

Density and wood biomass development in whole-tree analyses of Scots pine, and aspects on heritability estimates

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(Received 25th January 2011)

Abstract

Twelve trees in a 36 year old full-sib progeny plantation, testing a part of the Scots pine breeding population, were analysed for wood density and the width of the earlywood and latewood sections in each annual ring. Wood samples (stem discs) were taken with 1 m intervals along the stem and the analyses covered thus the whole stem. Based on these data, the biomass of the earlywood and latewood of each annual ring in each 1 meter stem section was estimated. Latewood density increased from pith to bark while it decreased from stem base to top. Earlywood density was of similar size both radially and vertically. The biomass in each annual ring increased until around ring number 10 from pith for both wood types. For earlywood it then decreased while it remained quite constant for latewood. Latewood biomass decreased more rapidly towards the top of the tree than earlywood biomass. Heritabilities for earlywood and latewood in each annual ring at breast height (estimated in the same material in a previous study) were related to the corresponding biomasses to indirectly estimate overall heritability for wood density valid for the whole stem. The analyses indicate that the decrease in heritability for latewood density and increase for earlywood density, from the pith to bark, is compensated by the increase in latewood biomass in relation to earlywood biomass. Thus, the heritability of the latewood density and earlywood density seems to have the same influence on the overall heritability for density in the whole stem.

Key words: *Pinus sylvestris*, wood density, biomass, stem, earlywood, latewood, heritability, selection, genetic improvement.

Introduction

The demand for more effective utilization of the forest wood resource increases continuously and the recent focus on the forest resources for the development of a sustainable society has intensified this trend. The forest used for commercial wood supply is to an increasingly extent planted forests (c.f. CARLE and HOLMGREN, 2008) in which use of genetically improved plant materials is an important mean to improve growth and wood properties. This also means that the forests are more intensively managed and the trees are harvested at younger ages thanks to an increased use of the wood from trees felled in thinnings regimes and shorter rotations.

Biomass production and the allocation to the stem in relation to branches are important aspects when evaluating productivity of merchantable wood. Important factors are then the crown architecture through branching and leaf area (CHMURA et al., 2007) and the stand treatment, as was shown for Scots pine (*Pinus sylvestris* L.) in EGNELL and VALINGER (2003). The development of biomass can thus vary between trees depending on its competitive situation in the stand and silviculture regime. Besides stem volume is wood density an important component in stem biomass, and due to the heterogeneity of the wood in the stem of a forest tree, such as Scots pine (*Pinus sylvestris* L.), can the wood density vary considerably, making the stem biomass to a complex trait. There are different models for the wood structure in a stem, but a traditional description is to define the first growth rings from the pith as juvenile wood and after a transition zone, mature wood is formed (ZOBEL and SPRAGUE, 1998). The transition from juvenile to mature wood is difficult to define and varies between species and for different wood properties. For pines there are often large differences in wood properties between juvenile and mature wood, and the transition is often rather abrupt (BENDTSEN, 1978; KENNEDY, 1995). Examples of transition ages are 10-14 years for loblolly pine (*Pinus taeda* L.) (LOO et al., 1985; SZYMANSKI and TAUER, 1991) and radiata pine (*Pinus radiata* D. Don) (ZAMUDIO et al., 2005), whereas 12-30 growth rings has been reported for Scots pine (SAUTER et al., 1999; MATSSON et al., 2002; ELIASSON, 2003; FRIES and ERICSSON, 2009). Another definition of the different wood types is made by COWN (1992) and BURDON et al. (2004) who name the central cylinder from the base to the top of the tree corewood. This is furthermore differentiated from the ground in juvenile, transition, mature and top corewood. These vertical delineations are rather determined by height from ground than by growth stage. In addition, there is another vertical differentiation so that below ca 5 m height there is a cone-formed part of the corewood named juvenile wood. Factors that influence the change from juvenile wood to mature wood are claimed to be the culmination of annual height increment (KUČERA, 1994) and silvicultural measures which affect initial growth rate (COWN, 1992; AMARASEKARA and DENNE, 2002).

It is well known that young trees, e.g. from thinnings, contain a large fraction of juvenile wood with specific characteristics such as shorter fibres with thinner cell walls, lower wood density, lower modulus of elasticity (MOE), higher microfibril angle (MFA), higher coarseness, and higher lignin-percentage but lower α -cellulose-percentage (cf. BENDTSEN, 1978; DUCHESNE et al., 1997; ZOBEL and SPRAGUE, 1998; GROOM et al., 2002a and b; MOTT et al., 2002; BURDON et al., 2004).

