-by-environment interaction

In forestry, the genotype-by-environment interactions (G x E) describe the performance of a genotype, an individual or a family at different locations. G x E for several traits have been evaluated especially in fast growing pines and eucalypts in the past. But the practical significance has been reported to be little for growth, wood density and wood stiffness (McKeand et al. 1997 and references herein, McKeand et al. 2006; Wielinga et al. 2009). Only Baltunis et al. (2010) reported some evidence for G x E of tree diameter and branch size in their study of Australian radiata pine. Some G x E interaction was also reported for wood chemical properties in loblolly pine by Sykes et al. (2006). However, there appears to be a lack of knowledge of G x E of wood traits in other species, especially in spruces. The investigation of G x E in this species is crucial as breeding programs often aim to identify genotypes with a good performance on a broad variety of sites and silvicultural regimes.

Genetic testing for quantitative traits

The previous section introduced the concept of heritability as being the ratio of genetic (G) and phenotypic (P) effects. Estimating heritability assumes that the magnitude of these effects including the environmental effects is known. A key preoccupation in genetics and breeding is to precisely separate G and E effects that are confounded in phenotypic observations. This is done by genetic testing.

A genetic test is a comparative plantation on a specific site following a statistical structure in order to compare sometimes hundreds of genetic elements at a time. The test can be replicated on several sites to study the performance of elements in different environments. Genetic elements can be represented by different species, varieties, provenances, families or clones (Nanson 2004). Testing assumes that the elements that are compared are randomly selected among a larger set. The three types of tests that are most frequently used are the provenance, the progeny and the clonal test. Brief descriptions follow.

(a) A **provenance test** often stands in the beginning of a genetic program. The aim is to compare seed lots from different origins of a species' distribution. It serves to assess the genetic value of a provenance and to describe the species' genetic variation.

(b) A **progeny test** is an experiment where the offspring of several parents (i.e. several families) are compared. Progeny testing is sometimes combined with provenance testing in a single experiment. The progeny test is mostly used to estimate the genetic value of the descendants' parents and to select the best genitors (backward selection). In the case of forward selection, the test can also be used to directly select the best families or individuals for further breeding.

One differentiates between half-sib and full-sib families. Full-sib families are issued by controlled pollination of one female tree and one male; in this case parents of all offspring are the same. Half-sib families are generated by polycrosses or several matings between a female tree and several known males. A special case is open-pollination, where a female tree is pollinated with a load of pollen from different trees; all progenies have hence one parent (female) in common. However, open-pollinated families are not strictly half-sibs, but a mix of half and full-siblings, depending on the effective number of pollinator males.

(c) To be able to capture, the entire genetic variance, a **clonal test** needs to be used. Comparing different individuals with the same genotype (clones) allows to estimate non-additive genetic effects and also to optimize the assessment of additive effects. This increases the determinable amount of genetic effects and leads to high heritability estimates. Additionally, superior clones matching the objectives of a breeding program can be easily identified. Nevertheless, the production of clones is expensive and the establishment of clonal breeding trials is often reserved to advanced breeding generations.

Statistical methods in quantitative genetics

In each genetic test, control of the environment cannot be ignored. To be able to precisely estimate genetic effects, environmental effects on each individual need to be as homogenous as possible. This is achieved by homogenous and wide planting distances to avoid competition. But also the choice of a homogenous site for example with uniform soil

and drainage is important. Statistical experiment designs using randomization and blocking are used to account for residual within-site variation.

An accurate determination of genetic and environmental effects also relies on the statistical analysis of the field experiment. Phenotypic data from genetic tests are usually analyzed with ANOVA (analysis of variance) or ANOVA-like methods. Statistical models contain the different genetic effects (provenance, family or clone) to be tested and the effects to better control the environmental influence (block, site in test). The standard ANOVA uses least-square regression to estimate variance and covariance matrices from which magnitude of genetic and environmental effects as well as significance of effects are estimated. But the classical approach has limitations for tree breeders and can lead to biased estimates, especially when unbalanced data is used. In reality, the loss of individuals, families or entire blocks in field experiments is common and analysis techniques appropriate for unbalanced data need to be used. Today, most quantitative genetic analyses rely on mixed models using the REML (restricted maximum likelihood) approach. REML is herein a powerful iterative method and can deliver statistically unbiased estimates of variance components (Saxton 2004). Additionally, the mixed model approach enables analyses of more complex statistical designs found in advanced-generation programs such as analyses including several mating designs or different generations or designs with non-random mating (White et al. 2007).

1.3.4 Molecular genetics in forestry

While some of the basic concepts of quantitative genetics evolved over centuries, the rapid evolution of molecular biology during recent decades had a large effect on forest genetic research. The outcomes of this research will most likely influence management practices in the near future. The following paragraphs give an overview of some major developments in molecular forestry research.

Since the 1960s, biochemical markers such as allozymes have been used by forest geneticists to investigate genetic variation and diversity of natural and artificial populations. The application of molecular genetic techniques to forest trees was well established by the early 1990s (White et al. 2007). The development of restriction fragment

length polymorphisms (RFLP) markers and their application to organelle genomes allowed inheritance studies of organelles (Neale and Sederoff 1989; Neale et al. 1986) and provided unique opportunities to study genetic diversity and phylogeography in tree species. Many other markers mainly based on amplification of DNA sequences using the polymerase chain reaction (PCR) were developed for the nuclear genome. The markers were used to study temporal and spatial patterns of genetic variability in populations, human or natural influences on variation, phylogenetics, fingerprinting or for the construction of genetic maps (Strauss et al. 1992).

In the late 1990s, the genomic era came to forest genetics, opening possibilities for the concurrent study of many genes. Constant advances in DNA sequencing techniques allowed building gene catalogues and methods to study gene function were first introduced (Pavy et al. 2005; White et al. 2007). Still a young science, genomics already has highly specialized areas such as the fields of structural and functional genomics. **Structural genomics** focuses on the overall sequencing of genes in a species as well as on genome mapping representing the relative position of genes on the chromosomes (Pavy et al. 2008). **Functional genomics** for its part deals with the individual and combined influence of genes on a given trait (Bousquet et al. 2007).

In forest genetics, there is a common interest to use outcomes of both areas of genomics in order to investigate allele–gene combinations that govern phenotypic variation of commercially valuable traits. The identification of such candidate genes follows two different strategies: The first involves the analysis of quantitative traits in segregating pedigrees and the identification of quantitative trait loci, known as QTLs. A second approach is based on the identification of DNA polymorphisms and their direct association to phenotypic variation in a population which is estimated to be unstructured (Bousquet et al. 2007).

Until now, very few studies have been published where candidate genes could be associated to a phenotype in forest trees. Eckert et al. (2009) reported genetic association of 12 candidate genes and 14 traits related to cold hardiness in Douglas–fir. In a study on Sitka spruce, Holliday et al. (2010) detected associations to 28 candidate genes related to

cold hardiness and bud set. Associations to wood traits are even rarer: significant SNP associations for two genes related to wood density in radiata pine were found by Dillon et al. (2010). González-Martínez et al. (2007, 2008) published statistical correlations between SNPs from several candidate genes and quantitative wood traits as well as carbon isotope discrimination (CID, related to water use efficiency) in loblolly pine. Six genotype–phenotype associations for three wood traits were significant: earlywood density, latewood proportion and earlywood MFA. As might be expected due to the quantitative nature of these traits, individual candidate genes only explain a small proportion of the overall phenotypic variation. Individual SNPs are expected to account for 1 to 10 percent of the phenotypic variation (Neale and Ingvarsson 2008).

One of the most obvious outcomes of association studies is the application of validated SNP markers or QTN in **gene-assisted breeding** (GAS) (see section below: 1.4.3 Molecular genetics in service of tree improvement). But successful associations will also elucidate the genetic control of wood traits. This will help to better understand their genetic architecture and to answer questions, such as (a) how many genes are associated to complex traits, e.g. wood density? (b) Which specific alleles are responsible for superior traits? Or (c) is superiority more related to variation in regulatory regions? Even if the numbers are still modest to date, association studies on plants and trees have yielded some interesting genes.

1.4 Breeding for improved wood traits

For many years, breeding programs were focussed on growth, adaptability or pest resistance of trees. Although these traits have an indirect impact on wood yield and quality, wood traits directly related to its utilization have been surprisingly neglected, considering that the aim of forestry is to produce wood suitable for a multitude of different applications. Authors like Zobel (1964) and Curro (1972) suggested early on to include wood traits along with growth into breeding programs. Zobel (1974) noted that moderate change of wood properties could be achieved without negative impact on desired form, growth and adaptability.

However, it took until the 1990s for first selections in breeding for fast growing pine species such as radiata pine (Wu et al. 2008) to be based on indices including wood density. There are several reasons for the long delay between the recognition of importance of wood quality and the actual insertion of wood traits into tree improvement. (a) A common problem has been the **lack of** large test and breeding populations with a **sufficient wood volume for testing**. For example, extensive white spruce progeny tests were established in Canada only by the end of the 1970ies. Relatively slow growth only permitted the comprehensive analysis of wood properties in recent years. (b) Even if tests with acceptable tree size have been available earlier in other, fast growing species, the analysis of wood traits in large genetic experiences remains **tedious and expensive**. The development of tools that allow the quick evaluation of complex traits such as MOE or methods that correlate wood traits to spectral information will facilitate the effort of intensive phenotyping of wood traits in the near future. (c) For a long time, there was a **lack of pressure** from consumers or industry on breeding programs to regenerate seedlings with improved wood quality. Wu et al. (2008) noted that stiffness of older radiata pine trees from Australia was deemed acceptable for structural timber for a long time. The problem became more apparent in recent years when more and more wood from short rotation plantations could be found on the market. This wood contains more of the weaker juvenile wood or is sown from trees that are *only* improved for growth, thanks to achievements from previous breeding generations. In other words, the combination of selection for faster growth and the use of more intensive silviculture methods together have had a detrimental effect on wood quality.

Radiata pine programs are probably the most advanced in breeding for wood properties. In New Zealand, ranking of families for wood density using Pilodyn penetration started in the mid 1970ies. But “High wood density” breeding populations were established only in 1995 (Jayawickrama and Carson 2000). Serious consideration of wood density into Australian radiata pine breeding was implemented only in recent years (Wu et al. 2008).

It seems difficult to acquire detailed information on which wood trait is about to be included in tree improvement programs. Some hints can be found in a comparison table published by Apiolaza (2009). This author put together information about different

measurement methods for early selection of wood quality and their application in different countries and tree species. This information leads to the conclusion that selection for wood density is incorporated in major breeding programs for radiata pine (Australia, New Zealand, Chile, and South Africa) as well as for loblolly and slash pine (USA). New Zealand and Australia are furthermore implementing acoustic MOE in selection and surveying MOE and MFA on a research base by SilviScan measurements. Occasional application of NIR predicted lignin or chemical composition of radiata pine wood (New Zealand, Chile) and loblolly pine wood (USA) hints towards an inclusion in breeding programs in the near future.

1.4.1 Genetic gain

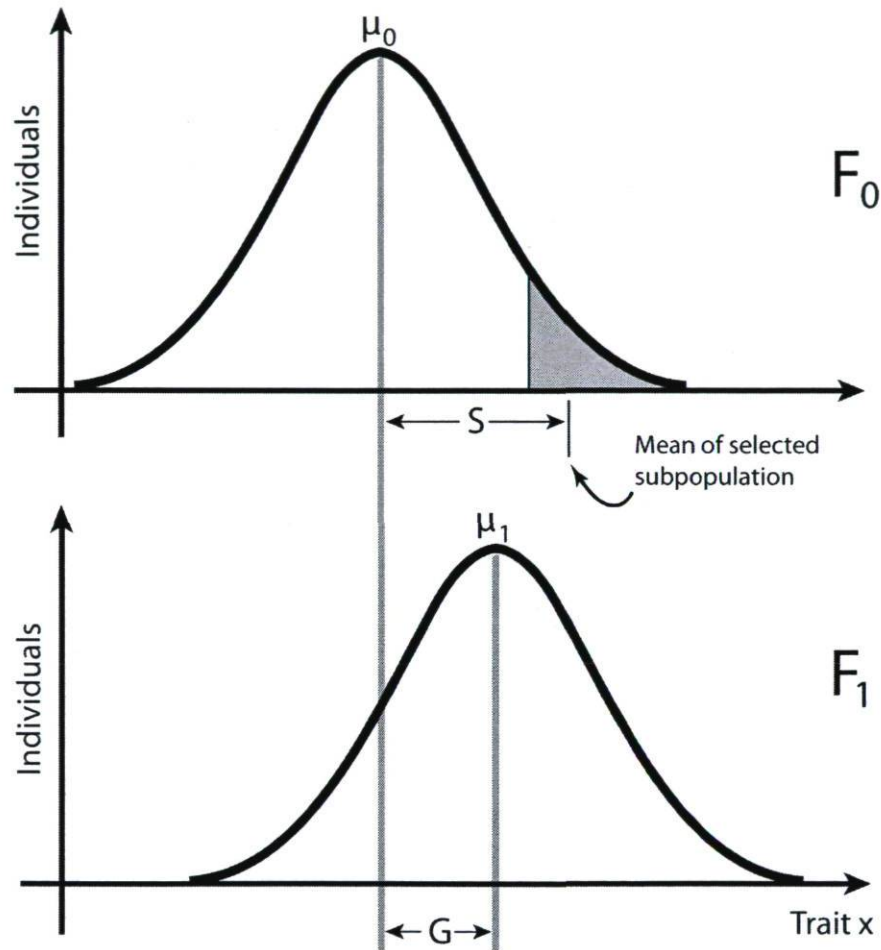
The ultimate aim of each breeding program, whether in an agricultural or a forestry context, is to improve one or more traits of interest. The most important driver in shaping a tree breeding program is economics, i.e., one aims to achieve a monetary advantage for future plantations through higher yield, e.g. by increased growth, or a higher value, e.g. wood quality (White et al. 2007). This section gives an overview of the concept of genetic gain.

As most wood properties are quantitative traits, there are always individuals whose traits are considerably different than the population mean. By selection, mating and propagation of the *best* individuals, one is trying to increase the mean value of a trait in following breeding cycles. The difference of a trait between the current and a following breeding generation is called **genetic gain** (Fig. 1.6). This improvement can be expressed in absolute values or in percentage of the original value. One must distinguish between expected and realized genetic gain. Realized gain is based on actual measurements of both base and improved populations; the expected gain is estimated *a priori* using information of a population that is considered for selection. The mathematical expression for the genetic gain (G) is:

$$[1.3] \quad G = h^2 * S \quad \text{with} \quad S = i * \sigma_p,$$

where h^2 is the narrow sense heritability and S is the selection differential. S can be split up into selection intensity i and the phenotypic standard deviation σ_p of the trait under consideration.

Fig. 1.6. The concept of genetic gain. Selection in the current generation (F_0) influences the expected gain (G) in the next generation (F_1). Breeders aim to maximize the selection differential (S). The selection differential is the difference between the actual population mean and the mean of the selected sub population.



The most straightforward way to alter the amount of expected genetic gain is to raise the selection differential or rather the selection intensity. In other words, to increase the difference between the mean of the selected parents and the total population mean (Fig. 1.6).

The mean of the selected subpopulation is influenced through the shape of the statistical distribution of the entire population, expressed by the phenotypic standard deviation, and how many individuals are selected compared to the total population, in short the selection intensity. Its value is calculated through a logarithmic function or can be found in tables

such as on page 134 in Zobel and Talbert's book on "Applied Forest Tree Improvement" (1984). The smaller the portion of selected individuals, the more extreme are their phenotypes compared to the entire population. As a consequence, a higher mean and thus gain can be expected in the offspring population obtained by inter-mating of these selected individuals.

Usually only a part of the superiority of selected parents is due to heredity, which explains that heritability influences the linear relationship between genetic gain and selection differential (Fig. 1.6). Superiority due to environmental effects cannot be passed from one generation to another. Therefore, tree breeders seek to maximize the estimate of genetic control in the base population through the choice of uniform sites and the control of the environment (Zobel and Talbert 1984). The high level of genetic control that has been estimated for wood properties together with a considerable variation of traits thus promises considerable gains in breeding for wood quality.

However, expected gains reported in the literature are variable because they highly depend on the specifics of a selection scenario, including the population size, the selection intensity or the economic weight in cases of multi-trait selection (e.g. Gapare et al. 2009). For wood density in spruce, Zhang and Morgenstern (1995) expected a response of selection around 3.3% in black spruce, whereas 4.4% was reported for Norway spruce (Costa E Silva et al. 2000).

1.4.2 Selection strategies

Optimizing genetic gain in a cost effective manner is the main focus and objective of a tree improvement program. To achieve this goal effectively, tree breeders have the choice between different methods of selection of the best genitors, dependent on the species genetics, on the information available and the product goals. The three main methods will be presented in the following paragraphs.

(a) **Mass or individual selection** involves that individuals are selected based on their phenotype only. The performance of ancestors, siblings or other relatives is not considered. This selection method is mostly used when the pedigree is unknown, for example, in plantations or natural stands (Zobel and Talbert 1984). It works best for traits showing high

heritability, which means that the phenotype is a good reflection of the genotype or genetic potential.

(b) **Family selection** means that the choice of entire families is based on the average performance of family members. It is applied in cases of low heritability (Nanson 2004). Environmental effects can be compensated to some degree, if family averages are calculated from a large number of individuals (Falconer and Mackay 1996). Family averages then become a good estimate for the average genetic effect. However, in forestry family selection is often combined with other methods in order to achieve larger genetic gains. There is another inconvenience when selection is based on families only: it can reduce the genetic base and increase the risk of inbreeding (Zobel and Talbert 1984).

(c) **Intra-family (mass) selection** relies on the choice of individuals in many families that bare better characteristics than other family members. This method implies a low rate of inbreeding, but gains are mostly small. It is thus often combined with family selection. The combined selection, family selection in a first step followed by intra-family selection, is frequently applied in forestry. In cases of low heritability of the trait to be improved, the intensity of selection is shifted towards the family selection; if the heritability is high, the intensity is shifted towards within-family selection. This way, the genetic gain can be optimized (Nanson 2004).

Some authors also recognize further selection methods such as provenance, sib and clonal selection. These methods are quite self-explanatory and were mentioned already above in section 1.3.2 (subsection: genetic testing for quantitative traits).

Selection for multiple traits

Most breeding programs aim to incorporate gains for several traits at a time in order to meet different needs through future plantations. If one wishes to alter a trait through breeding, it is fundamental to know its relationship to other traits of value, whether those traits are finally included in a breeding program or not. An important step is the investigation of correlations between traits, especially at the genotypic level where environmental effects are not taken in account (see section 1.3.2). Some opposing (unfavourable) correlations can cause problems and it is difficult to combine traits in a

breeding program. A classic example is the negative correlation between growth traits and wood density (Zobel and Jett 1995). It has been often reported that increased tree growth often causes a lower wood density and a decrease of related mechanical traits such as strength (Rozenberg and Cahalan 1997; Beaulieu et al. 2006; Steffenrem et al. 2009). Problems due to negative correlation between traits can only be overcome by knowledge of the genetics of traits and optimized selection strategies. There are three essential systems that pertain to multi-trait selection:

(a) In the case of **tandem selection**, a given trait is targeted alone and improved over several breeding generations until a sufficient level is achieved. The next trait is improved thereafter in following cycles. In forestry where breeding cycles are of long duration, this approach is rarely considered from the beginning of a breeding program. However, with the shift from breeding for quantity to wood quality this approach is considered in some programs today. There are variations of tandem selection where two or more traits are selected one at a time within a breeding cycle (two-stage selection). For example, early selection for a growth trait is followed by a selection for another trait from the individuals remaining after the first screen. In all cases, the expected gain depends on the order of selection and on the correlation between traits (White et al. 2007).

(b) **Independent culling** means that minimum values are set and only trees that meet these minimum criteria are selected. This selection has intuitive appeal and can be applied by tree breeders in a straightforward manner. However, it does not consider economic weight neither the heritability of different traits (Nanson 2004). White et al. (2007) indicate that independent culling is best applied in combination with index selection, where high priority traits are included in the selection index and low culling levels are set for low priority traits. This way, only individuals with unacceptable values of low priority traits are not retained for selection; concentrating on the more important economical values.

(c) **Index selection** is a multivariate approach to combine all traits of interest into a single index. A score is assigned to each individual using the formula

$$[1.4] \quad P \times b = G \times a \quad \text{leading to:} \quad b = P^{-1} \times G \times a,$$

where P and G represent the variance–covariance matrices of phenotypic and genotypic effects, and b and a are the vectors of phenotypic and economic weights, respectively. By solving the set of simultaneous equations, the breeder derives a vector of phenotypic weights. It is dependent on the heritabilities, correlations among traits and the economic weight of each trait (Baker 1986). Theoretically, index selection leads to the optimum genetic gain for all traits. A crucial and often very difficult issue is to estimate the elements of the vector of economic weights. Several case studies have been published in the past that investigated optimum relative weights based on lumber value (Aubry et al. 1998) or the impact of different economic weights on genetic gain of pulp wood traits (Silva et al. 1998) in conifer species. However, it appears problematic to generalize results because tree species show large differences in their wood, its application as well as the value of wood products due to local market demands. Tree breeders need to evaluate economic weights anew for each species and breeding program.

Indirect selection

There are several situations where it is very expensive, difficult or yet impossible to measure a trait of interest in a direct manner. In order to improve such a trait, breeders apply a method where they select for a trait that is related to the trait of interest but measurable without difficulty. This approach is called indirect selection.

Besides adequate genetic control of both traits, the key requirement is that traits – the trait to be improved and the trait on which selection is done – are highly correlated; otherwise genetic gain will be small and the results uncertain (Falconer and Mackay 1996). An example for indirect selection in the widest sense is the improvement of wood density. Compared with other wood traits, density can be easily measured and tree breeders aim to use it to improve wood quality traits, due to good correlations between density and pulp yield as well as density and mechanically important wood traits such as strength and MOE.

A special case of indirect selection is **early selection**. It implies that individuals are selected based on their juvenile performance with the aim to enhance mature qualities. Again juvenile and mature traits need to be highly correlated in order to achieve appropriate gains. Before early selection is implicated into a breeding program, tests are necessary to study the genetics of the trait of interest at a juvenile and a mature state as well as to

estimate correlations between both ages. Several studies have recently confirmed the possibility for early selection of mainly wood density in fast growing pines. Optimal gain of density per unit time is reported to be possible around cambial age 5 in loblolly pine (Gwaze et al. 2002) and radiata pine (Li and Wu 2005); which is much earlier than rotation age. In tree breeding there is a special interest on early selection; as forest trees are slow growing, an important objective for breeders is to reduce the length of breeding cycles in order to reduce costs and increase efficiency, in terms of genetic gain per unit of time.

1.4.3 Molecular genetics in service of tree improvement

The constant development of molecular genetic techniques such as high-throughput DNA sequencing and genotyping technology opens new possibilities for forest tree breeders. The possibility of early selection as described above would help to reduce breeding cycles. Even with early selection, there is testing of wood properties and the costly establishment and the maintenance of field tests. The development of genetic markers coding for wood quality traits would allow for testing based on genotypes instead of phenotypes. Genotype testing could be carried with seedlings at the nursery stage for future wood properties and make selection at a very early stage.

Selection

Genetic markers can be used in different ways for selection: (1) by application of statistical associations between a phenotype and one or more chromosome regions (quantitative trait locus, QTL). This is known as QTL mapping and represents an approach to identify DNA markers that can be used in **marker-assisted selection** (MAS). This is usually done with full-sib families where linkage disequilibrium (LD) is extensive (Grattapaglia et al. 2009). The markers linked to a QTL typically span a portion of a chromosome that may encompass several tens or hundreds of genes; and, their physical location relative to the gene that controls the trait is not determined. (2) Another approach for developing of MAS is to search for markers such as gene SNPs that can more robustly be shown to govern phenotypic effects (Wilcox et al. 2007). This is some times referred to as **gene-assisted selection** (GAS). From a tree breeding prospective, MAS based on QTLs can represent a good technology for within family selection when few families are considered as in Eucalyptus breeding programs developed in Brazil. However, when many families are

considered for selection (as in white spruce breeding programs), this approach can be costly if applied at the genome-wide level. For GAS, no prior pedigree information is needed and selection can be applied on a family level additionally to individual genotypes within families (Wilcox et al. 2007). On the other hand, QTL studies remain a powerful tool of forest geneticists to study the genetic architecture of quantitative traits in all tree species.

The advantages of using markers in tree breeding are multiple, the most important are: (1) **early selection** and identification of superior genotypes at an early seedling stage will significantly reduce generation intervals. (2) It basically **eliminates or substantially reduces field testing**, which is the most expensive component in breeding programs. (3) An **increased selection intensity** can be realized thanks to high throughput genotyping technologies that allow the screening of many more individuals than can be analyzed by field testing (Wilcox et al. 2007).

From a practical perspective, much research and development is still needed before markers can be extensively applied in breeding. There are some promising results; but there are only few reports of significant markers that have been identified to date and each one of them only accounts for a small proportion of phenotypic variation in traits of interest (see above: 1.3.3 Molecular genetics in forestry). In order for markers to become of value for application, larger proportion of the overall variation must be explained by markers. Therefore, it is to be expected that several markers will need to be used in combination to be used as selection tools.

Population management

In population management, genetic markers have already been used for a number of applications. They can help to characterize and choose the base population material. In breeding, markers can further be used to assess diversity (Williams et al. 1995) and verify parentage (Grattapaglia et al. 2004), which will help to avoid inbreeding and erosion of the genetic base (White et al. 2007). A more sophisticated but technically attainable application is pedigree reconstruction, in order to obtain most of the benefits of pedigree information without controlled crossing (Lambeth et al. 2001).

A very interesting and practical application of pedigree reconstruction was recently suggested by El-Kassaby and Listiburek (2009). They promoted the idea of identifying naturally created half-sib families with informative markers and to combine this information with quantitative genetic analyses in order to identify elite genotypes without field testing. In a case study, they obtained up to 85% of the gain of conventional breeding by this approach they call “breeding without breeding”. This study presents a very promising example of application of biotechnology in breeding where breeding cycles can be reduced significantly and promising genetic gains can be expected in the near future.

1.4.4 Biotechnology

Different approaches of biotechnology have been used in forestry. Probably the most debated is the **genetic modification** of forest trees. The production of genetic modified organisms (GMO) has been of interest mainly to study the introduction of new characters such as pest or insect resistance genes transferred from diverse organisms which cannot be crossed with trees. Although genetically modified trees have been produced and established in field plantings in Canada and Quebec, strong environmental regulations were put in place to confine field testing and avoid uncontrolled propagation (Beaulieu et al. 2009). Some large-scale planting of genetically modified poplar has been done in China; also in the United States and South America, the genetic modification of several species including poplars, pines and eucalypts is investigated (White et al. 2007). However in Canada, the plantation of genetically modified trees for purposes other than experimental testing has not been done nor is it considered in the near future (Beaulieu et al. 2009).

Clonal forestry

There are several methods for the production of clones. **Grafts** or **rooted cuttings** are routinely used to conserve and propagate valued genotypes, for example in seed orchards. For several years, the Quebec ministry of Natural Resources and Wildlife has produced rooted cuttings for conifers, mainly spruces, as well as poplars to establish tree plantations (Beaulieu et al. 2009). This represents the first step to clonal forestry. Advanced techniques of **somatic embryogenesis** are also used at a small or pre-commercial scale in North America (Beaulieu et al. 2009; Grossnickle and Pait 2008). In a breeding context, the main

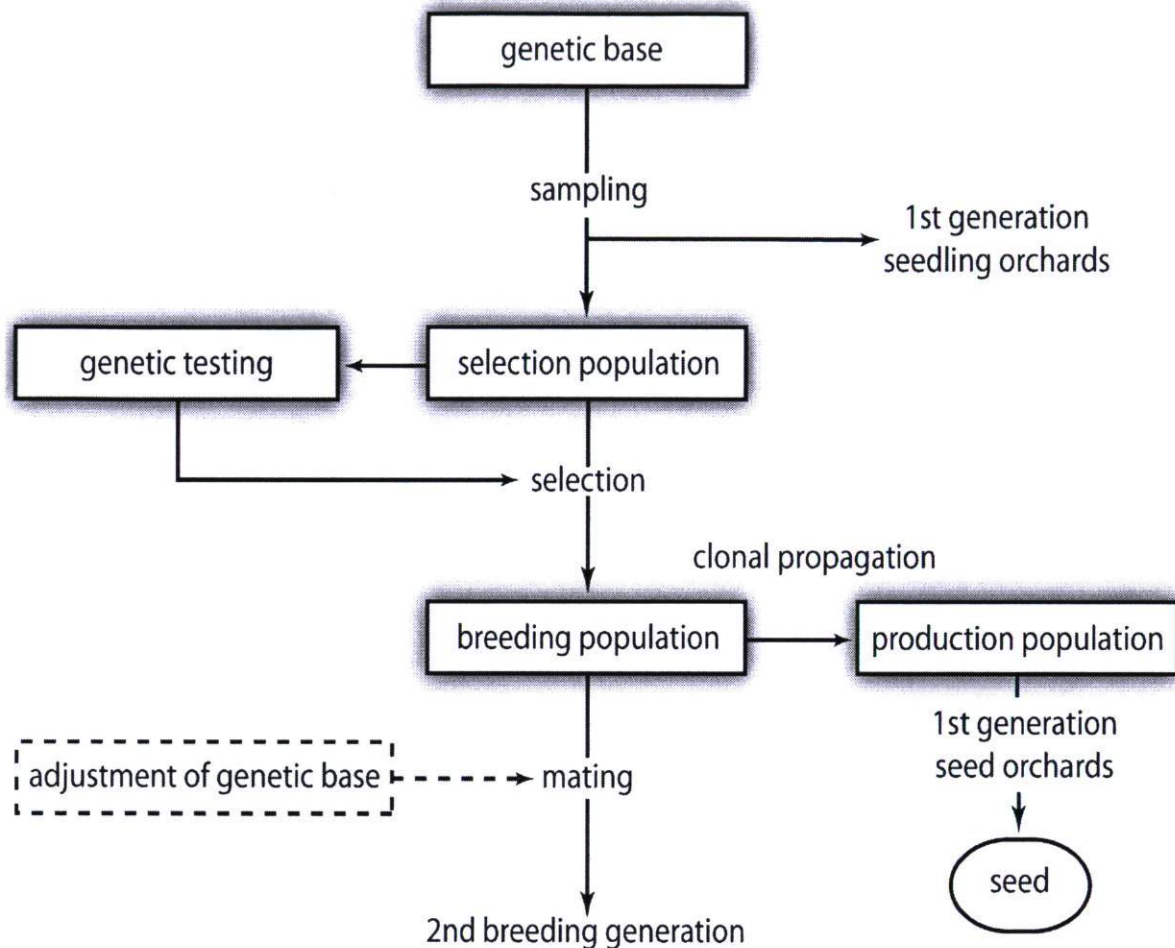
objective is to multiply and propagate high value seed obtained from controlled pollination of superior trees. The genetically superior clones could be used to establish high producing plantations.

1.4.5 Putting everything together – the breeding program

Breeding is characterized through the recurrent application of **selection**, **testing** and **mating**. Fig. 1.7 shows a general breeding program, but variations around this scheme are many fold. Breeding strategies need to be adapted to a species' characteristics such as economic interests, genetic and phenotypic variation of the traits of interest and the species reproduction biology.

A breeding program generally starts with the sampling of the genetic base from natural populations covering genetic diversity of a species. Seed of different provenances or progeny is then planted and evaluated by genetic testing. The best performing progeny is retained in breeding populations. The best individuals are then selected from the breeding population and clonal propagation is used to construct production populations. Those are often seed orchards that produced the improved seed for reforestation. The next breeding generation starts if progeny or individuals are selected from the first generation breeding population for further improvement. The steps to be taken for testing, selecting and breeding in following generations may be identical to the first breeding cycle.

Fig. 1.7. Schematic representation of a standard breeding program. Translated and adapted from Beaulieu et al. (2009).



1.4.6 The state of the white spruce breeding program in Quebec

In the Quebec province, 15 to 20% of the harvested area is planted aiming to compensate for the lack of natural regeneration on sites (Beaulieu et al. 2009). For this purpose, about 150 million seedlings mainly black spruce, jack pine and white spruce are produced every year, and more than 80% of them come from improved seed sources (Rainville and Beaulieu 2007). Enhanced growth of these sources is expected to increase forest productivity in the near future. In turn, enhanced productivity can be leveraged to increase the area of forest land that is protected, respecting new laws and policies of sustainable forest management.

The province of Quebec maintains tree improvement programs for different conifers i.e. black, white and Norway spruce; jack pine and larch (Rainville et al. 2003). The white spruce breeding program is the most advanced improvement program among these. Provenances from the species entire distribution and progeny from all over Quebec have been analysed in about twenty trials since the 1950s. The Canadian Forest Service, in collaboration with the Quebec Ministry of Natural Resources and Wildlife, set up an enhanced structured breeding program in the 1970s and as a first outcome, seventeen clonal first generation seed orchards have been established since the 1980s. Two second generation orchards were then set up in 1999. Important gains in merchantable volume have been realized throughout the first breeding generations: 14 to 28 m³/ha at 45 years. For the second generation, about 40 m³/ha of gain are expected. The merchantable value will be additionally increased through improvement of stem straightness (Despouts et al. 2007).

The first phases of improvement focussed on volume production, stem straightness and pest resistance (Beaulieu 1994). Hence, different studies (Beaulieu and Corriveau 1985; Corriveau et al. 1987; Corriveau et al. 1990) recognized the importance to consider wood quality traits in white spruce breeding, but until now only some of the selections for the second generation included wood density. However, strategies are currently being modified to include several wood and fibre quality traits into the program (J. Beaulieu, personal communication).

1.5 Objectives and Hypotheses

The previous sections illustrate the need and intention to include wood traits into breeding programs. Additionally, there is an increased interest in developing molecular markers indicative of wood trait variation in white spruce through genomics research projects, such as Arborea (www.arborea.ca). A few years ago, it thus became obvious that a more comprehensive and detailed understanding of quantitative genetics of wood traits would be of considerable value both to advance traditional breeding goals and help develop the modern approach of gene association studies. Essential information such as the genetic control or genetic correlations among white spruce wood traits is still lacking. The general

goal of this thesis is to elucidate the genetics of white spruce wood traits in order to enable their efficient inclusion in breeding programs.

The material used for the study relied on a provenance–progeny test established in 1979 by the Canadian Forest Service in the province of Quebec, Canada. The test is replicated on three sites located in the main reforestation zones for white spruce (for details see chapter II, table 2.1.). In total, 375 trees were sampled including 25 families and 5 trees per family and site. A 12–mm increment core was extracted from each tree and analyzed with the SilviScan system at FPInnovations – Paprican Division in Vancouver, BC. High resolution pith–to–bark profiles were obtained for density, MFA, bending MOE and cell anatomy related traits such as radial and tangential cell diameter, cell wall thickness, fibre coarseness as well as specific fibre surface (further described in material and methods of chapter II). The experimental layout and the high resolution of wood properties allowed for estimation of genetic parameters such as heritability and correlations between traits, and to investigate their radial variation from the pith to the bark. Furthermore, the consequences of this variation on decision making in tree improvement programs are also discussed.

Objective I

To evaluate if genetic gains can be expected by selection in order to economically justify genetic improvement of white spruce wood traits.

Hypotheses:

- a. The genetic control of wood traits is moderate to high.
- b. Heritability varies with cambial age.

Objective II

To investigate possibilities to reduce time for breeding cycles for a more cost-efficient breeding.

Hypotheses:

- c. For individual wood traits, there are strong correlations between juvenile and transition wood.
- d. Early selection for wood properties is effective.
- e. The optimal moment for early selection varies from one trait to another.

Objective III

To study interactions between different wood traits to estimate the effect of selection for one trait on other wood traits.

Hypothesis:

- f. Genetic correlations between different traits vary from the pith to the bark.

Chapter II

Genetic control of wood properties in *Picea glauca* – an analysis of trends with cambial age

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2.1 Résumé

Le contrôle génétique des propriétés du bois selon l'âge cambial a été étudié dans le but d'évaluer la possibilité d'améliorer les attributs du bois juvénile chez l'épinette blanche (*Picea glauca* (Moench) Voss). Des carottes ont été extraites de 375 arbres choisis aléatoirement parmi 25 familles issues de pollinisation libre dans un test de provenance–descendances répété sur trois stations. Des profils à haute résolution allant de la moelle à l'écorce ont été obtenus pour l'angle de microfibrilles de cellulose (AMF), le module d'élasticité (MOE), la densité du bois, le diamètre des trachéides, l'épaisseur des parois, la masse linéique et la surface spécifique des cellules, au moyen de la technologie SilviScan. Les héritabilités estimées indiquent que le contrôle génétique des caractéristiques d'anatomie cellulaire augmentent avec l'âge cambial, tandis que le contrôle génétique du MOE et de AMF est constant et plus faible que ce qui a été rapporté précédemment chez d'autres conifères. La densité du bois, le diamètre radial, l'épaisseur des parois cellulaires et la surface spécifique étant fortement héritables, des gains importants sont anticipés par le biais de programmes d'amélioration génétique. Toutefois l'âge cambial lors de la sélection pourrait grandement influencer les gains réalisés. À l'opposé, l'héritabilité des caractères de croissance comme la largeur des cernes, la longueur des carottes ou la hauteur de l'arbre était faible ou négligeable. Des corrélations défavorables entre des propriétés mécaniques et des propriétés anatomiques liées à la qualité de la pâte à papier indiquent que l'amélioration de la qualité du bois doit tenir compte des deux types de caractères en fonction de différentes utilisations.

2.2 Abstract

We investigated the genetic control of wood properties as a function of cambial age to enable improvement of juvenile wood attributes in white spruce (*Picea glauca* (Moench) Voss). Increment cores were taken from 375 trees randomly selected from 25 open-pollinated families in a provenance-progeny trial repeated on three sites. High-resolution pith-to-bark profiles were obtained for microfibril angle (MFA), modulus of elasticity (MOE), wood density, tracheid diameter and cell wall thickness, fibre coarseness, and specific fibre surface with the SilviScan technology. Heritability estimates indicated that genetic control of cell anatomy traits and wood density increased with cambial age, whereas the genetic control of MFA and MOE remained relatively low across growth rings. Wood density, radial cell diameter, cell wall thickness, and specific fibre surface were highly heritable, indicating that significant genetic gains could be expected in tree improvement programs, although cambial age at selection may strongly influence the magnitude of realized gains. In contrast, growth-related properties, such as ring width, core length, and tree height gave weak or non-significant heritability estimates. Adverse correlations between mechanical strength and properties related pulp quality suggest that breeding strategies must incorporate both types of traits to improve white spruce wood quality for different end uses.

2.3 Introduction

White spruce, *Picea glauca* (Moench) Voss, is a major sub-boreal species that spans the entire North American continent. Like many other conifers, it plays an important role in diverse forest ecosystems. It lends itself well to reforestation and silviculture for timber production. In Canada alone, more than 150 million seedlings of white spruce and its hybrids are planted yearly, spanning almost all forested regions, a variety of soils types and a wide range of climatic conditions (Canadian Council of Forest Ministers 2009). Numerous studies since the 1950s have shown important genetic and phenotypic variation in the growth and adaptive characteristics of white spruce (Dhir 1976; Li et al. 1997). Others have aimed to obtain better knowledge regarding variation in wood characteristics such as wood density and fibre length, and their impacts on the properties of wood products (Beaulieu 2003; Corriveau et al. 1991; Hernandez et al. 2001). Breeding programs were initiated in the late 1960s to make use of this existing genetic variation and to improve planted stocks. Yet, selection criteria have been mainly focused on height growth or stem straightness and not on end-use properties.

The testing of wood properties and their incorporation into an improvement program is both time consuming and costly; therefore, they need to be justified by economic gain in a reasonable time frame (White et al. 2007). Moreover, genetic trials that are old enough to provide samples with sufficient wood must be available in order to test wood properties accurately. Both issues have been problematic for eastern white spruce because this subboreal tree species is slow growing compared with other softwoods like loblolly pine or Douglas-fir (Burns and Honkala 1990). In view of an increasing demand for plantation-grown wood and shorter rotation ages, there is also a need to incorporate wood properties into white spruce breeding programs. Numerous authors have highlighted the negative impact that intensive plantation management has had on the quality of wood (Bendtsen 1978; Kennedy 1995). Furthermore, different studies have revealed negative correlations between radial growth and wood properties in various conifers, primarily for density (Ivkovich et al. 2002b; Myszewski et al. 2004), but also for wood stiffness (Baltunis et al. 2007). These problems can be most reliably overcome by careful design of mating and selection strategy, which in turn require a detailed understanding of genetic parameters.

Quantitative genetic analyses of coniferous wood properties have recently focused on fast-growing and economically important species like Monterey (radiata) pine or loblolly pine (Baltunis et al. 2007; Kumar et al. 2006; Myszewski et al. 2004). Most of these studies were aimed at characterizing mechanical properties, such as stiffness and related traits, including wood density and microfibril angle. Only a few genetic studies have looked at anatomical issues like cellular dimensions, wall thickness, or fibre coarseness, which are important for the pulp and paper industry (Gwinyai Nyakuengama et al. 1997; Ivkovich et al. 2002b; Kibblewhite 1999). Furthermore, no comprehensive study has estimated genetic parameters for mechanical and anatomical wood properties of white spruce in the eastern part of its geographical range.

