J Wood Sci (2002) 48:467–472

ORIGINAL ARTICLE

Petri P. Kärenlampi · Mika Riekkinen

Pine heartwood formation as a maturation phenomenon

Received: June 13, 2001 / Accepted: December 19, 2001

Abstract The inverse of the relative increment rate of size is proposed as a measure of the maturity of a forest tree. The heartwood content within bole cross sections is modeled semiempirically using asymptotic fitting. It is shown that the present proposal for a definition of maturity statistically explains heartwood content far better than age or size. The heartwood content appears to be independent on growth rate and tree size.

Key words Age · Growth rate · *Pinus silvestris* · Size

Introduction

In many tree species the permeability of heartwood to liquid and gas is less than that of sapwood.[1,2] In some tree species, heartwood has chemical constituents that inhibit fungal activity.[3–5] These two properties make heartwood a material with natural decay resistance. Heartwood, with a significant extractives content, also has more stable dimensions when subjected to varying air humidity.[4,6,7]

Heartwood formation appears to take place only in trees exceeding a specified age; thereafter the proportion of heartwood increases with age.[6,8–11] On the other hand, the amount of heartwood appears to be negatively correlated with the growth rate of any tree.[8,6,11,12] However, fast-grown trees have a lower heartwood content only when they are compared with more slowly grown trees of the same size.[13,14] When the age is the same, large diameter trees appear to have a greater relative proportion of heartwood.[13,14]

The maturation of any plant is manifested in a variety of physiological changes. The sexual maturation of trees appears to be related to the accumulated number of cell divisions in the meristems, rather than age or size per se.[15–19] Some observations suggest that pine cambium maturity, judged on the basis of the change in wood basic density, is better described in terms of chronological age than in terms of the accumulated amount of production.[20]

It is well known that the decline in the relative increment rate of size due to age takes longer as growing conditions worsen. In other words, the relative growth at forest sites on poor soil or in a cool climate declines at an older age than the relative growth at sites where the soil is good and the climate is warm.[21–23] On the other hand, with favorable conditions for growth, trees tend to grow larger.[13,21–23] The relative proportions of biomass compartments (heartwood, sapwood, foliage, branches, roots) change along with tree maturation in a similar pattern at good and poor sites, although at good sites such transitions take place at a younger age and larger size.[24] Thus, it appears that within a particular tree species maturity cannot be described solely in terms of tree age, cambium age, or tree size.

No tree grows to infinite size. Thus, at some stage the increment rate of size declines and ultimately approaches zero. Observations propose that the relative increment rate of size generally decreases with maturation.[25–27] Thus, the inverse of the relative increment rate of size generally increases monotonically. We propose that the inverse of the relative increment rate of size can be used as a measure of maturity.

This proposed measure of maturity has the dimension of time. The ultimate outcome of maturation being death, the ultimate relative increment rate of size corresponds to zero per time unit, maturity thus approaching infinite time. On the other hand, because the size of a very young individual is small, the relative increment rate of size may be large and the proposed measure of maturity has a low value. The maturity of a newly established individual, however, does not correspond to zero. Also, this asymptote has a physiological correspondence: The establishment of an individual does not correspond to the origin of life.

Heartwood formation is a phase transition, where tissue that includes living cells becomes a tissue that no longer

---

P.P. Kärenlampi (✉) · M. Riekkinen
Faculty of Forestry, University of Joensuu, PO Box 111, FIN-80101 Joensuu, Finland
Tel. +358-13-251-4009; Fax +358-13-251-3590
e-mail: petri.karenlampi@joensuu.fi

includes cells with any metabolism. Furthermore, considering that the extreme outcome of maturation is death – a state where there is no metabolism – it is obvious that the extreme outcome of maturation refers to heartwood content of unity.

We intended to clarify experimentally to what degree heartwood content can be explained in terms of the proposed measure of tree maturity (i.e., the inverse relative increment rate of size). Heartwood content is modeled semiempirically using asymptotic fitting. The coefficient of determination by the achieved model is compared with the corresponding coefficients of determination by models based on age or size. We also intended to clarify whether the heartwood content at a specified maturity depends on the *growth rate* or the *tree size*.

Materials and methods

The experimental material consists of two independent datasets. Two datasets were collected to clarify the repeatability of the results.

Dataset 1 was acquired during March 2000. One hundred Scots pine (*Pinus silvestris L.*) butt sawlogs entering a sawmill in eastern Finland were sampled. Sampling was designed to represent the volume-weighted diameter distribution and geographic yield of Kainuu Province. Sample disks were sawn 55 cm from the top of the sampled butt log, the logs being 3–6 m in length. Circular specimens (28 mm diameter) were cut from the middle of the sapwood zone of the disk along a sampling line that corresponds to the greatest diameter of the disk. The average annual ring width within each specimen was measured, as was the distance from the tree pith, in terms of millimeters as well as in terms of the number of annual rings.

Dataset 2 was acquired during August 2000. Forty logs were sampled from the same sawmill as was used to obtain Dataset 1. These logs also represented the volume-weighted diameter distribution and geographic yield of Kainuu Province. A sample disk was sawn from these logs at 90% of the log length, and specimens were produced as for Dataset 1.

For the sample disks a coordinate system was established by taking the line of greatest diameter as the reference line and the center point of this line as the origin. The distance of the heartwood–sapwood boundary from the origin, as well as the distance of the wood–bark boundary, was measured at angular intervals of π/6. The location of the geometric center of the heartwood cross-sectional area and the center of the log cross-sectional area were calculated; the location of the pith of the tree was also determined. The geometric area centers were taken where the sum of the squared differences of distances from the center to any of the boundaries was least; thus the geometric center did not exactly coincide with the pith. The cross-sectional area of the wood disks and the cross-sectional area of the heartwood were determined on the basis of the average distance of the 12 boundaries from the center of the disk and from the center of the heartwood, respectively.