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In addition to the above wood types includes each annual ring an earlywood and a latewood part, also with large differences in cell structure, moisture content and wood density. In the earlywood dominates long and slender fibres, while the latewood has cells with thick walls and they give lower strength of the pulp and paper (WATSON and BRADLEY, 2004). Furthermore has in Scots pine the latewood more than twice as high density as the earlywood (FRIES and ERICSSON, 2009).

The genetic parameters for wood and fibre traits for earlywood and latewood differ (see e.g. LOO et al., 1984; HANNRUP and EKBERG, 1998; LOUZADA and FONSECA, 2002; FRIES and ERICSSON, 2009), and to estimate more correct genetic parameters for the whole stem, the proportions of the different wood types in the stem for trees of different ages is needed to be known.

In the present study we analysed wood density and ring width at different height levels and for earlywood and latewood separately. Using those measures we then determined the wood biomass for each component of all annual rings and all heights and by this totally in the stem. The studied trees were 12 windthrows in a 35 year old progeny test of Scots pine which is included in the Swedish breeding population of Scots pine for north-central Sweden. Due to the value of the progeny test, only windthrows could be used making the study limited. The relative amounts of earlywood and latewood biomasses in the stem were related to the heritabilities of earlywood and latewood densities, respectively, thus obtaining a weighed heritability for whole-tree density valid for the whole stem. The heritabilities that were used were estimated in FRIES and ERICSSON (2009) and were based on 5 mm increment cores taken at breast height (1.3 m height), and including annual ring numbers 12–21 from pith. The aims with the present study were thus:

- 1) to analyse the development of the wood density, ring width and biomass of the earlywood and latewood sections, from pith to bark and from the stem base to the top,
- 2) to estimate the total biomass of the earlywood and latewood in each annual ring from pith to bark, along the stem to the top and totally for the stem, and
- 3) to weigh the above biomasses with heritabilities for earlywood and latewood density for each annual ring (estimated in an earlier study of the same full-sib progeny material), and by this to approximate a more relevant heritability for total wood density the whole stem.

Material and Methods

Test material and sample collection

The study examines wood samples collected from full-sib progenies of plus trees in the Swedish Scots pine breeding program for use at latitude 62–64°N in Sweden. The progeny test, Grundtjärn (S23F711261, at 63°33'N, 17°25'E and 320 m elevation), was established by Skogforsk at a non-sloping sandy moraine with an average site index for the locality, i.e. ca T20 (projected dominant height after 100 years equals ca 20 m corresponding to a site productivity of about 3 m³sk per

hectare and year (HÄGGLUND and LUNDMARK, 1982)). It was planted in single tree plots in September 1971 with plants seeded in April 1971, i.e. after one growing season, and the test includes 184 full-sib families from controlled crosses between 50 phenotypically selected first generation parents. In early October 2007, stem discs were collected from 12 well growing trees that in autumn 2006 had blown down after a thinning in February 2006, i.e. at the age 36 growing seasons. Since the trees were left after a thinning they could be defined as a sample of well growing trees in the trial. The positions of the trees were not identified, and thus not which full-sib families they represented. From each sample tree, stem discs of about 5 cm in thickness were cut at height intervals of 1 meter starting at 1 meter height. Tree height varied between 10.1 m and 13.5 m (mean 12.1 m, standard deviation 0.95 m) and between 10 and 12 stem discs could be collected from each tree. Identification (tree number and sample height), and north and south direction were indicated on each disc. If the sample height coincided with a whorl, adjustment up or down was made for this sample height, but the ordinary 1 meter-interval was kept above the adjusted sample. After collecting the stem discs, they were stored in +8°C cold room before preparation of samples for analyses.

Sample preparation

From each disc two radial wood strips were prepared in two steps. In the last step, the strips were sawn to 8–10 mm longitudinal height and 2.2 ± 0.1 mm tangential thickness using a twin-blade circular saw making very even surfaces (the exact thickness was adjusted for in the X-ray analysis). For six trees, the strips represented north-south direction and for six trees they represented the east-west direction. The strips were conditioned in the chamber of the density scanner for about 1 week in relative air humidity of about 15–25% prior to analysis.