A major inconvenience for the genetic selection of wood traits is that most wood properties change with cambial age and stabilize only with cambial maturity. Relatively strong correlations have been reported between juvenile and mature wood properties inter alia for density in spruce (Blouin et al. 1994); nevertheless, a detailed determination of wood properties and their variation with cambial age remains crucial for the estimation of genetic parameters. New technologies, especially the SilviScan system (Evans 1994, 2006), enable high-resolution analysis to determine several anatomical and mechanical wood characteristics on a sub-ring basis. Additionally, techniques requiring only small increment cores, like the SilviScan system, help to preserve valuable comparative plantations and allow additional testing in the future.

Like radial variation, the genetic control of wood properties may also vary with cambial age, which influences the optimal moment for selection in a tree improvement program. Several studies have described the influence of cambial age on the heritability of wood density or density components (Hannrup et al. 1998; Ivkovich et al. 2002a; Zamudio et al. 2005), and a few studies have also looked at mechanical properties such as rigidity or the closely related microfibril angle (Baltunis et al. 2007; Dungey et al. 2006). In contrast, knowledge regarding trends in genetic control of cellular properties is generally lacking.

To enhance the knowledge on quantitative genetics of wood traits in eastern white spruce, this study aimed to address the following key questions:

Table 2.1. Location and site characteristics of the provenance–progeny tests.

Site	Geographic coordinates	Elevation (m)	Average temperature July, August (°C)	Annual precipitation (cm)	Number of frost-free days	Eco-logical region	Surface deposit	Site treatment before planting
La Patrie (Estrie)	45°20' N, 71°15' W	389	16.8	107	120–130	Maple – yellow birch	Silty limestone till	Clear cut, piling of logging waste
Dablon (Lac St Jean)	48°21' N, 72°13' W	323	17.2	74	110	Balsam fir – Paper birch	Till	Clear cut, piling of logging waste
Mastigouche (Mauricie)	46°31' N, 73°13' W	223	17.4	97	110	Maple – yellow birch	Glacial till	Clear cut and burning

(1) How do different anatomical and mechanical wood properties vary as a function of cambial age? (2) What is the influence of cambial age on genetic control of these wood properties? (3) Are genetic control trends observed in white spruce similar to those observed in other conifers? (4) What is the relative magnitude and variability of genetic correlations for different wood properties?

2.4 Materials and methods

Wood samples from provenance–progeny trials

Wood cores were collected at breast height (130 cm) from 375 trees in a white spruce (*Picea glauca* (Moench) Voss) provenance–progeny test that was replicated on three sites in Quebec, Canada (see Table 2.1 for site descriptions). The trial was established by the Canadian Forest Service in 1979 using 4-year-old seedlings raised in a nursery. The provenance–progeny test includes 250 open-pollinated families from 50 wide-ranging provenances from the province of Quebec that were set up in a randomized complete block design with 6 blocks on each site.

In each block, families are represented by row plots each with five trees with 1.2 m between trees within plots and 2.4 m between rows. For this study, 25 families represented on each site were randomly selected. They represent 20 different populations. Five trees per family were randomly sampled across blocks on each of the three sites in November 2005. The 12-mm-diameter increment cores were extracted from the same side (southern face) of the trees to minimize the variation due to sample orientation.

Sample treatment and data acquisition

After its removal from the tree, each wood core was put in a plastic labelled vial, stored in a cooler for transportation, and then frozen at -10°C until it could be shipped to FPInnovations – Paprican Division (Vancouver, British Columbia), where it was stored at -10°C until further treatment. Before analysis with the SilviScan3 system (Evans 1994; Evans et al. 1996), samples were thawed and subjected to soxhlet acetone extraction, after which a 7-mm-high by 2-mm-thick strip (with respect to the grain) was cut from each core. Air-dried (20°C , 40% relative humidity) wood strips were scanned with image analysis and x-ray densitometry systems in $25\ \mu\text{m}$ steps, and with the x-ray diffractometry system in 1 mm steps. These components of the SilviScan system provide measurements and estimates for several important physical, mechanical, and anatomical wood traits (Table 2.2). All raw data were stored in a PostgreSQL database.

The method used to determine growth ring boundaries was similar to that used by Pernestål et al. (1995), with the following modifications. Raw density profiles are scanned for radical changes. The first derivative (slope) of the density function was averaged over 10 readings because SilviScan data have high resolution, and therefore, the raw profiles are irregular. Extreme negative slopes of the density profile were identified as ring boundaries. Earlywood-latewood boundary determinations used the method of Mäkinen et al. (2002). These boundaries were assumed to be at 50% of the difference between the maximum (ρ_{\max}) and minimum (ρ_{\min}) densities of a growth ring; therefore, the following formula was used to calculate the earlywood-latewood transition density (ρ_{trans}):

$$[2.1] \quad \rho_{\text{trans}} = \frac{\rho_{\min} + \rho_{\max}}{2}.$$

Each growth ring was thus treated individually to account for density variation between different rings and wood cores. VisualBasic routines were developed to automatically delineate earlywood and latewood as well as growth ring boundaries from the raw density profiles. Manual verifications of growth rings and earlywood–latewood boundaries were made to minimize the risk of errors. The mean wood properties were determined for each growth ring. The earlywood and latewood traits were considered on an individual ring basis and on a cumulative basis, which was calculated as the sum of single–ring means up to and including the specified ring. Single means were weighted by their individual ring areas.

Table 2.2. Wood properties analyzed in this study.

Property	Abbreviation	Way of determination
Wood Density	Dens	Obtained through x–ray densitometry
Fibre Coarseness	Coars	Calculated with RadDiam, TanDiam and Dens
Radial Cell Diameter	RadDiam	Obtained through image analysis system
Tangential Cell Diameter	TanDiam	Obtained through image analysis system
Cell Wall Thickness	Wt	Isotropic thickness; calculated with Dens, RadDiam and TanDiam
Specific Fibre Surface	SpecSurf	Calculated through tracheid perimeter and Coars
Angle of Cellulose Microfibrils in Secondary Cell Walls	MFA	Obtained through azimuthal x–ray diffraction pattern
Longitudinal Stiffness (Modulus of Elasticity)	MOE	Calculated with Dens and the azimuthal intensity profile of x–ray diffraction pattern

Note: More detailed information on the determination of wood properties by the SilviScan system can be found for anatomical properties in Evans (1994), for MFA in Evans et al. (1996), and for MOE in Evans (2006).

Statistical analysis and estimation of genetic parameters

The MIXED procedure in SAS (Littell et al. 2006; SAS Institute Inc. 2002) was used to analyze the data. Variance components were estimated via restricted maximum likelihood (REML). Wald *Z*–statistics were computed and tested using normal distribution to

determine whether or not variance components were significantly different from zero. The following linear random model was used in the analyses:

$$[2.2] \quad Y_{ijkm} = \mu + f_i + s_j + fs_{ij} + p_k + b_{m(j)} + e_{ijkm},$$

where Y_{ijkm} is the observation on the $ijkm^{\text{th}}$ tree, μ is the general mean, f_i is the random effect of the i^{th} half-sib family, the random site effect is represented by s_j and the interaction between sites and families by fs_{ij} , p_k is the random provenance effect and $b_{m(j)}$ is the random effect of the m^{th} block within the j^{th} site, and e_{ijkm} represents the residual error term. A χ^2 -test, performed on the difference in the -2 residual log likelihood of the model before and after iterative removal of the block, provenance, and site effects as well as the site-family interaction, was used to select the final model (Saxton 2004). On one hand, removal of the site effect significantly changed the -2 residual log likelihood in all analyses, indicating that this source of variation was different from zero and could not be eliminated from the linear model. On the other hand, the family-site interaction, the block and provenance effect were removed from the analysis, as their contribution to the total variance was negligible, and in many cases, the variance component for these terms could not be estimated or was otherwise insignificant. Equation 2.2 was thus reduced to:

$$[2.3] \quad Y_{ijk} = \mu + f_i + s_j + e_{ijk}.$$

Normality of studentized residuals was verified using Kolmogorov-Smirnov (D -statistic) and Shapiro-Wilk (W -statistic) tests in the UNIVARIATE procedure of SAS. In a few marginal cases, a graphic residual analysis was also performed; however, no data transformation was deemed necessary. On average, depending on the wood trait and the analyzed ring, two to three extreme observations with studentized residuals greater than $|3|$ were detected and removed from calculations as outliers.

In a half-sib design with random mating, members of the same family are presumed to share one-quarter of their genes (White et al. 2007); therefore, individual heritability was estimated as:

$$[2.4] \quad h^2_i = \frac{4 \times \sigma^2_f}{\sigma^2_f + \sigma^2_e},$$

where σ^2_f is the estimated family variance and σ^2_e is the residual variance. The associated error of heritability estimates was calculated, as recommended by Dieters et al. (1995), as:

$$[2.5] \quad S_{h^2} = \frac{4 \times s_{\sigma^2_f}}{\sigma^2_{\text{tot}}},$$

where $s_{\sigma^2_f}$ represents the error associated with family variance component estimates and σ^2_{tot} is the total phenotypic variance.

Genetic correlations between two traits were obtained with:

$$[2.6] \quad r_{A(x,y)} = \frac{COV_{f(x,y)}}{\sqrt{\sigma^2_{f(x)} \times \sigma^2_{f(y)}}}, \quad \text{with } COV_{f(x,y)} = (\sigma^2_{f(x+y)} - \sigma^2_{f(x)} - \sigma^2_{f(y)})/2,$$

where $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the estimated family variance components for characteristics x and y, respectively. The method is described in greater detail by Williams et al. (2002). Standard errors associated with genetic correlations were estimated using the method initially presented by Robertson (1959):

$$[2.7] \quad \sigma(r_A) = \frac{1 - r_A^2}{\sqrt{2}} \times \sqrt{\left[\frac{\sigma(h^2_x) \times \sigma(h^2_y)}{h^2_x \times h^2_y} \right]}$$

Phenotypic correlations were calculated as Pearson product–moment correlations (r) using the CORR procedure in SAS.

2.5 Results

High resolution pith–to–bark profiles of eight major traits for 375 wood cores, representing nearly 6500 growth rings, were derived from SilviScan readings generating more than 500,000 lines of data (Table 2.2). Although all trees were of the same age, the cores taken at breast height had variable numbers of growth rings from one tree to the next. The mean number (\pm Standard Error) of rings across the 375 cores was 17.3 ± 2.8 rings, and the observed number overall ranged from 8 to 24 rings because of particularly slow–growing or vigorous trees, respectively.

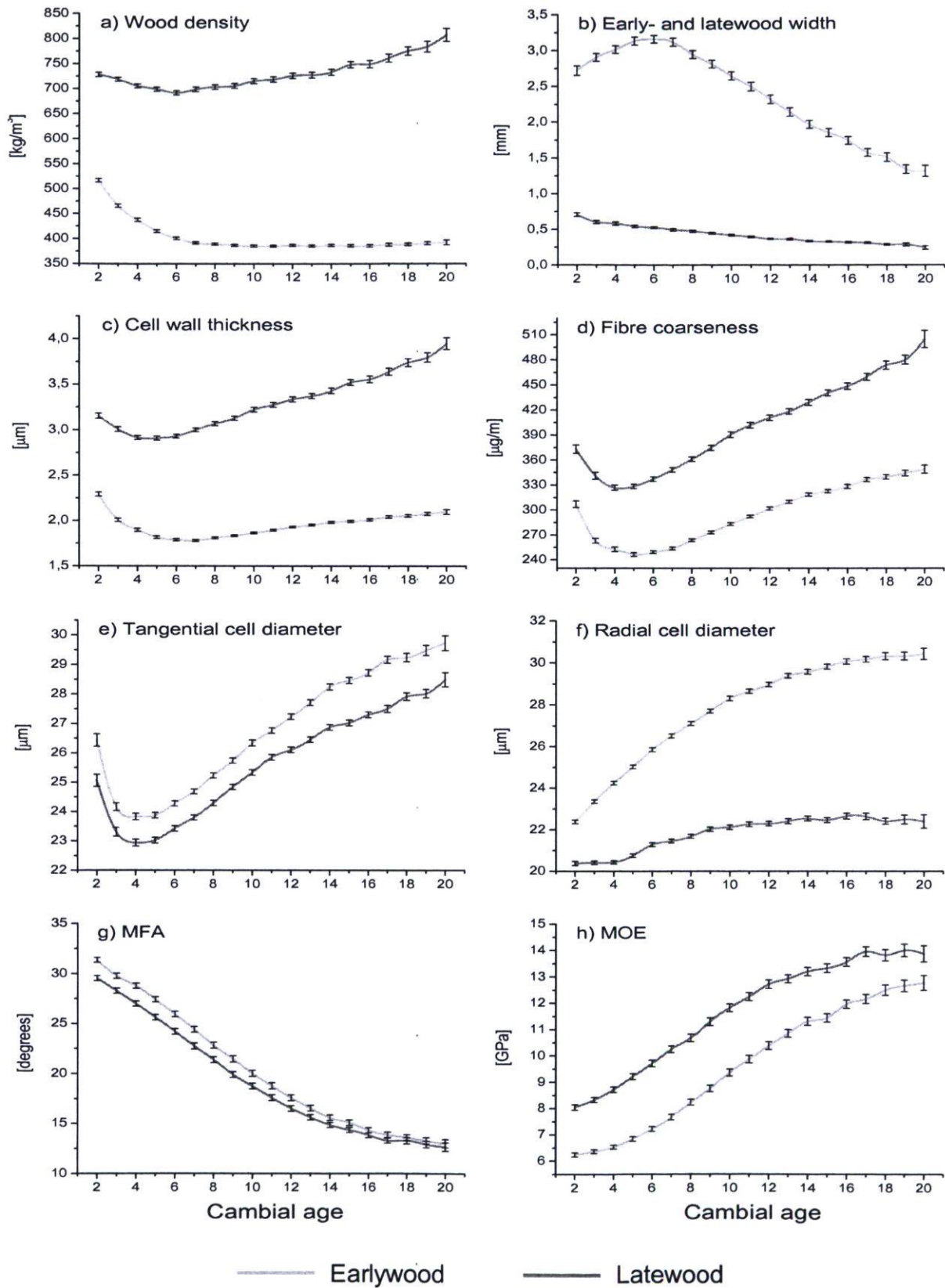
Phenotypic trends

Cambial age had a moderate to strong influence on the wood properties that we investigated. Fig. 2.1 shows the trends in the means of the earlywood and latewood properties as a function of cambial age. Overall, properties of the whole growth increments (spanning the early and latewood) followed the earlywood trends very closely, with a minor exception for wood density; therefore, whole increment properties are not presented. Mean earlywood density decreased from the pith to a cambial age of 7 years, and remained constant thereafter at around 385 kg/m^3 (Fig. 2.1a). In contrast, latewood density reached a minimum at around 6 years and increased constantly toward the bark, resulting in a slightly increasing overall mean density beyond a cambial age of 13 years. The mean proportion of earlywood is high (between 80% and 85%) and stable (data not shown). The largest growth rings are found at around age 5–6 years, because of a maximum in earlywood width at 6 years (Fig. 2.1b). Thereafter, earlywood and latewood widths appeared to decrease at similar rates.

Similar phenotypic trends for both early and latewood were observed for cell wall thickness (Fig. 2.1c), fibre coarseness (Fig. 2.1d) and tangential tracheid diameter (Fig. 2.1e). From the pith outward, the means decreased and reached a minimum at a cambial age of 4 years for the tangential diameter, 4 to 5 years for coarseness, and 5 to 6 years for wall thickness. Afterwards, they steadily increased toward the bark. Tangential diameter gave a similar trend, but it began to level off in cores with rings older than 17 years.

In contrast, radial cell diameter (Fig. 2.1f) did not decrease in the first rings away from the pith, and appeared to level off at a younger age than tangential diameter, in addition to diverging between early and latewood. A somewhat similar trend was observed for stiffness (MOE; Fig. 2.1h); however, the difference between earlywood and latewood MOE decreased with cambial age. Cellulose MFA decreased quite rapidly and steadily from the pith outward, and began to level off at cambial age 17, where very little difference was observed between earlywood and latewood (Fig. 2.1g).

Fig. 2.1. Trends of mean wood properties as a function of cambial age for earlywood and latewood.



Genetic analysis of wood core means

Quantitative genetic analyses were carried out using arithmetic means of wood cores regardless of the number of rings per core, which produced similar results to those using cumulative area-weighted wood core means (not shown). Table 2.3 provides an overview of narrow sense individual heritability as well as genotypic and phenotypic correlations in the earlywood and the latewood. In the earlywood, wood characteristics that are related to mechanical properties, such as MOE ($h^2 = 0.27$) and MFA ($h^2 = 0.28$) were under moderate genetic control. Whereas, wood density was highly heritable in our data set ($h^2 = 0.69$). In contrast, the genetic influence on wood properties related to cell anatomy was variable. Namely, radial cell diameter ($h^2 = 0.62$), cell wall thickness ($h^2 = 0.52$), and specific fibre surface ($h^2 = 0.48$) were under strong genetic control, whereas fibre coarseness ($h^2 = 0.14$) and tangential cell diameter ($h^2 = 0.20$) showed low inheritance.

Latewood characteristics generally had lower and less significant family variance components. Thus, heritability estimates were lower than in the earlywood, except for MOE ($h^2 = 0.41$) and MFA ($h^2 = 0.34$). The genetic control of cell anatomy traits and density was very low or could not be estimated, e.g., specific fibre surface. The only exception was the moderate estimate of heritability ($h^2 = 0.35$) for latewood radial cell diameter.

Genetic and phenotypic correlations were examined separately among earlywood and latewood properties (Table 2.3). Both the genetic and phenotypic relationships (r_G and r_P) between MOE and MFA were strongly negative in the earlywood and the latewood ($r_G \approx r_P \approx -0.80$). Strong genetic correlations in both tissues were also found between MOE and density, while density and MFA were weakly correlated. In the earlywood, there was a negative genetic correlation between MOE and the radial cellular dimensions ($r_G = -0.52$); the corresponding phenotypic correlation was also negative, albeit weak ($r_P = -0.25$). Interestingly, the negative relationship between wood density and cell size varied from moderate in earlywood ($r_G = -0.36$ and $r_P = -0.55$) to strong in the latewood ($r_G = -0.81$ and $r_P = -0.67$).

Table 2.3. Genetic correlations (above diagonal), phenotypic correlations (below the diagonal) and heritability estimates (on the main diagonal) based on wood core means.

(a) Earlywood properties

	SpecSurf	Wt	MOE	MFA	Coars	TanDiam	RadDiam	Dens	Height
SpecSurf	0.48** (0.20)	-0.96 (0.02)	-0.79 (0.13)	0.12 (0.34)	-0.82 (0.14)	0.15 (0.37)	0.66 (0.16)	-0.91 (0.05)	0.69 (0.20)
Wt	-0.98*	0.52*** (0.22)	0.64 (0.20)	-0.11 (0.33)	0.75 (0.19)	-0.04 (0.37)	-0.69 (0.15)	0.70 (0.14)	-0.71 (0.19)
MOE	-0.48*	0.47*	0.27** (0.15)	-0.71 (0.19)	0.87 (0.11)	0.44 (0.35)	-0.57 (0.22)	0.69 (0.17)	-0.25 (0.40)
MFA	0.22*	-0.19*	-0.88*	0.28** (0.15)	-0.11 (0.47)	-0.38 (0.37)	0.15 (0.32)	0.28 (0.29)	-0.35 (0.37)
Coars	-0.86*	0.85*	0.30*	-0.21*	0.14 (0.12)	0.20 (0.51)	0.82 (0.14)	0.94 (0.05)	-1.14 (0.17)
TanDiam	-0.44*	0.41*	0.05	-0.16*	0.75*	0.20* (0.13)	0.12 (0.36)	0.62 (0.22)	-0.01 (0.47)
RadDiam	0.04	-0.08	-0.25*	-0.01	0.40*	0.43*	0.62*** (0.24)	-0.36 (0.23)	0.52 (0.26)
Dens	-0.80*	0.83*	0.50*	-0.11	0.42*	-0.09	-0.55*	0.69*** (0.26)	-0.72 (0.17)
Height	-0.11	0.09	-0.13	-0.01	0.35*	0.40*	0.50*	-0.22*	0.20* (0.13)

(b) Latewood properties

	SpecSurf	Wt	MOE	MFA	Coars	TanDiam	RadDiam	Dens	Height
SpecSurf	0	— ^a	—	—	—	—	—	—	—
Wt	-0.97*	0.06 (0.06)	0.90 (0.09)	-0.42 (0.42)	—	—	-1.02 (0.02)	0.46 (0.54)	-0.67 (0.32)
MOE	-0.26*	0.33*	0.41** (0.19)	-0.81 (0.12)	—	—	-0.07 (0.34)	0.78 (0.17)	-0.16 (0.38)
MFA	0.15*	-0.19*	-0.89*	0.34** (0.17)	—	—	-0.49 (0.27)	-0.06 (0.46)	-0.21 (0.39)
Coars	-0.91*	0.93*	0.25*	-0.17*	0.04 (0.09)	—	—	—	—
TanDiam	-0.63*	0.60*	0.05	-0.13	0.80*	0.02 (0.08)	—	—	—
RadDiam	0.48*	-0.46*	-0.15	0.05	0.17*	0.01	0.35** (0.17)	-0.81 (0.16)	0.65 (0.23)
Dens	-0.92*	0.95*	0.36*	-0.19*	0.77*	0.38*	-0.67*	0.13 (0.11)	-1.07 (0.08)
Height	-0.14	0.15	0.03	0	0.28*	0.33*	0.27*	0.02	0.20* (0.13)

Note: Errors for heritability and genetic correlation estimates are given in parentheses. Significance levels of Z-tests for family variance components used in heritability estimates are given as *, p = 0.1; **, p = 0.05 and ***, p = 0.01. Phenotypic correlations are significant at the 0.01 level. Variables are defined in Table 2.2.

^a Dashes indicate genetic correlations that cannot be estimated due to very low or nonestimable family variance components.

Non-significant family variance component estimates were obtained for growth-related properties, such as mean ring width or mean ring area that had been derived from wood cores and tree diameter (at breast height); the sole exception among growth-related properties was tree height, which was estimated to be under low genetic control ($h^2 = 0.20$). Thus, tree height was included in the genetic analyses to provide an indication of the relationship between wood properties and tree growth (Table 2.3). We found that phenotypic correlations between tree height and earlywood properties were generally low to moderate, whereas the corresponding genetic correlations ranged more widely. For example, both the genetic and phenotypic correlations between tree height and radial cell diameter were moderate ($r_P = 0.50$ and $r_G = 0.52$). In contrast, strong negative genetic correlations were observed between tree height and wood density ($r_G = -0.72$) and between tree height and cell wall thickness ($r_G = -0.70$); however, the corresponding phenotypic correlations were weak ($r_P = -0.22$, for density) or very weak ($r_P = 0.09$ for cell wall thickness). The correlations between latewood traits and tree growth were similar to those observed for earlywood, whereas the genetic correlations between tree height and latewood density or radial cell diameter were somewhat stronger ($r_G = -1.07$ and $r_G = 0.65$) than in the earlywood. In contrast, phenotypic correlations were weaker (tree height and radial cell diameter: $r_P = 0.27$) or negligible (tree height and density: $r_P = 0.02$).

In general, genetic correlations between wood properties with low genetic control were inaccurate and prone to carry high associated errors; this was especially the case for latewood properties.

Ring-by-ring analysis of genetic parameters

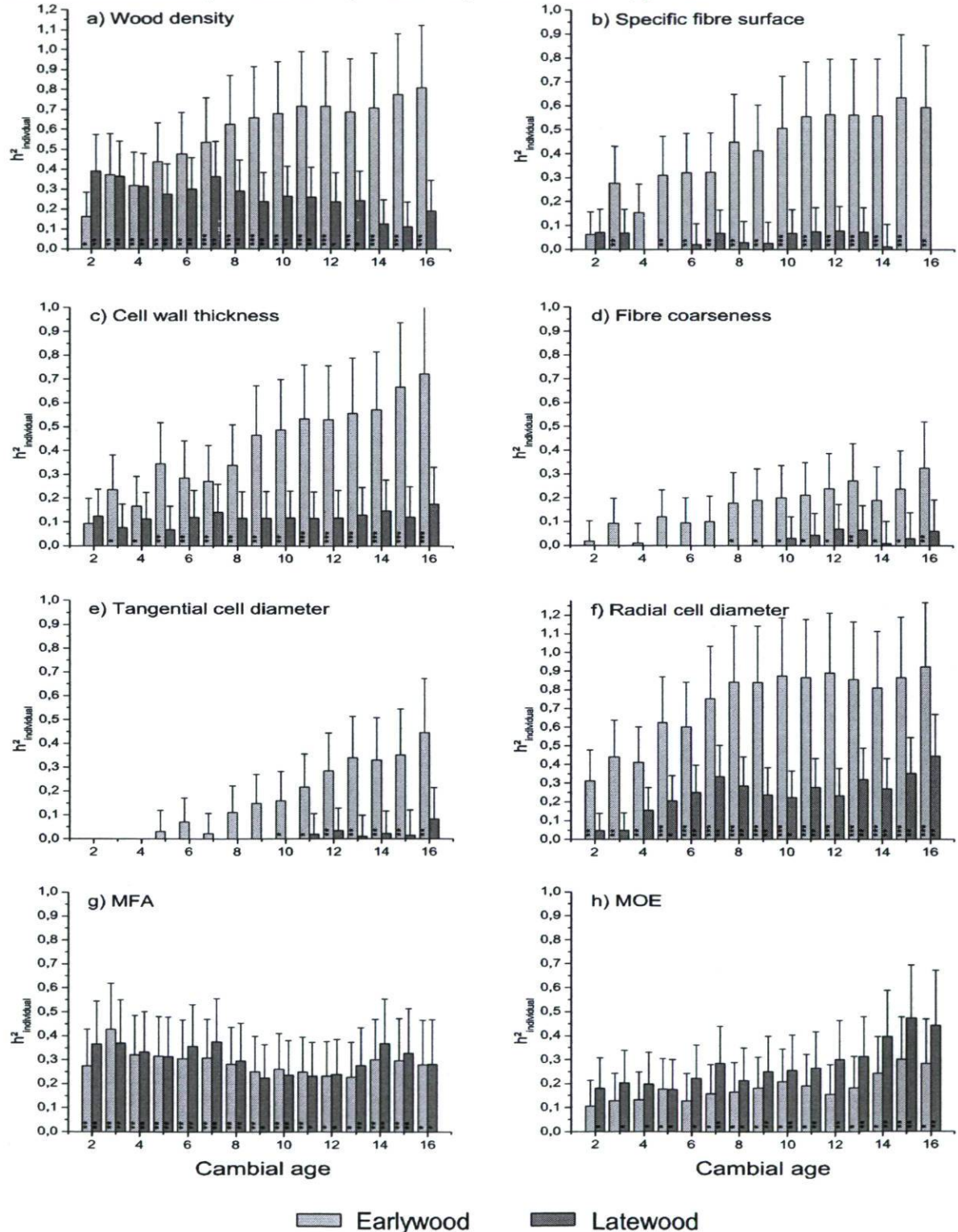
The genetic control of most traits varied with cambial maturity, and the profiles produced shared similarity with the phenotypic profiles for many of the traits. Heritability estimates for early and latewood were obtained from cumulative area-weighted means (Table 2.3). Likewise, heritability estimates were also computed, based on arithmetic growth ring means, and found to follow the same trends as estimates from cumulative weighted-averages. The latter estimates were slightly lower and more variable from ring to ring (not shown). Beyond a cambial age of 16 years, heritability estimates became less accurate and their associated errors became large because of an increasing number of missing

observations (cores had 17 growth rings on average). Because of the small proportion of latewood in all rings, estimates of genetic control for whole-ring wood properties are similar to earlywood estimates.

Three major trends were identified regarding the variation of genetic control with cambial age (Fig. 2.2; earlywood heritability estimates). First, there was a rapid increase in heritability from the pith to the ninth or tenth growth ring. As the cambium begins to mature (past ring 10), estimates level off and fluctuate around an asymptotic value. This was the case for wood density (Fig. 2.2a), radial cell diameter (Fig. 2.2f) and specific fibre surface (Fig. 2.2b) where heritability levelled off at around 0.6, 0.8, and 0.5, respectively. Second, for other traits related to wood anatomy, namely cell wall thickness (Fig. 2.2c), fibre coarseness (Fig. 2.2d) and tangential cell diameter (Fig. 2.2e), genetic control increased steadily and did not level off in the investigated age range. For example, heritability of cell wall thickness increased from around 0.1 near the pith to approximately 0.6 at a cambial age of 16 years. Genetic control of coarseness was lower and reached a heritability close to 0.3 in ring 16. The tangential cell size represents an extreme case because no family influence could be found in the first four rings close to the pith. Heritability in subsequent rings was low but rapidly increased to 0.45 by ring 16. Third, trends were found in MFA (Fig. 2.2g) and MOE (Fig. 2.2h). Moving outward from the pith, genetic control of these properties was almost constant over the range of cambial ages that we investigated. Heritability estimates for MFA fluctuated between 0.25 and 0.30, whereas estimates for MOE were between 0.15 and 0.20, but increased slowly with cambial maturity.

The latewood estimates of heritability were much more variable from trait to trait. Most of these estimates were lower than the corresponding earlywood estimates, and statistically non-significant in several cases. Nonetheless, genetic control of latewood MFA and MOE was as high or even higher (for MOE) than that estimated for earlywood. Latewood heritability of MOE increased above 0.40 in the last three growth rings. In contrast, no family variance could be estimated for latewood coarseness and latewood tangential diameter close to the pith, while estimates were very low and carried large errors for some older rings.

Fig. 2.2. Individual heritability trends as a function of cambial age for earlywood and latewood. Each heritability estimate is the heritability of the area-weighted mean up to and including the specified growth ring. Error bars are the associated standard error of the heritability estimates. Asterisks indicate the significance level of the Z-test for family variance components that are used in heritability estimates: *, $p = 0.1$; **, $p = 0.05$; and ***, $p = 0.01$.



The specific fibre surface of latewood also gave very low latewood heritability estimates, and wall thickness heritability estimates were around 0.1 throughout all growth rings. Inheritance of latewood density presented a unique case, as it was higher than that of earlywood density close to the pith, but decreased with cambial maturity, thus following a trend opposite to that of earlywood.

2.6 Discussion

High-resolution descriptions of several anatomical traits and mechanical properties were utilized to obtain pith-to-bark phenotypic trends and to evaluate the degree of genetic control in white spruce. Wood properties are strongly influenced by cambial maturity, which in turn is determined by the relative distance from the live crown and by physiological signals, such as the concentration of growth regulators produced in the apical meristems (Barnett and Jeronimidis 2003). Wood traits can change significantly from one growth ring to the next, especially in juvenile wood formed within or close to the live crown. The detailed description of phenotypic variability over several growth rings represents the basis for genetic analysis and the estimation of quantitative genetic parameters in relation to developmental age.

Phenotypic variability across cambial ages

The phenotypic trends observed for MFA and MOE were consistent with previous reports in other conifers. High MFA and low MOE in rings close to the pith ensure flexibility and protect the young shoots from wind damage. In Monterey pine, MOE increased up to 17–20 GPa at ring 17 (Dungey et al. 2006), whereas our observations for white spruce MOE were lower and consistent with the general trend that pines have higher mechanical stiffness than spruces. Additionally, MOE in spruce wood seemed to stabilize at a later age than in pine, as was reported by Alteyrac et al. (2006) in black spruce. MFA profiles were similar to those from Monterey pine (Dungey et al. 2006) and black spruce (Alteyrac et al. 2006); however, MFA was lower near the pith (around 30°) and ring-to-ring variation was smaller in our study.

Cell anatomy traits (diameter and wall thickness) and diameter growth (ring width) are interrelated. Juvenile growth close to the pith produces smaller cells with thicker walls and

more compression wood and has lower mechanical resistance. Increasing diameter growth and ring width in the juvenile phase likely result in frequent anticline divisions of cambial initials, thus leading to cell files with a low tangential diameter around cambial age 4. Afterwards, larger cells with a thicker cell wall form as the cambial age increases and radial growth slows.

Pith-to-bark characterizations of wood anatomy have become relatively routine with the automation of imaging methods. Earlier reports described trends in different conifers using more tedious data collection methods (Gwinyai Nyakuengama et al. 1997; Mitchell and Denne 1997). The trends that we observed in white spruce are consistent with these earlier reports, but our results were more uniform because of the higher resolution and a large sample size. For example, cell wall thickness data (decreasing until ring 6, then increasing steadily toward the bark) are in sharp contrast with the more irregular increase from the pith to the bark found in Sitka spruce by Mitchell and Denne (1997).

Variation of cell anatomy traits is of interest to the pulp and paper industry because paper sheet properties are directly related to the structure of the wood fibres used as raw material (Da Silva Perez and Fauchon 2003; Zhu et al. 2008). Fibre coarseness determines sheet formation, tensile strength, absorption capacity, and bulk (Zhu et al. 2008). Juvenile and earlywood fibres have thin walls and low coarseness resulting in superior sheet formation and surface properties, whereas coarse fibres (e.g., in latewood) make stronger paper products. Fibre coarseness is influenced by cell geometry and density; therefore, it is not surprising that the coarseness profiles were similar to profiles for tangential cell diameter and cell wall thickness.

Wood density strongly affects pulp yield and solid wood product performance (Barnett and Jeronimidis 2003; Einspahr et al. 1969). Density profiles for white spruce have been reported to decrease steadily until ring 15 (ring 6 in our data) and then to increase (Corriveau et al. 1990). The trend that we observed was slightly different and closer to black spruce, where overall density was found to be constant up to ring 13 and to slowly increase afterwards (Alteyrac et al. 2006).

The increment cores we analyzed consisted largely of juvenile wood, as indicated by the anatomical traits MFA and MOE, which levelled off at ring 20. Only the outer rings of larger trees were transition wood. As rotation ages of plantations constantly decrease, the proportion of juvenile and transition wood will increase, which will have negative impacts on timber quality and pulp yield. Hence, tree improvement efforts must select for more favourable juvenile wood properties to counterbalance anticipated negative effects on wood quality.

Genetic control of wood properties

MFA and MOE

Latewood usually represents a small proportion of the annual growth, and consequently, few quantitative genetics studies have differentiated between earlywood and latewood MFA or MOE. In white spruce, most traits gave significantly higher levels of genetic control for earlywood than for latewood, except for MFA (levels were similar) and MOE where latewood had stronger heritability estimates.

Genetic control of MFA was moderate and quite stable with cambial age in our study. Ivkovich et al. (2002b) reported somewhat higher heritability estimates for two progeny tests of interior hybrid spruce (i.e., white spruce x Engelmann spruce) from British Columbia. Their heritability estimates varied somewhat between sites and the site effect was significant in their statistical analysis, which is in contrast to our analysis.

Heritability estimates of MFA and MOE are generally higher in fast-growing Monterey and loblolly pines (Baltunis et al. 2007; Myszewski et al. 2004). This response could be related to estimates having been derived from controlled pollinated or full-sib families that were previously selected for growth and wood properties. Dungey et al. (2006) analyzed cumulative area-weighted MOE and MFA from open-pollinated Monterey pine families in a ring-by-ring analysis; the heritability estimates obtained were moderate to high in rings close to the pith but low in rings closer to the bark. Decreasing heritability from pith to bark was also described by Kumar et al. (2006) in Monterey pine. In contrast, heritabilities of MFA and MOE in our white spruce cores varied very little between rings (except for the latewood MOE, which increased toward the bark), suggesting that the MFA and MOE profiles themselves may be under strong genetic control.

Cell anatomy–related traits and density

Cell anatomy traits are reported to be highly heritable (Zobel and Jett 1995), as we observed for many of them in our study. Here, we focus on earlywood because genetic control in latewood was not always statistically significant. Strong genetic control was found especially for earlywood properties including radial cell diameter, wall thickness and specific fibre surface, which is closely related to fibre dimensions. In contrast, tangential tracheid diameter and fibre coarseness were under weak genetic control, especially in rings close to the pith where heritability was negligible.

The high heritability estimates for radial cell diameter that we observed in white spruce are consistent with literature reports for other coniferous species, including Monterey pine (Gwinyai Nyakuengama et al. 1997; Riddell et al. 2005) and interior British Columbia spruces (i.e., white spruce, Engelmann spruce, and their hybrids). Ivkovich et al. (2002b) found moderate estimates, where radial diameter was generally more heritable than tangential diameter (Ivkovich et al. 2002b; Riddell et al. 2005). Heritability of radial diameter and other cell anatomy traits was especially strong in older rings and lower in rings close to the pith, indicating that the environmental influence on cell anatomy is strongest in the young shoot.

Tangential cell diameter is primarily influenced by the width of cambial initials. To keep pace with radial growth, either cambial cells increase in tangential width or new cambial cells must be formed by anticlinal division (Sanio 1873). Our tangential diameter results suggest that the rate of anticlinal cambial divisions in the rings close to the pith was more randomly controlled than genetically controlled. In larger stems, cambial cells divide only infrequently (Larson 1994) and were clearly related to heritable family differences. Individual heritability estimates for tangential cell diameter in older rings were low to moderate, both in the interior spruces (Ivkovich et al. (2002b) and in our study. In contrast, very high broad–sense heritability estimates were reported for tangential diameter and fibre coarseness, respectively, in 16–year–old Monterey pine clones (Kibblewhite 1999; Riddell et al. 2005). The low genetic control of fibre coarseness compared with other investigated traits possibly reflects its complex nature. Coarseness is controlled by other traits, such as

fibre cross-section (radial and tangential diameter) and wall thickness, which are under various levels of genetic control.

Investigations of the genetic control of fibre wall thickness have arrived at divergent conclusions. Our results for white spruce show low and variable inheritance of wall thickness close to the pith, but heritability estimates increased with age to become moderate or high in older rings. Kibblewhite (1999) also found strong narrow-sense heritability in Monterey pine clones. In contrast, Ivkovich et al. (2002b) were unable to estimate heritability for fibre wall thickness in one test and found only low genetic control in another test in a study about open-pollinated interior spruces. Similar conclusions were reported for juvenile wood from a Monterey pine diallel experiment (Gwinyai Nyakuengama et al. 1997).

Earlywood density followed a trend that was highly similar to that of the cell anatomy traits. This is consistent with the fact that density is mainly determined by cell wall thickness and tracheid cross-section, which are both under stronger environmental influence in the younger stems. Interestingly, genetic control of latewood density followed an opposite trend, going from moderate in rings close to the pith to low in older rings. This may suggest that the deposition of cell wall material in young shoots is more tightly controlled in latewood, perhaps to ensure mechanical stability. Earlywood and latewood thus seem to be under different biological constraints during development. Similarly, Zhang and Morgenstern (1995) found evidence that earlywood and latewood densities are controlled by different sets of genes, because the traits were negatively correlated in black spruce.

Our findings show that heritability estimates based on whole-core averages can be of limited value, especially when genetic control varies largely with cambial age. For example, heritability of cell anatomy traits based on core means overestimated genetic control and the potential for genetic gains close to the pith but underestimated them in rings close to the bark. Ring-by-ring analyses are clearly more accurate in estimating heritability and, thus, in predicting genetic gains at a given age. Nonetheless, core means gave a

reasonable indication of heritability for some highly heritable traits like earlywood density when comparing the core mean versus the older rings, for example.

Growth traits

We were able to estimate family variance for total tree height and obtained a low heritability that is comparable to findings in different conifers (Hannrup et al. 1998), but which is lower than those of Ivkovich et al. (2002a), who reported high individual heritability estimates around 0.7 for interior British Columbia spruces. In contrast, no significant family variance components could be estimated for traits related to the annual diameter growth, including ring width, and the width and proportion earlywood and latewood. This response was likely due to a strong environmental influence on annual increment. The influences of different growth seasons and their interaction with genotype are confounded in analyses based on cambial age. Low genetic variance estimates for ring width and its components have been reported in pine species (Gaspar et al. 2008; Zamudio et al. 2005).

Precision of heritability estimates

Heritability estimates that we reported for earlywood density and radial cell diameter appear to be very high. This raises a question regarding the reliability of our estimates. The errors associated with heritability estimates are comparable to errors reported in literature (Baltunis et al. 2007; Kumar et al. 2006; Myszewski et al. 2004). Replication of the genetic test on three different sites covering both white spruce breeding zones in Québec (Li et al. 1997) and the sampling of 20 independent populations from all over Québec are expected to lead to reliable estimates. The number of families included in this study (25) probably presents a lower limit, but overall, the statistics and the experimental layout suggest good reliability of heritability estimates (Lynch and Walsh 1998). Nonetheless, it was surprising that traits like density and cell size, which are known to be influenced by environmental conditions within a season, would give nearly maximal genetic control (heritability near 1) in an analysis based on cambial age.

Overestimation of heritability and additive variance can occur under specific inbreeding conditions (Namkoong 1966). Coles and Fowler (1976) reported inbreeding among

neighbouring trees in white spruce populations in the province of New Brunswick. Open-pollinated seeds were used for this particular study, and no information was available related to inbreeding and the number of effective population sizes. Inbred half-sibs theoretically have more than one-quarter of their genes in common, which is contrary to our assumption for calculating additive variance components (equation 4). Therefore, one explanation for the strong heritability estimates is that they were overestimated because of inbreeding effects. The additive variance might be more accurately estimated by multiplying the family variance components by a factor between 3 and 3.5, which would decrease heritability estimates by as much as 25% but would not change trends of genetic control across cambial ages.

Correlation between traits

Our data showed a very strong relationship between MFA and MOE in latewood and earlywood, as has also been observed in loblolly pine (Baltunis et al. 2007). A strong relationship between MOE and MFA has been widely reported. For example, more than 70% of the variation in MOE could be explained by MFA in black spruce (Alteyrac et al. 2006). Wood density is also related to mechanical properties such as MOE. In our study based on cores containing a major proportion of juvenile wood, density and MOE were moderately but positively correlated. These findings are consistent with the results of Baltunis et al. (2007) in loblolly pine and of Alteyrac et al. (2006) in black spruce.

Although MOE is strongly linked to both MFA and density, the relationship between MFA and wood density appears to be negligible in our study. The relationship between MFA and cell anatomy traits was more difficult to interpret. Weak relationships suggest that larger cells and thicker cell walls lead to lower MFA, but this trend may be related to variation in the relative amount of juvenile wood and mature wood, which differ with regard to MFA and cell diameter. Although some of the genetic correlations were moderate (e.g., latewood MFA and wall thickness: -0.42 ; latewood MFA and radial diameter: -0.49), they were prone to carry large errors, probably due to low family variance estimates. Further research to elucidate correlations may require larger sample sets to obtain estimates with smaller error.

A strongly negative genetic correlation was observed between growth and wood density, as shown in several previous reports on spruces (Ivkovich et al. 2002a; Zhang and Morgenstern 1995; Zobel and Jett 1995). For white spruce, Corriveau et al. (1991) and Yanchuk and Kiss (1993) reported negative phenotypic correlations but contrasting results for genetic correlations. Vigorous trees appear to allocate available carbon differently to produce tracheids with larger diameters and thinner walls compared with smaller trees. The corresponding phenotypic correlations are slightly lower. Our results for genotypic and phenotypic correlations clearly indicate that selection for rapid tree growth alone would decrease wood density, as was shown for hybrid white x Engelmann spruce (Ivkovich et al. 2002a), and thus, would likely decrease MOE and have a negative impact on mechanical performance of wood products. In contrast, growth-based selection schemes that decrease density may lead to better paper sheet formation and surface properties of pulp fibres, because of increased cell diameter and specific fibre surface. Nevertheless, high wood density may also be favourable for the pulp and paper industry because it usually increases pulp yield. Because of the intensive use of white spruce for both paper manufacture and timber, tree breeders need to evaluate different strategies. One approach is to attempt to select for genotypes that do not follow the general trend regarding detrimental correlations between growth and wood properties and would be beneficial for both categories of products. Low to moderate correlations suggest that correlation breakers, exist as reported in many studies on spruces and other conifers (Corriveau et al. 1991; Yanchuk and Kiss 1993; White et al. 2007). An alternative approach would consist of establishing multiple breeding populations in improvement programs (Namkoong et al. 1988); one population would favour mechanical strength for construction materials, and the other would be bred for pulp and paper products.

2.7 Conclusions

The genetic parameter estimates reported here were based on samples from three different sites; therefore, the findings from our study are likely to be repeatable in other settings. Furthermore, the sites cover major bioclimatic zones for white spruce reforestation in eastern Canada; therefore, the findings are appropriate to help conduct genetic selections to enhance wood quality across most of this broad region. Heritability estimates for white

spruce wood properties were moderate to high, as in other conifers, indicating that significant gains may be expected in tree improvement programs. Variation of heritability with cambial age clearly showed how the time for selection may impact on potential genetic gains. Cell anatomy traits and wood density were under lower genetic control close to the pith. Good genetic gains would be expected when selection is based on ring 10 or older, but further analyses are needed to define the point of maximum selection efficiency. In contrast to studies of fast-growing pine species, MOE and MFA were under only moderate genetic control in white spruce. Interestingly, heritability for these traits was not very different in the latewood and earlywood and was quite constant (MFA) or increased slowly (MOE) with age. In the case of traits that have uniform (e.g. MFA) or high (e.g. density) genetic control, the estimation of heritability based on wood core means gave a good indication of genetic control in the older rings in our wood cores. Adverse correlation between mechanical properties and cell properties as well as tree growth point out the need of a careful selection strategy in order to balance trade-offs between mechanical suitability and pulp quality of white spruce wood.

2.8 Acknowledgements

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Chapter III

The influence of cambial age on breeding for wood properties in *Picea glauca*

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*Comment: Due to reviewer requests the word *cell* was replaced by the word *fibre* in this chapter. In regards to the entire document, the expressions cell diameter and cell anatomy, and fibre diameter and fibre anatomy are synonymous terms, respectively.

3.1 Résumé

L'influence de l'âge cambial sur les corrélations entre différentes propriétés du bois ainsi que le potentiel de la sélection précoce ont été étudiés afin d'aider la prise de décision en amélioration génétique du bois juvénile de l'épinette blanche (*Picea glauca* (Moench) Voss). L'analyse a porté sur des carottes de sondage extraites de 375 arbres représentant 25 familles issues de pollinisation libre et provenant d'un test de provenance–descendances de 30 ans au Québec, Canada. Les corrélations génétiques et phénotypiques entre différentes propriétés mécaniques et anatomiques du bois se sont avérées variables en fonction de l'âge cambial. La plupart des corrélations sont plus fortes dans les cernes proches de l'écorce. La corrélation entre l'angle de microfibrilles (AMF) et le module d'élasticité (MOE) fait exception : elle est demeurée fortement négative de la moelle à l'écorce. Des corrélations âge–âge élevées ont été déterminées et les gains attendus par sélection précoce ont été estimés convenables à partir de l'âge de 8 ans pour la plupart des propriétés. L'AMF avait le plus haut potentiel de sélection précoce mais des corrélations désavantageuses avec la densité du bois pourraient présenter un inconvénient pour la sélection. Nos estimations montrent qu'une sélection basée sur des propriétés facilement mesurables comme la densité et la longueur des carottes donnerait des gains supérieurs pour des propriétés mécaniques ; toutefois, des impacts négatifs sont attendus sur l'anatomie des fibres qui est liée à la qualité de la pâte. Ces observations indiquent que les stratégies d'amélioration et de sélection doivent être prudemment planifiées si l'on cherche à améliorer plusieurs propriétés pour des utilisations variées des bois issus de plantation.

3.2 Abstract

We investigated the influence of cambial age on correlations between different wood traits and the possibility of early selection in order to help decision making for the improvement of juvenile wood in white spruce (*Picea glauca* (Moench) Voss). Increment cores were analysed from 375 trees covering 25 open pollinated families from a 30 year old provenance–progeny trial in Quebec, Canada. Genetic and phenotypic correlations between different mechanical and fibre anatomy related wood traits were found to vary with cambial age. Most correlations became stronger in magnitude in rings closer to the bark. An exception is the correlation between microfibril angle (MFA) and the modulus of elasticity (MOE) where correlations were strongly negative from the pith to the bark. Age–age correlations for different wood traits were found to be high and possible gains from early selection were estimated to be good in ring eight and older for most traits. MFA was the trait with the strongest potential for selection as early as ring 4, but a detrimental correlation with wood density may represent a drawback of such a juvenile selection approach. Estimates showed that selection concentrated on a few easily measurable traits such as wood density and core length, holds promise to obtain superior genetic gains for mechanical properties, but negative impacts would be expected on fibre anatomy traits related pulp quality. These findings show the need for more carefully planned breeding and selection strategies if one wishes to improve several traits for different end uses.

3.3 Introduction

White spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Miller) BSP) are transcontinental in their distributions and form the backbone of the forest products industry in boreal North America. Genetic improvement of the planting stock has so far focussed mainly on growth and adaptive traits, which have been reported to vary widely in these species (Khalil 1984; Li et al. 1993; Nienstaedt 1985). Variation in wood density and the effects of genetic variation on wood transformation have been studied, but both are not routinely considered in tree breeding programmes (Corriveau et al. 1987; Zhang and Morgenstern 1995; Zhang et al. 2004).

Quantitative genetic research on wood properties in spruce has concentrated on wood density (Rozenberg and Cahalan 1997) and upon the genetic control of density components (Corriveau et al. 1991; Hysten 1999; Ivkovich et al. 2002a). Several authors have established relationships between density and growth traits in white and black spruces (Corriveau et al. 1987; Zhang and Morgenstern 1995). Moreover, wood density is a very important wood trait that is highly correlated with different mechanical and anatomical wood traits (Zobel and Van Buijtenen 1989), and which potentially determines its end use. For example, the wood of white spruce has a wide range of applications, but it is mainly used as solid wood products for construction and as fibres for pulp and paper manufacture. In view of changes in the economy of forest products towards creating a value-added industry, other wood traits and fibre properties are also likely to play a significant role. Consequently, there is a need to investigate relationships among key traits for both areas of application to optimise breeding strategies, especially if one wishes to satisfy multiple user needs. Possibilities for genetic selection and improvement of relevant mechanical and anatomical wood traits thus need to be examined.

Several studies already have confirmed strong genetic control, together with the potential of successful breeding for mechanical (Baltunis et al. 2007; Dungey et al. 2006) and anatomical traits (Gwinyai Nyakuengama et al. 1997), particularly radiata or Monterey pine (*Pinus radiata* D. Don). Genetic correlations between different mechanical and anatomical wood traits, however, have rarely been investigated in conifers in general, and in species other than pine in particular. Baltunis et al. (2007) published correlation estimates between

wood quality traits such as MOE (modulus of elasticity), MFA (microfibril angle), and density in radiata pine. Ivkovich et al. (2002b) presented the relationship between different wood anatomy traits, including MFA and density, for selected growth rings sampled in spruces from the British Columbia interior (where extensive hybridisation occurs between *P. glauca* and *P. engelmannii* Parry ex Engelm., i.e., Engelmann spruce). Yet no study has investigated genetic correlations between fibre anatomy and mechanical traits such as wood stiffness in spruce.

Most wood properties and their genetic controls vary with cambial age and follow distinct trends throughout the juvenile and transition wood, which implies that correlations among different wood traits also vary with development. The very few reports that have been made, mainly in radiata pine (e.g. Baltunis et al. 2007; Kumar et al. 2006), have investigated genetic correlations between different wood traits in different growth rings. A relationship that varies with cambial age would appear to be crucially important when selection is performed simultaneously on different traits in tree improvement programs. Therefore, a detailed analysis of genetic correlations at different ages is of particular value because it may help predict the relationships among diverse traits at the time of selection.

The optimal age of selection maximises the gain that can be achieved by unit time. To reduce costs and proceed with breeding and selection cycles as quickly as possible, there is considerable value in selecting as early as possible and predicting adult traits from juvenile properties. In recent years, many genetic studies of wood properties have examined age–age correlations and the efficiency of early selection of wood traits, mainly density (Gwaze et al. 2002; Kumar and Lee 2002; Li and Wu 2005). Only a few studies have looked at wood quality traits and fibre anatomy traits have mainly been ignored (Wu et al. 2007). Information on conifers other than fast–growing pines is also generally lacking.

The assessment of most wood traits is time–consuming and expensive. This is why most breeding efforts have focussed on improving easily measurable traits such as wood density, ring width, or annual increment. A more informed understanding is also needed on the impact of selection and breeding based on such traits in regard to wood traits including mechanical properties or fibre anatomy.

In a previous study, we investigated phenotypic variation in white spruce wood traits and presented results concerning trends in their genetic control as a function of cambial age (Lenz et al. 2010). The present report focuses on the genetic relationships between different wood traits and subsequent implications for tree improvement. To address key questions related to breeding of wood traits in spruce, our main objectives were: (I) To estimate genetic and phenotypic correlations between different anatomical and mechanical wood traits to evaluate their relationships as a function of cambial age; (II) to assess the possibilities of early selection of wood properties, with the aim of shortening breeding cycles; and (III) to estimate the effects of selection based on easily measurable traits, such as wood density and core length, upon fibre anatomy and wood mechanics.

3.4 Materials and Methods

Sampling and data acquisition

A total of 375 wood cores representing 25 open-pollinated families were extracted at breast height (1.37 m) from a white spruce provenance progeny test. The trial was 30 years old at the time of sampling and is repeated on three sites in the central and southern parts of the Province of Quebec, Canada. Each randomly selected family was represented by five trees per site, and one core was extracted per tree. The increment cores were analysed with the SilviScan system at FPInnovations, PAPRICAN Division (Pulp and Paper Research Institute of Canada), in Vancouver, British Columbia. High-resolution pith-to-bark profiles were obtained for microfibril angle (MFA, deg), modulus of elasticity (MOE, GPa), wood density (kg m^{-3}), radial and tangential fibre diameter (μm), fibre coarseness ($\mu\text{g m}^{-1}$), fibre wall thickness (μm), and specific fibre surface ($\text{m}^2 \text{kg}^{-1}$). The SilviScan 3 system uses X-ray densitometry to determine wood density as well as image analysis for measuring fibre sizes and estimating coarseness and specific fibre surface (Evans 1994). X-ray diffraction is used to determine MFA and MOE. MFA determination uses the width and positions of diffraction peaks (Evans et al. 1996) whereas MOE is calculated with density and the variation coefficient of the azimuthal intensity profile (Evans 2006). Unless otherwise stated, traits have been presented on a cumulative basis, which was calculated as

the sum of single ring means up to and including the specified ring. Single means were thereby weighted by their individual ring areas. More detailed information concerning the progeny test and sample analysis can be found in Lenz et al. (2010).

Statistical analysis

Variance components were estimated using the restricted maximum likelihood (REML) algorithm of the SAS MIXED procedure (Littell et al. 2006) and the following linear random model was fitted:

$$[3.1] \quad Y_{ijk} = \mu + f_i + s_j + e_{ijk}$$

where Y_{ijk} is the observation on the ijk^{th} tree, μ is the grand mean, f_i is the random effect of the i^{th} family, the random site effect is represented by s_j , and e_{ijk} is the residual error term. The site–family interaction was removed from the model as it was previously shown to be non–significant in all analyses (Lenz et al. 2010). A Chi–square test on the difference in the –2 Res Log–Likelihood before and after removal of the interaction (Saxton, 2004) revealed a negligible contribution to the total variance of the model. Genetic correlations between two traits and age–age correlations were obtained with:

$$[3.2] \quad r_{A(x,y)} = \frac{COV_{f(x,y)}}{\sqrt{\sigma^2_{f(x)} \times \sigma^2_{f(y)}}}, \quad \text{and}$$

$$[3] \quad COV_{f(x,y)} = (\sigma^2_{f(x+y)} - \sigma^2_{f(x)} - \sigma^2_{f(y)}) / 2,$$

where $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the estimated family variance components for characteristics x and y , or a single characteristic at two different ages, respectively, as described by Williams et al. (2002). Standard errors associated with genetic correlations were estimated using the method of Robertson (1959):

$$[3.4] \quad \sigma(r_A) = \frac{1 - r_A^2}{\sqrt{2}} \times \sqrt{\left[\frac{\sigma^{(h^2x)} \times \sigma^{(h^2y)}}{h^2_x \times h^2_y} \right]},$$

where h^2_x and h^2_y are the heritability estimates of trait x and y ; $\sigma^{(h^2x)}$ and $\sigma^{(h^2y)}$ are the associated standard errors of heritability estimates.

Phenotypic correlations were calculated as Pearson product–moment correlations (r) using the CORR procedure in SAS. Significance levels were calculated with respect to the null hypothesis $r = 0$.

The efficiency of early selection (E_{gen}) versus an adult reference age can be understood as the ratio of the correlated response between both ages to the direct response at the reference age (White et al. 2007). This interrelationship can be reduced to the formula:

$$[3.5] \quad E_{\text{gen}} = r_A \times \frac{i_E \times h_E}{i_A \times h_A} = r_A \times \frac{h_E}{h_A},$$

where r_A is the additive genetic correlation between the wood characteristic at the early selection age and the adult reference age, while h_E and h_A are the square roots of individual narrow sense heritability estimates at the juvenile and adult reference age. Heritability was estimated as presented in an earlier study (Lenz et al. 2010); the estimates used in this study are assembled in table 3.1. To facilitate calculations, selection intensities at the early selection age (i_E) and the adult reference age (i_A) were assumed to be equal. In this report, adult reference age was set at a cambial age of 16 years.

Wood density and core length, up to and including a specified growth ring, were considered to be easily measurable traits. The two traits were combined into an index to evaluate their influence on other wood traits in a selection process (Baker, 1986). The vector of index coefficients b was found by solving the set of simultaneous equations:

$$[3.6] \quad b = P^{-1} \times G \times a, \quad \text{where } a = (1, \dots, 1),$$

which gave uniform weighting to traits included in the index. Elements of the genotypic (G) and phenotypic (P) variance–covariance matrices were estimated with the MIXED procedure and through the aid of formula 3.3. Matrix calculations were then performed in the SAS IML procedure (SAS Institute 1999). Genetic and phenotypic correlations between wood traits and the index were calculated as described above for correlations between traits using equations 3.2 to 3.4. The efficiency of index selection compared to direct selection of wood traits was calculated using formula 3.5. For this purpose r_A is defined as the additive

genetic correlation between a specific wood trait and the index, while h_E and h_A are the square roots of individual narrow sense heritability estimates of the index and the trait respectively.

Table 3.1. Heritability estimates and their associated errors used for calculations.

Cambial age	Density		Fibre wall thickness		Specific fibre surface		Radial fibre diameter		MOE		MFA	
	h^2	error	h^2	error	h^2	error	h^2	error	h^2	error	h^2	error
2	0.28**	0.15	0.14*	0.10	0.09	0.09	0.31**	0.16	0.12	0.10	0.33**	0.16
3	0.40**	0.18	0.17*	0.11	0.19**	0.11	0.38**	0.18	0.14	0.11	0.38**	0.17
4	0.28**	0.15	0.12*	0.09	0.13*	0.09	0.38**	0.18	0.12	0.10	0.32**	0.16
5	0.35**	0.17	0.21**	0.11	0.24**	0.12	0.52***	0.22	0.15*	0.11	0.28**	0.14
6	0.42**	0.18	0.18**	0.11	0.20**	0.11	0.54***	0.22	0.16*	0.12	0.30**	0.15
7	0.47***	0.20	0.24**	0.12	0.26**	0.13	0.67***	0.26	0.17*	0.12	0.29**	0.15
8	0.47***	0.20	0.28**	0.14	0.31**	0.14	0.77***	0.28	0.17*	0.12	0.26**	0.14
9	0.49***	0.20	0.30**	0.14	0.34**	0.15	0.75***	0.28	0.18*	0.12	0.24**	0.14
10	0.54***	0.22	0.34**	0.16	0.36**	0.16	0.73***	0.27	0.21*	0.13	0.25**	0.14
11	0.61***	0.24	0.38**	0.17	0.48**	0.20	0.73***	0.27	0.21*	0.13	0.24**	0.14
12	0.60***	0.23	0.47***	0.19	0.49***	0.20	0.74***	0.27	0.18*	0.13	0.22*	0.14
13	0.59***	0.23	0.47***	0.19	0.50***	0.20	0.70***	0.26	0.21*	0.14	0.25**	0.15
14	0.63***	0.24	0.51***	0.21	0.52***	0.22	0.68***	0.26	0.27**	0.16	0.33**	0.17
15	0.68***	0.26	0.59***	0.23	0.60***	0.24	0.70***	0.27	0.35**	0.19	0.33**	0.18
16	0.68***	0.27	0.64***	0.26	0.62***	0.25	0.78***	0.30	0.32**	0.19	0.32**	0.19

Note: Asterisks indicate the significance level of the Wald Z-test for family variance components that are used in heritability estimates: *, $p = 0.1$; **, $p = 0.05$; and ***, $p = 0.01$

3.5 Results

The results of this study show that it is important to consider cambial age when selection is made for wood traits in tree improvement programs. Correlations between different wood traits vary with cambial age; furthermore, not all wood traits show the same potential for early selection, the best age for early selection may vary from one trait to another.

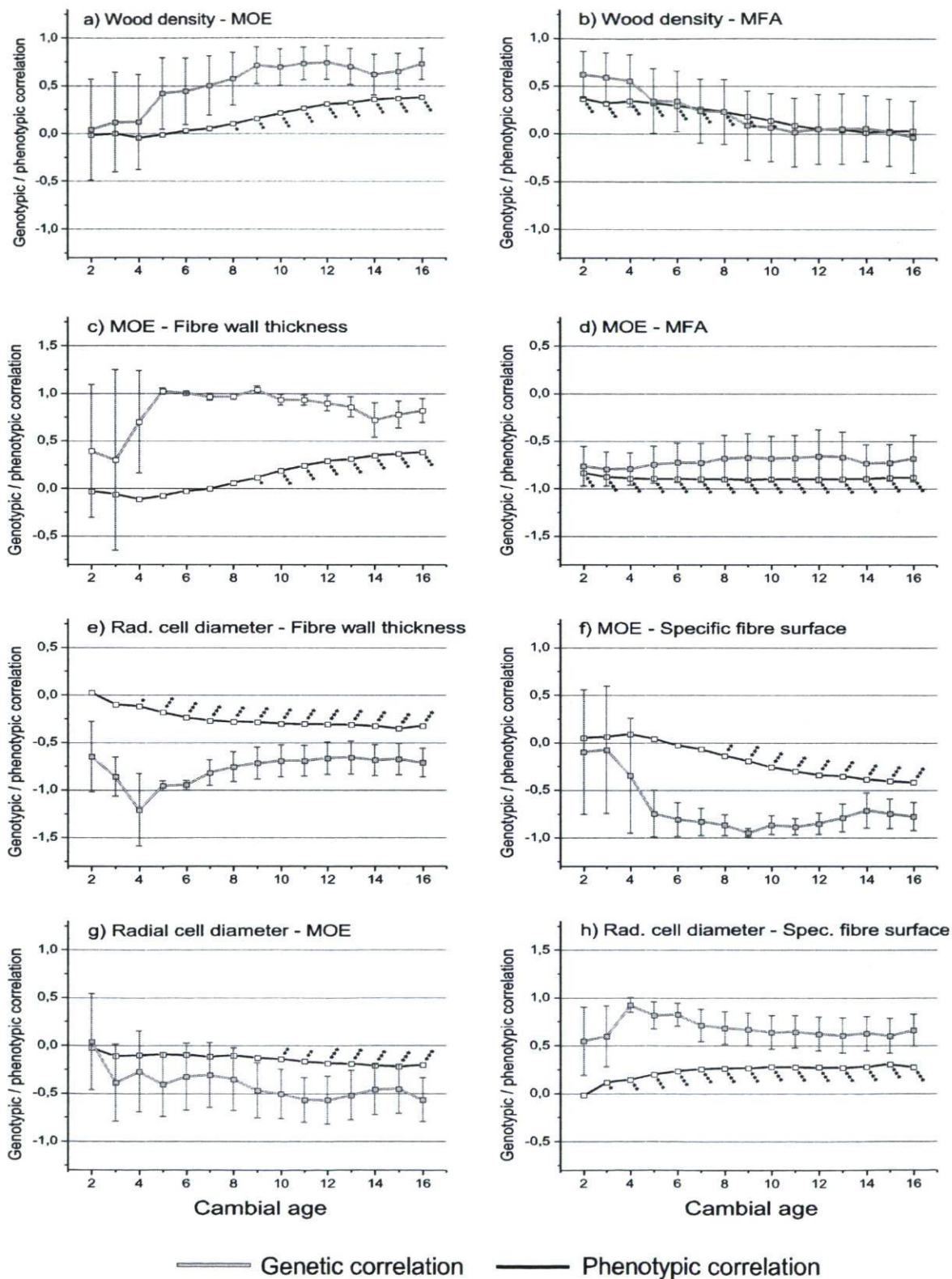
Correlations between traits

Genetic and phenotypic correlations were calculated from cumulative area-weighted means for wood density, MOE and radial fibre diameter, each with two or three other traits including MOE, MFA, fibre wall thickness, and specific fibre surface. The two types of correlations for a given pair of traits usually followed similar trends as a function of cambial age (Fig. 3.1). Absolute values of the genetic correlation estimates were larger than the corresponding phenotypic estimates, regardless of whether the correlations were positive (see Fig. 3.1a, c, h) or negative (see Fig. 3.1e, f, g). Correlations involving MFA (with wood density and MOE) did not follow this trend (Fig. 3.1b and 1d).

Some of the genetic and phenotypic correlations for a given trait differed considerably in magnitude. For example, phenotypic correlations between MOE and fibre wall thickness increased gradually from about 0 near the pith to 0.4 near the bark (Fig. 3.1c). In contrast, the corresponding genetic correlations abruptly increased to around 1.0 and remained relatively constant over several rings. A similar pattern was observed for MOE and specific fibre surface, except that the correlations were negative (Fig. 3.1f).

Most phenotypic correlations increased gradually in magnitude (whether positive or negative) and became significant or more significant with cambial age (Fig. 3.1, except 3.1b). For example, wood density and MOE did not give significant phenotypic correlation estimates in the first seven growth rings and increased from around 0 near the pith to 0.4 in rings near the bark (Fig. 3.1a). As exceptions to this trend, phenotypic correlations involving MFA (with wood density and MOE) were highly significant close to the pith (Fig. 3.1b, 3.1d) and did not increase in magnitude closer to the bark. As a rule, the corresponding genetic correlations varied most in magnitude between rings 2 to 6 (with the exception of MOE and MFA) and remained rather constant beyond that point.

Fig. 3.1. Pair-wise phenotypic correlations and genetic correlations between different wood traits based on cumulative area-weighted means. Standard errors of genetic correlations are given by error bars. Asterisks indicate the significance level of phenotypic correlations: *, $p = 0.05$; **, $p = 0.01$; and ***, $p = 0.001$.



Significant correlations were observed between MFA and both MOE and wood density; however, they followed very different trends with age. MFA and MOE gave the most consistent and largest negative correlations over the entire age range, with phenotypic correlations close to -0.9 and genetic correlations varying between -0.65 and -0.8 (Fig. 3.1d). Positive correlations (genetic and phenotypic) were found between MFA and wood density in rings closest to the pith, but they decreased to about 0 beyond ring 11 (Fig. 3.1b).

Correlations between radial fibre diameter and other wood anatomy traits, including fibre wall thickness and specific fibre surface, as well as MOE, were following quite similar trends with cambial age. Phenotypic correlations with fibre wall thickness were significant in rings 4 and older but remained rather weak (-0.25 and -0.30), while the genetic correlations were consistently less than -0.60 and peaked at ring 4 (Fig. 3.1e). Similarly, phenotypic correlations with specific fibre surface increased in magnitude with cambial age and stabilised around 0.25, while the genetic correlations were consistently above 0.6 and had a maximum in ring 4 (Fig. 3.1h). With MOE, phenotypic correlations were also very weak in rings close to the pith but slowly became more negative, reaching -0.2 near the bark (Fig. 3.1g).

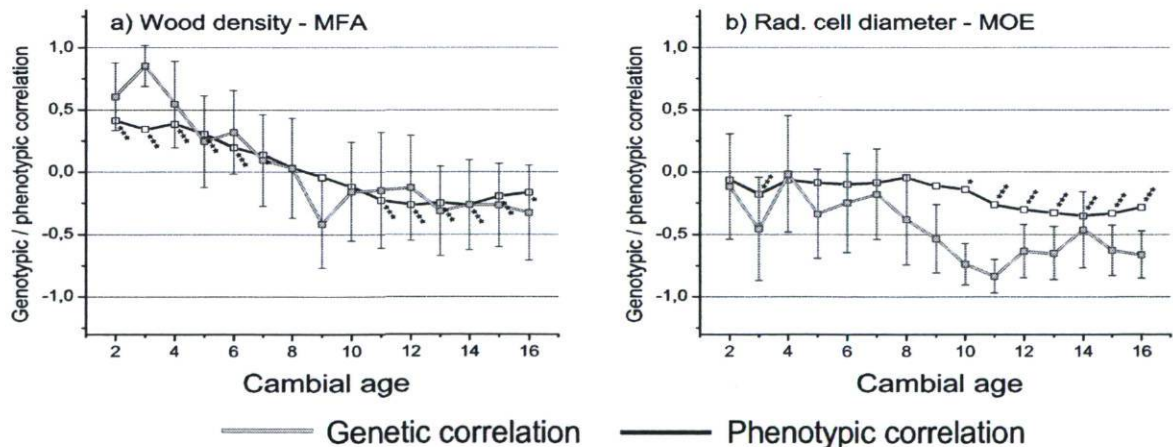
The corresponding genetic correlations were more irregular from ring to ring, varying between -0.35 and -0.55 , and decreasing slightly toward the bark. In contrast to the above, the genetic correlations with wood density were highly negative (around -0.8) and did not vary significantly between rings (results not shown), and the corresponding phenotypic correlations were moderate close to the pith and gradually decreased to a value around -0.6 in older growth rings.

We also calculated correlation coefficients based on individual ring means to evaluate the effect of area-weighting and accumulation of data from earlier growth rings (Fig. 3.2). The correlation profiles across rings were more irregular from one ring to the next when based on single ring data. The irregularity in correlation estimates was more pronounced for specific pairs of traits. For example, genetic correlation estimates for rings 3 and 9 appeared

to diverge from the overall trend between wood density and MFA (Fig. 3.2a). Both phenotypic and genetic correlations (Fig. 3.2a) were moderate close to the pith, but decreased more suddenly than correlations based on cumulative means (Fig. 3.1b). They even became negative beyond ring 9, which was not observed with the cumulative means.

Similarly, genetic correlations between radial fibre diameter and MOE were very irregular when based on single growth ring data (Fig. 3.2b) compared to the trend presented in Fig. 3.1g. Correlations were weak to moderate close to the pith and decreased to about -0.65 in older rings. Corresponding phenotypic correlations were largely non-significant up to ring 10, but decreased more rapidly than correlations based on cumulative means (Fig. 3.1g), reaching -0.3 in rings that were close to the bark. In both examples in Fig. 2, errors associated with the genetic correlations were generally larger than errors estimated for correlations based on cumulative means (Fig. 3.1).

Fig. 3.2. Pair-wise phenotypic correlations and genetic correlations between different wood traits based on single ring means. Standard errors of genetic correlations are given by error bars. Asterisks indicate the significance level of phenotypic correlations: *, $p = 0.05$; **, $p = 0.01$; and ***, $p = 0.001$.

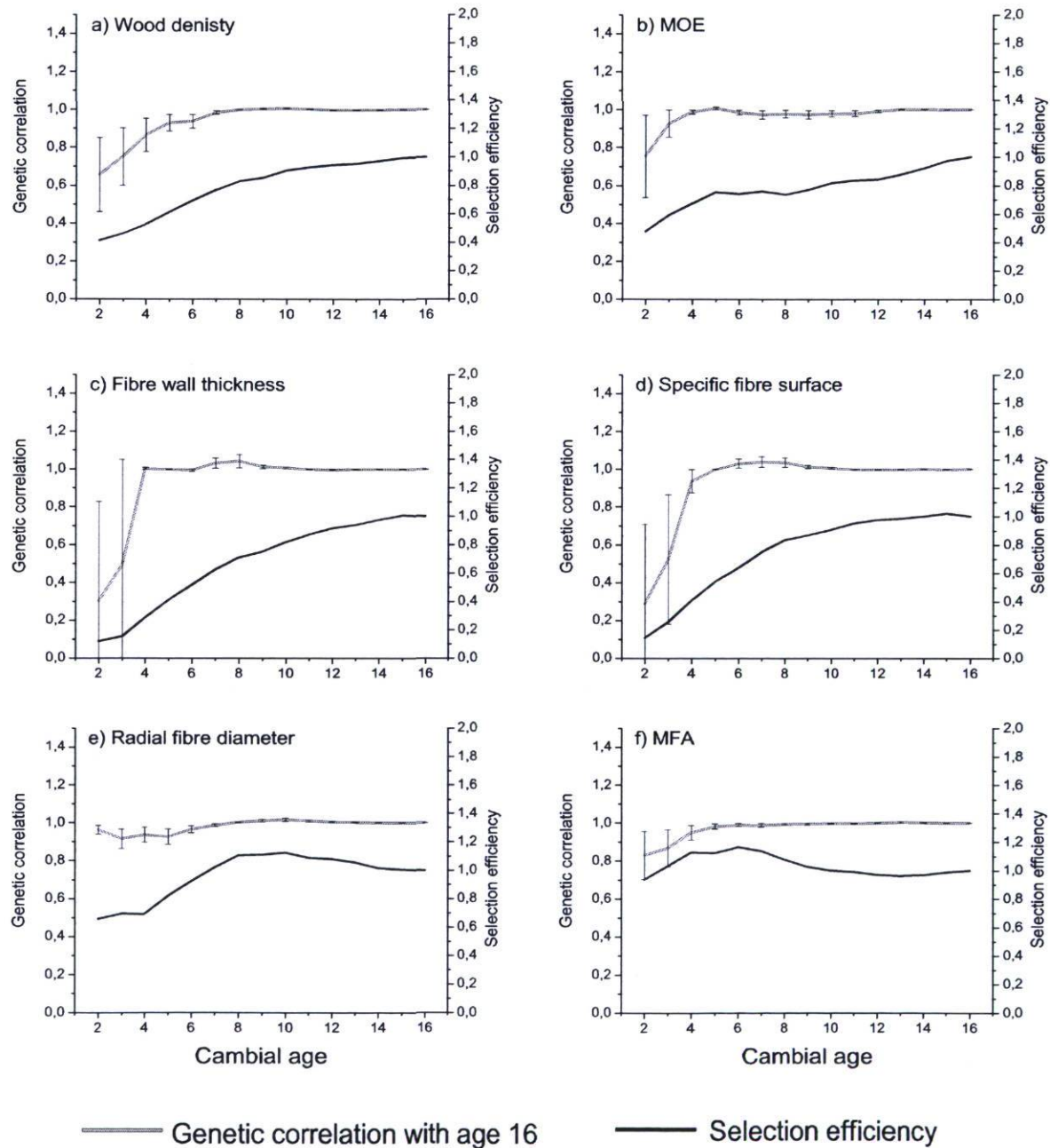


Age-age correlations

Information on juvenile-mature correlations is required to evaluate the opportunity of carrying out selection on a given trait as early as possible during the breeding cycle. In this study, genetic correlations between each of the rings and ring 16 were calculated with the

aim of describing the relationship that may exist for wood traits between early and more mature cambial ages (Fig. 3.3). Correlations were generally high and very close to one, except for rings immediately next to the pith.

Fig. 3.3. Age–age correlations and selection efficiencies in reference to ring 16. Standard errors of genetic correlations are given by error bars.



For example, genetic correlations between ring two and ring 16 for MOE and MFA were around 0.8, but increased immediately in subsequent rings and approached 1 in rings 4 to 5 (Fig. 3.3b, 3.3f). Inter-ring correlations for fibre wall thickness and for specific fibre surface (Fig. 3.3c, 3.3d) were low to moderate, with very large errors associated with rings 2 and 3, but the correlations increased rapidly and stayed close to 1 from ring 4 onwards.

In contrast, correlations for radial fibre diameter were very high (0.9 and 1) in rings close to the pith and remained close to 1 throughout the profile (Fig. 3.3e). More complex wood properties that are influenced by several wood anatomy traits generally reached a correlation close to 1 at an older cambial age. For example, genetic correlations for wood density (Fig. 3.3a) were around 0.6 close to the pith and increased over several rings to reach 1 at ring 7. A more extreme case was observed for fibre coarseness. The variance components could not be estimated in rings close to the pith (not shown); further, correlations were highly variable and had large errors associated with rings 6 to 9, but were close to 1 in rings 10 and higher.

Early selection efficiency

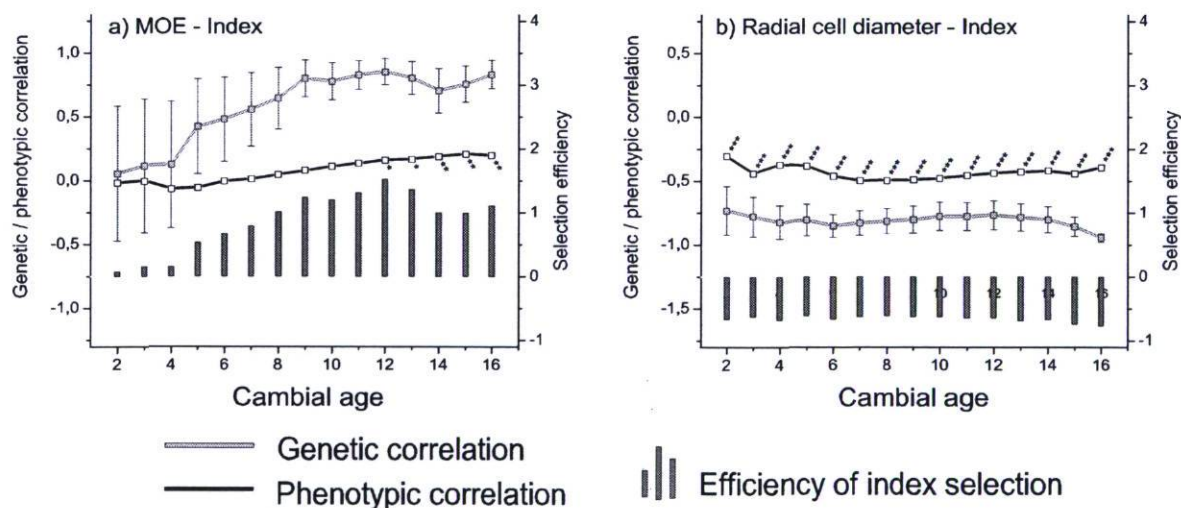
Using the age-age correlations and the heritability estimates presented in table 3.1, we calculated selection efficiency to evaluate the potential of early selection compared to selection based on ring 16. Wood density, fibre wall thickness and specific fibre surface gave similar trends for selection efficiency (Fig. 3.3a, 3.3c, 3.3d). In all three traits, efficiency was low in rings close to the pith, but increased to about 0.8 in ring 8, and gradually approached 1 in older rings. Selection efficiency of MOE reached 0.55 by ring 5, did not change from 5 to 8 and further increased in approaching the bark. Selection efficiency estimates above 1 were found in some growth rings for MFA and for radial fibre diameter. Moving away from the pith, efficiency for fibre diameter increased slowly and reached a peak at age 10 ($E_f \approx 1.1$). Following a slightly different trend, the efficiency for MFA increased quickly in the first few rings to reach a maximum of 1.2 in ring 6 but decreased in subsequent rings, stabilising around 1 from age 8 to 16.

Correlations with a multiple trait index

To evaluate the possibility of using indirect phenotypic data for genetic selection, the index based on the easily measurable traits of core length and wood density was correlated with

wood traits and used to estimate selection efficiencies. Correlation trends between different traits and the index were consistent with pairwise correlation trends between different traits and density. However, absolute values were quite different: genetic correlation coefficients between MOE and the index were lower in rings close to the bark (Fig. 3.4a) than coefficients of correlations between MOE and density (Fig. 3.1a); by comparison, the phenotypic correlations between the index and density were higher. Genetic correlations between radial fibre diameter and the index (Fig. 3.4b) were more irregular than pairwise correlations between wood density and radial fibre diameter (data not shown). On the other hand, phenotypic correlations between the index and MOE, as well as with fibre diameter, were up to 40% lower in rings close to the bark.

Fig. 3.4. Phenotypic correlations and genetic correlations between the index (containing wood density and core length) and (a) MOE or (b) the radial fibre diameter. Estimates are based on cumulative area-weighted means. Standard errors of genetic correlations are given by error bars. Asterisks indicate the significance level of phenotypic correlations: *, $p = 0.05$; **, $p = 0.01$; and ***, $p = 0.001$.



The trends in index selection efficiency followed trends for genetic correlations between the index and the different traits (Fig. 3.4). Selection efficiency of MOE increased from the pith to the bark; from ring 8 onwards; the correlated gain between MOE and the index was higher than the possible gain of direct selection on MOE. Index selection efficiency reached

a maximum value of 1.5 in ring 12 and declined slightly approaching the bark. When compared to direct selection, the efficiency of index selection on radial fibre diameter was negative and quite constant from one ring to another. Values fluctuated between -0.6 and -0.75 .

3.6 Discussion

In addition to the level of genetic control, optimal selection schemes for breeding depend upon the relationship between the different traits of interest as well as the potential for early selection. Our results show a strong influence of cambial age on inter-trait correlations, generally leading to stronger correlations in older rings than in rings close to the pith. The data also indicate that it should be possible to select for wood traits at an early age, as indicated by high age-age correlations. The choice of traits to be included in improvement programmes often depends on their ease of assessment or determination; therefore, a selection strategy that combined the easily measurable traits of wood density and core length was evaluated and it was found that this approach holds promise for improvement of mechanical wood properties.

Correlations between traits

The increment cores that were used for this study spanned on average 17 growth rings and mostly contained juvenile wood, which is characterised by significant variation in wood traits and their genetic control from one ring to the adjacent ring. Only a few rings close to the bark can be considered as transition wood where traits are less variable from one ring to another. It was found that correlation estimates based on entire wood core means published in an earlier study (Lenz et al. 2010) give good indications for genotypic and phenotypic correlations in transition wood rings. We showed that correlations in juvenile wood can differ considerably from transition wood correlations. This becomes an important factor if early selection of wood traits is considered.

Overall, the use of area-weighted cumulative means seems appropriate because the correlation trends are less variable and clearly show developmental trends with cambial age. Our data show that including all growth rings of wood cores in analyses is preferable even if it might be more time-consuming and costly. In cases where only data for single

rings is available, one must take into account that correlations based on single ring means are more variable from one ring to another and might not give as precise estimates as needed for tree improvement programmes.

The fact that genetic correlations are stronger than phenotypic correlations is probably explained by environmental influences that weaken phenotypic correlations between wood traits in comparison to genetic correlations. This seems to be an important issue especially in young shoots where marked differences in genetic and phenotypic correlations were observed. This is consistent with findings from an earlier study showing a strong environmental influence on fibre anatomy-related wood traits as well as density of rings close to the pith, whereas the genetic influence increases in more mature growth rings (Lenz et al. 2010).