Wood density measurements

Wood density was measured using an Itrax Wood scanner (Cox Analytical Instruments, Gothenburg, Sweden, [<http://coxsys.se/>, June 2011]). The instrument is a direct X-ray scanning instrument with a resolution of $25 \times 25 \mu\text{m}$. Procedure for the measurements is described in LINDBERG (2001) and BERGSTEN et al. (2001). The technical data for the X-ray measurements are given in FRIES and ERICSSON (2006). Around 30 wood samples and one reference strip made of cellulose acetate with a gradient of thicknesses, corresponding to known wood densities, were included in each run. The X-ray images were then analysed by the software WinDendro (Regent Instruments Inc., Quebec, Canada, [<http://www.regentinstruments.com/>, June 2011]) for density calculations. Grey scales in the X-ray images were transferred to wood densities based on the reference strip. For each growth ring, ring width, average ring density, earlywood density, latewood density, early- and latewood proportions and minimum and maximum density were calculated. The earlywood was defined as the wood with density up to 0.50 g/cm^3 and the latewood with density above 0.50 g/cm^3 . The borders between

annual rings were set automatically but were then adjusted manually in case of e.g. leaning annual rings. Each image was visually examined, and for 45 annual rings (1.3%) density measurements were potentially unreliable due to wood irregularities, such as compression wood and cracks, and were consequently excluded and treated as missing values.

Data treatment

Wood biomass at the different heights was calculated for each 1 meter section and each direction separately using the wood biomass estimate in the middle of the 1 meter-section. A perfect circular stem and even taper was approximated, and the total latewood biomass for the 1 m height interval x , i.e. LWmass (Height inter-

val x), (e.g. $x=0.5-1.5$ m) was then based on the following equation:

$$LWmass(\text{Height interval } x) [\text{gram}] = \sum_{n=1}^n LD \text{ ring}_{1 \rightarrow n} \quad [1]$$

$$[\text{gram} \times \text{cm}^{-3}] \times LW \text{ arearing}_{1 \rightarrow n} [\text{mm}^2] \times 1000 \text{ mm} \times 0.5$$

where $LD \text{ ring}_{1 \rightarrow n}$ is the latewood density for ring 1 to n , $LW \text{ arearing}_{1 \rightarrow n}$ is the cross-section area of ring 1 to n , and n is the ring number of the outermost annual ring. The corresponding equation was used for EWmass. The cross section area of ring n was estimated using the equation for circle area:

$$\text{circle area} = r^2 \times \pi. \quad [2]$$

For each ring section (earlywood and latewood), the accumulated ring section areas inside that ring section