Modulus of elasticity (MOE), a determinant of wood stiffness, is influenced by wood density and MFA. Wood density is reported to strongly influence MOE in other conifers (Bendtsen and Senft 1986; Cown et al. 1999). Our results show that correlations between density and MOE were virtually nonexistent in very juvenile wood of white spruce. However, the correlation estimates that we found in rings close to the bark are very similar to estimates that Kumar et al. (2002) reported for small clear wood samples in radiata pine. No exceptionally strong correlations between MOE and density were found and there is no indication of autocorrelation as it could be expected because the SilviScan system uses density and variation of the diffraction pattern to estimate MOE.

In any case, our observations show that making predictions of genetic gain pertaining to wood stiffness based on the relationship between wood density and MOE requires some caution: Data reported here indicate that improvement of stiffness through selection of density would fail at an early age.

Strong, negative correlations between MFA and MOE have been reported in earlier studies on different conifers (Baltunis et al. 2007; Cave and Walker 1994; Evans and Ilic 2001). For our results, the absolute correlation coefficients were slightly stronger than those reported by Alteyrac et al. (2006a) for black spruce. It was interesting that the correlations were stable from juvenile through to transition wood and did not change with cambial age,

unlike correlations between density and MOE, or other correlations between wood traits. These findings confirm that MFA is a valuable predictor of wood stiffness.

The trend in correlations between density and MFA is particularly interesting in comparison to other trends that were found in this study. It is the only correlation that decreased in magnitude with increasing cambial age at both genetic and phenotypic levels. Although samples for this study had been screened for abnormal growth rings and compression wood, we can assume that a young shoot potentially contains more compression and flexure wood due to effects of wind on the young stem (Telewski 1989). In compression wood in conifers, elevated density is accompanied by elevated microfibril angles compared to normal wood (Donaldson, 2008). As the stem grows older and reaction wood becomes less abundant, high density measurements may not necessarily be correlated with high MFA. The presence of more compression wood in younger growth rings, in turn, could explain the absence of correlation between wood density and MOE at young ages. Furthermore, the high to moderate genetic correlations between wood density and MFA in rings that were close to the pith suggested that both traits could be genetically linked in the formation of conifer juvenile wood.

Relationships between density and MFA are the subject of conflicting reports in the literature (Baltunis et al. 2007; Donaldson 2008; Evans et al. 1996). Evans et al. (1996) found an inverse relationship between these two traits on an inter-ring basis when they analyzed high resolution profiles of density and MFA of radiata pine and shining gum trees (*Eucalyptus nitens* H.Deane & Maiden). Baltunis et al. (2007) found also slightly negative genetic and phenotypic correlations in radiata pine, whereas Bergander et al. (2002) found no correlations in Norway spruce (*Picea abies* (L.) H. Karst.). The differences in wood anatomy as well as reaction wood formation between angiosperms and conifers might partly explain the discrepancy between these reports. However, the declining correlation trend – from moderate correlations near the pith to correlation coefficients close to zero in more mature rings – suggests a complex relationship between wood density and MFA.

The absence of correlations between MFA and wood density, and MFA and fibre anatomy-related properties such as fibre diameter, wall thickness and also density makes MFA a

useful trait for tree breeding; this is especially true in the transition wood. Breeding strategies that would aim to reduce MFA, and thus, increase MOE would be predicted to have negligible influence on fibre anatomy. Mechanical traits could thus be improved without detrimental effects on pulp fibre quality through the production of coarse fibres with a low specific surface.

The high degree of similarity between correlation trends that included fibre wall thickness and specific fibre surface (i.e. MOE vs. fibre wall thickness and MOE vs. specific fibre surface) was related to a very high, but negative correlation between the two traits. Yet, even if fibre diameter is moderately or even highly correlated with fibre surface, it was surprising that correlation trends did not follow those of fibre surface and wall thickness. As a consequence, only weak phenotypic correlations and weak to moderate genetic correlations between MOE and radial fibre diameter were found. Fibre size apparently plays a less important role for mechanical traits such as MOE than does fibre wall thickness.

Our findings confirmed those of earlier studies, which revealed anatomical traits like fibre diameter and especially fibre wall thickness represented important components of wood density (Zobel and Van Buijtenen 1989). However, our results disagreed with those of Hannrup et al. (2001), who found no relationship between wood density and fibre wall thickness.

Genotypic and phenotypic correlations between different fibre anatomy-related traits such as fibre diameter, fibre wall thickness or specific fibre surface were similar and did not markedly change from one ring to another, except for the first few rings. Thus, it appears that environmental influences on young shoots and growth stress due to rapidly increasing circumference influence the relationship between wood anatomy related traits up to approximately ring 6.

The negative correlations that exist between wood density and traits such as fibre diameter and specific fibre surface are expected to result in a reduction of quality in the latter traits when genetic selection is weighted toward density. Selection for density would negatively influence fibre diameter and thus have a detrimental impact on pulp and paper properties

such as collapsibility in fibre processing, smoothness and opacity (Zhu et al. 2008). One approach to overcome this limitation is to identify trees or genotypes that represent correlation breakers, which may be suggested to exist by the moderate correlations between these traits.

Potential for early selection of wood traits

Genetic correlations with reference age 16 were generally high, which shows that expression of genes coding for different wood traits is fairly stable as a function of cambial age. This stability opens up opportunities for early selection of white spruce wood traits, especially for radial fibre diameter and mechanically related wood traits such as MFA and MOE. Transition wood properties of more complex traits, such as density and specific fibre surface, were predicted less accurately from rings closer to the pith. Poor prediction was probably related to both traits being influenced by combinations of different anatomical traits, such as fibre diameter and fibre wall thickness. Higher correlations have been reported for density between early ages and older reference ages in Norway spruce by Hylen (1999; reference age 12 years) and in radiata pine by Kumar and Lee (2002; reference age 30 years). Correlation trends similar to those estimated in our study were reported by Li and Wu (2005) for radiata pine and by Gwaze et al. (2002) for loblolly pine (*P. taeda* L.).

Nevertheless, these aforementioned studies suggest selection of wood density at ages as early as six–years or even younger, which is considerably earlier than our findings for white spruce. In addition to high age–age correlations, the ratio of heritability estimates at the young and adult reference ages plays an important role in estimating early selection efficiency. The strong environmental influence on wood anatomy and density compared to older rings, where heritability is high (Lenz et al. 2010), led to low selection efficiency estimates close to the pith in our study. We do not recommend selection before ring 8 or 9 to achieve 80% of the possible genetic gain expected for selection at age 16. Similar results were found by Gwinyai Nyakuengama et al. (1997) in a study of radiata pine pulpwood quality traits including density, specific fibre surface, and fibre perimeter. In our data set, selection for radial fibre diameter between cambial age 8 and 10 would be more effective than selection in the transition wood, which is related to slightly stronger heritability

estimates relative to the reference age of 16 years. Nevertheless, lumber quality remains the main interest of most tree improvement programmes. Low priority has been given to improving specific fibre traits for pulp and paper manufacture from spruce. Direct improvement with the aim to increase fibre diameter, specific fibre surface, or coarseness would probably decrease density and have a detrimental effect on pulp yield, but such changes also would have a negative influence on the suitability of the wood in mechanical applications.

Wu et al. (2007) found that early selection of MFA and MOE would be effective from age 4 to 8 in radiata pine. Our study showed similar findings for MFA in white spruce, but early selection of MOE seems to come with significant challenges. An increase in genetic control towards the end of the age range we investigated (Lenz et al. 2010) resulted in correlated gains that are consistently smaller than possible gains at the reference age. Improvements to MOE could come through its strong relationship with MFA and based on the high selection efficiency for MFA in rings 4 to 7. However, the moderate correlation between density and MFA at this age seems to be problematic. Further research on the economic impact of both traits would be helpful in developing decision-making strategies related to these traits, especially since the heritability of MOE and MFA are moderate and gains are expected to be modest.

Impact of selection for easily measurable traits

With the development of automated technologies like the SilviScan system, analyses of MFA and MOE have become widespread but still, processing numerous samples from a breeding population remains expensive. By combining wood density and core length into a selection index we tried to evaluate the effect on different mechanical and wood anatomy-related traits when selection strategies are based on easily measurable traits. These two traits have been reported to be negatively correlated in spruce (Corriveau et al. 1991; Zhang and Morgenstern 1995), which has led tree breeders to consider multi-trait selection strategies to avoid losses in either density or increment growth (Vargas-Hernandez and Adams 1991). Density dominates the selection index in our case as it is under much higher genetic control than radial growth. This explains why correlation trends between wood traits and the index are very similar to pairwise correlations with wood density. In several

cases it is advantageous to include growth traits, as the genetic impact is reinforced through the combined selection compared to pairwise correlations involving density alone. It is interesting that higher genetic gains can be achieved through indirect selection on density and core length compared to direct selection on MOE. This is due to the strong relationship between density and MOE as well as the high genetic control of wood density. Under these circumstances there seems to be no need to evaluate MOE in the entire breeding population. Control samples on subsets would be sufficient and represent a cost-effective alternative to monitor genetic control and correlations with different traits in the breeding population. However, more research is needed to evaluate the genetics of mechanical wood traits in white spruce. Recently developed methods to evaluate wood stiffness with acoustical sensors appears to be an inexpensive way to assess what is conceivably the most important mechanical wood trait and can be applied to large breeding populations (Huang et al. 2003; Jayawickrama 2001). However, the applicability of acoustic devices in small stemmed and branchy white spruce trials is widely untested – compared to their application in fast growing radiata and loblolly pine trials.

3.7 Conclusions

This study used high resolution data to precisely describe ring-by-ring profiles of genetic and phenotypic correlations over a range of 16 growth rings and to investigate the potential for early selection of wood traits in white spruce. Most of the correlations of fibre anatomy-related traits, together with density and MOE, were weak or close to zero near the pith, but increased in rings close to the bark. Only the correlations of MFA with MOE and density did not follow this trend. A strongly negative correlation, which does not vary in different growth rings, is indicative of the strong predictive value of MFA for MOE. Wood density and MFA were moderately correlated in rings close to the pith, but correlations were virtually absent in transition wood; this information may help to elucidate apparent contradictions in the literature.

We conclude that early selection of wood traits in white spruce should be based on a cambial age greater than eight years to capture highly correlated gains due to elevated age-age correlations (the reference age is 16 in this study). MFA represents the only exception,

where a higher genetic gain relative to the reference age can be expected between ages 4 to 6. Although attention must be paid to negative effects that may result from positive correlations with density up to age 8, MFA seems to be a promising trait for wood improvement in white spruce. The lack of correlation between MFA and fibre anatomy opens possibilities for indirectly selecting for MOE with little impact on pulp properties.

Another strategy to improve stiffness is presented by multi-trait selection on wood density and core length. Very promising and even stronger genetic gains were predicted for combined selection on density and core length than from direct selection on MOE. Disadvantages of strategies employing wood density are represented by unfavourable correlations between density and fibre anatomy-related traits that would negatively affect some pulp quality traits. A combined selection for pulp quality and mechanically relevant traits only seems to be possible when traits that are more expensive to access, such as MFA, are considered in selection programmes.

3.8 Acknowledgements

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Chapter IV – General Conclusions

White spruce (*Picea glauca* [Moench] Voss) is one of the most important tree species for the Canadian forest industry with over 100 million seedlings planted yearly for reforestation purposes in the whole country. In Quebec alone every year, about 25 million seedlings are produced, the majority coming from genetically improved sources mainly for growth (Beaulieu et al. 2009). Several studies on spruce and other conifers revealed that breeding only for growth leads to significant loss of wood quality, especially in mechanical traits (Zobel and Jett 1995; Jayawickrama 2001; Wu et al. 2008). To avoid detrimental effects of increased growth on wood application, wood quality traits are soon to be included into selection criteria of white spruce breeding programs. Research is also focussing on genomics, to set the scene for potential future breeding strategies based on molecular markers and the association of DNA markers to phenotypic variation. Both traditional breeding techniques and modern molecular genetics rely on the knowledge of quantitative genetic characteristics of traits. In this thesis, wood traits assessed from increment cores were analyzed, in order to study pith-to-bark variation of genetic control (chapter II) and correlations between different wood traits (chapter III). Additionally, correlations between juvenile wood and transition wood were calculated and the efficiency of early selection of wood traits was evaluated.

4.1 Review of results and hypotheses

This study presents genetic parameter estimates of white spruce wood traits which were assessed using pith to bark wood cores and the SilviScan system. The investigated traits, which are related to wood mechanics, included wood density, modulus of elasticity or cellulose microfibril angle; others traits were related to cell anatomy and pulp and paper properties such as tangential and radial cell diameter, fibre wall thickness or fibre coarseness. For all of these traits, genetic control was estimated for each ring from the pith to the bark separating earlywood and latewood. Correlations between different traits were estimated. A focus was set on the variability of parameters from the pith to the bark. For

each trait, correlations were also calculated between juvenile wood rings and rings of transition wood to help evaluate the efficiency of early selection. The main results are reviewed following the objectives and hypotheses, as stated at the end of chapter I.

Objective I. To evaluate if genetic gains can be expected by selection in order to justify genetic improvement of white spruce wood traits.

Each tree improvement program aims to increase the value of the targeted tree species; the improvement of a trait is thereby referred to as genetic gain. Besides variability of a trait, its genetic control strongly influences the gain that can be obtained from one generation to another. These first hypotheses aimed to evaluate the heritability of wood traits in white spruce.

Hypotheses

- a. The genetic control of wood traits is moderate to high.

The hypothesis can largely be accepted for earlywood traits; but it needs to be rejected for the latewood. The heritability of latewood traits could not always be estimated; else it was generally low or moderate. This did not considerably influence the whole ring heritability of traits, as the latewood proportion was low. However, the heritability of MFA and MOE was generally low to moderate and there were no major differences between earlywood and latewood.

- b. Heritability varies with cambial age.

This hypothesis is principally true. Heritability followed discernable trends from the pith to the bark. The genetic control of most wood traits was small in rings close to the pith, which is probably due to important environmental influences, especially on cell anatomy and on MOE, in young stems. These environmental effects most likely cause an irregular formation of reaction tissues, such as compression wood, in rings close to the pith. Consequently, heritability increased with cambial age. However, the heritability of latewood traits did not always follow this trend. For example, the heritability of latewood density was moderate close to the pith and decreased in the transition zone. The MFA

seemed to be an exception to these trends: the genetic control of this trait seemed fairly independent of age and did not vary significantly in different growth rings.

The high heritability estimates for cell anatomy-related traits as well as for wood density are consistent with previous studies on different conifers (e.g. radiata pine Gwinyai Nyakuengama et al. 1997; interior spruce Ivkovich et al. 2002b; or white spruce Corriveau et al. 1991). In contrast to our results, MFA and MOE have been reported to be under moderate to high genetic control in fast growing conifers, as discussed in detail in chapter II. Our results indicate that significant genetic gains can be expected if selections are conducted on wood traits in tree improvement programs. This conclusion is mainly based on the high genetic control of traits especially in rings older than age 10, which along with the observed variation of traits, influences the expected genetic gain.

Expected genetic gains have not been presented in the previous chapters, as the focus of this study was on the variation of genetic parameters with cambial age and not on determinations of gain in a breeding population. But conservative estimations from our data predict the possibility to improve density by about 8% (40 kg/m³) in ring 8 and by more than 14% (60 kg/m³) when selection is based on rings closest to the bark; whereas cell anatomy related traits such as radial cell diameter could only be improved by 9% (2.5 µm). This is largely due to the little variation observed in cell structure, even though some anatomy-related traits were found to be under strong genetic control. These calculations are based on a selection intensity of $i = 1.76$ (Zobel and Talbert 1984) for the case that 10% of the population is selected.

Although we found that mechanically important traits, such as MOE, were under low to moderate genetic control and MFA under moderate control, noteworthy gains for both traits were estimated. MFA could be altered for 2 to 3 degrees, representing a gain of 10% in rings close to the pith and 13% close to the bark. MOE shows potential for increase of 11 to 12% (1 GPa) in rings close to the bark. It is interesting to note that the estimated gain for MOE is of the same magnitude as the difference between white spruce and red spruce as well as black spruce wood; both latter species were reported to have slightly superior mechanical properties (Jessome 1977). Improvement of mechanics-related wood traits,

especially MOE, has the potential to result in white spruce trees that are similar to other spruces which have slightly superior wood quality. Thus, there is potential to increase the mechanical performance of white spruce wood compared with that from trees in primary forests. Although growth may remain the primary trait of interest in tree improvement, wood traits could be successfully included into selection schemes, especially if breeding populations are big so that individuals can be detected that do not follow the general negative correlation between growth and wood quality. This would help to reduce or even avoid potential losses in wood quality associated with rapid growth.

Objective II. To investigate possibilities to shorten breeding cycles for a more cost-efficient breeding.

The long life cycle of forest trees retards the selection of traits only after many years of testing. Tree breeders are thus constantly seeking to shorten breeding cycles without decreasing the efficiency or the expected genetic gain. In the context of this objective, we examined correlations between juvenile and older transition wood rings aiming to test if they are strong enough for successful early selection.

Hypotheses

- c. For individual wood traits, there are strong correlations between juvenile and transition wood.

Our findings agree with this hypothesis. Correlations above 0.9 were found among all rings older than age 4. Only for rings very close to the pith, some density related traits such as cell wall thickness and specific fibre surface show moderate correlation with the transition wood.

- d. Early selection for wood properties is effective.

Yes, there are possibilities for effective early selection. Selection efficiency increased from the pith to the bark for most traits. For radial cell diameter and MFA maximum selection, efficiency could be achieved before transition age. However, our data showed that very early selection at a cambial age of 5 years, as it was reported for some fast growing pine

species (Gwaze et al. 2002; Li and Wu 2005), would not be possible in white spruce. For most traits, at least 80% of the transition wood gain could be realized by selection around a cambial age of 8 to 10 years.

- e. The optimal moment for early selection varies from one trait to another.

Although the early selection efficiency was not the same for all wood traits, early selection around age 8 to 10 seemed optimal for most of the traits. The hypothesis thus needs to be rejected. An exception was MFA that had maximum selection efficiency around age 6. Very early selection only seems possible for MFA; for other wood properties, heritability increases with cambial age. Selection on the phenotype would be more effective and expected gain would increase at a cambial age of 8 years or more.

Objective III. To study interactions between different wood traits to estimate the effect of selection for one trait on other wood traits.

Most improvement programs focus on a few key traits at a time, for practical and economic reasons; therefore, not all of the end-product relevant properties can be targeted at once. In the choice of selection traits, one needs to consider interactions between traits in order to avoid detrimental effects resulting in potential loss of wood quality. With the knowledge that the phenotype as well as the genetic control of wood properties vary with cambial age, we may also assume that correlations between traits would vary from the pith to the bark.

Hypothesis

- f. Genetic correlations between different traits vary from the pith to the bark.

The hypothesis was found to be true especially in rings close to the pith. Most of the correlations between traits increased in magnitude from the pith to the bark, but sooner or later levelled off as cambial age increased, and then did not change significantly from one ring to another. The correlation between MFA and MOE was unique because it remained constant from the pith to the bark. The variability of correlations especially in rings close to the pith might have a significant influence on selection strategies. However, correlations

did not change a lot beyond a cambial age of 8 years, when selection became most efficient for the majority of traits.

Selection for wood density, often considered as one of the most important wood traits, showed a negative impact on cell size and fibre surface. This would influence detrimentally traits that are important for pulp and paper manufacture, such as fibre collapsibility and sheet formation (Smook 2002). However, wood density was positively correlated to the mechanically important trait MOE. It was also found that indirect selection of MOE, using an index combining density and core length, was found to be highly effective. This is a very interesting approach, because direct selection on MOE was penalized by low heritability and moderate expected gain. Length of increment cores, as a measure of growth, and wood density can be determined with relatively simple techniques. This approach using indirect selection could thus help increase cost effectiveness without trade-offs concerning the improvement of the mechanically important trait MOE.

Taken together, the findings of this study offer valuable quantitative genetic estimates necessary for genetic research of white spruce wood traits. Additionally, they bare information for decision making concerning breeding strategies for improvement of white spruce wood traits. More implications for breeding strategies resulting from our findings are discussed in section 4.3.1 below.

4.2 Critical discussion

The focus of the study was put on the investigation of variation of quantitative genetic parameters as a function of cambial age. This information is valuable for tree improvement on the one hand, but is also fundamental for bio-molecular research such as gene expression studies. Some of the heritability estimates that we obtained appeared surprisingly high and it raises questions concerning the accuracy of our quantitative parameter estimates. This section discusses factors related to this issue and other potential limitations of this study that may be related to sampling and experimental design.

4.2.1 Statistical layout and sampling

For this study, we analysed 375 wood cores from 25 open-pollinated families, with each family being represented by five trees on each site. The analysis of different sites is helpful in a genetic study, because the genetic variance component as part of the total variance is highly influenced by environmental and thus site effects. Such sampling layouts permit to measure the extent of genotype-by-environment interaction. The inclusion of site effects or also block-within-site effects allows for a better control of environmental influences and makes heritability estimates more representative (Zobel and Talber 1984). The study of these aspects can be seen as an advantage of our study in comparison to previous investigations that did not consider different environments (e.g. Zamudio et al. 2005).

Nevertheless, our analysis revealed no or a negligible genotype-by-environment interaction of white spruce wood traits. The site-family-interaction was even removed from our statistical model as described in the material and methods section of chapter II (refer to formulas 2.2 and 2.3). The site effect was however not negligible, although it was statistically non-significant in our analysis. Wood trait means differ from one site to another (see tables of family means in appendix 2). Additionally, variance components of the site effect can be as high as or in some cases even higher than the more significant family effect (see variance estimates in appendix 3). The fact that the site effect remains statistically non significant is probably due to the small number of sites (three sites, and only two degrees of freedom) and the large errors associated with the variance estimates (see variance estimates and associated errors in appendix 3).

The number of families analysed in this study probably presents a lower limit for quantitative genetic analysis. Some of the published studies on wood traits included 20 to 30 families (Dungey et al. 2006; Zamudio et al. 2005), but most studies targeted more (Ivkovich et al. 2002 a, b; Kumar and Lee 2002), in some cases over 200 families (Baltunis et al. 2007) to capture the existing variation among different provenances. As the total number of trees is often limited by the cost of analyses, the number of families, sites, and trees per site and per family need to be balanced in order to maximize precision of estimates. In our case, unpublished analyses including 165 families and 3 trees per family

on one site led to large errors associated with heritability estimates. Additionally, there was a lack of power to estimate genetic variance components for some of the traits including wood density and MOE. For the present multi-site analysis, we thus decided to reduce the family number in order to be able to sample five trees per site and family and thus to more accurately represent intra-family variation.

In this study, the number of families is considered sufficient for describing the variation of genetic parameters with cambial age; nevertheless, absolute values such as heritability may be different in other populations. Especially in the context of a breeding program, there is a need for reliable determination of quantitative genetic estimates, such as heritability of traits, which will allow to precisely evaluate the expected gain and thus the economic base of the improvement program across one or more breeding zones. The white spruce families used in this study, come from provenances covering both breeding zones that were suggested earlier by Li et al. (1997) for the province of Québec. They represent the geographic variation; but nevertheless, the sampling of more families and sites would improve estimates of the genetic variance components. It would likely also allow the estimation of the site-family interaction and thus better separate environmental genetic influences in the statistical model. These options should be considered in future studies on genetics of white spruce wood properties.

As discussed in chapter 2, the genetic variance and the heritability were higher than expected in some cases. For instance, some heritability estimates for the radial cell diameter were close to one, which would imply that the trait is almost entirely genetically controlled. Blaming a possible overestimation of the genetic variance components on the low number of families may be a little bit short-sighted. Instead, the way of calculating the genetic variance as four times the family variance might be too optimistic and only true for strict half-sib families. Open-pollinated families, as used in this study, may contain a mix of half-sibs and full-sibs due to relatedness and spatial relationship among parents (Zobel and Talbert 1984, Coles and Fowler 1976). For a more realistic estimate of the additive genetic effect, the family variance is probably more correctly multiplied by a factor between 3 and 3.5, which would lower the heritability estimates but not alter the described trends observed with cambial age.

4.2.2 Material

Sampling one wood core per tree at breast height (as was done in this study) is a standard procedure often used in forestry and forest genetics. It allows investigating inter-annual variation of wood traits and inter-tree variation, but leaves longitudinal variation along tree height unconsidered. Variation of wood traits with tree height was reported earlier (for example by Alteyrac et al. 2005) and it is assumed that it somewhat follows the juvenile – mature wood pattern with a shorter juvenile phase (Alteyrac et al. 2006). In our study on white spruce, which is slower growing compared with radiata or loblolly pines, the number of growth rings in wood cores was highly variable from one tree to another. This implies that trees were not at the same developmental age stage when they reached breast height. The analysis of data with respect to cambial age brings the focus on the important radial variation of wood traits; however, it may overlook possible variation of wood traits along tree height, which also influences homogeneity of wood traits and thus wood quality. The investigation of genetics of wood variation along tree height could represent an interesting and challenging subject for future studies.

The low number of growth rings in our white spruce wood samples represented a disadvantage compared with faster growing pine species that reach breast height within two to three years after planting (compare to data from Li and Wu 2005; Dungey et al. 2006). Although the trees were 30 years old when sampled, only 17 growth rings could be found on average in wood cores. This long tree establishment phase is primarily due to the general slower juvenile growth of white spruce, but also to site conditions before or in the beginning of the establishment of the progeny test. Prior to its installation most of the organic matter and probably nutrients were removed from the site (see material and methods of chapter II). Additionally, we cannot exclude competition by herbaceous species in the early years after the establishment. In any case, a quicker growth and thus wood samples with more growth rings would have helped to extend the reference age for early selection efficiency or age–age correlations closer to the approximate rotation age. It would have also covered a few mature wood rings and given a more complete picture of the wood actually available at rotation.

4.2.3 Investigated traits

To our knowledge, no prior study analysed different traits related to wood mechanics and cell anatomy on a single ring basis. We covered most traits of interest for the use of white spruce wood as lumber in construction or for its fibres in pulp and paper manufacture. Our data allowed us to investigate the complex relationship between wood mechanics relevant traits and pulp and fibre properties. There are only very few wood traits that are relevant for the end-use of wood that have not been investigated here. A trait that is very important for wood mechanics is the modulus of rupture (MOR). It is related to the maximum strain a piece of wood can withstand before breaking and is determined by destructive tests. Another trait that has not been analyzed, but which plays an important role in fibre and pulp characterization is fibre length. Fibre length influences inter-fibre bounding and is highly correlated to tear strength of paper (Smook 2002). MOR and fibre length cannot be analysed with the SilviScan system but it may be of interest to include both traits in future studies to give a more complete view of interactions between traits related to wood mechanics and pulp properties.

The consideration of more growth traits, such as height or tree volume measurements repeated at different ages may help to better describe the relationship between growth and wood quality in future studies. We only found very low genetic control of single ring increment, which may be considered as a measure related to tree growth. Growth related traits have been previously reported to be under weak genetic control, especially diameter growth (e.g. Merrill and Mohn 1985). In this study, early wood and late wood width, and their percentage did not allow for the successful modelling of genetic variance components. Nevertheless, a more complete description of correlation between wood and growth traits, such as height or tree volume would likely be of value to tree improvement programs aiming to breed for growth and wood quality at the same time.

4.3 Perspectives

The results of this study indicate that there is a very good potential to include wood properties into white spruce breeding programs. The encouraging trends observed for heritability, early selection or correlations between traits represent valuable information for

decision making and selection strategies. The absolute values of heritability and expected gain likely need to be confirmed in the breeding populations, including as many families as possible. An increase of provenances and sites uniformly covering the two white spruce breeding zones (Li et al. 1997) will help to broaden the applicability of results. This section discusses selection strategies for breeding programs and examines what kind of information still needs to be acquired to optimize such strategies. Some future study subjects concerning breeding for wood quality are also discussed.

4.3.1 Implications for selection strategies

The moderate to high heritability observed for most wood traits gives the possibility to pursue individual selection strategies or combined strategies such as intra-family mass selection with a strong weight on individual selection. Such strategies would allow maintaining a high level of genetic diversity in the breeding population and promise considerable gains as the phenotypes are a good indicator of the genetic potential of individuals.

In the unlikely case that only a few traits are targeted in an improvement program, the selection could be done by independent culling, selecting the individuals that meet minimum criteria for the traits of interest. It represents a relatively simple approach, but in most programs, the consideration of many traits is expected. Index selection would hence be a better choice because it allows the breeder to cope with traits with different levels of genetic control through the multivariate analysis of the matrices of genetic and phenotypic effects. Additionally, index selection offers the opportunity to weight traits by their economic value. Index selection seems to offer more advantages than independent culling methods; however, it has the potential to decrease genetic diversity in cases of strong adverse correlations, for example, between growth traits and wood density. Concluding from Monte-Carlo allele-based simulations, Sanchez et al. (2008) reported a loss of heterozygosity and a higher variance of response when applying index selection methods. These results should however be verified on a white spruce data set.

Before choosing a selection strategy that incorporates wood traits into white spruce breeding programs in a profitable manner, breeding objectives must be clearly defined. In

the recent years, breeding objectives for other conifer species and especially radiata pine have been developed that include wood quality traits (Berlin 2009; Ivkovich et al. 2006a,b; Shelbourne et al. 1997). The analysis of the economic value of different traits starting from the plantation owner, the transforming industry up to the end product needs to be implemented in order to find the optimal weight of each trait in a selection strategy. Economic studies would additionally give an integrated view of the value chain for forest products; therewith each industry involved in the processing of trees could identify how it would benefit from tree improvement. This could help justify breeding for wood quality and stimulate industrial support for this activity. Ultimately, developing a partnership with industry may help to strengthen applied breeding programs, which in turn could deliver optimal raw material for the industry.

For white spruce wood, the primary utilization will likely remain for structural purposes. Pulp and paper fabrication from spruce is mainly based on sawmill residues and lower quality logs. The alignment of a whole breeding program on specially improved pulp and paper qualities appears unprofitable in the current economic situation: the Canadian pulp and paper industry is facing a deep crisis, hampered by a poor image in the investment community, decreasing paper prices and a rising importance of the overseas competition from fast growing tree plantations (Tang 2008). Under these conditions, it seems doubtful that the use of improved fibres for pulping would result in higher revenues. Still, spruces have some very interesting pulp properties, as described in chapter I, and future research might consider the improvement potential focussing on specialised pulp products, or even biorefinery products that may promise higher revenues than the standard pulp products (Chambost and Stuart 2007).

From a breeding point of view, the simultaneous consideration of cell anatomy and mechanical wood properties into breeding programs seems difficult due to strong adverse correlations. Our results suggest that the use of MFA for improvement of wood mechanics could possibly overcome those adverse correlations, because it appears unrelated to cell anatomy. The high cost of MFA evaluation may only be justified when very early selection is considered in a white spruce breeding program. In this case, one could profit from the potential for very early selection of MFA in rings close to the pith. An assessment is needed

to estimate the costs and the expected gain of wood mechanical properties that could be achieved by this indirect early selection strategy.

Overall, a relatively high priority may be assigned to improving mechanical traits such as MOE and the correlated traits MFA and wood density. Based on cost, SilviScan analyses for the determination of MOE and MFA profiles may not be feasible in entire breeding populations. The use of acoustic tools for the assessment of dynamic MOE should be considered also in white spruce. Several studies showed their satisfactory application in slash and radiata pine breeding (Kumar 2002, Li et al. 2007). Low costs and the large number of individuals that can be analyzed make acoustic tools interesting for integration into breeding programs. In any case, the results from the third chapter of this thesis show that an index combining annual increment and wood density would allow for effective indirect improvement of MOE. Direct measurements of MOE may be only needed for validations of this relationship.

The white spruce breeding program of Québec is less advanced than programs for radiata pine in the southern hemisphere, loblolly pine in the United States or Norway spruce and Scots pine in Scandinavia. Wood traits were only recently included into selection of white spruce so that the widespread availability of seed resulting from selections for improved wood quality is still several years away. Nevertheless, the negative correlation observed between growth and mechanical wood traits suggest that efforts to improve wood quality in the planted stock should be increased as soon as possible. A short-term solution might be the screening and selective thinning of current seed orchards for mechanical wood traits such as MOE and density. Due to the high heritability of wood density in particular, seeds of mother-trees with high density wood are expected to carry genes that will also lead to superior wood density in seedlings used for reforestation. With the advance of the breeding program, new orchards will be established including seed trees improved for wood quality. Additionally, elite populations could be developed for an enhanced focus on particular end-product qualities, such as mechanical wood traits or pulp traits; although we previously argued that pulp traits are of lower priority. Especially in these elite populations, clonal testing and replication could enhance genetic gain, due to better delineation of genetic and

environmental effects. Weng et al. (2009; 2010) showed some of the benefits of clonal testing for improved gain of volume in spruce. However, traits showing high heritability, such as wood traits, may also be effectively tested with open-pollinated material as a higher number of families and individuals per family may be tested; this was also suggested for the new Australian radiata pine breeding strategy (Dungey et al. 2009).

The installation of small specialized populations would also allow for testing different environments and silvicultural treatments to better document the extent of G x E interaction. This might be especially necessary for growth. Our analysis on wood traits revealed no G x E influence, but a non-negligible contribution of environment to the total variance. Silviculture treatments such as thinning and spacing were reported to have significant impact on realized gain in Douglas-fir volume and growth (Ye et al. 2010). There seems to be a need for investigating different climatic environments but also different silvicultural regimes in order to make the best selections for improvement of white spruce.

The high cost of many wood property determinations, the long growth period of up to 20 years or more before wood traits can be evaluated in spruces, the diversity of traits to consider and the complexity of these traits has encouraged the development of new tools including DNA markers. The possibility of developing DNA markers for many different traits could simplify and strengthen selection methods, in addition to shortening the breeding cycle. Genomic investigations also have the potential to shed new light on the genetic architecture of wood traits. To date, successfully associated markers explain only a small percentage of the phenotypic variation of wood traits ranging from 1 to 5% (González-Martínez et al. 2007; Dillon et al. 2010; Thumma et al. 2010). Additionally, the variation noted in heritability estimates and genetic correlations suggests that gene expression and also linked expression of genes is variable, especially in young stems. Together, these observations and findings indicate that effective DNA marker selection will require a large number of markers associated with the traits of interest. Association studies aiming to discover market-trait associations were almost exclusively based on coding regions of genomes and usually target a rather small number of genes. Dillon et al. (2010)

also considered upstream regulatory regions and scanned one of the largest sets of genes with close to 100 different genes. A broader and more comprehensive analysis of the genome appears to be needed to develop a set of markers that will be of value to tree breeding. Much larger set of candidate genes (several hundred genes) are being tested in more recent studies (e.g. Beaulieu et al. 2011). They suggest that a significantly larger proportion of the phenotypic variation may be explained by several markers considered together. It remains to be shown that they will be sufficient to enable marker-assisted selection.

To overcome some of the problems, authors like Grattapaglia et al. (2009) advocated the development of genome-wide and cost efficient marker systems applying thousands of markers covering the entire genome. This approach relies on linkage disequilibrium (LD) among genes so that the marker-trait linkage may be detected in the test population (Grattapaglia and Resende, 2010). However, it is well established that conifer populations – both natural and those used for breeding – have very low LD because they are essentially undomesticated; they have large effective population sizes and outcrossing mating systems. LD, being a function of population size, could be improved through small breeding population sizes, which could be the case in advanced programs or small elite populations. In any case, the genome of spruces and conifers in general is among the largest of living organisms (about 300 billion base pairs, Murray 1998) and genome-wide scanning remains unaffordable despite the advances in sequencing technologies. The dream of powerful molecular breeding tools that would allow for cost-effective scanning of many more individuals than in field tests is still far from reality. In any case, the genetic gain that can be meanwhile achieved through traditional breeding techniques will benefit from the high heritability of wood traits.

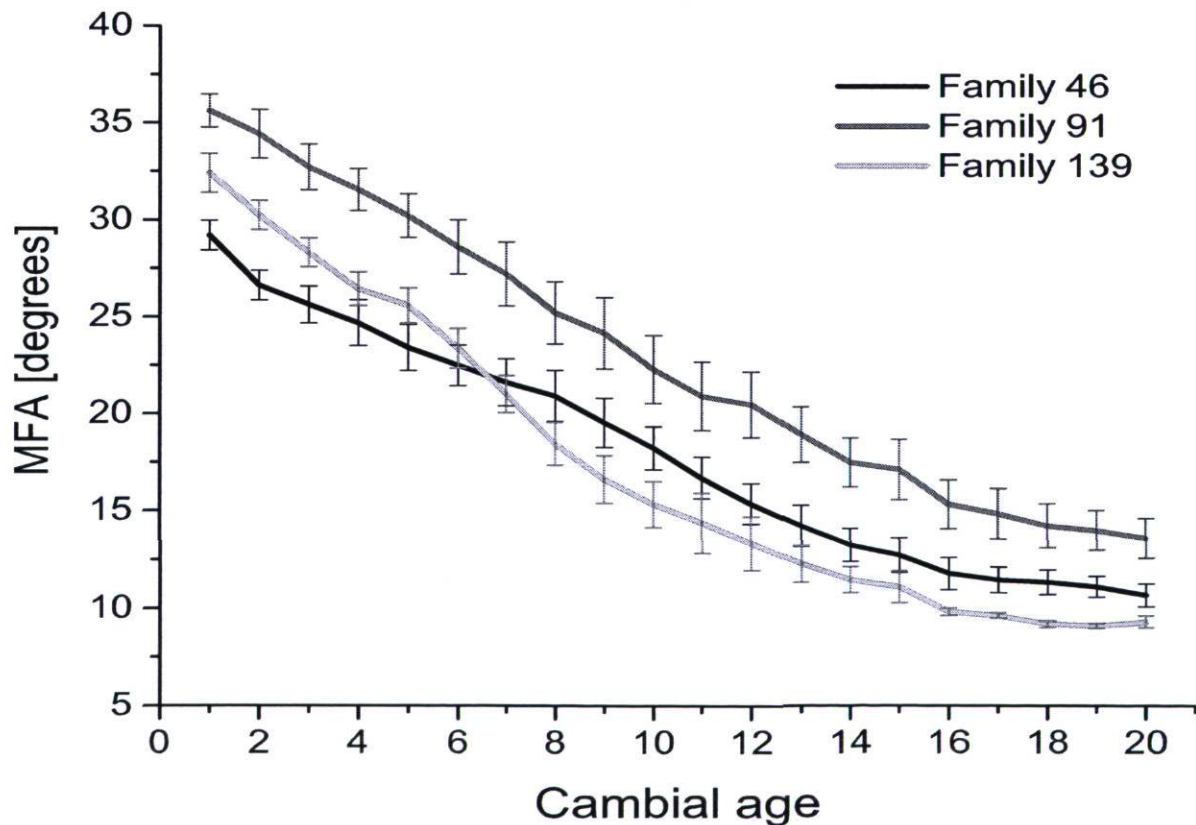
4.3.2 Future studies

Some of the results and discussions presented in this thesis suggest future research projects. These include: a) the study of different environments to better describe G x E interaction; b) economic studies to identify the economic weight of each wood trait and c) the improved characterization of intra-tree variation of traits and its impact on selection. Especially radial

variation of wood traits appears to be often neglected although it impacts on different features of the challenges met in wood quality improvement (Apiolaza 2009); this issue will be developed in more detail in the following paragraphs.

As the rotation ages continue to decrease owing to more intensive silviculture and genetic selection for growth, breeding strategies need to focus on the improvement of juvenile traits. Individuals showing good juvenile traits and especially quick improvement of mechanical wood traits in the first rings close to the pith should be preferred in selection. But genetic studies of wood traits are generally performed on single ring analysis, regarding each cambial age in isolation, as also presented in this thesis. This approach neglects between-ring variation in wood cores although it is highly informative. In the example of fig. 4.1, family 139 has the quickest decrease of MFA and should be preferred in selection to overall improve the juvenile and transition wood MFA.

Fig. 4.1. The informative character of inter-ring variation of MFA. Family 139 shows the quickest decrease of MFA from the pith to the bark. Dependent on the age, family 46 or 139 has the lowest MFA and might be preferred in selection. Each family is represented by 15 trees; the standard error of family means is represented by the error bars.



Taking into account the inter-ring variation or the entire phenotypic trend from the pith to the bark in quantitative genetic analysis comes with statistical challenges. Models that consider a given trait in each ring as a repeated measure on a wood core may help account for inter-ring variance, but they require complex variance-covariance matrices. Exploratory analyses that have not been included in this thesis showed that the interpretation of results is not straightforward and that the models require considerable computational time and capacities. The fitting of non-linear function to traits like MOE and MFA appears to be more encouraging; the fitting parameters such as slopes, asymptotes or curve shape could be thereafter analyzed with quantitative genetic models. Preliminary analyses (not been shown in this thesis) were very promising and encourage the further investigation of non-linear function in future modelling studies.

A different approach to address radial variation wood traits is presented by Apiolaza (2009) in his opinion paper “Very early selection for solid wood quality: screening for early winners”. The author suggested the introduction of threshold selection values for a given age. This idea represents a practical approach that does not rely on the costly analysis of all of the growth rings of a tree. For different wood traits, technical threshold values already exist, for example minimal loads or stiffness requirements in building codes. These values could be transformed into breeding objectives, rejecting individuals that do not meet the threshold criteria and would else only produce low quality wood, such as pulp wood. Stiffness thresholds could be easily evaluated with acoustic tools at a given age, with the advantage of cost effective screening of large populations as described above. Some basic work on several eastern Canadian species was already presented by Achim et al. (2010) who investigated relationship between dynamic MOE of standing trees and static bending MOE of the subsequently produced lumber. However, there is still a need to enhance correlations and to study the utility of acoustic tools in an actual breeding context for the improvement of Canadian (sub-) boreal tree species.

Although very promising, there are also some drawbacks of threshold selection that need further investigation. The example in fig. 4.1 shows that the time of selection may influence which individuals or families are selected. This illustrates how threshold selection may neglect variation before and also after the selection point. There is a need of understanding

at which age a threshold would best reflect end-product quality for optimal use of threshold selection.

Another point that needs consideration is the statistic analysis of data in threshold selection strategies. At a first glance, it appears to fit a binomial approach with two possibilities, whether a tree meets the threshold criteria or is rejected. Statistical models would then need to account for non-Gaussian distribution of traits and would be different to standard approaches of quantitative genetics.

Overall, threshold selection appears to be a very interesting way of selection because it is simple to apply. Although it contrasts with quantitative selection strategies aiming to identify the best individuals, it should be considered for breeding strategies aiming to select individuals or families with desired variation trends. This goes along with the main results of this thesis that clearly show the importance of phenotypic and genotypic inter-ring variation for the improvement of white spruce wood traits.

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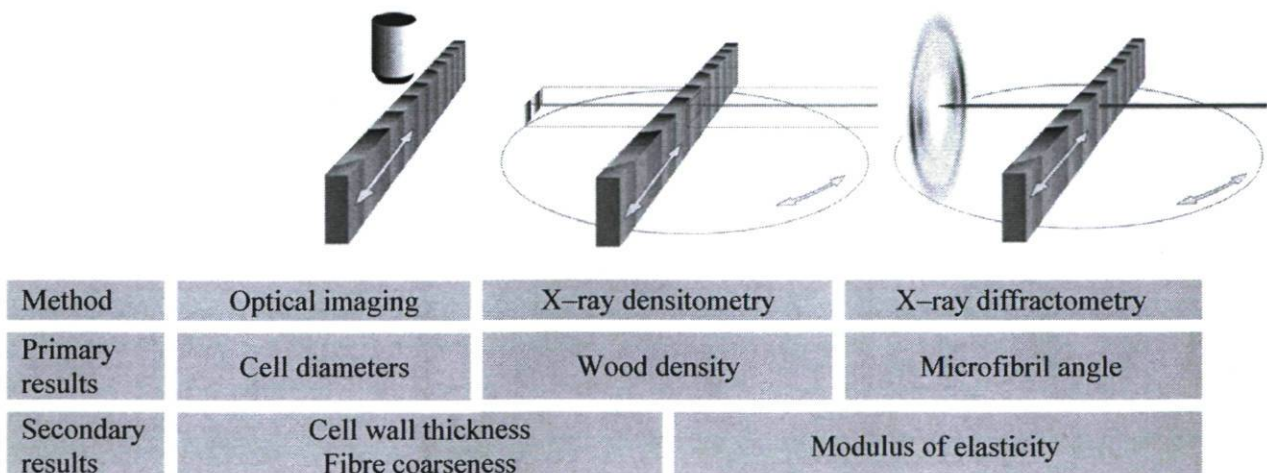
Appendix 1

The SilviScan system

The SilviScan system was developed by researchers lead by Robert Evans at the CSIRO, division of Forestry and Forest Products, in Melbourne, Australia during the late 1980s (Evans 1994; Evans et al. 1999). Wood trait determination using SilviScan has become a routine analysis during recent years, allowing the measurement of high resolution pith to bark profiles of density, fibre width and cellulose microfibril angle (MFA). From these data many more wood traits may be calculated; these traits are related to cell anatomy and wood mechanics that are of industrial importance (Evans et al. 1995; Lundqvist and Evans 2004), see Fig. A.1 for an overview of traits.

Usually, analyses are made on increment cores with diameters around 10 mm or sections from wood disks. The samples are acetone extracted and are air-dried (conditioned to 20 C and 40% relative humidity). They are cut into cants of 7 mm (longitudinal) by 3 mm (tangential) using a twin blade circular saw and one top-surface is polished with a series of fine abrasive sheets to reveal fibre cross-sections (Evans 1994). The cants are mounted on a computer-controlled stage and analyzed with the three components of the SilviScan system: microscopic image analysis, X-ray densitometry, and X-ray diffraction. Readings can be taken down to every 25 μ m.

Fig. A.1. SilivScan measurement principles. Secondary results are not directly measured and calculated from primary results. Adapted from Keunecke et al. (2009).



Wood traits related to cell anatomy and wood density

In the beginning, SilviScan consisted only of the imaging system and X-ray densitometry. With these components cell diameters and wood density can be directly measured and a number of other traits can be calculated (Evans 1994; Evans et al. 1995) based on some simple approximations for softwoods in which tracheids are the most abundant cell type (e.g. Stamm 1964; Britt 1965, 1966; Scallan and Green 1974, 1975; Yao and Ching Ma 1978).

$$[A.1] \quad P = 2 \times (R + T)$$

$$[A.2] \quad N = \frac{l}{R \times T}$$

$$[A.3] \quad C = \frac{D}{N} = R \times T \times D$$

$$[A.4] \quad S = \frac{P}{C}$$

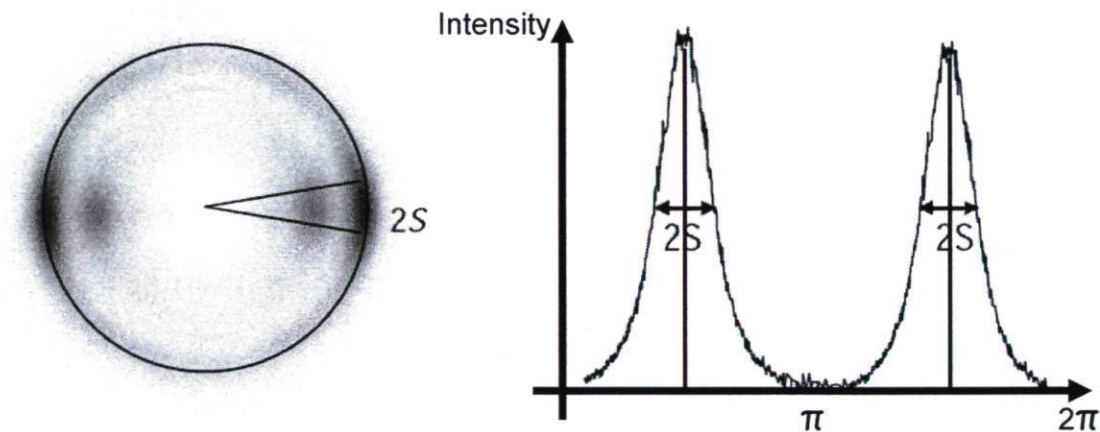
$$[A.5] \quad w = \frac{P}{8} - \frac{l}{2} \times \sqrt{\frac{P^2}{16} - \frac{C}{d}}$$

The primary, measured traits are: **R**, the **radial cell diameter** (in the pith to bark direction); **T**, the **tangential cell diameter** (parallel to the ring boundary); and **D**, the **wood density**. These measures serve the calculation of **P**, the (external) **perimeter** of a tracheid that is approximately rectangular in its cross-section; **N**, the **number of cells** per mm²; **S**, the **specific surface** of a fibre and **C**, the **fibre coarseness**. SilviScan uses a coarseness definition based on cell cross section and density as it was done earlier by Britt (1964; 1965) in solid wood. This definition is contrast to pulp fibre coarseness that is often calculated with density and fibre length; the latter trait is not determined by the SilviScan system to date. However, pulp fibre coarseness can be estimated by multiplying wood fibre coarseness with pulp yield (Evans 1994). Cell **wall thickness**, **w**, is calculated with an earlier established relationship (Kibblewhite and Bailey 1988; Evans et al. 1995) involving the **tracheid wall density**, **d**, that has been shown to be rather constant (1500 kg/m³) in different softwoods and hardwoods (Kellogg and Wangaard 1969; Kellogg et al. 1975).

X-ray diffractometry

Towards the end of the 1990s, different components were added to the SilviScan system allowing for the analysis of the x-ray diffraction pattern: this includes a copper rotating anode in point focus, a nickel filter, a capillary focussing system to produce beam cross-sections of 0.2 mm as well as a CCD (charge-coupled device) area detector (see Evans et al.1999 for further details). The deflection of the x-ray beam is mainly due to the crystalline nature of cellulose microfibrils. The angle of these microfibrils in the secondary cell wall (short **MFA**) presents an important measure as it is believed to have a significant influence on the tensile strength, stiffness, and shrinkage of wood (Cave and Walker 1994; Evans and Ilic 2001).

Fig. A.2. X-ray diffraction pattern and microfibril angle. MFA is calculated from the length of the intense diffraction arcs. Adapted from Lundqvist and Evans (2004).



Evans (1999) argued that the width of the diffraction peaks due to the strong (002 azimuthal) equatorial reflection is directly linked to MFA (Fig. A.2). It is calculated by the SilviScan system using the formula:

$$[A.6] \quad MFA \approx \sqrt{2} \times S$$

where S is the standard deviation of the peak profiles corrected for local dispersion.

It should be noted that Verrill et al. (2010) mentioned several concerns about this approach in a very recent publication. For example, the authors believe that the justification for a base assumption that led to equation A.6 is not strong; they also criticize that a possible tilt in fibre

orientation remains unconsidered. These concerns have not been regarded in this thesis but may be of importance for future research projects.

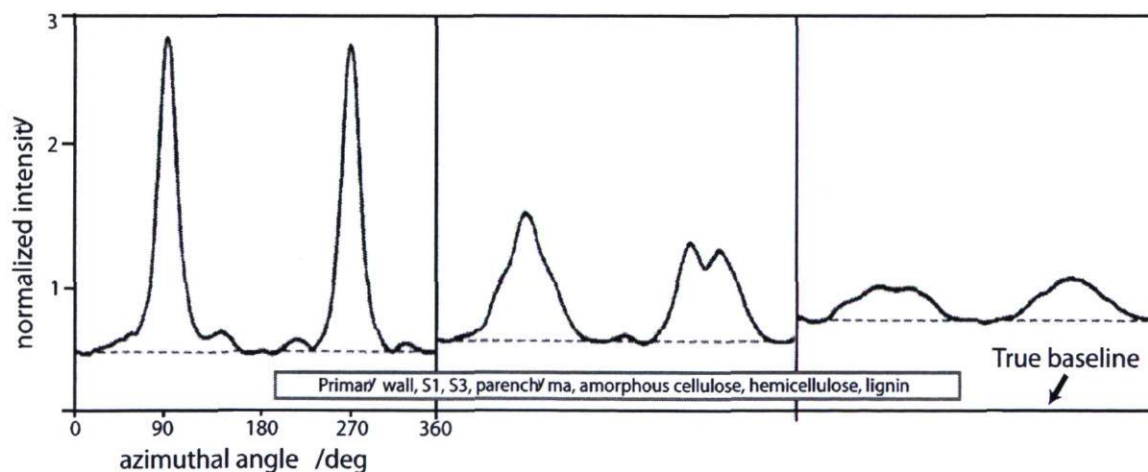
Wood stiffness by X-ray diffractometry

Evans and Illic (2001) present an approximate estimate of **modulus of elasticity** (MOE) involving SilviScan MFA and wood density. However, Evans (2006) introduces an ameliorated semi-empirical approach to determine MOE with the SilviScan technology and developed the following formula:

$$[A.7] \quad MOE = a \times (I_{cv} \times D)^b$$

where D is the wood density and I_{cv} the variation coefficient of the normalized intensity profile. There is an advantage of using the I_{cv} because it enables to account for background scattering of all components that are present in the cell wall matrix (such as lignin and hemicelluloses) and does not rely only on cellulose MFA (figure A.3).

Fig. A.3. Typical normalized azimuthal diffraction profiles. From left to the right: High, medium and low MFA. The amplitude of the intensity profile decreases and the proportion of background scattering increases with increasing MFA. Adapted from Evans (2006).



The coefficients a and b in formula A.7 are determined empirically through correlation with the dynamic longitudinal MOE measured by the resonance method. The values of the coefficients seem to be determined mainly by instrumental conditions rather than differences between tree species (McLean et al. 2010; Evans 2006).

Future applications of SilviScan X-ray diffractometry

Two traits that can be measured with SilviScan, but that are rarely used for wood characterization until now are **crystallinity** and **crystallite width**. These traits describe the part of crystalline cellulose in the wood matrix as well as their crystalline structure. Some authors investigated SilviScan crystallite width and established correlations between growth strain (Yang et al. 2006) or tension wood (Washusen and Evans 2001) and the crystalline character of wood cellulose. However, crystallinity and crystallite width appear to be two essential traits in view of an increasing interest into the production and application of nano crystalline cellulose in the near future.

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Appendix 2

Family means (tables)

The following tables present an overview of family means (mean), the standard deviation (stddev), the coefficient of variation (CV), the minimum (min) and maximum (max) of investigated wood traits in the earlywood and the latewood. Means are presented for individual test sites and for all sites combined. Families are sorted by their overall mean of the respective trait in the earlywood. The data may give a rough indication of superior families. However, the values are based on arithmetic core means; growth and cambial age of family members as well as the radial phenotypic variation (see chapter II, figure 2.1) remains neglected.

Site codes:

E560A1: La Patrie, Éstrie

E560A2: Dablon, Lac St. Jean region

E560A3: Mastigouche, Mauricie

More information on site characteristics is given table 2.1. in the section *materials and methods* in chapter II.

Traits:

- a) Wood density
- b) Cell wall thickness
- c) Radial cell diameter
- d) Tangential cell diameter
- e) Specific fibre surface
- f) Fibre coarseness
- g) Number of cells per mm²
- h) Earlywood and latewood width
- i) Earlywood and latewood proportion
- j) Microfibril angle (MFA)
- k) Modulus of elasticity (MOE)

a) Wood density

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
84	364,34	320,10	426,96	27,19	7,46	686,56	514,94	811,29	93,79	13,66
52	367,89	344,59	390,28	14,79	4,02	669,69	542,17	773,77	73,01	10,90
172	370,96	323,49	465,13	45,09	12,16	675,78	539,53	905,56	107,68	15,93
155	374,20	333,89	445,04	28,38	7,58	700,41	557,39	798,61	78,21	11,17
55	374,86	307,64	420,98	29,91	7,98	700,09	568,17	823,74	65,61	9,37
98	379,44	334,22	454,79	36,14	9,53	686,06	559,43	809,30	80,79	11,78
70	380,46	324,45	424,17	28,41	7,47	698,86	502,28	797,57	93,55	13,39
170	381,09	343,03	448,92	31,82	8,35	718,73	549,55	845,40	89,92	12,51
197	382,19	318,70	428,90	28,35	7,42	702,05	569,94	810,47	74,19	10,57
201	383,18	339,19	452,96	30,54	7,97	678,98	560,16	773,30	76,46	11,26
31	383,24	332,63	443,59	30,60	7,98	703,04	506,24	852,02	89,88	12,78
178	386,61	326,99	427,51	22,67	5,87	714,66	571,56	806,05	77,22	10,81
15	397,01	344,73	474,08	34,72	8,75	704,49	583,20	796,42	64,58	9,17
30	397,62	341,96	443,06	32,63	8,21	701,54	553,49	813,38	87,88	12,53
16	398,40	332,43	448,99	33,76	8,47	702,56	545,80	829,05	86,36	12,29
91	400,96	355,41	469,12	26,29	6,56	729,62	575,55	872,51	87,40	11,98
83	401,62	352,34	457,99	35,10	8,74	705,87	586,66	833,26	62,98	8,92
171	405,48	348,58	455,47	32,23	7,95	722,34	568,25	838,42	64,98	9,00
137	406,12	352,44	445,92	24,48	6,03	718,41	563,96	843,92	76,22	10,61
139	406,41	359,46	470,22	33,24	8,18	750,98	590,07	854,22	101,30	13,49
38	406,61	360,31	504,52	34,96	8,60	747,65	643,27	875,17	69,33	9,27
46	406,74	368,26	467,91	29,40	7,23	730,81	583,84	814,60	77,87	10,66
189	408,18	365,90	451,77	25,79	6,32	732,22	617,37	848,11	81,43	11,12
4	412,54	364,19	475,58	33,71	8,17	723,03	568,19	845,23	93,10	12,88
208	416,51	372,37	459,21	24,75	5,94	739,62	614,14	874,40	76,13	10,29

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
84	375,80	36,96	733,66	68,73	354,11	30,39	689,61	115,00	363,12	1,20	636,42	83,13
52	377,06	11,45	720,59	26,53	360,28	16,90	672,63	74,95	366,33	12,99	615,84	73,91
172	370,88	53,35	714,03	59,79	381,44	57,98	713,84	145,97	360,57	25,25	599,48	69,16
155	382,97	17,31	754,15	37,70	372,25	43,76	687,46	88,18	367,37	21,07	659,62	79,44
55	368,83	40,01	705,19	54,54	386,01	20,82	736,24	59,22	369,74	29,38	658,83	69,21
98	401,81	18,47	728,98	36,01	361,26	28,76	690,42	77,67	375,27	48,41	638,76	101,94
70	391,83	23,65	759,84	34,36	379,62	36,62	689,26	123,27	369,94	24,98	647,50	78,68
170	398,84	38,89	787,96	74,14	382,83	29,82	726,56	69,27	361,62	16,41	641,66	67,18
197	389,43	30,83	735,07	49,23	386,26	38,54	729,45	74,80	370,88	11,48	641,62	66,17
201	389,10	44,12	696,17	81,89	394,94	23,33	700,85	72,21	365,49	12,88	639,92	75,27
31	396,13	41,88	755,27	92,41	386,76	8,17	724,81	50,76	366,84	29,95	629,05	79,45
178	396,65	20,54	752,07	32,09	387,92	15,98	728,30	84,91	375,27	28,87	663,60	85,98
15	402,42	48,04	731,31	34,71	408,18	31,75	719,07	82,62	380,41	19,13	663,08	57,07
30	414,82	17,92	764,89	43,61	399,94	37,79	708,68	54,17	378,09	33,53	631,05	104,41
16	412,56	24,38	759,19	40,25	405,55	38,99	709,16	85,42	377,09	31,51	639,33	90,15
91	397,06	18,84	769,62	35,69	421,70	29,00	782,07	77,13	384,12	17,68	637,16	58,20
83	397,19	33,60	740,29	52,91	412,36	38,59	715,18	60,05	395,30	38,43	662,13	59,13
171	400,73	30,39	754,00	57,76	412,95	34,21	701,50	84,85	402,08	39,56	708,79	40,11
137	416,10	21,73	767,11	31,69	399,44	31,21	717,55	100,66	402,81	21,38	670,58	58,06
139	427,24	24,99	827,82	30,66	419,41	29,41	774,39	85,79	372,58	13,91	650,73	83,58
38	418,17	54,89	812,56	46,24	414,98	8,52	741,49	56,16	386,67	21,00	688,89	43,59
46	434,35	31,86	785,82	31,47	398,23	10,77	747,57	68,62	387,63	19,86	659,03	70,35
189	430,98	12,91	795,30	64,87	401,64	19,35	740,38	67,03	391,91	27,45	660,98	55,74
4	417,67	42,47	768,80	101,91	421,53	34,37	715,72	104,65	398,43	24,67	684,57	66,79
208	437,27	19,54	810,37	40,52	413,49	13,03	744,71	59,34	398,76	25,46	663,77	40,49
site	401,84	35,07	757,20	58,84	394,52	33,58	720,27	79,71	378,54	26,47	651,23	68,73

b) Cell wall thickness

Fam	All sites				
	Earlywood		Latewood		
	mean	min	max	stddev	CV
172	1,798	1,558	2,395	0,226	12,551
52	1,806	1,603	1,923	0,091	5,035
155	1,831	1,550	2,223	0,173	9,438
70	1,837	1,549	2,120	0,148	8,084
84	1,839	1,592	2,100	0,138	7,524
178	1,843	1,588	2,037	0,113	6,138
98	1,843	1,661	2,258	0,170	9,209
197	1,868	1,712	2,030	0,094	5,022
170	1,869	1,656	2,193	0,165	8,846
31	1,869	1,584	2,233	0,184	9,854
55	1,886	1,697	2,133	0,119	6,313
16	1,895	1,551	2,262	0,178	9,416
201	1,897	1,433	2,397	0,219	11,531
15	1,907	1,653	2,315	0,178	9,310
30	1,920	1,595	2,383	0,220	11,453
46	1,923	1,730	2,194	0,133	6,894
91	1,933	1,705	2,303	0,160	8,275
83	1,933	1,664	2,188	0,156	8,092
4	1,954	1,720	2,169	0,155	7,936
189	1,956	1,715	2,300	0,172	8,791
137	1,979	1,784	2,178	0,113	5,733
38	1,980	1,693	2,388	0,176	8,906
171	1,982	1,649	2,233	0,166	8,368
139	1,987	1,723	2,320	0,152	7,666
208	2,008	1,729	2,264	0,150	7,451

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
172	1,785	0,202	3,199	0,270	1,876	0,316	3,311	0,772	1,733	0,155	2,692	0,419
52	1,878	0,046	3,363	0,126	1,817	0,071	3,161	0,370	1,722	0,079	2,708	0,399
155	1,889	0,095	3,478	0,249	1,865	0,239	3,175	0,450	1,738	0,147	2,880	0,513
70	1,946	0,105	3,506	0,195	1,833	0,155	3,136	0,497	1,731	0,116	2,799	0,472
84	1,899	0,136	3,417	0,356	1,811	0,182	3,219	0,557	1,808	0,094	2,901	0,375
178	1,877	0,102	3,376	0,189	1,877	0,077	3,261	0,376	1,774	0,140	2,882	0,481
98	1,953	0,067	3,279	0,261	1,737	0,086	3,065	0,347	1,840	0,244	2,913	0,639
197	1,904	0,119	3,351	0,198	1,881	0,106	3,265	0,345	1,820	0,026	2,887	0,338
170	1,945	0,170	3,610	0,392	1,909	0,187	3,385	0,467	1,753	0,075	2,874	0,269
31	1,998	0,222	3,594	0,411	1,844	0,092	3,286	0,355	1,766	0,161	2,819	0,382
55	1,895	0,149	3,327	0,249	1,940	0,115	3,410	0,358	1,821	0,072	2,983	0,387
16	1,909	0,063	3,340	0,143	1,974	0,217	3,224	0,459	1,801	0,203	2,818	0,521
201	1,982	0,261	3,282	0,437	1,964	0,154	3,236	0,389	1,744	0,176	2,786	0,423
15	1,996	0,210	3,372	0,199	1,953	0,125	3,223	0,357	1,772	0,124	2,892	0,358
30	2,076	0,220	3,567	0,469	1,910	0,125	3,168	0,196	1,773	0,218	2,777	0,610
46	2,033	0,128	3,517	0,083	1,912	0,072	3,316	0,272	1,823	0,110	2,898	0,366
91	1,917	0,143	3,383	0,255	2,057	0,147	3,532	0,420	1,824	0,115	2,814	0,307
83	1,965	0,183	3,429	0,289	1,980	0,154	3,214	0,275	1,855	0,129	2,892	0,266
4	2,011	0,190	3,514	0,517	2,009	0,144	3,305	0,474	1,844	0,066	2,962	0,328
189	2,076	0,167	3,639	0,452	1,908	0,107	3,345	0,385	1,884	0,192	2,922	0,397
137	2,034	0,121	3,521	0,156	1,937	0,120	3,257	0,450	1,965	0,098	3,024	0,324
38	2,074	0,225	3,796	0,304	2,000	0,090	3,357	0,340	1,865	0,148	3,030	0,290
171	1,983	0,212	3,527	0,439	2,021	0,157	3,283	0,454	1,932	0,142	3,121	0,443
139	2,106	0,127	3,881	0,183	2,027	0,070	3,504	0,311	1,827	0,092	2,906	0,386
208	2,164	0,058	3,739	0,235	1,971	0,110	3,346	0,351	1,888	0,114	2,884	0,204
site	1,972	0,167	3,480	0,320	1,920	0,154	3,279	0,388	1,811	0,139	2,881	0,378

c) Radial cell diameter

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
16	27,07	23,80	29,58	1,49	5,50	21,60	19,25	24,13	1,22	5,64
46	27,07	24,49	29,50	1,43	5,29	21,55	19,18	24,14	1,55	7,17
91	27,50	25,94	29,69	1,10	4,00	21,42	19,51	24,19	1,45	6,75
171	27,55	23,69	31,62	2,24	8,15	22,28	20,07	25,52	1,55	6,97
208	27,55	25,53	29,16	1,06	3,86	21,65	19,86	23,18	0,90	4,16
137	27,66	25,18	30,16	1,63	5,89	22,10	20,29	24,96	1,59	7,18
189	27,69	25,59	30,41	1,35	4,86	21,99	20,40	23,80	1,04	4,71
178	27,80	24,30	29,86	1,40	5,03	21,59	19,95	24,45	1,22	5,65
4	27,83	24,89	31,59	1,61	5,78	22,37	20,53	25,21	1,46	6,51
15	27,84	25,71	30,18	1,22	4,37	22,29	20,38	24,27	1,22	5,48
83	27,94	24,71	30,54	1,81	6,49	22,31	20,37	24,67	1,38	6,19
197	28,01	25,49	30,81	1,51	5,39	22,11	20,21	24,84	1,38	6,24
70	28,05	24,76	30,78	1,79	6,39	21,97	19,75	25,92	1,92	8,75
170	28,11	23,90	31,97	1,97	7,01	22,17	19,31	24,96	1,44	6,49
30	28,12	26,04	33,38	1,86	6,63	22,28	20,33	24,59	1,34	6,02
38	28,13	26,03	30,13	1,47	5,21	21,90	20,57	23,36	0,78	3,58
139	28,19	25,49	30,77	1,80	6,39	22,08	20,15	25,30	1,89	8,55
98	28,38	25,71	30,97	1,56	5,49	22,24	20,49	25,29	1,32	5,92
172	28,48	24,36	30,92	1,91	6,70	22,59	19,73	25,52	1,77	7,83
155	28,51	24,52	30,72	1,83	6,41	22,20	20,30	25,99	1,68	7,58
31	28,61	26,39	31,49	1,56	5,44	22,99	20,16	26,62	1,79	7,79
201	28,92	24,38	32,29	1,84	6,36	22,65	20,52	24,96	1,22	5,37
55	29,60	26,40	33,40	2,17	7,33	22,91	20,80	25,30	1,28	5,57
52	29,76	27,47	32,98	1,35	4,53	23,39	21,76	25,88	1,18	5,05
84	30,51	27,84	33,53	1,66	5,46	23,21	21,41	27,25	1,60	6,90

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
16	25,60	1,11	20,46	0,87	27,73	0,86	21,89	0,76	27,88	1,32	22,44	1,12
46	25,76	1,45	20,66	1,07	27,54	1,15	21,12	1,61	27,90	0,69	22,87	1,11
91	27,39	1,07	20,28	0,56	27,31	1,47	21,08	1,07	27,80	0,87	22,89	1,17
171	27,59	1,94	21,77	1,60	27,43	2,61	23,05	1,74	27,62	2,77	21,95	1,19
208	27,23	1,32	20,94	0,71	27,36	0,87	21,58	0,62	28,05	0,98	22,42	0,77
137	27,14	0,74	21,13	0,34	27,59	2,14	22,16	1,99	28,26	1,83	23,02	1,58
189	26,66	1,10	20,99	0,52	27,61	0,90	21,95	0,49	28,80	1,20	23,04	0,79
178	27,46	0,46	21,11	0,54	27,98	1,36	21,42	1,41	27,97	2,14	22,23	1,44
4	27,93	2,54	21,89	1,45	27,52	1,37	22,62	1,73	28,04	0,74	22,58	1,38
15	28,03	1,23	22,08	0,70	27,60	1,73	22,11	1,85	27,89	0,74	22,68	1,01
83	28,68	1,55	22,30	1,54	27,48	1,73	21,88	1,18	27,67	2,26	22,76	1,55
197	27,56	0,85	21,72	0,99	27,52	2,12	21,20	0,99	28,96	1,03	23,40	1,18
70	28,36	1,25	21,35	0,62	28,03	2,37	22,40	2,95	27,77	1,96	22,17	1,76
170	27,46	2,93	21,17	1,42	28,71	1,76	22,43	0,80	28,16	0,97	22,90	1,61
30	28,85	2,76	21,98	1,79	27,56	1,64	21,83	1,20	27,94	0,88	23,04	0,76
38	28,43	1,76	21,53	0,64	27,66	1,68	21,89	0,88	28,29	1,09	22,26	0,80
139	27,78	1,12	21,30	0,68	27,58	2,18	21,61	2,09	29,20	1,86	23,33	2,16
98	28,16	2,43	21,51	0,83	27,93	1,25	21,57	0,84	29,04	0,41	23,64	1,00
172	28,04	2,11	21,36	0,79	28,13	2,28	22,47	2,07	29,28	1,37	23,94	1,37
155	28,52	1,83	21,61	1,29	28,92	1,73	22,49	2,11	28,08	2,21	22,51	1,77
31	29,14	1,85	22,95	2,48	27,51	1,34	21,99	0,46	29,17	0,99	24,02	1,52
201	29,50	1,94	22,93	1,32	28,58	0,78	22,37	0,51	28,70	2,61	22,65	1,73
55	30,17	2,17	22,97	1,47	29,28	1,93	22,35	1,15	29,34	2,72	23,41	1,23
52	29,42	0,85	22,57	0,57	30,71	1,44	23,92	1,33	29,14	1,34	23,69	1,22
84	30,42	2,27	22,66	0,75	30,60	1,26	22,79	1,20	30,50	1,72	24,17	2,28
site	28,05	1,95	21,65	1,27	28,08	1,76	22,09	1,45	28,47	1,60	22,97	1,39

d) Tangential cell diameter

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
4	25,41	21,56	28,63	1,94	7,63	24,97	21,15	27,59	1,77	7,07
178	25,91	24,59	27,27	0,78	3,00	25,25	22,87	26,66	1,14	4,50
52	25,93	22,20	27,89	1,49	5,75	25,39	22,50	27,44	1,50	5,89
46	25,95	24,00	27,89	1,23	4,76	25,12	23,47	26,81	0,94	3,74
189	26,07	23,06	31,11	1,90	7,27	25,22	22,49	29,72	1,70	6,75
30	26,14	23,67	32,04	2,00	7,65	25,30	23,34	29,41	1,51	5,98
15	26,25	23,37	29,21	1,70	6,48	25,11	22,97	28,18	1,52	6,07
83	26,28	23,04	27,93	1,29	4,92	25,17	21,79	27,07	1,57	6,22
16	26,32	24,00	28,15	1,36	5,15	25,50	23,64	27,27	1,17	4,58
31	26,33	22,66	29,36	1,67	6,33	25,58	22,62	28,18	1,60	6,27
208	26,38	24,02	29,79	1,49	5,66	25,31	22,88	27,77	1,38	5,45
38	26,45	23,59	28,93	1,65	6,23	25,28	22,58	27,88	1,66	6,57
70	26,52	23,14	29,49	1,67	6,30	25,94	22,60	28,35	1,78	6,85
98	26,53	24,26	30,34	1,50	5,64	25,58	23,80	28,43	1,22	4,79
172	26,57	22,56	31,01	2,23	8,41	25,87	22,99	28,59	1,70	6,56
91	26,63	24,19	28,98	1,45	5,44	25,32	23,22	27,17	1,23	4,85
139	26,74	24,49	28,39	1,12	4,21	25,86	24,18	28,05	1,16	4,48
155	26,78	22,72	30,08	1,85	6,90	25,76	21,41	29,18	1,97	7,64
201	26,83	22,83	29,43	1,75	6,52	25,85	22,38	28,33	1,64	6,34
84	26,89	23,50	28,74	1,37	5,08	25,87	22,72	27,57	1,26	4,86
137	27,05	23,22	28,96	1,56	5,76	25,96	22,97	27,56	1,23	4,72
197	27,20	25,41	30,38	1,47	5,40	25,81	23,80	28,53	1,30	5,02
170	27,25	25,68	30,63	1,23	4,53	26,00	24,49	28,15	0,93	3,59
171	27,35	24,22	30,52	2,09	7,64	26,11	23,01	29,44	2,07	7,92
55	27,37	24,21	29,83	1,53	5,60	26,18	23,45	28,07	1,40	5,37

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
4	25,98	1,71	25,45	0,83	25,85	1,33	25,98	1,28	24,39	2,55	23,49	2,07
178	25,67	0,59	25,74	0,88	26,49	0,89	25,69	0,73	25,58	0,59	24,33	1,27
52	26,77	0,59	26,40	0,77	26,61	0,77	26,02	0,76	24,42	1,59	23,75	1,25
46	26,41	1,36	25,69	0,34	26,33	1,07	25,18	0,29	25,10	1,00	24,49	1,40
189	26,90	2,51	26,29	2,03	25,73	1,62	25,03	1,36	25,60	1,55	24,32	1,29
30	27,10	2,81	26,23	1,90	26,23	1,01	25,15	0,71	25,10	1,61	24,51	1,41
15	27,69	1,11	26,37	1,17	26,15	1,65	25,03	1,39	24,90	1,12	23,94	1,05
83	27,01	0,93	26,09	1,02	26,45	1,16	25,26	1,51	25,40	1,41	24,16	1,71
16	26,13	1,33	25,70	1,07	26,78	0,87	25,91	1,25	26,06	1,88	24,89	1,15
31	27,45	1,26	26,65	1,33	26,06	1,55	25,41	1,70	25,48	1,78	24,67	1,36
208	27,84	1,20	26,49	0,94	26,01	1,12	25,21	0,98	25,27	0,86	24,21	1,25
38	26,95	1,94	26,23	1,71	26,29	1,56	25,18	1,21	26,13	1,68	24,44	1,80
70	27,52	1,43	27,01	1,12	26,74	1,05	26,30	0,77	25,29	1,85	24,52	2,25
98	26,49	2,29	25,64	1,76	26,63	1,24	25,52	0,92	26,48	1,01	25,58	1,14
172	26,63	0,51	25,84	0,41	27,57	3,07	26,36	2,29	25,52	2,27	25,40	2,02
91	26,92	1,51	25,55	1,14	27,16	1,38	25,65	0,97	25,82	1,37	24,76	1,57
139	27,25	0,86	26,79	1,10	26,50	1,40	25,43	0,77	26,47	1,12	25,35	1,12
155	27,03	1,36	26,58	1,53	27,61	1,44	26,41	0,58	25,71	2,38	24,28	2,60
201	27,75	1,62	27,05	1,16	27,33	1,32	26,26	1,17	25,42	1,58	24,25	1,23
84	26,90	1,02	25,84	1,07	27,56	1,10	26,48	0,78	26,20	1,77	25,30	1,70
137	27,59	1,37	26,71	0,81	26,94	1,25	25,81	0,96	26,64	2,12	25,36	1,58
197	27,48	1,76	26,10	0,93	27,52	1,85	25,88	1,86	26,59	0,56	25,46	1,14
170	27,51	1,88	26,19	1,26	27,38	0,98	26,19	0,85	26,85	0,74	25,61	0,66
171	27,85	1,49	26,98	0,74	27,46	2,59	26,34	2,31	26,58	2,41	24,75	2,61
55	28,10	1,20	27,01	0,83	27,31	0,98	26,24	1,21	26,69	2,14	25,28	1,69
site	27,08	1,50	26,26	1,17	26,75	1,44	25,76	1,22	25,74	1,63	24,68	1,54

e) Specific fibre surface

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
208	370,16	331,17	421,65	26,25	7,09	249,47	205,61	305,17	33,98	13,62
137	373,65	342,28	406,65	19,70	5,27	251,47	215,91	302,43	30,49	12,13
139	374,01	325,70	423,62	25,55	6,83	244,07	200,94	318,28	40,30	16,51
171	374,54	333,66	441,26	30,51	8,15	248,19	199,33	299,37	31,58	12,73
38	377,01	320,22	432,97	30,29	8,03	243,96	199,49	305,37	31,12	12,76
189	379,15	324,53	424,29	29,76	7,85	252,24	196,12	320,86	35,48	14,07
4	381,34	344,09	426,56	26,66	6,99	256,44	205,48	312,32	37,37	14,57
91	382,75	325,57	429,85	28,85	7,54	253,99	206,88	317,36	36,43	14,34
83	382,96	338,94	436,88	29,20	7,63	256,91	212,07	332,01	30,81	11,99
46	385,54	339,58	420,17	23,94	6,21	254,69	223,94	309,54	33,34	13,09
30	387,18	310,27	455,07	41,11	10,62	261,03	192,27	355,36	45,85	17,56
15	388,71	324,72	441,03	31,72	8,16	260,10	220,86	329,86	31,56	12,13
55	390,40	347,41	426,27	21,68	5,55	251,64	212,53	297,56	29,73	11,81
201	390,52	310,21	502,89	43,93	11,25	265,06	212,97	372,94	44,29	16,71
16	391,37	330,15	469,07	34,16	8,73	264,09	222,91	343,88	38,48	14,57
197	393,21	364,31	425,05	17,64	4,49	258,32	224,20	300,48	29,04	11,24
31	396,61	330,63	460,42	36,52	9,21	256,63	203,50	341,03	41,85	16,31
170	397,25	338,27	442,05	31,31	7,88	252,12	204,52	313,40	35,83	14,21
84	399,22	355,86	454,73	27,55	6,90	259,93	212,91	334,11	38,78	14,92
178	399,75	363,73	458,09	23,18	5,80	259,32	220,39	334,28	36,45	14,06
98	400,90	343,36	435,56	29,24	7,29	265,64	212,27	340,80	37,62	14,16
70	401,47	349,99	467,00	30,69	7,64	261,87	216,58	335,53	43,99	16,80
155	404,18	336,45	467,85	35,51	8,78	262,04	215,85	356,17	44,01	16,79
52	405,79	383,87	450,71	19,53	4,81	263,67	220,38	325,25	36,40	13,81
172	411,81	309,62	466,43	42,11	10,23	271,38	190,18	349,22	48,45	17,85

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
208	343,75	7,20	218,49	11,40	376,04	20,82	243,01	21,36	390,68	22,02	286,92	21,24
137	365,19	21,34	228,45	9,09	381,87	20,02	251,65	30,97	373,89	18,12	274,29	29,98
139	354,91	18,41	211,33	8,60	366,61	12,34	233,14	18,98	400,51	19,79	287,74	37,12
171	375,86	39,34	231,80	24,89	366,62	28,23	249,53	31,45	382,78	26,63	267,02	35,41
38	365,24	35,48	217,47	15,01	369,65	16,89	241,99	23,23	396,15	31,10	272,43	27,00
189	358,86	26,04	230,31	27,07	386,61	19,35	244,16	26,24	391,99	35,45	282,26	34,29
4	371,73	34,63	236,23	38,89	373,52	22,72	252,62	34,60	398,78	14,15	280,47	30,45
91	385,42	28,97	238,15	16,24	360,24	22,03	231,27	24,73	402,58	21,32	292,54	30,87
83	377,77	33,34	234,44	15,54	373,71	27,84	248,73	19,46	397,40	26,38	287,57	28,51
46	366,82	22,11	230,29	4,05	385,97	14,09	244,44	18,64	403,82	21,51	289,33	33,92
30	359,13	37,72	228,73	27,18	386,56	22,37	252,30	15,73	415,85	44,48	302,07	53,54
15	373,91	33,70	238,94	13,61	377,45	21,98	253,91	28,48	414,75	24,97	287,46	30,76
55	389,22	27,64	238,51	14,98	380,62	19,79	238,40	24,13	401,35	14,75	278,01	31,34
201	375,85	45,10	246,36	34,60	375,14	29,54	247,59	31,36	420,56	46,42	301,24	47,22
16	387,33	12,00	242,25	10,69	376,71	35,76	255,21	34,27	410,07	43,97	294,81	44,94
197	387,06	23,74	240,76	12,26	391,32	19,38	248,61	25,33	401,24	4,13	285,60	26,96
31	374,20	44,18	225,35	23,29	399,53	19,39	249,20	29,27	416,11	35,03	295,35	39,55
170	384,25	34,02	226,96	22,46	388,65	34,44	241,65	29,58	418,84	14,23	287,75	24,47
84	387,93	23,27	236,94	22,12	405,61	37,52	253,85	40,22	404,10	21,65	288,99	37,33
178	394,33	18,77	239,01	9,44	391,71	13,63	247,76	25,61	413,20	31,61	291,19	44,20
98	377,89	13,18	244,21	15,93	420,46	17,29	259,77	26,33	404,36	36,94	292,95	49,57
70	379,65	18,64	229,67	10,82	401,26	31,85	259,07	44,01	423,49	27,07	296,86	43,37
155	392,59	19,57	233,44	12,46	396,98	46,79	256,19	34,48	422,97	34,15	296,49	53,71
52	391,07	8,65	236,90	7,33	402,31	15,40	252,65	24,59	423,98	17,99	301,45	33,87
172	415,09	37,82	250,84	18,33	398,13	56,38	252,05	51,49	422,21	34,87	311,25	47,41
site	377,40	29,67	233,43	19,32	385,33	28,19	248,35	27,61	406,25	28,82	289,46	35,26

f) Fibre coarseness

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
178	276,06	231,38	306,68	19,77	7,16	380,30	282,85	449,43	46,72	12,29
172	276,70	227,55	389,08	40,18	14,52	382,04	287,79	540,20	67,08	17,56
70	280,06	218,25	328,08	27,72	9,90	388,07	283,42	456,16	60,22	15,52
16	281,62	234,37	349,14	31,01	11,01	377,42	299,86	454,05	50,21	13,30
52	281,94	230,84	310,52	22,72	8,06	389,67	290,08	463,28	51,78	13,29
98	282,16	255,71	347,29	27,66	9,80	380,43	311,61	506,04	53,01	13,93
46	282,90	251,25	313,31	20,63	7,29	385,19	320,48	428,08	38,09	9,89
155	283,58	212,07	338,25	36,80	12,98	393,30	259,20	530,96	68,31	17,37
15	286,51	231,46	339,83	30,04	10,48	383,68	284,19	448,36	47,18	12,30
31	287,14	225,70	358,97	36,39	12,67	401,93	295,36	510,84	63,38	15,77
197	287,66	262,97	314,84	15,38	5,35	388,67	322,14	436,27	39,04	10,04
4	288,16	245,38	358,29	28,27	9,81	392,11	317,86	485,69	54,29	13,85
170	288,67	249,15	359,27	32,54	11,27	404,87	332,28	508,54	55,88	13,80
30	290,83	224,59	433,90	49,72	17,10	388,13	277,14	578,61	75,39	19,42
91	290,87	245,53	341,69	30,27	10,41	386,36	316,58	459,44	49,99	12,94
83	291,01	251,52	343,75	26,47	9,10	388,03	293,21	462,27	47,65	12,28
189	292,36	243,98	375,21	35,19	12,04	397,04	295,06	537,68	62,43	15,73
84	295,66	240,11	332,40	25,75	8,71	401,41	303,08	477,90	49,01	12,21
201	295,88	189,95	386,08	44,53	15,05	389,56	252,58	490,60	62,34	16,00
55	300,09	254,97	338,45	25,23	8,41	409,18	335,16	470,88	49,90	12,20
38	300,12	245,95	365,16	33,18	11,06	407,79	315,49	516,87	58,07	14,24
137	300,30	257,62	343,26	24,95	8,31	400,78	308,30	448,09	42,35	10,57
208	300,32	255,89	339,84	27,63	9,20	396,71	318,66	468,80	51,64	13,02
139	302,76	255,70	346,82	24,08	7,95	415,22	312,98	518,88	54,09	13,03
171	302,97	248,26	373,57	41,45	13,68	412,35	308,98	528,40	70,27	17,04