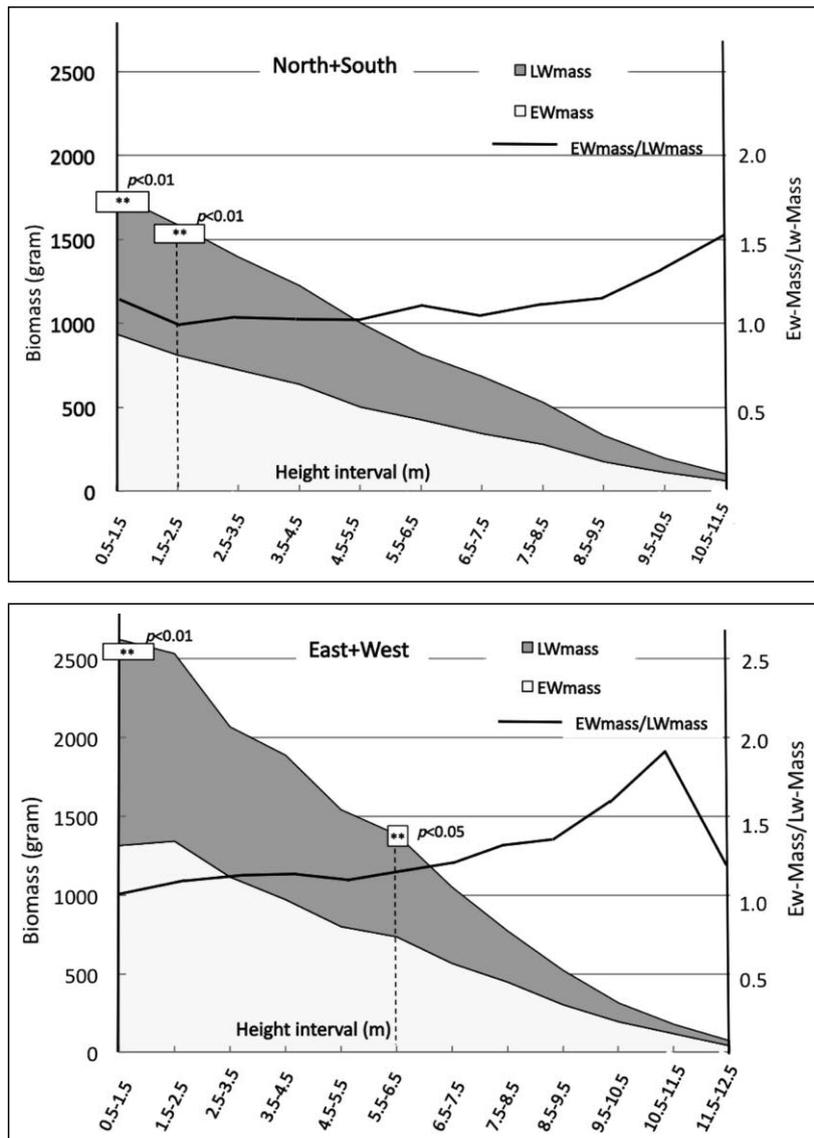


Figure 1. – Development of the biomass of the earlywood and latewood for different height intervals (1 meter sections) from height interval 0.5-1.5 m to the top, and the development of the quotient EWmass/LWmass. All growth rings are included for the different intervals. Significant differences between directions are indicated.

- a) Average of the north and south directions (tree nos. 2, 3, 4, 6, 8 and 10).
- b) Average of the east and west directions (tree nos. 1, 5, 7, 9, 11 and 12).

was subtracted from the accumulated ring section areas including the ring section in question. Multiplication by 0.5 is necessary for keeping the different directions separate.

To be able to compare annual rings at different heights in the tree but of the same degree of juvenility, ring number from pith was used. The disadvantage with this is that annual rings compared between height levels (the same ring number from the pith) could be formed under different weather conditions. Both factors (ring number from pith and annual weather conditions) can however not be kept identical, and since the same age from pith is more important for wood traits (COWN,

1992) we chose this factor determining the age. The genetic parameters used were estimated in a previous study of the same progeny test (FRIES and ERICSSON, 2009).

Results

Difference between directions

Differences between directions for the same annual ring number from bark over all trees and height levels and within the same height level over all trees were tested statistically, but there was with a few exceptions no significant difference between the directions for any