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
178	277,59	14,77	403,58	26,56	285,05	14,88	393,95	30,58	265,55	26,21	343,36	58,17
172	271,18	18,14	388,83	21,81	291,68	60,74	413,40	89,23	267,22	34,64	343,90	64,87
70	302,86	14,45	433,35	21,92	279,81	19,43	393,29	41,02	257,52	28,60	337,58	68,90
16	273,73	12,19	391,88	18,97	299,02	34,90	394,84	50,32	272,10	37,80	345,55	63,41
52	294,79	9,56	425,14	17,24	292,22	11,59	409,14	36,43	258,80	23,95	334,75	44,06
98	297,84	31,37	399,14	46,27	264,95	8,95	374,10	28,92	283,70	30,53	368,05	78,60
46	292,50	17,22	413,58	12,56	286,70	20,80	391,57	18,52	269,50	20,07	350,42	44,80
155	293,59	27,53	432,73	56,73	294,85	40,10	401,11	50,02	262,29	39,03	346,06	76,18
15	307,50	23,82	417,95	27,95	290,99	25,42	387,50	38,56	261,05	23,62	345,59	47,13
31	314,73	40,04	453,86	53,63	276,34	28,02	400,39	51,61	270,36	28,23	351,55	44,43
197	292,38	20,21	410,53	22,48	287,86	17,90	393,77	41,66	282,73	6,41	361,71	39,43
4	300,43	38,17	420,04	54,58	295,20	16,16	408,74	40,64	268,84	19,05	347,57	43,42
170	297,11	39,53	432,93	52,68	298,72	36,16	422,71	59,64	270,19	13,93	358,99	24,13
30	324,73	66,76	441,03	87,67	284,98	9,82	383,84	14,55	262,78	40,43	339,50	74,29
91	289,54	30,22	394,86	35,99	310,15	28,62	418,56	42,52	272,90	24,57	345,65	46,74
83	303,79	28,62	424,86	35,21	295,61	19,61	391,67	30,07	273,61	25,29	347,55	45,19
189	308,74	44,04	433,70	68,10	282,91	22,69	401,87	43,93	285,42	37,04	355,54	56,69
84	303,49	16,88	424,96	39,92	295,52	31,39	409,46	51,93	287,98	30,01	369,83	45,77
201	316,41	47,58	423,73	56,12	305,74	31,00	407,54	45,45	265,49	43,73	337,42	55,93
55	308,31	17,92	430,44	30,41	306,11	23,04	423,88	47,18	285,84	31,49	373,23	55,81
38	317,73	33,55	456,34	46,65	300,02	30,79	404,83	44,63	282,61	31,75	362,20	45,60
137	307,56	21,90	430,27	14,68	292,99	24,12	396,85	40,03	300,35	31,37	375,23	50,39
208	329,32	13,10	445,95	23,49	291,66	25,22	399,95	40,16	280,00	14,26	344,24	26,16
139	319,86	20,43	467,70	30,45	304,07	19,80	417,00	18,31	284,34	20,72	360,97	43,01
171	306,63	46,98	439,65	64,49	308,70	47,23	417,06	66,52	291,22	35,60	372,32	80,83
site	302,09	31,40	425,48	43,43	292,87	27,54	402,28	42,41	274,36	28,44	352,59	50,44

g) Number of cells per mm²

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
84	1259,0	1105,5	1540,1	111,4	8,8	1756,9	1528,5	1990,1	135,7	7,7
55	1277,9	1024,2	1592,7	154,1	12,1	1757,7	1471,5	2041,6	147,5	8,4
52	1332,3	1195,0	1627,5	124,4	9,3	1765,9	1591,0	1937,0	118,8	6,7
201	1334,2	1085,4	1833,4	172,2	12,9	1792,2	1549,3	2219,5	168,1	9,4
170	1352,9	1055,7	1534,7	129,2	9,5	1817,0	1584,6	1995,7	133,0	7,3
197	1353,9	1092,7	1535,5	122,4	9,0	1835,5	1604,1	2051,5	139,3	7,6
155	1361,1	1131,4	1845,3	180,0	13,2	1846,9	1546,7	2376,1	200,4	10,9
31	1369,0	1109,1	1625,0	140,6	10,3	1791,2	1364,3	2053,6	176,8	9,9
139	1370,3	1172,3	1625,4	109,4	8,0	1849,4	1627,7	2064,9	134,5	7,3
98	1370,7	1123,4	1521,5	117,1	8,5	1848,6	1654,4	2030,1	114,6	6,2
172	1376,5	1102,5	1740,2	180,4	13,1	1813,1	1503,8	2202,0	191,1	10,5
137	1378,2	1208,0	1677,3	138,1	10,0	1825,1	1624,0	2056,9	133,4	7,3
171	1382,6	1103,3	1729,0	199,9	14,5	1810,3	1398,0	2167,7	218,5	12,1
38	1388,4	1186,3	1550,1	141,2	10,2	1883,4	1680,3	2088,8	138,6	7,4
70	1390,3	1206,1	1688,0	133,6	9,6	1852,1	1512,5	2221,0	184,8	10,0
91	1409,2	1203,0	1559,6	110,6	7,8	1924,0	1688,3	2153,4	132,7	6,9
83	1409,4	1257,6	1794,0	144,1	10,2	1866,5	1615,3	2348,1	184,1	9,9
30	1411,5	962,8	1622,7	164,2	11,6	1859,7	1465,7	2053,9	156,4	8,4
15	1412,1	1167,7	1626,4	130,9	9,3	1870,6	1628,0	2087,4	147,8	7,9
208	1418,7	1252,4	1573,2	88,7	6,3	1902,9	1768,7	2107,7	87,9	4,6
178	1428,8	1312,2	1699,5	96,5	6,8	1919,2	1775,2	2225,5	124,7	6,5
189	1433,2	1174,0	1666,6	136,6	9,5	1895,5	1616,6	2096,7	129,6	6,8
16	1446,4	1282,8	1722,4	120,9	8,4	1895,3	1729,0	2119,1	120,7	6,4
4	1460,4	1150,0	1762,1	146,3	10,0	1879,0	1627,8	2273,2	161,3	8,6
46	1462,9	1253,7	1668,1	104,9	7,2	1932,9	1757,7	2075,1	99,1	5,1

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
84	1259,6	126,6	1771,9	116,4	1220,4	41,3	1725,8	82,2	1297,1	148,5	1773,1	205,9
55	1219,3	134,1	1678,7	124,2	1280,5	98,2	1784,4	135,6	1333,8	217,6	1810,1	173,9
52	1297,0	57,0	1739,8	83,7	1253,4	58,6	1677,5	95,1	1446,5	147,8	1880,4	79,6
201	1257,9	139,0	1679,1	137,4	1318,4	101,6	1760,0	85,9	1426,3	236,4	1937,4	170,4
170	1380,8	188,2	1866,6	167,6	1306,2	117,8	1769,8	92,1	1371,7	70,6	1814,7	139,5
197	1363,9	128,1	1824,4	129,3	1364,6	177,8	1891,9	186,8	1333,2	60,3	1790,2	98,0
155	1346,1	149,7	1828,9	155,3	1288,2	127,8	1750,2	149,8	1449,0	240,9	1961,6	255,9
31	1287,0	131,8	1704,8	228,5	1435,9	144,7	1864,0	127,2	1384,1	128,9	1804,9	157,5
139	1358,5	56,7	1812,9	109,0	1417,8	166,7	1905,0	167,2	1334,5	79,3	1830,2	132,4
98	1390,5	173,4	1882,8	145,6	1381,9	113,3	1885,9	87,8	1339,6	57,3	1777,1	86,5
172	1381,6	126,1	1866,7	76,1	1353,8	255,5	1788,1	259,2	1394,2	177,8	1784,5	222,5
137	1371,0	64,6	1821,9	41,6	1383,3	158,4	1826,0	169,2	1380,3	193,3	1827,5	178,5
171	1347,0	146,1	1771,3	141,2	1384,6	264,2	1723,7	215,3	1424,5	217,1	1967,2	265,6
38	1351,0	169,8	1830,9	145,7	1423,6	154,7	1886,3	131,3	1390,7	117,0	1932,9	149,0
70	1317,6	64,1	1791,1	48,0	1379,2	95,9	1791,9	198,1	1474,3	183,2	1973,2	224,6
91	1400,7	112,1	1985,0	117,4	1389,1	129,8	1918,6	63,8	1437,7	108,5	1868,5	187,8
83	1327,1	63,4	1775,7	126,5	1420,8	114,4	1874,9	102,7	1480,4	201,5	1948,8	270,6
30	1338,6	228,0	1811,4	236,6	1424,2	118,4	1880,6	116,3	1471,8	130,1	1887,0	107,9
15	1322,7	94,1	1777,2	105,8	1426,2	159,6	1885,5	184,2	1487,3	91,5	1949,0	111,6
208	1360,4	87,3	1847,9	71,9	1445,6	99,9	1906,6	43,4	1450,1	59,7	1954,1	113,7
178	1457,5	49,0	1897,7	99,2	1385,2	70,5	1889,8	98,0	1443,8	146,7	1970,1	173,5
189	1441,6	167,4	1888,6	159,9	1446,4	130,7	1899,0	99,8	1411,5	139,0	1898,8	152,1
16	1527,8	130,2	1968,3	133,7	1385,4	76,0	1824,6	72,8	1426,0	122,4	1892,9	122,1
4	1424,3	173,3	1863,5	103,6	1445,6	86,6	1783,8	126,4	1511,2	179,7	1989,6	193,5
46	1505,9	115,4	1940,1	111,4	1416,2	107,0	1947,9	109,3	1466,6	93,1	1910,8	95,1
site	1361,4	138,2	1825,1	142,7	1375,1	137,7	1833,7	143,1	1414,6	147,2	1884,7	168,5

h) Earlywood and latewood width

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
16	35,16	17,15	51,93	10,08	28,66	7,00	2,98	12,28	2,87	41,04
4	35,83	19,65	53,38	9,67	26,99	8,57	3,98	20,75	3,89	45,40
30	36,25	18,78	55,33	10,85	29,93	7,51	3,68	13,90	2,78	37,00
139	37,32	22,40	59,05	9,65	25,87	7,96	3,23	11,53	2,14	26,94
171	37,81	13,35	64,58	14,91	39,43	7,98	4,85	14,08	2,58	32,36
38	38,46	24,00	60,43	12,09	31,45	8,82	5,35	13,75	2,47	28,01
91	39,56	21,15	54,13	9,34	23,62	7,92	5,18	11,13	1,65	20,76
70	39,78	19,43	55,48	11,82	29,73	7,68	3,50	10,70	2,16	28,14
52	39,97	11,98	65,55	14,59	36,50	7,96	5,30	12,68	2,06	25,84
137	40,18	16,78	69,20	14,00	34,85	8,73	3,98	14,43	2,76	31,63
189	40,82	23,35	62,20	12,42	30,42	8,88	6,23	16,35	2,61	29,36
46	41,05	12,33	61,00	12,63	30,77	7,43	3,35	12,33	2,12	28,51
15	41,35	17,93	65,45	11,37	27,50	9,81	5,73	16,93	3,42	34,86
83	41,76	22,70	61,70	12,21	29,25	9,14	5,05	17,45	3,06	33,48
208	41,92	23,65	60,90	12,18	29,06	9,02	3,08	15,43	2,95	32,69
178	42,71	21,08	62,78	12,97	30,37	9,07	5,68	15,10	2,81	30,93
155	42,95	23,20	75,63	15,75	36,67	8,38	4,65	17,05	2,85	34,00
98	44,41	16,60	72,95	19,27	43,38	8,73	3,33	15,83	3,59	41,14
197	45,60	23,60	88,40	17,94	39,35	8,31	4,58	14,43	3,11	37,47
170	45,92	20,08	61,08	12,54	27,31	9,82	5,28	16,18	3,16	32,22
31	46,92	23,73	93,68	17,72	37,76	8,79	4,88	18,48	3,32	37,72
55	47,02	25,90	76,80	16,60	35,30	9,67	5,80	16,80	3,00	31,01
84	47,20	24,88	69,75	13,41	28,40	8,87	4,83	13,93	2,74	30,87
201	48,68	18,75	77,95	16,51	33,91	9,26	4,18	19,18	3,71	40,14
172	49,05	22,88	72,80	16,48	33,60	9,05	4,95	15,45	3,21	35,49

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
16	25,80	7,93	4,56	1,96	40,80	8,74	8,12	2,29	38,88	7,05	8,31	2,94
4	34,53	12,39	6,87	2,00	40,33	7,56	11,11	5,90	32,64	8,75	7,72	1,24
30	35,77	8,68	6,66	1,08	35,25	16,67	7,26	3,98	37,74	7,38	8,61	2,74
139	34,82	7,02	6,95	2,78	35,58	9,73	8,27	2,10	41,58	12,16	8,66	1,39
171	42,24	15,03	8,02	1,91	31,93	14,39	7,15	2,70	39,64	17,07	8,96	3,44
38	40,28	13,08	8,05	1,12	35,63	14,83	8,33	2,32	39,47	10,27	10,09	3,42
91	43,72	9,19	7,92	2,35	38,47	10,41	7,65	1,79	36,49	8,83	8,21	0,72
70	46,77	9,69	8,60	2,15	34,46	11,41	6,85	2,39	38,10	12,85	7,60	2,03
52	38,70	15,14	7,35	1,84	48,48	6,44	8,57	2,46	32,74	17,79	7,98	2,10
137	35,26	7,91	8,09	1,40	44,85	19,42	9,98	4,15	40,42	13,75	8,12	2,12
189	36,29	11,90	8,19	1,67	40,98	9,52	7,79	1,00	45,19	16,06	10,65	3,74
46	31,26	12,73	6,71	2,68	52,52	7,56	8,48	2,21	39,39	7,18	7,10	1,22
15	40,95	5,71	11,26	4,82	46,01	11,89	9,37	2,61	37,11	15,13	8,79	2,58
83	48,02	13,68	8,03	1,96	37,36	8,33	10,37	4,40	39,89	13,71	9,03	2,47
208	40,54	13,89	7,23	2,41	40,26	11,13	9,95	1,84	44,96	13,60	9,89	3,90
178	40,13	8,84	8,62	1,47	43,07	15,71	8,64	3,83	44,94	15,79	9,96	3,04
155	38,56	13,88	7,17	2,18	52,83	20,92	9,84	4,26	37,48	7,39	8,13	0,97
98	40,67	25,33	6,84	2,84	46,77	15,37	8,62	2,44	45,79	19,86	10,75	4,65
197	47,99	16,40	8,89	4,63	43,69	25,98	6,37	1,09	45,12	13,06	9,67	1,98
170	38,81	14,53	8,18	3,51	51,90	7,18	10,88	3,92	47,05	13,35	10,40	1,47
31	50,93	25,02	9,59	5,00	45,06	14,71	7,56	2,09	44,79	15,03	9,23	2,49
55	50,11	19,69	9,89	4,11	50,24	15,85	9,86	3,58	40,71	15,83	9,25	1,17
84	42,77	12,25	8,18	3,35	52,98	15,22	9,78	2,25	45,86	13,38	8,65	2,88
201	46,87	21,38	9,45	5,86	49,15	4,31	9,15	1,61	50,02	21,71	9,17	3,36
172	50,11	19,61	9,92	3,03	50,34	18,73	8,99	4,52	46,69	14,30	8,24	2,17
site	40,87	14,49	8,05	3,01	43,56	13,96	8,76	3,05	41,32	13,14	8,92	2,52

i) Earlywood and latewood proportion

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
4	0,806	0,649	0,875	0,061	7,504	0,193	0,125	0,351	0,061	31,494
15	0,808	0,735	0,849	0,037	4,551	0,192	0,151	0,265	0,037	19,191
38	0,808	0,728	0,867	0,042	5,163	0,192	0,133	0,272	0,042	21,781
171	0,814	0,734	0,898	0,055	6,795	0,186	0,102	0,266	0,055	29,835
189	0,816	0,713	0,864	0,044	5,349	0,184	0,136	0,287	0,044	23,765
83	0,817	0,655	0,867	0,053	6,500	0,183	0,133	0,345	0,053	29,003
52	0,817	0,614	0,884	0,077	9,483	0,183	0,116	0,386	0,077	42,361
137	0,817	0,760	0,882	0,031	3,741	0,183	0,118	0,240	0,031	16,749
178	0,818	0,697	0,890	0,057	6,915	0,182	0,110	0,303	0,057	31,051
55	0,821	0,674	0,889	0,062	7,534	0,179	0,111	0,326	0,062	34,480
208	0,822	0,714	0,885	0,044	5,380	0,178	0,115	0,286	0,044	24,766
139	0,822	0,773	0,896	0,036	4,436	0,178	0,104	0,227	0,036	20,552
170	0,823	0,778	0,884	0,033	4,021	0,177	0,116	0,222	0,033	18,660
98	0,828	0,666	0,886	0,054	6,565	0,172	0,114	0,334	0,054	31,640
30	0,828	0,770	0,878	0,031	3,778	0,172	0,122	0,230	0,031	18,246
91	0,828	0,740	0,907	0,041	4,938	0,172	0,093	0,260	0,041	23,851
155	0,832	0,751	0,882	0,039	4,740	0,168	0,118	0,249	0,039	23,400
201	0,835	0,647	0,899	0,059	7,083	0,165	0,101	0,353	0,059	35,906
70	0,836	0,791	0,886	0,029	3,418	0,164	0,114	0,209	0,029	17,370
16	0,837	0,774	0,882	0,031	3,644	0,163	0,118	0,226	0,031	18,781
84	0,838	0,737	0,897	0,043	5,074	0,162	0,103	0,263	0,043	26,332
31	0,840	0,780	0,879	0,028	3,288	0,160	0,121	0,220	0,028	17,236
197	0,840	0,746	0,927	0,042	5,052	0,160	0,073	0,254	0,042	26,573
172	0,841	0,775	0,892	0,037	4,359	0,159	0,108	0,225	0,037	23,107
46	0,842	0,786	0,891	0,030	3,605	0,158	0,109	0,214	0,030	19,250

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
4	0,831	0,027	0,169	0,027	0,791	0,084	0,209	0,084	0,797	0,062	0,200	0,063
15	0,792	0,052	0,208	0,052	0,831	0,011	0,169	0,011	0,801	0,030	0,199	0,030
38	0,825	0,039	0,175	0,039	0,804	0,045	0,196	0,045	0,796	0,044	0,204	0,044
171	0,832	0,057	0,168	0,057	0,808	0,044	0,192	0,044	0,801	0,075	0,199	0,075
189	0,808	0,055	0,192	0,055	0,836	0,035	0,165	0,035	0,805	0,042	0,195	0,042
83	0,856	0,009	0,144	0,009	0,784	0,075	0,216	0,075	0,811	0,031	0,189	0,031
52	0,833	0,047	0,167	0,047	0,849	0,042	0,151	0,042	0,769	0,112	0,231	0,112
137	0,811	0,028	0,189	0,028	0,816	0,019	0,184	0,019	0,825	0,045	0,175	0,045
178	0,819	0,036	0,181	0,036	0,830	0,046	0,170	0,046	0,805	0,086	0,195	0,086
55	0,824	0,087	0,176	0,087	0,836	0,035	0,164	0,035	0,802	0,062	0,198	0,062
208	0,849	0,030	0,151	0,030	0,795	0,055	0,205	0,055	0,821	0,033	0,179	0,033
139	0,836	0,049	0,164	0,049	0,809	0,025	0,191	0,025	0,822	0,034	0,178	0,034
170	0,823	0,041	0,177	0,041	0,832	0,035	0,168	0,035	0,814	0,026	0,186	0,026
98	0,843	0,031	0,157	0,031	0,842	0,023	0,158	0,023	0,800	0,085	0,200	0,085
30	0,841	0,020	0,159	0,020	0,827	0,042	0,173	0,042	0,817	0,030	0,183	0,030
91	0,846	0,035	0,154	0,035	0,829	0,051	0,171	0,051	0,810	0,035	0,190	0,035
155	0,837	0,049	0,163	0,049	0,839	0,040	0,161	0,040	0,818	0,033	0,182	0,033
201	0,823	0,104	0,177	0,104	0,844	0,014	0,156	0,014	0,839	0,030	0,161	0,030
70	0,845	0,025	0,155	0,025	0,835	0,018	0,165	0,018	0,827	0,042	0,173	0,042
16	0,852	0,023	0,149	0,023	0,833	0,039	0,167	0,039	0,828	0,029	0,172	0,029
84	0,839	0,040	0,161	0,040	0,835	0,064	0,165	0,064	0,842	0,024	0,158	0,024
31	0,841	0,024	0,159	0,024	0,854	0,023	0,146	0,023	0,825	0,032	0,175	0,032
197	0,850	0,032	0,150	0,032	0,855	0,047	0,145	0,047	0,817	0,044	0,183	0,044
172	0,825	0,050	0,175	0,050	0,852	0,029	0,148	0,029	0,848	0,030	0,152	0,030
46	0,820	0,032	0,180	0,032	0,861	0,027	0,139	0,027	0,846	0,019	0,154	0,019
site	0,832	0,044	0,168	0,044	0,829	0,043	0,171	0,043	0,816	0,048	0,184	0,048

j) Microfibril angle (MFA)

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
139	17,00	12,69	27,13	3,75	22,06	16,10	12,50	23,53	3,14	19,50
46	17,12	10,28	19,97	2,26	13,22	16,00	10,16	19,50	2,15	13,42
137	17,60	14,20	21,63	1,92	10,92	16,77	13,14	21,14	2,41	14,35
31	17,74	11,55	26,11	4,49	25,29	16,75	11,47	23,78	4,20	25,06
171	18,20	14,00	24,43	3,20	17,56	16,88	12,44	23,82	3,47	20,54
197	18,72	10,95	24,16	3,62	19,34	17,59	10,39	22,70	3,65	20,75
170	18,96	12,36	26,18	3,40	17,93	18,31	12,57	25,87	3,37	18,39
55	19,58	12,76	30,68	4,34	22,19	18,71	12,54	33,06	4,81	25,72
52	19,61	11,80	29,02	4,80	24,50	18,62	10,43	28,48	5,10	27,40
201	19,66	12,69	25,87	3,52	17,90	19,01	13,09	29,89	4,27	22,44
16	19,84	15,52	26,26	3,16	15,92	18,81	14,47	24,27	3,16	16,83
172	19,99	12,60	26,07	4,30	21,49	19,10	13,06	24,88	3,66	19,15
83	20,02	14,34	34,44	6,11	30,51	19,13	12,84	33,75	6,44	33,66
178	20,37	14,61	26,74	3,89	19,11	19,34	13,96	23,56	3,20	16,54
70	20,48	14,43	29,88	4,23	20,65	19,95	13,40	29,61	4,07	20,39
84	20,56	12,79	31,13	5,26	25,56	19,67	11,73	31,14	5,13	26,11
155	20,59	14,81	30,63	4,45	21,61	19,46	13,40	28,81	4,26	21,87
208	20,81	14,62	26,98	3,55	17,06	19,70	13,86	25,29	3,29	16,69
189	20,83	13,36	25,82	3,79	18,19	19,85	12,63	24,18	3,52	17,71
15	21,14	13,64	29,56	5,07	24,00	20,21	13,25	29,06	4,98	24,64
38	21,44	13,41	30,64	4,89	22,79	20,15	12,84	28,66	4,25	21,07
30	21,52	12,69	30,44	4,74	22,03	20,75	12,08	27,62	4,46	21,49
4	21,53	14,03	32,82	4,78	22,21	20,18	13,20	33,39	5,00	24,76
91	22,55	15,42	32,28	5,14	22,81	21,23	14,67	29,81	4,68	22,07
98	22,67	13,02	29,68	5,29	23,36	21,70	12,66	32,98	5,36	24,70

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
139	15,67	2,63	15,40	3,03	15,50	1,64	14,69	1,34	19,84	4,96	18,22	3,86
46	18,04	1,68	16,96	2,05	17,85	0,99	16,81	0,80	15,46	2,99	14,22	2,32
137	18,77	2,09	18,62	2,37	16,91	1,61	15,87	2,42	17,13	1,85	15,82	1,54
31	17,69	6,56	17,03	5,73	16,26	3,37	14,51	2,86	19,29	3,22	18,70	3,09
171	18,76	3,99	17,58	4,49	18,75	3,45	17,26	3,78	16,83	1,91	15,54	1,68
197	20,51	3,25	19,29	3,47	18,37	3,84	17,07	3,85	17,30	3,73	16,40	3,74
170	18,57	5,02	18,09	4,94	19,54	1,23	18,72	0,89	18,77	3,62	18,11	3,76
55	21,98	4,91	21,16	6,68	18,42	5,01	17,33	4,47	18,34	2,46	17,65	2,29
52	22,59	5,43	21,47	5,49	15,86	3,66	14,32	3,33	20,37	2,91	20,08	3,74
201	19,90	3,10	19,76	5,85	19,60	5,25	19,11	4,46	19,48	2,45	18,16	2,83
16	18,55	2,14	17,15	2,64	19,33	2,93	19,13	3,05	21,63	3,92	20,14	3,61
172	21,14	3,53	21,05	3,20	20,34	5,31	19,04	4,27	18,49	4,40	17,21	3,03
83	19,57	4,48	18,30	4,04	20,40	6,17	20,56	7,78	20,10	8,49	18,53	8,03
178	22,55	2,49	21,34	1,94	17,79	2,56	17,12	2,21	20,77	5,08	19,57	3,99
70	19,04	2,72	18,38	2,85	20,06	3,31	19,88	2,64	22,33	6,09	21,60	6,03
84	22,55	5,54	21,56	5,77	20,12	6,15	19,42	5,87	19,00	4,46	18,03	4,08
155	20,27	5,45	19,28	5,53	20,03	2,08	18,99	1,98	21,45	5,82	20,13	5,29
208	20,24	3,15	19,11	3,17	20,38	3,45	19,92	3,00	21,81	4,51	20,08	4,25
189	22,41	4,02	21,53	3,71	18,86	4,87	17,85	4,20	21,23	1,50	20,18	1,78
15	23,43	5,59	23,04	5,22	20,67	3,72	19,20	3,37	19,34	5,84	18,39	5,73
38	21,57	3,62	19,69	2,54	17,92	3,52	17,34	3,32	24,84	5,30	23,42	4,71
30	22,12	4,55	21,42	4,43	20,97	5,58	20,48	5,65	21,46	5,10	20,36	4,16
4	19,53	2,92	18,57	2,55	24,50	6,79	23,40	7,22	20,57	2,88	18,58	3,06
91	26,37	4,62	25,00	3,98	17,43	2,34	16,28	1,81	23,85	3,56	22,42	2,75
98	23,70	4,48	22,73	3,99	23,37	6,16	21,52	5,04	20,93	5,86	20,86	7,55
site	20,62	4,35	19,74	4,38	19,17	4,26	18,23	4,19	20,05	4,51	18,92	4,33

k) Modulus of elasticity (MOE)

Fam	All sites									
	Earlywood					Latewood				
	mean	min	max	stddev	CV	mean	min	max	stddev	CV
98	8,275	5,179	12,746	2,098	25,351	10,309	6,515	15,409	2,275	22,070
84	8,722	4,557	11,931	2,242	25,702	11,019	6,090	15,873	2,784	25,267
172	8,799	5,743	13,938	2,336	26,548	10,900	8,273	15,282	1,906	17,483
52	8,957	6,629	11,346	1,429	15,951	11,128	8,166	13,994	2,048	18,404
91	9,025	5,174	12,460	2,080	23,051	11,258	7,917	14,355	2,244	19,933
70	9,063	5,400	11,787	1,960	21,626	10,822	7,153	13,835	2,118	19,573
155	9,073	5,092	11,674	1,898	20,915	11,548	6,669	14,262	1,985	17,193
55	9,074	5,741	13,251	1,995	21,990	11,786	6,073	15,464	2,283	19,366
30	9,100	6,589	13,049	1,963	21,568	10,769	7,796	14,376	2,025	18,807
15	9,189	6,200	12,304	1,694	18,437	11,377	7,772	15,496	2,066	18,161
201	9,212	7,451	12,657	1,425	15,465	11,471	8,387	14,991	1,914	16,686
189	9,264	7,567	11,958	1,482	16,003	11,423	9,367	13,941	1,517	13,281
16	9,497	6,558	11,266	1,477	15,550	11,369	7,951	13,822	1,558	13,702
178	9,517	6,207	12,454	1,744	18,328	11,566	8,494	15,156	1,661	14,363
83	9,574	4,496	13,224	2,480	25,905	11,879	5,641	16,255	3,077	25,905
4	9,577	6,140	13,937	2,063	21,539	11,769	6,589	16,622	2,953	25,094
197	9,584	7,766	13,151	1,338	13,958	12,205	9,007	16,432	1,617	13,249
38	9,652	5,820	12,930	2,201	22,802	12,145	8,456	15,086	1,917	15,783
170	9,768	6,602	14,509	1,979	20,255	12,540	8,339	15,847	1,884	15,025
208	10,087	7,481	12,366	1,347	13,357	12,351	9,446	15,584	1,507	12,203
31	10,303	6,196	14,582	2,410	23,396	12,695	8,316	17,089	2,398	18,889
171	10,504	6,826	12,621	1,598	15,215	13,160	9,124	16,929	2,293	17,424
137	10,602	9,480	12,501	0,857	8,086	13,010	11,036	16,137	1,436	11,041
46	10,858	8,870	14,574	1,406	12,947	13,290	11,414	17,046	1,443	10,858
139	11,012	6,954	13,376	1,713	15,558	13,484	10,768	15,466	1,469	10,895

Fam	E560A1				E560A2				E560A3			
	Earlywood		Latewood		Earlywood		Latewood		Earlywood		Latewood	
	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev	mean	stddev
98	8,284	0,896	10,045	1,584	7,832	3,022	10,513	2,865	8,707	2,233	10,370	2,694
84	8,414	2,621	10,173	2,880	8,465	2,648	10,895	3,321	9,287	1,762	11,988	2,391
172	8,290	1,801	10,178	1,756	9,036	3,590	11,333	2,728	9,071	1,575	11,188	1,094
52	8,359	1,829	10,091	1,931	9,594	1,252	12,920	1,147	8,918	1,130	10,373	1,888
91	7,703	1,796	9,841	2,236	11,257	0,940	13,650	0,475	8,116	1,262	10,282	1,245
70	9,630	1,250	11,742	1,514	9,084	2,005	10,351	2,335	8,474	2,651	10,372	2,524
155	9,538	2,155	11,697	2,144	8,828	1,494	11,669	1,084	8,853	2,307	11,278	2,808
55	7,880	1,811	10,093	2,543	10,008	2,454	12,788	1,988	9,336	1,294	12,478	1,543
30	9,310	2,130	10,605	2,263	9,235	2,349	10,687	2,495	8,754	1,788	11,014	1,700
15	8,541	1,622	9,903	1,486	9,429	0,992	11,776	1,290	9,595	2,372	12,452	2,590
201	9,183	1,323	10,595	1,955	9,532	2,034	12,032	2,004	8,921	0,990	11,787	1,874
189	9,152	1,697	10,735	1,456	9,755	1,816	11,791	2,044	8,884	1,009	11,744	0,933
16	10,039	1,021	11,417	1,313	9,808	0,987	11,769	1,224	8,645	2,055	10,922	2,196
178	9,141	1,313	10,967	1,027	10,361	1,564	12,675	1,481	9,048	2,266	11,057	2,026
83	9,352	1,930	11,740	2,075	9,383	2,468	10,984	3,493	9,987	3,375	12,914	3,778
4	10,053	1,320	12,169	2,581	8,860	3,029	10,528	3,811	9,818	1,725	12,609	2,517
197	8,923	1,067	11,207	1,295	9,624	1,028	12,482	0,995	10,205	1,743	12,926	2,120
38	10,026	2,149	12,301	1,751	10,830	1,821	13,342	1,382	8,100	2,024	10,791	1,942
170	10,440	2,852	12,661	2,727	9,365	1,036	12,256	1,494	9,500	1,906	12,704	1,613
208	10,463	0,930	12,360	1,302	10,141	1,462	12,190	1,214	9,657	1,715	12,503	2,173
31	10,744	3,883	12,696	3,607	10,843	1,069	13,742	1,380	9,322	1,519	11,647	1,571
171	10,142	2,349	12,789	3,169	10,293	1,368	12,634	1,987	11,221	0,490	14,281	1,326
137	10,490	0,702	12,157	1,185	10,462	0,732	12,862	1,079	10,855	1,193	14,010	1,570
46	10,909	1,337	12,603	1,267	10,380	0,636	13,371	1,126	11,285	2,051	13,896	1,832
139	11,816	0,937	13,564	1,116	11,981	1,030	14,629	0,912	9,240	1,559	12,259	1,398
site	9,473	1,950	11,373	2,132	9,775	1,918	12,155	2,123	9,337	1,864	11,895	2,180

Appendix 3

Variance components (tables)

The following tables include variance components and their associated errors of investigated wood traits. The estimates are based on cumulative area-weighted ring data and result from a statistical model including only site and family effects (equation 2.3). Variance components are shown for the earlywood and the latewood as well as the entire ring combining both tissues. Additionally, the probability of the Wald Z-test is given for the site and family effect.

- a) Wood density
- b) Cell wall thickness
- c) Radial cell diameter
- d) Tangential cell diameter
- e) Specific fibre surface
- f) Fibre coarseness
- g) Number of cells per mm²
- h) Increment, based on ring width
- i) Earlywood and latewood proportion
- j) Microfibril angle (MFA)
- k) Modulus of elasticity (MOE)

a) Wood density

		Whole ring					
ring	estimate	Site error	Prob Z	Fam estimate	Fam error	Prob Z	Residual estimate error
1	0			225.73	153.77	0.0711	4492.41
2	130.71	155.49	0.2003	235.70	129.05	0.0339	3056.74
3	143.13	163.58	0.1908	293.83	134.51	0.0145	2513.64
4	218.55	236.21	0.1774	182.96	96.49	0.0290	2198.33
5	257.90	272.61	0.1721	202.65	94.57	0.0161	1825.16
6	219.59	231.98	0.1719	205.03	89.33	0.0109	1525.97
7	179.16	190.18	0.1731	202.36	85.25	0.0088	1356.53
8	179.08	189.96	0.1729	201.30	84.67	0.0087	1348.25
9	191.59	202.39	0.1719	210.05	87.04	0.0079	1324.88
10	187.12	197.08	0.1712	228.13	91.11	0.0061	1270.17
11	173.59	183.74	0.1724	252.51	97.17	0.0047	1216.49
12	201.92	211.30	0.1696	244.56	94.67	0.0049	1177.92
13	256.55	266.92	0.1682	246.05	95.10	0.0049	1171.24
14	274.98	286.92	0.1689	278.20	107.18	0.0047	1220.49
15	322.71	336.21	0.1686	308.46	117.52	0.0043	1195.76
16	317.25	333.80	0.1710	321.85	126.37	0.0054	1256.29
17	296.44	321.66	0.1784	324.75	136.12	0.0085	1331.47
18	363.08	403.70	0.1842	389.21	162.68	0.0084	1301.66
19	52.37	105.24	0.3094	297.49	169.11	0.0393	1440.16
20	148.71	340.03	0.3309	220.43	227.31	0.1661	1643.44
core	274.08	283.94	0.1672	257.22	98.18	0.0044	1222.77
ring	estimate	Site error	Prob Z	Fam estimate	Fam error	Prob Z	Residual estimate error
1	0			620.14	313.60	0.0240	6839.95
2	0			444.58	208.57	0.0165	4103.25
3	103.05	128.37	0.2110	313.58	152.14	0.0196	3126.49
4	324.83	347.46	0.1749	238.79	124.41	0.0275	2796.89
5	622.22	644.31	0.1671	202.49	112.85	0.0364	2753.20
6	847.55	870.45	0.1651	229.57	122.51	0.0305	2850.07
7	1099.32	1122.25	0.1636	281.90	137.46	0.0201	2837.79
8	1433.21	1456.74	0.1626	229.21	124.37	0.0327	2944.06
9	1511.94	1537.46	0.1627	198.62	120.46	0.0496	3142.19
10	1713.29	1740.22	0.1624	231.35	132.39	0.0403	3284.78
11	1817.95	1846.41	0.1624	238.81	137.78	0.0415	3440.47
12	2045.97	2076.41	0.1622	225.36	138.16	0.0514	3579.11
13	2375.96	2407.76	0.1619	238.92	145.76	0.0506	3708.05
14	2111.18	2143.90	0.1624	129.60	124.44	0.1488	3967.09
15	2268.50	2313.75	0.1634	119.13	132.46	0.1842	4342.24
16	1996.73	2050.30	0.1651	216.95	175.47	0.1082	4342.24
17	1525.61	1599.22	0.1700	132.24	170.32	0.2187	4172.43
18	1515.09	1608.20	0.1731	464.05	261.18	0.0378	3172.22
19	833.53	993.06	0.2006	371.94	286.68	0.0972	3045.14
20	435.92	749.77	0.2805	552.95	374.17	0.0697	2270.59
core	2881.79	2918.41	0.1617	152.85	133.78	0.1266	4553.99
ring	estimate	Site error	Prob Z	Fam estimate	Fam error	Prob Z	Residual estimate error
1	101.58	774.43	0.0992	410.92	319.49	0.0992	10158
2	3431.96	261.76	0.0954	144.47	110.41	0.0954	3431.96
3	1938.40	148.88	0.0111	259.58	113.57	0.0111	1938.40
4	1716.32	131.06	0.0265	148.73	76.88	0.0265	1716.32
5	1364.80	104.21	0.0130	167.11	75.09	0.0130	1364.80
6	1155.13	88.33	0.0107	156.4	67.92	0.0107	1155.13
7	1031.17	78.85	0.0081	159.25	66.28	0.0081	1031.17
8	963.73	73.69	0.0057	177.78	70.28	0.0057	963.73
9	931.69	71.25	0.0051	183.42	71.44	0.0051	931.69
10	898.27	68.89	0.0048	183.21	70.73	0.0048	898.27
11	853.43	65.64	0.0042	185.97	70.62	0.0042	853.43
12	835.35	64.84	0.0044	181.86	69.47	0.0044	835.35
13	807.82	63.17	0.0050	167.60	65.01	0.0050	807.82
14	870.85	70.19	0.0053	186.85	73.04	0.0053	870.85
15	824.41	69.80	0.0051	198.79	77.18	0.0051	824.41
16	879.18	78.01	0.0050	229.57	89.48	0.0050	879.18
17	917.41	89.72	0.0091	213.14	90.28	0.0091	917.41
18	898.42	99.39	0.0088	250.93	105.64	0.0088	898.42
19	868.39	116.52	0.0368	190.25	106.34	0.0368	868.39
20	1065.05	201.02	0.1846	124.10	138.22	0.1846	1065.05
core	825.89	62.79	0.0044	173.71	66.22	0.0044	825.89

		Earlywood					
ring	estimate	Site error	Prob Z	Fam estimate	Fam error	Prob Z	Residual estimate error
1	100.31	182.31	0.2911	410.92	319.49	0.0992	10158
2	273.85	301.53	0.1819	144.47	110.41	0.0954	3431.96
3	148.27	164.17	0.1832	259.58	113.57	0.0111	1938.40
4	247.99	261.79	0.1717	148.73	76.88	0.0265	1716.32
5	251.08	262.10	0.1690	167.11	75.09	0.0130	1364.80
6	212.40	221.68	0.1690	156.4	67.92	0.0107	1155.13
7	168.77	177.06	0.1702	159.25	66.28	0.0081	1031.17
8	141.46	149.21	0.1715	177.78	70.28	0.0057	963.73
9	139.56	147.16	0.1715	183.42	71.44	0.0051	931.69
10	128.16	135.57	0.1722	183.21	70.73	0.0048	898.27
11	117.96	125.08	0.1728	185.97	70.62	0.0042	853.43
12	134.85	142.06	0.1712	181.86	69.47	0.0044	835.35
13	159.95	167.11	0.1693	167.60	65.01	0.0050	807.82
14	177.52	186.05	0.1700	186.85	73.04	0.0053	870.85
15	195.44	204.73	0.1699	198.79	77.18	0.0051	824.41
16	195.71	207.22	0.1725	229.57	89.48	0.0050	879.18
17	151.16	168.49	0.1848	213.14	90.28	0.0091	917.41
18	157.73	185.76	0.1979	250.93	105.64	0.0088	898.42
19	23.15	57.05	0.3424	190.25	106.34	0.0368	868.39
20	117.16	239.99	0.3127	124.10	138.22	0.1846	1065.05
core	126.30	132.97	0.1711	173.71	66.22	0.0044	825.89

		Latewood					
ring	estimate	Site error	Prob Z	Fam estimate	Fam error	Prob Z	Residual estimate error
1	620.14	313.60	0.0240	620.14	313.60	0.0240	6839.95
2	444.58	208.57	0.0165	444.58	208.57	0.0165	4103.25
3	313.58	152.14	0.0196	313.58	152.14	0.0196	3126.49
4	238.79	124.41	0.0275	238.79	124.41	0.0275	2796.89
5	202.49	112.85	0.0364	202.49	112.85	0.0364	2753.20
6	229.57	122.51	0.0305	229.57	122.51	0.0305	2850.07
7	281.90	137.46	0.0201	281.90	137.46	0.0201	2837.79
8	229.21	124.37	0.0327	229.21	124.37	0.0327	2944.06
9	198.62	120.46	0.0496	198.62	120.46	0.0496	3142.19
10	231.35	132.39	0.0403	231.35	132.39	0.0403	3284.78
11	238.81	137.78	0.0415	238.81	137.78	0.0415	3440.47
12	225.36	138.16	0.0514	225.36	138.16	0.0514	3579.11
13	238.92	145.76	0.0506	238.92	145.76	0.0506	3708.05
14	129.60	124.44	0.1488	129.60	124.44	0.1488	3967.09
15	119.13	132.46	0.1842	119.13	132.46	0.1842	4342.24
16	216.95	175.47	0.1082	216.95	175.47	0.1082	4342.24
17	132.24	170.32	0.2187	132.24	170.32	0.2187	4172.43
18	464.05	261.18	0.0378	464.05	261.18	0.0378	3172.22
19	371.94	286.68	0.0972	371.94	286.68	0.0972	3045.14
20	552.95	374.17	0.0697	552.95	374.17	0.0697	2270.59
core	152.85	133.78	0.1266	152.85	133.78	0.1266	4553.99

b) Cell wall thickness

ring	Whole ring			
	Site estimate	Site error	Prob Z	Fam estimate
1	0,0349	0,0363	0,1682	0,0058
2	0,0275	0,0283	0,1663	0,0050
3	0,0190	0,0196	0,1659	0,0039
4	0,0189	0,0193	0,1645	0,0024
5	0,0159	0,0162	0,1637	0,0031
6	0,0127	0,0130	0,1640	0,0021
7	0,0100	0,0102	0,1647	0,0025
8	0,0085	0,0087	0,1653	0,0028
9	0,0083	0,0085	0,1655	0,0030
10	0,0074	0,0076	0,1659	0,0032
11	0,0065	0,0068	0,1665	0,0034
12	0,0070	0,0072	0,1659	0,0042
13	0,0074	0,0076	0,1657	0,0042
14	0,0068	0,0071	0,1670	0,0046
15	0,0074	0,0077	0,1672	0,0054
16	0,0070	0,0073	0,1696	0,0060
17	0,0061	0,0066	0,1768	0,0063
18	0,0069	0,0076	0,1833	0,0082
19	0,0037	0,0050	0,2287	0,0079
20	0,0026	0,0060	0,3307	0,0047
core	0,0113	0,0115	0,1633	0,0046

ring	Earlywood				Latewood			
	Site estimate	Site error	Prob Z	Fam estimate	Site estimate	Site error	Prob Z	Fam estimate
1	0,0308	0,0332	0,1770	0,0048	0,0438	0,0456	0,1683	0,0149
2	0,0298	0,0307	0,1660	0,0027	0,0354	0,0369	0,1688	0,0060
3	0,0171	0,0175	0,1653	0,0036	0,0481	0,0493	0,1646	0,0028
4	0,0163	0,0166	0,1638	0,0018	0,0437	0,0446	0,1634	0,0030
5	0,0130	0,0132	0,1632	0,0028	0,0455	0,0463	0,1628	0,0016
6	0,0108	0,0110	0,1635	0,0020	0,0435	0,0442	0,1626	0,0027
7	0,0082	0,0083	0,1644	0,0017	0,0470	0,0477	0,1623	0,0031
8	0,0065	0,0066	0,1654	0,0020	0,0510	0,0517	0,1619	0,0025
9	0,0055	0,0057	0,1657	0,0026	0,0531	0,0538	0,1618	0,0025
10	0,0048	0,0049	0,1668	0,0027	0,0566	0,0573	0,1617	0,0026
11	0,0040	0,0041	0,1678	0,0028	0,0576	0,0583	0,1618	0,0026
12	0,0039	0,0041	0,1677	0,0027	0,0608	0,0616	0,1618	0,0028
13	0,0043	0,0044	0,1675	0,0029	0,0643	0,0652	0,1618	0,0032
14	0,0038	0,0040	0,1696	0,0030	0,0588	0,0597	0,1621	0,0037
15	0,0042	0,0043	0,1702	0,0036	0,0598	0,0609	0,1631	0,0032
16	0,0040	0,0042	0,1729	0,0040	0,0544	0,0557	0,1642	0,0048
17	0,0027	0,0030	0,1878	0,0037	0,0456	0,0474	0,1676	0,0041
18	0,0026	0,0031	0,2043	0,0051	0,0366	0,0392	0,1753	0,0086
19	0,0007	0,0014	0,3040	0,0044	0,0175	0,0215	0,2079	0,0103
20	0,0018	0,0037	0,3163	0,0030	0,0092	0,0162	0,2857	0,0186
core	0,0068	0,0069	0,1643	0,0029	0,0948	0,0958	0,1611	0,0030

ring	Residual error			
	estimate	error	Prob Z	estimate
1	0,2982	0,0227	0,2554	0,2153
2	0,1141	0,0087	0,1912	0,1889
3	0,0585	0,0044	0,0505	0,1462
4	0,0434	0,0033	0,0915	0,1064
5	0,0301	0,0023	0,0229	0,0975
6	0,0268	0,0020	0,0344	0,0892
7	0,0241	0,0018	0,0379	0,0873
8	0,0225	0,0017	0,0235	0,0861
9	0,0201	0,0015	0,0117	0,0851
10	0,0196	0,0015	0,0105	0,0873
11	0,0183	0,0014	0,0085	0,0903
12	0,0181	0,0014	0,0091	0,0938
13	0,0180	0,0014	0,0082	0,0981
14	0,0182	0,0014	0,0091	0,0976
15	0,0180	0,0015	0,0071	0,0985
16	0,0183	0,0016	0,0075	0,0985
17	0,0187	0,0018	0,0127	0,1023
18	0,0175	0,0019	0,0095	0,1045
19	0,0173	0,0023	0,0284	0,1028
20	0,0212	0,0040	0,1662	0,0893
core	0,0198	0,0015	0,0090	0,0636

c) Radial cell diameter

				Whole ring							
ring	estimate	Site error	Prob Z	estimate	Fam error	Prob Z	Residual estimate error	estimate	Fam error	Prob Z	Residual estimate error
1	0,123	0,156	0,2157	0,032	0,091	0,3627	4,079	0,312	0,094	0,4022	4,401
2	0,021	0,036	0,2827	0,166	0,086	0,0267	1,942	0,147	0,062	0,3051	2,672
3	0,019	0,032	0,2792	0,181	0,085	0,0169	1,685	0,128	0,048	0,2961	2,065
4	0	0		0,175	0,083	0,0182	1,686	0,127	0,050	0,1004	1,587
5	0	0		0,253	0,106	0,0085	1,687	0,127	0,051	0,0625	1,438
6	0	0		0,290	0,119	0,0076	1,839	0,139	0,054	0,0438	1,394
7	0,019	0,034	0,2834	0,373	0,143	0,0046	1,828	0,139	0,055	0,0240	1,294
8	0,028	0,042	0,2537	0,429	0,158	0,0034	1,787	0,135	0,056	0,0334	1,274
9	0,054	0,069	0,2159	0,433	0,160	0,0036	1,816	0,138	0,057	0,0497	1,334
10	0,072	0,087	0,2044	0,432	0,161	0,0038	1,864	0,142	0,058	0,0558	1,362
11	0,097	0,113	0,1945	0,442	0,165	0,0038	1,886	0,144	0,059	0,0625	1,358
12	0,160	0,177	0,1825	0,474	0,176	0,0036	1,886	0,144	0,060	0,0701	1,328
13	0,223	0,240	0,1768	0,465	0,174	0,0039	1,979	0,154	0,061	0,0801	1,459
14	0,306	0,326	0,1737	0,480	0,182	0,0043	2,022	0,162	0,062	0,0961	1,442
15	0,361	0,384	0,1738	0,512	0,199	0,0050	2,075	0,175	0,063	0,1171	1,442
16	0,286	0,313	0,1807	0,572	0,219	0,0045	2,078	0,184	0,064	0,1361	1,459
17	0,246	0,290	0,1978	0,544	0,225	0,0079	2,337	0,228	0,065	0,1551	1,459
18	0,304	0,374	0,2080	0,673	0,279	0,0079	2,297	0,254	0,066	0,1741	1,442
19	0,096	0,174	0,2900	0,727	0,329	0,0136	2,236	0,296	0,067	0,1931	1,442
20	0	0		0,421	0,354	0,1173	2,698	0,494	0,068	0,2121	1,595
core	0,045	0,066	0,2449	0,454	0,180	0,0060	2,551	0,194	0,069	0,2311	1,595
Latewood											
ring	estimate	Site error	Prob Z	estimate	Fam error	Prob Z	Residual estimate error	estimate	Fam error	Prob Z	Residual estimate error
1	0,261	0,297	0,1893	0,023	0,094	0,4022	4,401	0,334	0,094	0,4022	4,401
2	0,278	0,300	0,1766	0,031	0,062	0,3051	2,672	0,203	0,062	0,3051	2,672
3	0,184	0,201	0,1794	0,026	0,048	0,2961	2,065	0,156	0,048	0,2961	2,065
4	0,027	0,040	0,2480	0,063	0,050	0,1004	1,587	0,120	0,050	0,1004	1,587
5	0	0		0,078	0,051	0,0625	1,438	0,109	0,051	0,0625	1,438
6	0,030	0,041	0,2322	0,092	0,054	0,0438	1,394	0,106	0,054	0,0438	1,394
7	0,074	0,085	0,1905	0,117	0,059	0,0240	1,294	0,098	0,059	0,0240	1,294
8	0,156	0,166	0,1741	0,098	0,053	0,0334	1,274	0,097	0,053	0,0334	1,274
9	0,213	0,224	0,1707	0,084	0,051	0,0497	1,334	0,101	0,051	0,0497	1,334
10	0,298	0,309	0,1676	0,081	0,051	0,0558	1,362	0,104	0,051	0,0558	1,362
11	0,416	0,428	0,1651	0,100	0,056	0,0382	1,358	0,104	0,056	0,0382	1,358
12	0,511	0,523	0,1641	0,083	0,052	0,0561	1,358	0,105	0,052	0,0561	1,358
13	0,664	0,675	0,1628	0,114	0,061	0,0301	1,328	0,104	0,061	0,0301	1,328
14	0,674	0,688	0,1637	0,105	0,062	0,0463	1,459	0,118	0,062	0,0463	1,459
15	0,649	0,666	0,1647	0,146	0,079	0,0336	1,514	0,128	0,079	0,0336	1,514
16	0,535	0,554	0,1672	0,180	0,090	0,0228	1,442	0,128	0,090	0,0228	1,442
17	0,402	0,427	0,1732	0,160	0,089	0,0363	1,394	0,136	0,089	0,0363	1,394
18	0,438	0,470	0,1756	0,201	0,096	0,0183	1,040	0,115	0,096	0,0183	1,040
19	0,218	0,265	0,2058	0,277	0,126	0,0140	0,911	0,121	0,126	0,0140	0,911
20	0,015	0,072	0,4161	0,138	0,128	0,1409	1,026	0,191	0,128	0,1409	1,026
core	0,473	0,486	0,1651	0,150	0,074	0,0221	1,595	0,121	0,074	0,0221	1,595

d) Tangential cell diameter

ring	Whole ring				ring	Whole ring				ring	Whole ring										
	estimate	Site error	Prob Z	Fam error		estimate	Site error	Prob Z	Fam error		estimate	Site error	Prob Z	Fam error	estimate	Site error	Prob Z	Fam error			
1	15,175	15,275	0,1602	0	16,133	15,275	0,1602	0	16,133	15,275	0,1602	0	16,133	15,275	0,1602	0	16,133				
2	6,541	6,620	0,1616	0	10,765	6,620	0,1616	0	10,765	6,620	0,1616	0	10,765	6,620	0,1616	0	10,765				
3	3,263	3,305	0,1618	0	5,225	3,305	0,1618	0	5,225	3,305	0,1618	0	5,225	3,305	0,1618	0	5,225				
4	2,037	2,064	0,1618	0	3,266	2,064	0,1618	0	3,266	2,064	0,1618	0	3,266	2,064	0,1618	0	3,266				
5	1,345	1,362	0,1618	0	2,253	1,362	0,1618	0	2,253	1,362	0,1618	0	2,253	1,362	0,1618	0	2,253				
6	0,927	0,941	0,1624	0,01961	1,828	0,941	0,1624	0,01961	1,828	0,941	0,1624	0,01961	1,828	0,941	0,1624	0,01961	1,828				
7	0,661	0,674	0,1635	0,01543	1,669	0,674	0,1635	0,01543	1,669	0,674	0,1635	0,01543	1,669	0,674	0,1635	0,01543	1,669				
8	0,496	0,509	0,1651	0,01516	1,668	0,509	0,1651	0,01516	1,668	0,509	0,1651	0,01516	1,668	0,509	0,1651	0,01516	1,668				
9	0,400	0,413	0,1666	0,0134	1,640	0,413	0,1666	0,0134	1,640	0,413	0,1666	0,0134	1,640	0,413	0,1666	0,0134	1,640				
10	0,319	0,332	0,1680	0,0328	1,542	0,332	0,1680	0,0328	1,542	0,332	0,1680	0,0328	1,542	0,332	0,1680	0,0328	1,542				
11	0,243	0,255	0,1702	0,06712	1,434	0,255	0,1702	0,06712	1,434	0,255	0,1702	0,06712	1,434	0,255	0,1702	0,06712	1,434				
12	0,204	0,216	0,1725	0,08946	1,415	0,216	0,1725	0,08946	1,415	0,216	0,1725	0,08946	1,415	0,216	0,1725	0,08946	1,415				
13	0,146	0,158	0,1781	0,1095	1,400	0,158	0,1781	0,1095	1,400	0,158	0,1781	0,1095	1,400	0,158	0,1781	0,1095	1,400				
14	0,087	0,101	0,1942	0,1072	1,445	0,101	0,1942	0,1072	1,445	0,101	0,1942	0,1072	1,445	0,101	0,1942	0,1072	1,445				
15	0,059	0,075	0,2157	0,1248	1,471	0,075	0,2157	0,1248	1,471	0,075	0,2157	0,1248	1,471	0,075	0,2157	0,1248	1,471				
16	0,037	0,056	0,2540	0,1647	1,446	0,056	0,2540	0,1647	1,446	0,056	0,2540	0,1647	1,446	0,056	0,2540	0,1647	1,446				
17	0,010	0,036	0,3873	0,1197	1,624	0,036	0,3873	0,1197	1,624	0,036	0,3873	0,1197	1,624	0,036	0,3873	0,1197	1,624				
18	0	0	0	0,208	1,381	0	0	0,208	1,381	0	0	0,208	1,381	0	0	0,208	1,381				
19	0	0	0	0,1562	1,565	0	0	0,1562	1,565	0	0	0,1562	1,565	0	0	0,1562	1,565				
20	0	0	0	0,3716	1,576	0	0	0,3716	1,576	0	0	0,3716	1,576	0	0	0,3716	1,576				
core	0,487	0,503	0,1667	0,09285	2,040	0,503	0,1667	0,09285	2,040	0,503	0,1667	0,09285	2,040	0,503	0,1667	0,09285	2,040				
ring	estimate	Site error	Prob Z	Fam error	Residual estimate error	estimate	Site error	Prob Z	Fam error	Residual estimate error	estimate	Site error	Prob Z	Fam error	Residual estimate error	estimate	Site error	Prob Z	Fam error	Residual estimate error	
1	14,067	14,227	0,1614	0,161	20,166	14,227	0,1614	0,161	20,166	14,227	0,1614	0,161	20,166	14,227	0,1614	0,161	20,166	14,227	0,1614	0,161	20,166
2	6,542	6,734	0,1620	0	11,766	6,734	0,1620	0	11,766	6,734	0,1620	0	11,766	6,734	0,1620	0	11,766	6,734	0,1620	0	11,766
3	2,917	2,955	0,1618	0	4,812	2,955	0,1618	0	4,812	2,955	0,1618	0	4,812	2,955	0,1618	0	4,812	2,955	0,1618	0	4,812
4	1,835	1,861	0,1620	0	3,161	1,861	0,1620	0	3,161	1,861	0,1620	0	3,161	1,861	0,1620	0	3,161	1,861	0,1620	0	3,161
5	1,212	1,230	0,1621	0,017	2,243	1,230	0,1621	0,017	2,243	1,230	0,1621	0,017	2,243	1,230	0,1621	0,017	2,243	1,230	0,1621	0,017	2,243
6	0,840	0,854	0,1628	0,034	1,842	0,854	0,1628	0,034	1,842	0,854	0,1628	0,034	1,842	0,854	0,1628	0,034	1,842	0,854	0,1628	0,034	1,842
7	0,592	0,606	0,1644	0,010	1,771	0,606	0,1644	0,010	1,771	0,606	0,1644	0,010	1,771	0,606	0,1644	0,010	1,771	0,606	0,1644	0,010	1,771
8	0,392	0,405	0,1665	0,045	1,600	0,405	0,1665	0,045	1,600	0,405	0,1665	0,045	1,600	0,405	0,1665	0,045	1,600	0,405	0,1665	0,045	1,600
9	0,303	0,316	0,1684	0,059	1,524	0,316	0,1684	0,059	1,524	0,316	0,1684	0,059	1,524	0,316	0,1684	0,059	1,524	0,316	0,1684	0,059	1,524
10	0,255	0,268	0,1703	0,064	1,539	0,268	0,1703	0,064	1,539	0,268	0,1703	0,064	1,539	0,268	0,1703	0,064	1,539	0,268	0,1703	0,064	1,539
11	0,198	0,210	0,1732	0,085	1,482	0,210	0,1732	0,085	1,482	0,210	0,1732	0,085	1,482	0,210	0,1732	0,085	1,482	0,210	0,1732	0,085	1,482
12	0,164	0,177	0,1763	0,112	1,450	0,177	0,1763	0,112	1,450	0,177	0,1763	0,112	1,450	0,177	0,1763	0,112	1,450	0,177	0,1763	0,112	1,450
13	0,115	0,128	0,1838	0,134	1,467	0,128	0,1838	0,134	1,467	0,128	0,1838	0,134	1,467	0,128	0,1838	0,134	1,467	0,128	0,1838	0,134	1,467
14	0,062	0,076	0,2068	0,131	1,544	0,076	0,2068	0,131	1,544	0,076	0,2068	0,131	1,544	0,076	0,2068	0,131	1,544	0,076	0,2068	0,131	1,544
15	0,040	0,057	0,2405	0,149	1,523	0,057	0,2405	0,149	1,523	0,057	0,2405	0,149	1,523	0,057	0,2405	0,149	1,523	0,057	0,2405	0,149	1,523
16	0,023	0,043	0,2981	0,190	1,634	0,043	0,2981	0,190	1,634	0,043	0,2981	0,190	1,634	0,043	0,2981	0,190	1,634	0,043	0,2981	0,190	1,634
17	0	0	0	0,183	1,634	0	0	0,183	1,634	0	0	0,183	1,634	0	0	0,183	1,634	0	0	0,183	1,634
18	0	0	0	0,281	1,377	0	0	0,281	1,377	0	0	0,281	1,377	0	0	0,281	1,377	0	0	0,281	1,377
19	0	0	0	0,209	1,674	0	0	0,209	1,674	0	0	0,209	1,674	0	0	0,209	1,674	0	0	0,209	1,674
20	0	0	0	0,456	1,682	0	0	0,456	1,682	0	0	0,456	1,682	0	0	0,456	1,682	0	0	0,456	1,682
core	0,443	0,461	0,1679	0,115	2,154	0,461	0,1679	0,115	2,154	0,461	0,1679	0,115	2,154	0,461	0,1679	0,115	2,154	0,461	0,1679	0,115	2,154

e) Specific fibre surface

				Whole ring												
ring	estimate	Site error	Prob Z	estimate	Fam error	Prob Z	Residual estimate error	ring	estimate	Site error	Prob Z	Residual estimate error				
1	383,27	399,13	0,1685	50,12	53,25	0,1733	1946,50	1	446,82	500,88	0,1862	77,50	154,46	0,3079	6606,95	506,35
2	490,98	504,95	0,1654	51,99	49,54	0,1470	1744,27	2	616,21	633,16	0,1652	32,59	51,15	0,2620	2095,41	159,33
3	421,20	432,23	0,1649	90,58	53,26	0,0445	1358,64	3	470,47	482,24	0,1646	108,11	60,07	0,0359	1449,41	110,69
4	464,29	473,98	0,1637	57,33	40,57	0,0788	1196,47	4	522,69	533,09	0,1634	50,99	40,45	0,1037	1282,12	97,80
5	448,84	456,90	0,1630	90,53	46,02	0,0246	992,98	5	485,19	493,73	0,1629	88,30	46,52	0,0289	1052,74	80,40
6	392,11	399,65	0,1633	69,59	38,55	0,0355	932,91	6	412,75	420,42	0,1631	82,27	42,54	0,0266	946,92	72,31
7	314,79	321,93	0,1641	83,14	44,42	0,0224	882,70	7	326,06	333,58	0,1642	81,92	42,08	0,0258	936,10	71,37
8	269,83	276,93	0,1649	95,41	44,80	0,0167	877,12	8	261,95	269,17	0,1652	112,87	50,29	0,0124	892,78	68,08
9	237,86	244,51	0,1653	99,21	45,21	0,0141	836,57	9	223,57	230,53	0,1661	101,02	46,52	0,0150	878,42	66,99
10	211,49	217,84	0,1658	100,79	45,06	0,0127	804,87	10	182,57	188,96	0,1670	114,86	48,96	0,0095	791,22	60,60
11	166,88	172,41	0,1665	118,27	47,17	0,0070	701,01	11	147,49	153,37	0,1681	118,08	48,75	0,0077	733,55	56,34
12	167,91	173,68	0,1668	117,60	47,96	0,0071	683,20	12	147,34	153,47	0,1685	118,90	49,17	0,0078	726,55	56,23
13	174,17	180,07	0,1667	118,86	48,05	0,0067	665,05	13	150,49	156,63	0,1683	113,34	47,07	0,0080	694,39	54,14
14	150,67	157,04	0,1687	120,78	49,48	0,0073	648,81	14	125,79	132,47	0,1712	110,59	47,25	0,0096	682,12	55,00
15	161,07	167,94	0,1688	135,39	53,57	0,0058	607,10	15	135,32	142,59	0,1713	121,42	50,41	0,0080	644,22	54,43
16	153,22	161,58	0,1715	143,41	58,46	0,0071	632,98	16	111,11	120,07	0,1774	117,70	51,96	0,0118	675,46	59,93
17	107,23	118,66	0,1831	131,10	56,97	0,0107	613,75	17	89,09	100,59	0,1879	118,68	53,32	0,0130	613,30	60,09
18	103,32	120,70	0,1960	177,32	73,88	0,0082	569,65	18	83,47	100,89	0,2040	164,74	70,10	0,0094	563,80	62,79
19	26,39	49,04	0,2952	147,35	75,78	0,0259	550,51	19	23,89	46,88	0,3052	137,07	72,42	0,0292	544,43	111,79
20	48,51	112,86	0,3336	82,49	88,00	0,1743	611,04	20	199,27	204,96	0,1655	96,00	41,76	0,0108	581,44	111,28
core	242,90	248,32	0,1640	108,58	44,68	0,0076	668,98	core	199,27	204,96	0,1655	96,00	41,76	0,0108	506,32	53,79
				Latewood												
ring	estimate	Site error	Prob Z	estimate	Fam error	Prob Z	Residual estimate error	ring	estimate	Site error	Prob Z	Residual estimate error				
1	345,6	354,96	0,1651	46,51	37,03	0,1046	1180,37	1	446,82	500,88	0,1862	77,50	154,46	0,3079	6606,95	506,35
2	297,4	306,34	0,1658	20,04	28,13	0,2381	1125,93	2	616,21	633,16	0,1652	32,59	51,15	0,2620	2095,41	159,33
3	432,84	440,35	0,1628	16,03	23,09	0,2437	916,68	3	470,47	482,24	0,1646	108,11	60,07	0,0359	1449,41	110,69
4	491,17	497,58	0,1618	0	0	0	830,48	4	522,69	533,09	0,1634	50,99	40,45	0,1037	1282,12	97,80
5	531,15	536,97	0,1613	0	0	0	759,54	5	485,19	493,73	0,1629	88,30	46,52	0,0289	1052,74	80,40
6	553,76	559,82	0,1613	3,92	16,26	0,4046	748,96	6	412,75	420,42	0,1631	82,27	42,54	0,0266	946,92	72,31
7	600,38	606,05	0,1609	11,88	17,55	0,2493	701,71	7	326,06	333,58	0,1642	81,92	42,08	0,0258	936,10	71,37
8	655,47	661,16	0,1607	5,20	15,72	0,3703	704,31	8	261,95	269,17	0,1652	112,87	50,29	0,0124	892,78	68,08
9	663,07	668,56	0,1606	4,28	14,99	0,3875	675,40	9	223,57	230,53	0,1661	101,02	46,52	0,0150	878,42	66,99
10	678,99	684,44	0,1606	11,27	16,68	0,2496	664,74	10	182,57	188,96	0,1670	114,86	48,96	0,0095	791,22	60,60
11	663,31	668,69	0,1606	12,32	16,71	0,2305	651,42	11	147,49	153,37	0,1681	118,08	48,75	0,0077	733,55	56,34
12	680,02	685,54	0,1606	12,95	17,34	0,2275	658,17	12	147,34	153,47	0,1685	118,90	49,17	0,0078	726,55	56,23
13	689,89	695,25	0,1605	12,01	17,04	0,2405	653,69	13	150,49	156,63	0,1683	113,34	47,07	0,0080	694,39	54,14
14	616,05	622,20	0,1611	1,84	15,18	0,4516	648,48	14	125,79	132,47	0,1712	110,59	47,25	0,0096	682,12	55,00
15	597,53	603,92	0,1612	0	0	0	628,39	15	135,32	142,59	0,1713	121,42	50,41	0,0080	644,22	54,43
16	478,53	486,67	0,1627	0	0	0	644,96	16	111,11	120,07	0,1774	117,70	51,96	0,0118	675,46	59,93
17	335,23	344,38	0,1652	0	0	0	552,18	17	89,09	100,59	0,1879	118,68	53,32	0,0130	613,30	60,09
18	279,36	291,30	0,1688	0	0	0	423,10	18	83,47	100,89	0,2040	164,74	70,10	0,0094	563,80	62,79
19	153,16	171,82	0,1864	14,29	26,24	0,2930	362,69	19	23,89	46,88	0,3052	137,07	72,42	0,0292	544,43	111,79
20	118,52	187,58	0,2637	52,76	38,36	0,0845	223,16	20	199,27	204,96	0,1655	96,00	41,76	0,0108	581,44	111,28
core	843,97	849,99	0,1604	0	0	0	766,27	core	199,27	204,96	0,1655	96,00	41,76	0,0108	506,32	53,79

g) Number of cells per mm²

ring	Site			Fam			Whole ring			Site			Fam			Residual		
	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z
1	4547	46292.0	0,1631	976	2354.3	0,3391	104411	7936,4	1	85188	86192	0,1615	0	0	0	139860	10311,0	
2	30060	30513.0	0,1623	825	1369.4	0,2732	56363	4281,8	2	66442	67300	0,1618	0	0	0	125278	9223,0	
3	16561	16869.0	0,1631	1535	1211.3	0,1025	38890	2956,8	3	49123	49844	0,1622	0	0	0	97170	7153,7	
4	8806	9053.0	0,1653	714	816,1	0,1907	30365	2319,2	4	30605	31143	0,1629	0	0	0	70193	5160,7	
5	4724	4922.9	0,1686	1052	793.0	0,0922	24391	1862,9	5	18336	18745	0,1640	0	0	0	52011	3829,1	
6	3132	3310.2	0,1720	1738	936.0	0,0316	22014	1676,1	6	11008	11335	0,1657	646,1	992,3	0,2575	40371	3082,1	
7	1803	1959.8	0,1788	1972	951.5	0,0191	19437	1479,8	7	6406	6682	0,1688	454,7	806,8	0,2865	33918	2589,0	
8	1133	1277.6	0,1876	2182	981,9	0,0131	17951	1366,6	8	4129	4375	0,1727	649,8	794,1	0,2066	30571	2327,3	
9	676	803.6	0,1998	2168	938.5	0,0104	15828	1210,2	9	2752	2978	0,1777	569,5	721,7	0,2150	27957	2128,6	
10	444	567.0	0,2167	2195	937,7	0,0096	15379	1177,6	10	1059	1263	0,2009	668,6	691,7	0,1669	24747	1895,0	
11	133	248.8	0,2963	2280	940,0	0,0076	14177	1090,2	11	482	663	0,2332	985,5	723,2	0,0865	21662	1668,2	
12	0			2317	955,8	0,0077	14209	1097,8	12	121	299	0,3423	999,6	722,2	0,0832	21026	1631,4	
13	0			2207	914,5	0,0079	13526	1052,9	13	0	0		1073,1	707,9	0,0648	19176	1492,8	
14	1	129.4	0,4991	2306	948,9	0,0075	12882	1041,1	14	0	0		1425,9	815,0	0,0401	18674	1494,5	
15	15	168.2	0,4625	2230	966,7	0,0105	13073	1107,2	15	0	0		1656,7	910,3	0,0344	17429	1464,4	
16	0			2424	1031,7	0,0094	12581	1114,1	16	0	0		2201,6	1060,1	0,0189	16217	1427,6	
17	0			2020	997,9	0,0215	13761	1339,7	17	0	0		1682,2	984,0	0,0437	16742	1617,4	
18	0			2948	1320,2	0,0128	11865	1311,4	18	0	0		2071,6	1128,1	0,0331	14394	1575,4	
19	124	378.6	0,3712	2742	1444,2	0,0288	11532	1543,1	19	22	314	0,4713	2793,6	1527,8	0,0337	13633	1805,5	
20	24	679.5	0,4858	3004	2241,8	0,0901	14086	2680,1	20	0	0		1947,9	1888,3	0,1511	14851	2750,1	
core	340	477.6	0,2380	1745	838,9	0,0187	16955	1292,6	Core	527	692	0,2231	1203,7	745,3	0,0531	20238	1542,6	

Latewood

h) Increment (based on ring width)

ring	Earlywood			Whole ring			Latewood		
	Site estimate	Prob Z	Residual estimate error	Site estimate	Prob Z	Residual estimate error	Site estimate	Prob Z	Residual estimate error
1	0		170,47	4,89	0,3483	5,32	12,54	0,3483	920,06
2	0		4619,21	21,67	0,4140	98,31	99,76	0,4140	9396,26
3	0		20353	54,06	0,4390	1241,73	352,09	0,4390	36057
4	115,01	0,4281	62670	37,54	0,4834	935,98	900,54	0,4834	8024,89
5	0		171752	767,81	0,3919	1258,63	2799,57	0,3919	248569
6	0		336027	879,33	0,4269	2405,34	4771,84	0,4269	477141
7	0		8683072	4133	0,3452	19404	10374	0,3452	759096
8	0		1060431	11403	0,3005	31883	21804	0,3005	1277133
9	0		1228796	31084	0,2538	40365	46908	0,2538	1934238
10	0		1209094	100617	0,2068	70568	123075	0,2068	2717637
11	0		1355012	213382	0,1925	101406	245660	0,1925	3877559
12	0		1988365	441073	0,1822	121904	486248	0,1822	5427057
13	0		3251619	718329	0,1782	175944	778893	0,1782	8887279
14	0		46661	1245270	0,1745	408856	1329388	0,1745	718416
15	0		336027	2321256	0,1701	314325	2433485	0,1701	1122496
16	0		877675	2265820	0,1761	586297	2435085	0,1761	1411423
17	0		4136570	2313341	0,1838	953555	2567449	0,1838	1619682
18	0		5651380	4848476	0,1805	2097938	5307249	0,1805	1784385
19	0		6637205	1771676	0,2249	40614	2343772	0,2249	1899636
20	0		1802970	5374921	0,2406	1845384	7631777	0,2406	2287423
core	0		1802970	0		705917	669881		2354568
ring	estimate	Prob Z	Residual estimate error	estimate	Prob Z	Residual estimate error	estimate	Prob Z	Residual estimate error
1	0		13,11	0,82	0,4218	10,45	4,1971	0,4218	414,59
2	0		354,62	0		0	11,47	0,1820	1144,14
3	0		1562	21,28	0,3096	59,15	42,8217	0,2005	2621,61
4	115,01	0,4281	4819	43,22	0,3151	45,50	89,7703	0,3620	5697,66
5	0		12679	180,07	0,2467	76,32	262,85	0,3687	437,59
6	0		25620	451,80	0,2232	317,26	593,41	0,2358	10136
7	0		42381	1241,29	0,1962	531,87	1451,15	0,2136	17304
8	0		67316	2968,46	0,1836	1212,19	3292,26	0,1469	25597
9	0		103826	4619	0,1821	849,93	5090	0,2744	57967
10	0		157026	9139	0,1745	966,82	9759	0,2974	75317
11	0		233633	11979	0,1740	1549,66	12764	0,2571	7321
12	0		321339	21097	0,1699	880,46	22102	0,3804	9907
13	0		441453	31219	0,1692	1271,00	32609	0,4985	12398
14	0		537286	46572	0,1679	1798,64	48388	0,3545	193592
15	0		735852	71912	0,1673	0	74537	0,1673	238205
16	0		944517	83186	0,1680	0	86448	0,1680	276704
17	0		1205045	82527	0,1732	10669	87645	0,2041	310501
18	0		1355012	148851	0,1709	25280	156592	0,0898	282579
19	0		1988365	95541	0,1907	12412	109140	0,2713	317897
20	0		3251619	86695	0,2302	5686,31	117437	0,2968	473719
core	0		1372230	13912	0,2145	17592	17592	0,2145	452278

i) Earlywood and latewood proportion

(all estimates and errors need to be multiplied by 10^{-3})

ring	Site			Earlywood			Latewood			Residual estimate error	
	estimate	error	Prob Z	estimate	Fam error	Prob Z	estimate	Fam error	Prob Z		
1	0,246	0,747	0,3710	1,074	1,547	0,2438	62,200	4,729	4,729	62,200	4,729
2	0	0		0			16,240	1,201	1,201	16,240	1,201
3	0,029	0,084	0,3649	0			6,694	0,497	0,497	6,694	0,497
4	0,034	0,068	0,3079	0			4,177	0,309	0,309	4,177	0,309
5	0,020	0,041	0,3125	0,008	0,053	0,4435	2,527	0,194	0,194	2,527	0,194
6	0,063	0,080	0,2138	0			2,031	0,150	0,150	2,031	0,150
7	0,084	0,097	0,1941	0			1,631	0,121	0,121	1,631	0,121
8	0,089	0,101	0,1896	0,018	0,035	0,3027	1,499	0,115	0,115	1,499	0,115
9	0,075	0,085	0,1897	0,007	0,027	0,4024	1,256	0,096	0,096	1,256	0,096
10	0,081	0,090	0,1851	0,024	0,030	0,2115	1,137	0,087	0,087	1,137	0,087
11	0,080	0,090	0,1850	0,021	0,029	0,2341	1,116	0,086	0,086	1,116	0,086
12	0,054	0,063	0,1959	0,042	0,034	0,1092	1,058	0,082	0,082	1,058	0,082
13	0,061	0,071	0,1937	0,028	0,031	0,1822	1,080	0,085	0,085	1,080	0,085
14	0,046	0,057	0,2068	0,046	0,037	0,1071	1,061	0,086	0,086	1,061	0,086
15	0,018	0,029	0,2687	0,073	0,045	0,0534	0,996	0,085	0,085	0,996	0,085
16	0,015	0,028	0,2987	0,051	0,040	0,0998	0,956	0,086	0,086	0,956	0,086
17	0	0		0,049	0,044	0,1358	0,938	0,092	0,092	0,938	0,092
18	0	0		0,052	0,055	0,1725	0,999	0,111	0,111	0,999	0,111
19	0	0		0,044	0,075	0,2790	1,095	0,146	0,146	1,095	0,146
20	0	0		0			0,895	0,146	0,146	0,895	0,146

j) Microfibril angle (MFA)

ring	Whole ring				ring	Earlywood				ring	Latewood															
	estimate	error	Prob Z	Fam estimate error		estimate	error	Prob Z	Fam estimate error		estimate	error	Prob Z	Fam estimate error												
1	3,206	3,360	0,170	1,003	0,666	0,0660	18,994	1,452	1	3,467	3,638	0,1703	1,206	0,772	0,0592	21,333	1,629	1	1,710	1,857	0,1786	1,831	0,888	0,0196	18,156	1,384
2	1,770	1,906	0,1765	1,652	0,807	0,0204	16,821	1,280	2	1,816	1,948	0,1757	1,682	0,812	0,0192	16,475	1,258	2	1,710	1,857	0,1786	1,831	0,888	0,0196	18,156	1,384
3	1,635	1,759	0,1762	1,794	0,817	0,0142	15,289	1,164	3	1,928	2,058	0,1743	1,444	0,730	0,0240	15,888	1,213	3	1,816	1,948	0,1757	1,682	0,812	0,0192	16,475	1,258
4	1,864	1,993	0,1748	1,537	0,758	0,0214	15,983	1,217	4	1,673	1,804	0,1769	1,376	0,715	0,0272	16,122	1,230	4	1,928	2,058	0,1743	1,444	0,730	0,0240	15,888	1,213
5	2,322	2,451	0,1717	1,361	0,707	0,0271	15,951	1,216	5	1,471	1,606	0,1799	1,634	0,800	0,0206	16,679	1,271	5	1,673	1,804	0,1769	1,376	0,715	0,0272	16,122	1,230
6	2,044	2,179	0,1741	1,505	0,763	0,0243	16,720	1,274	6	1,534	1,674	0,1797	1,788	0,855	0,0183	17,208	1,314	6	1,471	1,606	0,1799	1,634	0,800	0,0206	16,679	1,271
7	1,893	2,037	0,1764	1,523	0,790	0,0270	17,845	1,360	7	1,362	1,516	0,1845	1,523	0,815	0,0309	19,032	1,451	7	1,471	1,606	0,1799	1,634	0,800	0,0206	16,679	1,271
8	1,625	1,782	0,1809	1,493	0,814	0,0334	19,503	1,484	8	1,434	1,601	0,1851	1,231	0,761	0,0531	20,585	1,569	8	1,625	1,782	0,1809	1,493	0,814	0,0334	19,503	1,484
9	1,495	1,662	0,1842	1,411	0,815	0,0418	20,704	1,578	9	1,244	1,412	0,1892	1,310	0,789	0,0484	20,683	1,581	9	1,495	1,662	0,1842	1,411	0,815	0,0418	20,704	1,578
10	1,323	1,493	0,1878	1,487	0,845	0,0393	20,983	1,604	10	1,135	1,304	0,1920	1,279	0,782	0,0509	20,671	1,585	10	1,323	1,493	0,1878	1,487	0,845	0,0393	20,983	1,604
11	1,221	1,393	0,1904	1,433	0,834	0,0429	21,125	1,620	11	1,144	1,309	0,1910	1,276	0,783	0,0517	20,107	1,559	11	1,221	1,393	0,1904	1,433	0,834	0,0429	21,125	1,620
12	1,095	1,268	0,1939	1,316	0,812	0,0525	21,029	1,628	12	1,250	1,402	0,1863	1,597	0,897	0,0375	17,831	1,505	12	1,095	1,268	0,1939	1,316	0,812	0,0525	21,029	1,628
13	1,212	1,375	0,1891	1,395	0,817	0,0439	19,825	1,548	13	1,212	1,370	0,1882	1,597	0,897	0,0375	17,831	1,505	13	1,212	1,375	0,1891	1,395	0,817	0,0439	19,825	1,548
14	1,140	1,300	0,1903	1,807	0,939	0,0271	19,090	1,540	14	1,250	1,402	0,1863	1,597	0,897	0,0375	17,831	1,505	14	1,140	1,300	0,1903	1,807	0,939	0,0271	19,090	1,540
15	1,113	1,273	0,1911	1,753	0,944	0,0317	18,138	1,535	15	1,212	1,370	0,1882	1,597	0,897	0,0375	17,831	1,505	15	1,113	1,273	0,1911	1,753	0,944	0,0317	18,138	1,535
16	1,409	1,573	0,1851	1,616	0,951	0,0446	17,405	1,553	16	1,135	1,304	0,1920	1,279	0,782	0,0509	20,671	1,585	16	1,409	1,573	0,1851	1,616	0,951	0,0446	17,405	1,553
17	1,555	1,752	0,1874	1,120	0,913	0,1100	17,746	1,750	17	1,144	1,309	0,1910	1,276	0,783	0,0517	20,107	1,559	17	1,555	1,752	0,1874	1,120	0,913	0,1100	17,746	1,750
18	2,256	2,565	0,1896	0,482	0,912	0,2986	17,910	2,008	18	2,011	2,285	0,1894	0,831	1,048	0,2140	17,759	1,993	18	2,256	2,565	0,1896	0,482	0,912	0,2986	17,910	2,008
19	2,291	3,038	0,2254	0,159	1,218	0,4479	19,710	2,644	19	2,721	3,366	0,2094	0,367	1,206	0,3802	18,307	2,460	19	2,291	3,038	0,2254	0,159	1,218	0,4479	19,710	2,644
20	0,070	0,811	0,4656	0	.	.	17,403	2,823	20	0,983	1,827	0,2944	0	.	.	16,478	2,692	20	0,070	0,811	0,4656	0	.	.	17,403	2,823
core	0,497	0,627	0,2161	1,252	0,690	0,0349	16,746	1,274	core	0,563	0,682	0,2042	1,354	0,681	0,0234	14,600	1,116	core	0,497	0,627	0,2161	1,252	0,690	0,0349	16,746	1,274