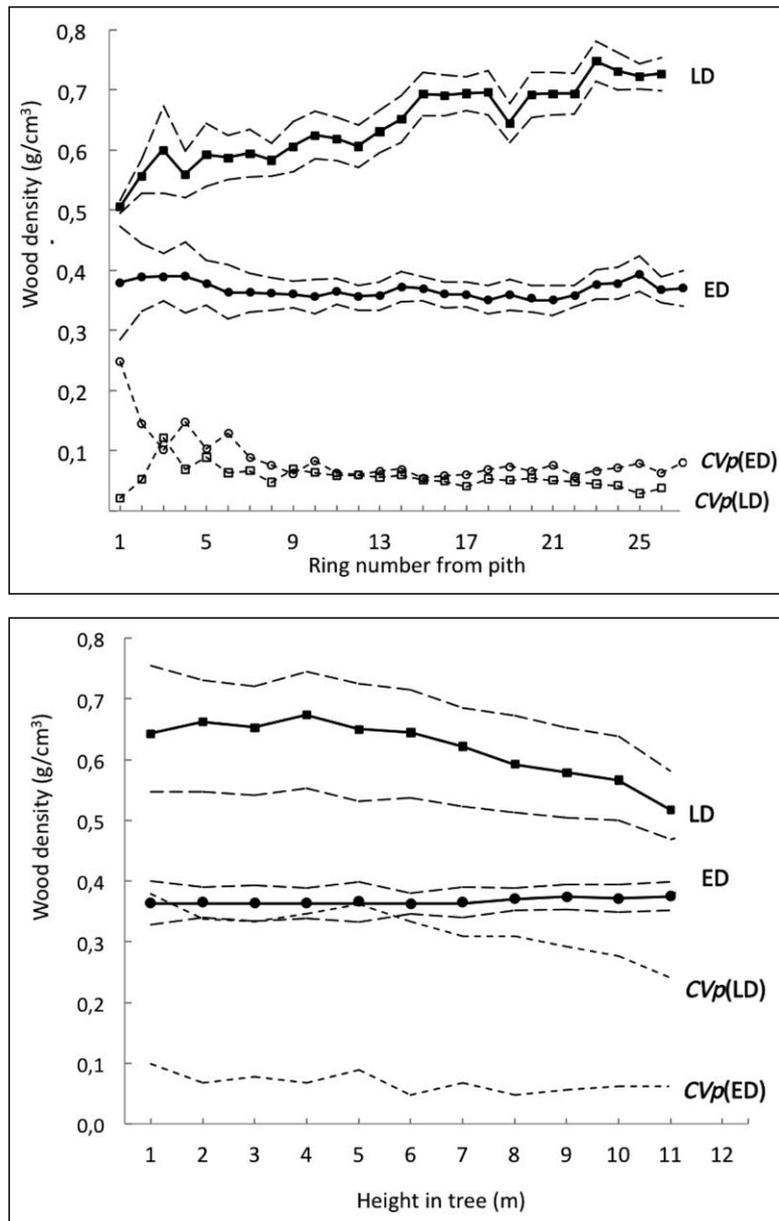


Figure 2. – Development of earlywood density (ED) and latewood density (LD) (broken lines shows ±1 standard deviation), and development for phenotypic coefficients of variations ($CV_p(ED)$ and $CV_p(LD)$, respectively).

- a) Development from pith to bark. Averages for each ring number over all heights levels.
- b) Development from the stem base to the top. Averages for each height level over all annual rings from pith to bark.

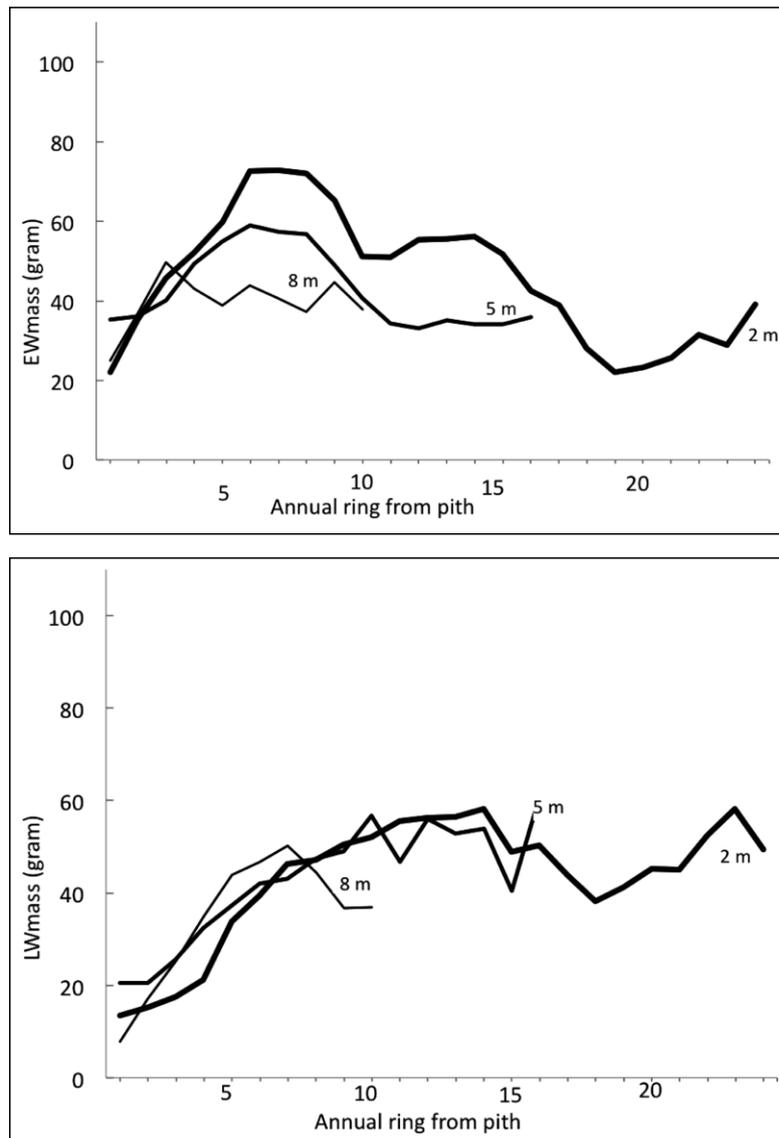


Figure 3. – Development of EWmass and LWmass per annual ring (EWmass/r and LWmass/r, respectively) at 2, 5 and 8 m height. All trees and all directions. Ring number one has been excluded due to low precision in measurements.