k) Modulus of elasticity (MOE)

ring	Site			Fam			Whole ring			Residual			
	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	estimate error	
1	0.599	0.623	0.1680	0.033	0.067	0.3080	0.599	0.623	0.1680	0.033	0.067	2.923	0.222
2	0.221	0.236	0.1749	0.068	0.057	0.1164	0.221	0.236	0.1749	0.068	0.057	1,911	0.145
3	0.198	0.212	0.1746	0.066	0.052	0.1019	0.198	0.212	0.1746	0.066	0.052	1,679	0.127
4	0.243	0.257	0.1714	0.057	0.049	0.1214	0.243	0.257	0.1714	0.057	0.049	1,640	0.124
5	0.200	0.214	0.1744	0.072	0.054	0.0896	0.200	0.214	0.1744	0.072	0.054	1,680	0.127
6	0.169	0.184	0.1789	0.082	0.060	0.0852	0.169	0.184	0.1789	0.082	0.060	1,843	0.140
7	0.163	0.179	0.1820	0.099	0.069	0.0763	0.163	0.179	0.1820	0.099	0.069	2,057	0.156
8	0.159	0.178	0.1852	0.107	0.076	0.0813	0.159	0.178	0.1852	0.107	0.076	2,313	0.175
9	0.149	0.170	0.1906	0.132	0.089	0.0709	0.149	0.170	0.1906	0.132	0.089	2,615	0.199
10	0.116	0.139	0.2021	0.166	0.104	0.0552	0.116	0.139	0.2021	0.166	0.104	2,837	0.216
11	0.091	0.117	0.2174	0.178	0.114	0.0586	0.091	0.117	0.2174	0.178	0.114	3,154	0.241
12	0.060	0.087	0.2464	0.158	0.114	0.0841	0.060	0.087	0.2464	0.158	0.114	3,350	0.258
13	0.053	0.080	0.2548	0.185	0.123	0.0668	0.053	0.080	0.2548	0.185	0.123	3,363	0.261
14	0.049	0.078	0.2635	0.259	0.151	0.0428	0.049	0.078	0.2635	0.259	0.151	3,478	0.279
15	0.073	0.103	0.2379	0.323	0.172	0.0306	0.073	0.103	0.2379	0.323	0.172	3,291	0.277
16	0.079	0.111	0.2375	0.302	0.182	0.0483	0.079	0.111	0.2375	0.302	0.182	3,362	0.298
17	0.070	0.109	0.2592	0.192	0.167	0.1258	0.070	0.109	0.2592	0.192	0.167	3,512	0.343
18	0.250	0.327	0.2224	0.237	0.200	0.1176	0.250	0.327	0.2224	0.237	0.200	3,328	0.368
19	0.123	0.292	0.3362	0.120	0.260	0.3223	0.123	0.292	0.3362	0.120	0.260	3,584	0.485
20	0	0	0	0	0	0	0	0	0	0	0	3,531	0.565
core	0.020	0.047	0.3363	0.291	0.152	0.0275	0.020	0.047	0.3363	0.291	0.152	3,450	0.261
	Latewood												
ring	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	Prob Z	estimate	error	estimate error	Residual
1	0.542	0.574	0.1722	0.174	0.128	0.0864	0.542	0.574	0.1722	0.174	0.128	3,898	0.298
2	0.331	0.358	0.1776	0.157	0.112	0.0795	0.331	0.358	0.1776	0.157	0.112	3,349	0.255
3	0.257	0.281	0.1800	0.158	0.104	0.0644	0.257	0.281	0.1800	0.158	0.104	2,953	0.225
4	0.240	0.262	0.1798	0.141	0.094	0.0674	0.240	0.262	0.1798	0.141	0.094	2,722	0.207
5	0.242	0.265	0.1808	0.131	0.094	0.0824	0.242	0.265	0.1808	0.131	0.094	2,881	0.219
6	0.184	0.209	0.1887	0.178	0.111	0.0548	0.184	0.209	0.1887	0.178	0.111	3,037	0.231
7	0.170	0.196	0.1931	0.247	0.135	0.0338	0.170	0.196	0.1931	0.247	0.135	3,239	0.246
8	0.184	0.213	0.1936	0.202	0.129	0.0586	0.184	0.213	0.1936	0.202	0.129	3,592	0.272
9	0.140	0.171	0.2055	0.249	0.145	0.0437	0.140	0.171	0.2055	0.249	0.145	3,732	0.284
10	0.142	0.174	0.2078	0.271	0.157	0.0420	0.142	0.174	0.2078	0.271	0.157	3,982	0.304
11	0.180	0.214	0.2001	0.296	0.168	0.0390	0.180	0.214	0.2001	0.296	0.168	4,179	0.319
12	0.157	0.192	0.2067	0.344	0.186	0.0325	0.157	0.192	0.2067	0.344	0.186	4,244	0.328
13	0.180	0.214	0.2003	0.352	0.188	0.0302	0.180	0.214	0.2003	0.352	0.188	4,170	0.324
14	0.193	0.228	0.1988	0.456	0.222	0.0202	0.193	0.228	0.1988	0.456	0.222	4,165	0.333
15	0.200	0.235	0.1976	0.534	0.251	0.0166	0.200	0.235	0.1976	0.534	0.251	4,001	0.336
16	0.266	0.303	0.1897	0.490	0.252	0.0261	0.266	0.303	0.1897	0.490	0.252	3,933	0.348
17	0.306	0.350	0.1909	0.407	0.250	0.0519	0.306	0.350	0.1909	0.407	0.250	4,071	0.396
18	0.526	0.584	0.1835	0.532	0.318	0.0474	0.526	0.584	0.1835	0.532	0.318	3,674	0.410
19	0.453	0.582	0.2181	0.342	0.358	0.1696	0.453	0.582	0.2181	0.342	0.358	4,031	0.545
20	0	0	0	0	0	0	0	0	0	0	0	4,831	0.773
core	0.146	0.179	0.2065	0.466	0.214	0.0147	0.146	0.179	0.2065	0.466	0.214	4,047	0.307

Appendix 4

Correlations between wood traits (tables)

The following tables present a detailed view of correlations between different wood traits that were investigated in this study. The genetic correlation and its associated error, as well as phenotypic (product moment) correlations including their P-value are given. Correlations are not differentiated in earlywood and latewood and are shown for the entire growth ring. Earlywood correlations are close to estimates for the entire growth ring; variance components for latewood correlations could not be estimated in many cases (see results of chapter III).

Abbreviations:

CoreLength	Increment or the length of the wood core at a specific age
Dens	Wood density
RadDiam	Radial cell diameter
TanDiam	Tangential cell diameter
Coars	Fibre coarseness
CellPop	Number of cells per mm ² , cell population
MFA	Microfibril angle
MOE	Modulus of elasticity
Wt	Cell wall thickness
SpecSurf	Specific fibre surface

ring	CoreLength vs. Dens				CoreLength vs. RadDiam				CoreLength vs. TanDiam			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-0,322	0,498	-0,273	0,0001	0,591	0,352	0,435	0,0001			-0,202	0,0001
3	-0,670	0,299	-0,291	0,0001	0,577	0,367	0,492	0,0001			-0,152	0,0033
4	-0,444	0,615	-0,303	0,0001	0,807	0,254	0,518	0,0001			-0,124	0,0164
5	-0,435	0,529	-0,363	0,0001	0,824	0,198	0,529	0,0001			-0,118	0,0225
6	-0,930	0,146	-0,390	0,0001	0,855	0,139	0,554	0,0001	-0,775	0,471	-0,071	0,1713
7	-0,580	0,298	-0,408	0,0001	0,724	0,204	0,572	0,0001	-0,227	1,030	-0,001	0,9902
8	-0,184	0,444	-0,428	0,0001	0,717	0,202	0,566	0,0001	0,614	0,676	0,047	0,3633
9	-0,475	0,447	-0,438	0,0001	1,191	0,229	0,558	0,0001	0,412	1,234	0,064	0,2164
10	-0,611	0,343	-0,462	0,0001	1,172	0,198	0,559	0,0001	1,799	2,152	0,070	0,1779
11	-0,889	0,112	-0,495	0,0001	0,922	0,081	0,586	0,0001	0,885	0,163	0,089	0,0874
12	-0,858	0,138	-0,523	0,0001	0,947	0,054	0,601	0,0001	1,160	0,232	0,113	0,0321
13	-0,782	0,204	-0,539	0,0001	0,659	0,296	0,618	0,0001	0,633	0,382	0,140	0,0079
14	-1,114	0,130	-0,568	0,0001	2,575	3,067	0,632	0,0001			0,131	0,0160
15	-1,154	0,185	-0,575	0,0001	0,942	0,064	0,633	0,0001	1,605	1,102	0,136	0,0168
16	-1,250	0,293	-0,586	0,0001	1,747	1,079	0,619	0,0001	2,498	3,256	0,162	0,0063
17	-0,949	0,053	-0,591	0,0001	1,347	0,440	0,627	0,0001	2,868	5,151	0,231	0,0003
18	-1,230	0,258	-0,603	0,0001	3,941	7,342	0,625	0,0001			0,245	0,0007

ring	CoreLength vs. Coars				CoreLength vs. CellPop				CoreLength vs. MFA			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-1,053	0,182	-0,146	0,0045			-0,028	0,5842	-0,427	0,429	-0,052	0,3157
3	-0,326	0,836	-0,111	0,0317	-1,173	0,440	-0,125	0,0158	-0,497	0,408	0,030	0,5581
4	-0,894	0,660	-0,097	0,0601	-1,017	0,052	-0,190	0,0002	-0,342	0,654	0,089	0,0852
5	-2,006	2,787	-0,131	0,0111	-0,822	0,317	-0,233	0,0001	-0,315	0,620	0,113	0,0287
6	-0,506	0,653	-0,119	0,0213	-0,799	0,224	-0,297	0,0001	-0,598	0,366	0,129	0,0127
7	-0,944	0,070	-0,091	0,0796	-0,882	0,111	-0,362	0,0001	-0,591	0,324	0,159	0,0020
8	-0,267	0,569	-0,086	0,0988	-0,902	0,088	-0,383	0,0001	-0,593	0,328	0,177	0,0006
9	-0,329	0,701	-0,083	0,1074	-1,139	0,184	-0,386	0,0001	-0,513	0,502	0,208	0,0001
10	-0,497	0,548	-0,097	0,0632	-1,334	0,451	-0,390	0,0001	-0,263	0,608	0,219	0,0001
11	-0,644	0,398	-0,096	0,0654	-1,471	0,673	-0,418	0,0001	-0,309	0,611	0,233	0,0001
12	-0,428	0,532	-0,093	0,0758	-1,425	0,572	-0,443	0,0001	-0,291	0,615	0,237	0,0001
13	-0,517	0,462	-0,081	0,1258	-1,108	0,127	-0,469	0,0001	-0,403	0,547	0,225	0,0001
14	-0,866	0,172	-0,108	0,0485	-1,499	0,713	-0,473	0,0001	0,403	0,533	0,230	0,0001
15	-1,605	1,037	-0,116	0,0424	-1,186	0,246	-0,478	0,0001	-0,173	0,650	0,199	0,0004
16	-1,573	0,902	-0,124	0,0373	-1,178	0,216	-0,478	0,0001	0,367	0,564	0,174	0,0033
17	-1,175	0,247	-0,075	0,2533	-0,548	0,417	-0,516	0,0001	-0,129	0,744	0,147	0,0239
18	-1,438	0,605	-0,088	0,2303	-1,203	0,237	-0,531	0,0001			0,129	0,0774

ring	CoreLength vs. MOE				CoreLength vs. Wt				CoreLength vs. SpecSurf			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-0,539	0,488	0,034	0,5180			-0,188	0,0003	0,611	0,459	0,189	0,0002
3	-0,829	0,222	-0,061	0,2372	-0,894	0,130	-0,180	0,0005	-1,053	0,067	0,197	0,0001
4	-0,408	0,813	-0,126	0,0147	-0,927	0,130	-0,179	0,0005	-1,256	0,512	0,224	0,0001
5	-0,618	0,510	-0,183	0,0004	-0,956	0,061	-0,232	0,0001	-0,322	0,610	0,281	0,0001
6	-0,226	0,649	-0,224	0,0001	-1,272	0,385	-0,249	0,0001	1,019	0,023	0,292	0,0001
7	0,057	0,576	-0,264	0,0001	-1,341	0,401	-0,255	0,0001	0,072	0,485	0,289	0,0001
8	0,121	0,571	-0,308	0,0001	-0,803	0,170	-0,271	0,0001	0,339	0,415	0,301	0,0001
9	0,675	0,403	-0,348	0,0001	-1,076	0,098	-0,284	0,0001	0,689	0,318	0,309	0,0001
10	0,799	0,249	-0,369	0,0001			-0,314	0,0001	1,780	1,257	0,336	0,0001
11	0,509	0,524	-0,395	0,0001			-0,341	0,0001	1,060	0,070	0,352	0,0001
12	1,019	0,028	-0,411	0,0001			-0,363	0,0001	1,255	0,315	0,362	0,0001
13	0,675	0,379	-0,413	0,0001			-0,372	0,0001	0,980	0,021	0,362	0,0001
14	2,295	2,876	-0,428	0,0001			-0,411	0,0001	1,519	0,740	0,396	0,0001
15	0,635	0,398	-0,414	0,0001			-0,425	0,0001	1,541	0,790	0,405	0,0001
16	0,749	0,290	-0,409	0,0001			-0,438	0,0001	1,813	1,240	0,415	0,0001
17	1,414	0,783	-0,402	0,0001			-0,422	0,0001	1,512	0,710	0,400	0,0001
18			-0,400	0,0001			-0,438	0,0001			0,422	0,0001

ring	Dens vs. RadDiam				Dens vs. TanDiam				Dens vs. Coars			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-0,767	0,173	-0,326	0,0001			0,414	0,0001			0,682	0,0001
3	-0,808	0,139	-0,439	0,0001			0,404	0,0001			0,705	0,0001
4	-0,862	0,106	-0,433	0,0001			0,389	0,0001			0,744	0,0001
5	-0,832	0,112	-0,470	0,0001			0,401	0,0001			0,766	0,0001
6	-0,861	0,085	-0,521	0,0001			0,347	0,0001			0,752	0,0001
7	-0,837	0,094	-0,553	0,0001			0,277	0,0001			0,734	0,0001
8	-0,821	0,097	-0,567	0,0001			0,194	0,0002			0,708	0,0001
9	-0,799	0,107	-0,580	0,0001			0,124	0,0167			0,676	0,0001
10	-0,789	0,108	-0,599	0,0001	-1,205	0,360	0,054	0,3004	1,016	0,028	0,644	0,0001
11	-0,795	0,104	-0,612	0,0001	-0,777	0,218	-0,003	0,9492	0,789	0,233	0,611	0,0001
12	-0,782	0,109	-0,622	0,0001	-0,548	0,310	-0,033	0,5296	0,678	0,268	0,585	0,0001
13	-0,788	0,108	-0,629	0,0001	-0,434	0,328	-0,058	0,2776	0,624	0,277	0,566	0,0001
14	-0,792	0,109	-0,642	0,0001	-0,649	0,239	-0,101	0,0646	0,597	0,330	0,548	0,0001
15	-0,793	0,108	-0,661	0,0001	-0,553	0,276	-0,118	0,0382	0,588	0,281	0,538	0,0001
16	-0,841	0,083	-0,647	0,0001	-0,402	0,322	-0,140	0,0186	0,598	0,269	0,534	0,0001
17	-0,865	0,077	-0,662	0,0001	-0,434	0,368	-0,176	0,0067	0,713	0,232	0,496	0,0001
18	-0,816	0,102	-0,662	0,0001	-0,497	0,328	-0,182	0,0122	0,573	0,290	0,506	0,0001

ring	Dens vs. CellPop				Dens vs. MFA				Dens vs. MOE			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2			-0,208	0,0001	0,622	0,261	0,369	0,0001	0,110	0,586	-0,018	0,7345
3			-0,095	0,0662	0,588	0,274	0,319	0,0001	0,208	0,580	-0,002	0,9744
4	3,624	16,310	-0,047	0,3666	0,543	0,300	0,347	0,0001	0,242	0,546	-0,044	0,3942
5	1,932	1,877	-0,002	0,9730	0,306	0,374	0,329	0,0001	0,566	0,345	-0,013	0,7966
6	1,478	0,575	0,090	0,0817	0,308	0,344	0,295	0,0001	0,565	0,319	0,031	0,5506
7	1,195	0,173	0,176	0,0006	0,204	0,359	0,262	0,0001	0,608	0,279	0,054	0,3009
8	1,079	0,060	0,238	0,0001	0,197	0,360	0,233	0,0001	0,670	0,241	0,102	0,0498
9	1,030	0,022	0,291	0,0001	0,039	0,383	0,183	0,0004	0,812	0,142	0,156	0,0025
10	0,973	0,018	0,349	0,0001	0,028	0,370	0,138	0,0076	0,762	0,161	0,214	0,0001
11	0,939	0,038	0,391	0,0001	-0,028	0,372	0,092	0,0787	0,803	0,134	0,263	0,0001
12	0,890	0,066	0,419	0,0001	0,002	0,383	0,053	0,3108	0,818	0,132	0,309	0,0001
13	0,863	0,081	0,440	0,0001	0,019	0,382	0,045	0,3930	0,741	0,171	0,322	0,0001
14	0,900	0,061	0,475	0,0001	0,059	0,360	0,018	0,7441	0,630	0,216	0,359	0,0001
15	0,885	0,069	0,502	0,0001	-0,005	0,370	0,030	0,5994	0,678	0,184	0,369	0,0001
16	0,857	0,083	0,504	0,0001	-0,066	0,401	0,031	0,6001	0,774	0,145	0,380	0,0001
17	0,867	0,085	0,528	0,0001	0,272	0,486	0,079	0,2295	0,648	0,257	0,350	0,0001
18	0,832	0,101	0,546	0,0001	-0,015	0,833	0,063	0,3868	0,823	0,140	0,371	0,0001

ring	Dens vs. Wt				Dens vs. SpecSurf				Wt vs. SpecSurf			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	1,808	2,937	0,876	0,0001	-1,250	0,435	-0,849	0,0001	-1,071	0,328	-0,966	0,0001
3			0,893	0,0001	-1,239	0,432	-0,869	0,0001			-0,961	0,0001
4			0,912	0,0001	-1,557	1,558	-0,877	0,0001			-0,943	0,0001
5	1,427	0,993	0,924	0,0001	-1,147	0,212	-0,885	0,0001	-1,033	0,101	-0,943	0,0001
6	1,179	0,243	0,925	0,0001	-1,043	0,046	-0,885	0,0001	-0,973	0,046	-0,949	0,0001
7	1,090	0,096	0,926	0,0001	-0,978	0,019	-0,885	0,0001	-0,993	0,009	-0,953	0,0001
8	1,049	0,044	0,923	0,0001	-0,965	0,027	-0,884	0,0001	-1,002	0,002	-0,956	0,0001
9	1,026	0,022	0,919	0,0001	-0,966	0,024	-0,883	0,0001	-1,003	0,002	-0,961	0,0001
10	1,008	0,006	0,916	0,0001	-0,957	0,029	-0,882	0,0001	-1,000	0,000	-0,968	0,0001
11	0,997	0,002	0,911	0,0001	-0,955	0,029	-0,878	0,0001	-0,999	0,001	-0,972	0,0001
12	0,983	0,012	0,908	0,0001	-0,949	0,032	-0,873	0,0001	-0,997	0,002	-0,976	0,0001
13	0,978	0,014	0,906	0,0001	-0,941	0,037	-0,869	0,0001	-0,995	0,003	-0,977	0,0001
14	0,980	0,014	0,906	0,0001	-0,944	0,036	-0,870	0,0001	-0,996	0,003	-0,979	0,0001
15	0,969	0,021	0,907	0,0001	-0,939	0,038	-0,870	0,0001	-0,996	0,002	-0,979	0,0001
16	0,970	0,019	0,906	0,0001	-0,939	0,037	-0,869	0,0001	-0,995	0,004	-0,980	0,0001
17	0,989	0,007	0,899	0,0001	-0,963	0,024	-0,861	0,0001	-0,998	0,001	-0,980	0,0001
18	0,952	0,032	0,905	0,0001	-0,918	0,052	-0,872	0,0001	-0,991	0,006	-0,980	0,0001

ring	RadDiam vs. TanDiam				RadDiam vs. Coars				RadDiam vs. CellPop			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	.	.	0,113	0,0286	.	.	0,204	0,0001	.	.	-0,500	0,0001
3	.	.	0,123	0,0173	.	.	0,122	0,0184	.	.	-0,576	0,0001
4	.	.	0,139	0,0072	.	.	0,108	0,0374	.	.	-0,634	0,0001
5	.	.	0,090	0,0826	.	.	0,051	0,3266	-1,398	0,557	-0,651	0,0001
6	.	.	0,117	0,0231	.	.	0,034	0,5128	-1,138	0,126	-0,699	0,0001
7	.	.	0,150	0,0037	.	.	0,032	0,5416	-1,073	0,054	-0,733	0,0001
8	.	.	0,194	0,0002	.	.	0,050	0,3317	-1,035	0,023	-0,756	0,0001
9	.	.	0,230	0,0001	.	.	0,075	0,1472	-1,017	0,011	-0,774	0,0001
10	0,386	0,623	0,257	0,0001	-0,193	0,761	0,091	0,0797	-0,997	0,002	-0,790	0,0001
11	0,294	0,468	0,288	0,0001	-0,154	0,560	0,118	0,0239	-0,981	0,011	-0,805	0,0001
12	0,243	0,391	0,302	0,0001	-0,068	0,463	0,137	0,0088	-0,962	0,022	-0,815	0,0001
13	0,213	0,364	0,313	0,0001	-0,064	0,425	0,152	0,0039	-0,954	0,027	-0,823	0,0001
14	0,377	0,335	0,337	0,0001	0,013	0,485	0,160	0,0033	-0,973	0,016	-0,838	0,0001
15	0,382	0,326	0,339	0,0001	-0,055	0,412	0,148	0,0093	-0,963	0,022	-0,843	0,0001
16	0,372	0,317	0,384	0,0001	-0,128	0,395	0,182	0,0022	-0,959	0,024	-0,861	0,0001
17	0,350	0,390	0,414	0,0001	-0,267	0,430	0,207	0,0014	-0,956	0,029	-0,869	0,0001
18	0,526	0,307	0,397	0,0001	-0,075	0,417	0,197	0,0065	-0,958	0,026	-0,874	0,0001

ring	RadDiam vs. MFA				RadDiam vs. MOE				RadDiam vs. Wt			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-0,577	0,265	-0,096	0,0640	0,102	0,547	-0,025	0,6335	-1,402	1,166	0,029	0,5799
3	-0,356	0,320	-0,040	0,4350	-0,382	0,453	-0,108	0,0375	.	.	-0,098	0,0584
4	-0,380	0,318	-0,039	0,4518	-0,270	0,470	-0,099	0,0561	.	.	-0,117	0,0234
5	-0,240	0,331	-0,052	0,3185	-0,437	0,349	-0,093	0,0723	-1,358	0,688	-0,181	0,0004
6	-0,323	0,300	-0,079	0,1293	-0,350	0,361	-0,097	0,0616	-1,125	0,146	-0,232	0,0001
7	-0,267	0,307	-0,069	0,1803	-0,334	0,347	-0,112	0,0299	-0,904	0,082	-0,268	0,0001
8	-0,272	0,310	-0,096	0,0650	-0,379	0,335	-0,102	0,0481	-0,804	0,141	-0,278	0,0001
9	-0,159	0,338	-0,083	0,1106	-0,502	0,282	-0,125	0,0160	-0,749	0,164	-0,284	0,0001
10	-0,103	0,337	-0,080	0,1230	-0,535	0,252	-0,140	0,0069	-0,698	0,176	-0,300	0,0001
11	-0,035	0,347	-0,061	0,2399	-0,600	0,225	-0,165	0,0015	-0,691	0,172	-0,304	0,0001
12	-0,046	0,359	-0,052	0,3257	-0,622	0,229	-0,184	0,0004	-0,648	0,185	-0,307	0,0001
13	-0,067	0,359	-0,052	0,3283	-0,552	0,249	-0,189	0,0003	-0,644	0,185	-0,311	0,0001
14	-0,075	0,340	-0,045	0,4111	-0,462	0,267	-0,206	0,0001	-0,650	0,191	-0,324	0,0001
15	-0,079	0,354	-0,058	0,3128	-0,465	0,257	-0,219	0,0001	-0,640	0,189	-0,349	0,0001
16	0,052	0,385	-0,078	0,1894	-0,607	0,219	-0,204	0,0006	-0,694	0,162	-0,324	0,0001
17	0,130	0,505	-0,076	0,2465	-0,774	0,174	-0,217	0,0008	-0,750	0,146	-0,325	0,0001
18	0,650	0,468	-0,084	0,2498	-0,845	0,120	-0,213	0,0033	-0,615	0,207	-0,336	0,0001

ring	RadDiam vs. SpecSurf			MOE vs. Wt			MOE vs. SpecSurf		
	genetic	phenotypic		genetic	phenotypic		genetic	phenotypic	
	corr.	error	Person r P-value	corr.	error	Person r P-value	corr.	error	Person r P-value
2	0,880	0,163	-0,015 0,7737	1,477	2,022	-0,030 0,5623	-0,566	0,696	0,052 0,3200
3	0,930	0,095	0,120 0,0202	.	.	-0,061 0,2377	-0,577	0,709	0,063 0,2246
4	1,715	1,855	0,145 0,0049	.	.	-0,113 0,0284	-1,362	1,150	0,094 0,0699
5	1,086	0,103	0,200 0,0001	.	.	-0,077 0,1377	-1,432	0,838	0,042 0,4203
6	0,979	0,019	0,233 0,0001	1,542	1,067	-0,026 0,6200	-1,275	0,406	-0,025 0,6269
7	0,780	0,150	0,258 0,0001	1,315	0,464	-0,001 0,9779	-1,141	0,163	-0,068 0,1874
8	0,721	0,165	0,264 0,0001	1,248	0,325	0,060 0,2494	-1,104	0,111	-0,136 0,0084
9	0,686	0,176	0,266 0,0001	1,286	0,344	0,119 0,0215	-1,147	0,148	-0,191 0,0002
10	0,638	0,187	0,280 0,0001	1,082	0,078	0,189 0,0003	-0,987	0,011	-0,254 0,0001
11	0,641	0,180	0,276 0,0001	1,073	0,066	0,241 0,0001	-0,996	0,003	-0,300 0,0001
12	0,608	0,190	0,274 0,0001	1,028	0,026	0,291 0,0001	-0,943	0,047	-0,338 0,0001
13	0,595	0,195	0,272 0,0001	0,915	0,069	0,312 0,0001	-0,832	0,124	-0,352 0,0001
14	0,593	0,205	0,282 0,0001	0,779	0,160	0,352 0,0001	-0,718	0,188	-0,385 0,0001
15	0,578	0,205	0,306 0,0001	0,814	0,126	0,370 0,0001	-0,769	0,147	-0,402 0,0001
16	0,649	0,176	0,276 0,0001	0,875	0,093	0,386 0,0001	-0,812	0,131	-0,416 0,0001
17	0,723	0,156	0,284 0,0001	0,691	0,252	0,352 0,0001	-0,647	0,275	-0,376 0,0001
18	0,573	0,216	0,302 0,0001	0,862	0,121	0,400 0,0001	-0,719	0,219	-0,425 0,0001

ring	TanDiam vs. Coars				TanDiam vs. CellPop				TanDiam vs. MFA			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	.	.	0,895	0,0001	.	.	-0,899	0,0001	.	.	0,109	0,0358
3	.	.	0,882	0,0001	.	.	-0,865	0,0001	.	.	0,128	0,0132
4	.	.	0,843	0,0001	.	.	-0,838	0,0001	.	.	0,164	0,0015
5	.	.	0,825	0,0001	.	.	-0,800	0,0001	.	.	0,156	0,0025
6	.	.	0,801	0,0001	.	.	-0,779	0,0001	.	.	0,089	0,0849
7	.	.	0,768	0,0001	.	.	-0,768	0,0001	.	.	0,044	0,3944
8	.	.	0,736	0,0001	.	.	-0,775	0,0001	.	.	-0,002	0,9680
9	.	.	0,712	0,0001	-1,582	13,923	-0,781	0,0001	.	.	-0,043	0,4053
10	.	.	0,686	0,0001	-0,466	0,666	-0,782	0,0001	.	.	-0,082	0,1127
11	-1,206	0,505	0,670	0,0001	-0,471	0,457	-0,787	0,0001	-1,621	1,095	-0,107	0,0405
12	-0,447	0,587	0,666	0,0001	-0,496	0,354	-0,786	0,0001	-1,118	0,141	-0,117	0,0257
13	-0,094	0,603	0,658	0,0001	-0,496	0,323	-0,784	0,0001	-0,910	0,088	-0,128	0,0155
14	-0,379	0,588	0,639	0,0001	-0,592	0,279	-0,783	0,0001	-0,742	0,218	-0,140	0,0099
15	-0,078	0,560	0,635	0,0001	-0,619	0,257	-0,780	0,0001	-0,682	0,259	-0,160	0,0048
16	0,147	0,529	0,624	0,0001	-0,618	0,248	-0,787	0,0001	-0,712	0,256	-0,154	0,0096
17	0,018	0,683	0,629	0,0001	-0,602	0,316	-0,797	0,0001	-0,700	0,387	-0,160	0,0138
18	0,156	0,582	0,603	0,0001	-0,747	0,200	-0,779	0,0001	-0,456	0,912	-0,235	0,0012

ring	TanDiam vs. MOE				TanDiam vs. Wt				TanDiam vs. SpecSurf			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	.	.	0,006	0,9047	.	.	0,747	0,0001	.	.	-0,748	0,0001
3	.	.	-0,056	0,2829	.	.	0,724	0,0001	.	.	-0,728	0,0001
4	.	.	-0,115	0,0265	.	.	0,679	0,0001	.	.	-0,693	0,0001
5	.	.	-0,089	0,0869	.	.	0,665	0,0001	.	.	-0,687	0,0001
6	.	.	-0,050	0,3336	.	.	0,621	0,0001	.	.	-0,646	0,0001
7	.	.	-0,032	0,5404	.	.	0,561	0,0001	.	.	-0,593	0,0001
8	.	.	-0,001	0,9867	.	.	0,498	0,0001	.	.	-0,528	0,0001
9	.	.	0,020	0,6941	.	.	0,446	0,0001	.	.	-0,472	0,0001
10	1,818	2,253	0,045	0,3927	-1,406	0,931	0,389	0,0001	1,168	0,317	-0,416	0,0001
11	1,102	0,146	0,049	0,3502	-0,970	0,038	0,346	0,0001	0,680	0,318	-0,375	0,0001
12	0,702	0,299	0,049	0,3486	-0,610	0,314	0,325	0,0001	0,425	0,388	-0,358	0,0001
13	0,511	0,377	0,052	0,3229	-0,397	0,380	0,304	0,0001	0,268	0,398	-0,341	0,0001
14	0,294	0,439	0,048	0,3799	-0,675	0,255	0,262	0,0001	0,551	0,311	-0,297	0,0001
15	0,192	0,430	0,056	0,3309	-0,495	0,329	0,243	0,0001	0,354	0,368	-0,283	0,0001
16	0,174	0,452	0,049	0,4121	-0,299	0,382	0,222	0,0002	0,178	0,395	-0,264	0,0001
17	0,142	0,628	0,048	0,4630	-0,331	0,439	0,202	0,0018	0,279	0,446	-0,249	0,0001
18	-0,232	0,567	0,122	0,0955	-0,308	0,430	0,177	0,0146	0,207	0,437	-0,213	0,0033

ring	MFA vs. MOE				MFA vs. Wt				MFA vs. SpecSurf			
	genetic		phenotypic		genetic		phenotypic		genetic		phenotypic	
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2	-0,743	0,252	-0,833	0,0001	0,642	0,723	0,321	0,0001	-0,614	0,458	-0,320	0,0001
3	-0,781	0,216	-0,876	0,0001	.	.	0,314	0,0001	-0,684	0,391	-0,315	0,0001
4	-0,776	0,209	-0,890	0,0001	.	.	0,362	0,0001	-0,581	0,654	-0,334	0,0001
5	-0,719	0,236	-0,893	0,0001	-0,145	0,906	0,350	0,0001	0,043	0,649	-0,303	0,0001
6	-0,702	0,240	-0,895	0,0001	-0,101	0,624	0,305	0,0001	0,047	0,527	-0,243	0,0001
7	-0,709	0,232	-0,897	0,0001	-0,163	0,522	0,272	0,0001	0,137	0,449	-0,197	0,0001
8	-0,661	0,277	-0,900	0,0001	-0,137	0,489	0,228	0,0001	0,122	0,426	-0,144	0,0051
9	-0,651	0,281	-0,903	0,0001	-0,308	0,439	0,171	0,0009	0,272	0,399	-0,091	0,0807
10	-0,668	0,252	-0,901	0,0001	-0,253	0,415	0,115	0,0273	0,234	0,384	-0,039	0,4510
11	-0,664	0,257	-0,901	0,0001	-0,292	0,395	0,063	0,2303	0,282	0,368	0,008	0,8727
12	-0,637	0,303	-0,899	0,0001	-0,215	0,414	0,018	0,7308	0,197	0,394	0,045	0,3949
13	-0,655	0,275	-0,898	0,0001	-0,182	0,412	0,003	0,9583	0,161	0,396	0,055	0,2954
14	-0,724	0,200	-0,893	0,0001	-0,097	0,406	-0,030	0,5877	0,081	0,389	0,082	0,1354
15	-0,720	0,201	-0,885	0,0001	-0,173	0,394	-0,028	0,6206	0,177	0,380	0,081	0,1573
16	-0,653	0,281	-0,880	0,0001	-0,176	0,426	-0,031	0,6091	0,214	0,409	0,083	0,1622
17	-0,484	0,568	-0,874	0,0001	0,193	0,549	0,021	0,7533	-0,185	0,540	0,025	0,7043
18	-0,414	0,948	-0,873	0,0001	-0,167	0,882	-0,017	0,8167	0,017	0,873	0,061	0,4076

ring	Coars vs. CellPop			Coars vs. MFA				Coars vs. MOE				
	genetic		phenotypic	genetic		phenotypic		genetic		phenotypic		
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2			-0,835	0,0001			0,237	0,0001			-0,020	0,6968
3			-0,752	0,0001			0,265	0,0001			-0,083	0,1083
4			-0,682	0,0001			0,328	0,0001			-0,144	0,0051
5			-0,627	0,0001			0,320	0,0001			-0,109	0,0354
6			-0,575	0,0001			0,265	0,0001			-0,061	0,2418
7			-0,528	0,0001			0,232	0,0001			-0,042	0,4193
8			-0,507	0,0001			0,176	0,0006			0,023	0,6628
9			-0,497	0,0001			0,114	0,0272			0,076	0,1448
10	0,926	0,132	-0,481	0,0001	-1,306	0,718	0,052	0,3166			0,140	0,0070
11	0,528	0,474	-0,480	0,0001	-1,163	0,265	0,002	0,9671	1,791	1,679	0,179	0,0006
12	0,251	0,492	-0,482	0,0001	-0,764	0,264	-0,040	0,4418	1,309	0,471	0,216	0,0001
13	0,136	0,471	-0,481	0,0001	-0,626	0,350	-0,060	0,2601	1,035	0,041	0,233	0,0001
14	0,173	0,517	-0,465	0,0001	-0,526	0,435	-0,090	0,0986	0,950	0,058	0,261	0,0001
15	0,126	0,443	-0,450	0,0001	-0,554	0,364	-0,103	0,0702	0,877	0,111	0,279	0,0001
16	0,079	0,436	-0,452	0,0001	-0,453	0,451	-0,109	0,0664	0,765	0,212	0,296	0,0001
17	0,303	0,469	-0,466	0,0001	0,094	0,783	-0,067	0,3026	0,488	0,509	0,256	0,0001
18	-0,043	0,446	-0,435	0,0001	0,064	1,135	-0,124	0,0883	0,445	0,475	0,325	0,0001

ring	Coars vs. Wt			Coars vs. SpecSurf				CellPop vs. MFA				
	genetic		phenotypic	genetic		phenotypic		genetic		phenotypic		
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2			0,947	0,0001			-0,915	0,0001			-0,064	0,2183
3			0,947	0,0001			-0,909	0,0001			-0,089	0,0873
4			0,950	0,0001			-0,899	0,0001	2,753	7,991	-0,101	0,0514
5			0,951	0,0001			-0,905	0,0001	1,532	0,894	-0,087	0,0940
6			0,944	0,0001			-0,906	0,0001	1,275	0,308	-0,015	0,7711
7			0,934	0,0001			-0,905	0,0001	0,940	0,050	0,016	0,7634
8			0,923	0,0001			-0,899	0,0001	0,823	0,131	0,063	0,2229
9			0,910	0,0001			-0,892	0,0001	0,674	0,227	0,078	0,1303
10	0,975	0,050	0,896	0,0001	-1,204	0,423	-0,886	0,0001	0,541	0,280	0,102	0,0508
11	0,848	0,200	0,881	0,0001	-0,978	0,028	-0,879	0,0001	0,459	0,314	0,101	0,0536
12	0,799	0,203	0,870	0,0001	-0,876	0,123	-0,874	0,0001	0,410	0,338	0,098	0,0623
13	0,781	0,197	0,861	0,0001	-0,849	0,134	-0,870	0,0001	0,396	0,342	0,106	0,0441
14	0,736	0,266	0,850	0,0001	-0,829	0,173	-0,862	0,0001	0,310	0,340	0,108	0,0480
15	0,778	0,186	0,842	0,0001	-0,823	0,147	-0,857	0,0001	0,295	0,355	0,129	0,0230
16	0,771	0,186	0,840	0,0001	-0,830	0,139	-0,857	0,0001	0,228	0,399	0,136	0,0222
17	0,817	0,171	0,825	0,0001	-0,890	0,105	-0,843	0,0001	0,260	0,535	0,134	0,0391
18	0,782	0,182	0,824	0,0001	-0,813	0,153	-0,836	0,0001	0,020	0,863	0,178	0,0141

ring	CellPop vs. MOE			CellPop vs. Wt				CellPop vs. SpecSurf				
	genetic		phenotypic	genetic		phenotypic		genetic		phenotypic		
	corr.	error	Person r	P-value	corr.	error	Person r	P-value	corr.	error	Person r	P-value
2			0,030	0,5586			-0,642	0,0001			0,655	0,0001
3	-1,890	8,598	0,118	0,0229			-0,521	0,0001	-1,138	1,316	0,533	0,0001
4			0,151	0,0034			-0,438	0,0001	-2,148	11,288	0,453	0,0001
5	-0,907	0,145	0,134	0,0093			-0,371	0,0001	-2,357	4,922	0,392	0,0001
6	-0,693	0,314	0,102	0,0490	2,438	3,977	-0,284	0,0001	-1,976	1,959	0,312	0,0001
7	-0,435	0,409	0,096	0,0640	1,593	0,892	-0,198	0,0001	-1,253	0,283	0,235	0,0001
8	-0,223	0,450	0,068	0,1889	1,267	0,291	-0,146	0,0047	-1,023	0,019	0,180	0,0005
9	0,021	0,452	0,072	0,1671	1,126	0,121	-0,102	0,0484	-0,945	0,043	0,135	0,0092
10	0,168	0,398	0,067	0,1994	0,982	0,014	-0,051	0,3265	-0,838	0,109	0,084	0,1050
11	0,251	0,377	0,083	0,1132	0,897	0,074	-0,019	0,7208	-0,784	0,135	0,057	0,2787
12	0,326	0,378	0,097	0,0646	0,787	0,137	0,003	0,9538	-0,703	0,172	0,040	0,4494
13	0,301	0,366	0,097	0,0680	0,729	0,167	0,022	0,6827	-0,643	0,199	0,027	0,6155
14	0,306	0,338	0,112	0,0391	0,791	0,136	0,061	0,2672	-0,706	0,174	-0,012	0,8295
15	0,339	0,316	0,115	0,0433	0,747	0,154	0,093	0,1026	-0,672	0,184	-0,041	0,4688
16	0,457	0,299	0,111	0,0636	0,700	0,173	0,095	0,1126	-0,628	0,200	-0,040	0,5013
17	0,570	0,327	0,121	0,0633	0,754	0,161	0,105	0,1068	-0,680	0,196	-0,052	0,4246
18	0,673	0,245	0,085	0,2429	0,625	0,217	0,140	0,0542	-0,558	0,236	-0,099	0,1761