- a) EWmass/r at 2, 5 and 8 m.
b) LWmass/r at 2, 5 and 8 m.

of the traits (EW, LW, ED LD, EWmass and LWmass). *Fig. 1a* includes thus both north and south direction and *Fig. 1b* east and west direction. The exceptions with significant differences were for LWmass between north and south side at height level 0.5–1.5 meter and 1.5–2.5 meter ($p \leq 0.01$) (*Fig. 1a*) and also for LWmass between east and west side for the height intervals 0.5–1.5 and 5.5–6.5 meter ($p \leq 0.01$ and $p \leq 0.05$, respectively) (*Fig. 1b*). In addition, LD and EW differed significantly between north and south directions for the interval 0.5–1.5 meter ($p < 0.05$) and ($p \leq 0.001$), respectively.

Development of wood density

Earlywood density (ED) was constant from pith to bark, while LD increased (*Fig. 2a*). Also from the stem

base to the top ED was constant, while LD showed a clear decrease (*Fig. 2b*).

Wood biomass

As expected, the biomass of the earlywood (EWmass) and latewood (LWmass) decreased from the stem base to the top (*Fig. 1a–b*). There the tree profiles show that the directions differed slightly in total biomass development along the stem, however generally not significantly. On the north and south sides both the EWmass and LWmass decreased more slowly than on the east and west sides. At the stem base EWmass and LWmass was similar. Towards the top of the tree, the quotient EWmass/LWmass increased indicating that LWmass decreased more rapidly than EWmass, to between 50

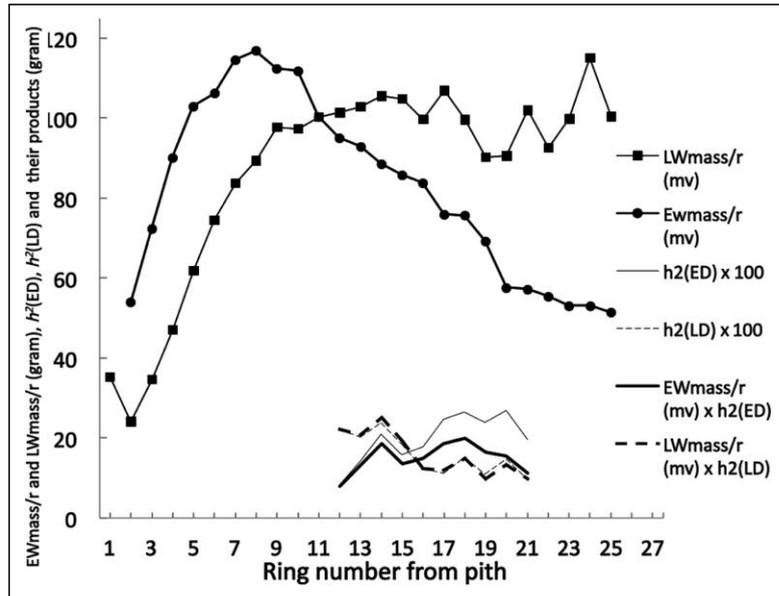


Figure 4. – Development of EWmass/r and LWmass/r (both directions and all height intervals), heritabilities of earlywood and latewood density (from FRIES and ERICSSON (2009)), and their products per annual ring in the whole stem from pith to bark (see also Fig. 5).

and 70% of the EWmass (Fig. 1a–b). Note that different trees were analysed in the north–south direction than in the east–west, so the levels of the biomasses are not comparable, but the pattern is the same: towards the top LWmass decreases in relation to the EWmass. Going from the pith to the bark, both EWmass and LWmass per annual ring (EWmass/r and LWmass/r) was lowest close to the pith and then increased to ring 8

(EWmass/r) and 13 (ca.) (LWmass/r) (Fig. 3; Fig. 4). Then EWmass/r decreased from nearly 120 to 40 gram per annual ring, while LWmass/r stabilized at ca 100 gram per annual ring (Fig. 4). Evaluations of each 11 or 12 height levels separately indicate that these trends were the same at different height levels, here exemplified by height levels 2, 5 and 8 meters (Fig. 3a–b). The standard deviations were however large. If EWmass/r is

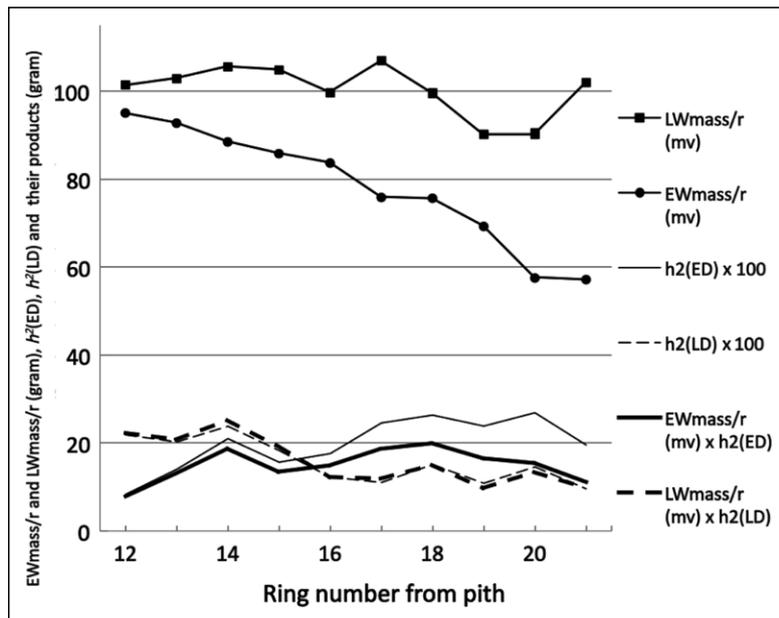


Figure 5. – Development of the heritabilities for ED and LD ($h^2(ED)$ and $h^2(LD)$) (from FRIES and ERICSSON (2009)), EWmass/r, LWmass/r (both directions), and the products $h^2(ED) \times EWmass/r$ and $h^2(LD) \times LWmass/r$, respectively. The presented section is between annual ring number 12 and 21, i.e. the section for which heritabilities were estimated.

multiplied with heritability for ED, $h^2(\text{ED})$, the decreasing trend for EWmass/r in *Fig. 4* is compensated by the increasing heritability for ED ($h^2(\text{ED})$), and $\text{EWmass}/r \times h^2(\text{ED})$ is quite constant (*Fig. 5*). $\text{LWmass}/r \times h^2(\text{LD})$ decreases on the other hand slowly and reaches the same level as $\text{EWmass}/r \times h^2(\text{ED})$ (*Fig. 5*).

Discussion

The trends in the present study agree on the whole with what has been stated in other studies. The increase in latewood density from pith to bark (here averages for all height levels) (*Fig. 2a*) was recognized also for e.g. *Pinus radiata* D. Don. (GAPARE et al., 2006) and in ZAMUDIO et al. (2005) (with the exclusion of ring nos. 1–8), for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (GARTNER et al., 2002), and in *Pinus pinaster* Ait. (GASPAR et al., 2008). Similarly, latewood density based on all annual rings from pith to bark, with the exception of the first 2 meters, decreased towards the top while earlywood density was quite constant (*Fig. 2b*). The same pattern was obtained for the three outermost annual rings in GARTNER et al. (2002), with the exception that LD was lower than expected and the initial increase continued to somewhat higher up. The increase in LD for the outermost annual rings both when going from the pith to bark and from the top to the stem base is logic since both transects imply a change from juvenile wood towards mature wood. In the present study, earlywood density was constant towards the top as also from pith to bark, as compared to the larger sample of the same material as in the present study in FRIES and ERICSSON (2009) which showed a slight tendency to increase: 0.345–0.360 with variation within the interval. ZAMUDIO et al. (2005), on the other hand, stated an apparent increase for ring number 9–14, while the pattern for lower ring numbers differed. According to *Fig. 3a–b*, the development of EWmass/r and LWmass/r at different height levels follow the same trend. For increasing height level, EWmass/r is however lower for the same annual ring from bark (*Fig. 3a*). LWmass/r is however similar for the different height levels although smaller diameter (*Fig. 3b*). The small sample size is however reflected in the large standard deviations. It is anyway noteworthy that the biomass of the earlywood (EWmass/r) decreases steadily from ring no. 8 although increasing stem diameter, while the biomass of the latewood (LWmass/r) is quite constant. The latewood increases thus its share of the wood biomass by increasing stem diameter at least up to annual ring 27. This is probably a combination of increasing density of the latewood from pith to bark while the earlywood density remains quite constant (*Fig. 2*), and that earlywood ring width decreases more rapidly than latewood ring width (FRIES and ERICSSON, 2009). This material was growing on lat. 63.5°N. According to STÄHL (1988), SAVVA et al. (2002) and ST-GERMAINE and KRAUSE (2008) have trees growing further to the north in comparable growth conditions lower wood density due to a thinner high density latewood section in relation to the earlywood section, as a result of a more rapid growth cessation in autumn

when the latewood is formed. It could thus be expected that by increasing ring number from the pith the development of LWmass/r , EWmass/r and the relation between them follow another pattern at other latitudes.

The similar development of the biomass at different height levels (*Fig. 3a–b*) indicate that the same properties for a certain ring number from pith independent of the height in the tree can be expected. Juvenility in Scots pine should thus be a general pattern for the whole stem, at least under similar growth conditions. This is in accordance with (COWN, 1992; BURDON et al., 2004) where it is claimed that the degree of juvenility of the wood is determined by the ring number from the pith.

In FRIES and ERICSSON (2009), large differences in heritability between earlywood density ($h^2(\text{ED})$) and latewood density ($h^2(\text{LD})$) were stated both for ring number 12 ($h^2(\text{ED})=0.083$ and $h^2(\text{LD})=0.22$) and up to ring number 21 ($h^2(\text{ED})=0.20$ and $h^2(\text{LD})=0.096$). These changes over years and between wood types indicate that a weighting of the heritabilities could improve the estimate for heritability for wood density for the whole stem. The biomasses the wood types represented (EWmass/r and LWmass/r , respectively) were thus multiplied with $h^2(\text{ED})$ and $h^2(\text{LD})$. For annual ring no. 12, the lower EWmass/r and lower $h^2(\text{ED})$ compared to $h^2(\text{LD})$ indicate that $h^2(\text{ED})$ has lower weight than $h^2(\text{LD})$ on the total heritability for wood density (*Fig. 4*; *Fig. 5*). However, at the end of the period (annual ring no. 21) the increase in $h^2(\text{ED})$ and decrease in $h^2(\text{LD})$ have resulted in equal influence from $h^2(\text{ED})$ and $h^2(\text{LD})$. The present data can't describe the development at higher ages, but if the trend with decreasing EWmass/r , rather unchanged LWmass/r (*Fig. 4*; *Fig. 5*) and unchanged $h^2(\text{ED})$ and decreasing $h^2(\text{LD})$ (*Fig. 4*; *Fig. 5*) remains, the rather equal influence of $h^2(\text{ED})$ and $h^2(\text{LD})$ should remain. According to our results, it should thus not be any reason to focus on the earlywood (thanks to higher heritability for the earlywood) or on the latewood (thanks to higher biomass of the latewood) when selecting for high total biomass. The high genetic and phenotypic correlations (0.72 and 0.57, respectively) between ED and LD obtained in FRIES and ERICSSON (2009) is a further argument for equal importance of $h^2(\text{ED})$ and $h^2(\text{LD})$ in genetic evaluation including wood density. Any of these heritabilities or whole ring heritability for density should thus be possible to use. This is in agreement with VARGAS-HERNANDEZ and ADAMS (1991) where it is claimed that the equal sizes of the heritability of the earlywood and latewood densities ($h^2_f=0.46$ and 0.51, respectively), and the high genetic correlation between them ($r_g=0.61$) makes the overall density equally effective as selection criteria as the separate components. LOUZADA and FONSECA (2002), on the other hand, claim that only earlywood density depends on genetic effects and could be used in selection, while latewood density shows large variation and is dependent on environmental effects. Referring to STÄHL (1988), SAVVA et al. (2002) and ST-GERMAINE and KRAUSE (2008) could latewood density be dependent on the duration of the growing season which could show annual (i.e. climatic) and latitudinal variation. Anyhow, using whole

ring density should eliminate the decrease in precision which is introduced when separating the earlywood and latewood in the density analysis. It should also reduce the time needed for measurements and so resources can instead be put on measuring additional trees.

As a summary, precise estimation of genetic parameters requires large data sets from progeny tests. The genetic parameters for the present material were estimated for breast height (FRIES and ERICSSON, 2009). To estimate the corresponding heritabilities for all height levels requires very large resources and is actually not realistic. According to the present limited study, it can be assumed that the genetic parameters for earlywood and latewood density are of similar size for the same ring number from the pith along the bole, at least for trees growing under the same growing conditions. The reason is that the degree of juvenility of the wood is determined by the ring number from the pith. It seems furthermore not necessary to focus on the earlywood (thanks to higher heritability for the earlywood) or on the latewood (thanks to higher biomass of the latewood) separately when selecting for high total biomass, at least at this age. Instead whole ring density and its heritability can be used.

Acknowledgements

The project was financed by Bo Rydins Stiftelse (Bo Rydin Foundation) and C.F. Lundströms Stiftelse who are acknowledged for economic support. The Forestry Research Institute of Sweden put the field test and information about it to our disposal.

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