Results

Heartwood formation as a maturation phenomenon

We have proposed the inverse of the relative increment rate of size as a measure of maturity. Such a quantity may achieve values between zero and infinity, having the dimension of time. To ensure that such a quantity is readily measurable from any cross section of a bole, we implemented the maturity characterization in terms of the inverse of the relative basal area increment rate. Assuming that the cross section of any bole is essentially circular, this measure can be written as

$$\text{Maturity} = \frac{\pi r^2}{2\pi r \frac{\mathrm{d}r}{\mathrm{d}t}} = \frac{r}{2\frac{\mathrm{d}r}{\mathrm{d}t}} \tag{1}$$

where r refers to the bole radius, and t refers to time.

For the present experimental material, the maturity according to Eq. (1) can be determined from wood specimens obtained to represent the sapwood of the sample disk. This is because the annual ring width, which is needed for Eq. (1), was measured in the circular specimens cut from the middle of the sapwood section. The calculated maturity thus corresponds to the maturity that prevailed some years before felling, during formation of the xylem, which presently constitutes the sapwood. The measured heartwood content, however, corresponds to the time of felling. Thus, there is a phase lag between the measurement of maturity and the heartwood content. The phase lag, however, is assumed here to be unimportant.

The heartwood content of any butt log top cross section as a function of the maturity of the cross section is shown in Fig. 1. We find that despite the phase lag in the measurements the heartwood content is accurately determined by maturity. Any function describing heartwood content as a function of maturity must approach zero at a small finite value of maturity and approach unity at infinite maturity. The function

$$\begin{aligned} &\text{Heartwood content} = 0, \text{ if maturity} < m_0 \\ &\text{Heartwood content} = 1 - \exp\left(-\left(\frac{\text{maturity} - m_0}{a}\right)\right) \\ &\quad \text{if maturity} \geq m_0 \end{aligned} \tag{2}$$

where m_0 is the maturity where heartwood formation initiates, and a and b are constants, satisfies these logical limit values. When fitted to Dataset 1, Eq. (2) provides a coefficient of determination of 0.76 (Fig. 1). Dataset 2 displays a trend of the heartwood content increment as a function of maturity, similar to that of Dataset 1.

Because maturity was defined above as the inverse of the relative increment rate of size, the heartwood content at a specified maturity does not need to be related to the width of the annual rings. Figure 2 shows that the normalized residuals of Eq. (2) do not correlate with the sapwood an-

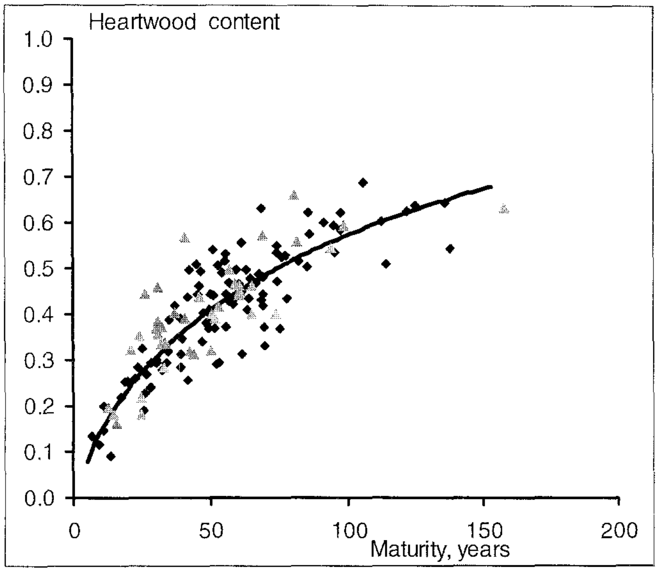

Fig. 1. Heartwood proportion of a cross-sectional area in a wood disk taken from the vicinity of the upper end of a butt log as a function of maturity, evaluated using Eq. (1). Eq. (2) is fitted to Dataset 1 (*diamonds*). Variation within Dataset 2 (*triangles*) can be reasonably described with the same model

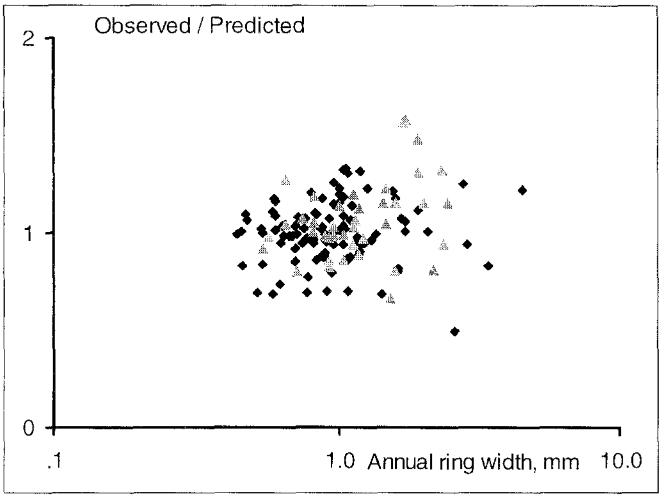

Fig. 2. Normalized residual variation of the heartwood proportion as a function of sapwood annual ring width after fitting Eq. (2) to Dataset 1 (*diamonds*). At a specified maturity, the heartwood content does not correlate with the annual ring width. Variation in Dataset 2 (*triangles*) can be reasonably described with the same model as used for Dataset 1

nual ring width, nor does the residual variation correlate with age or size.

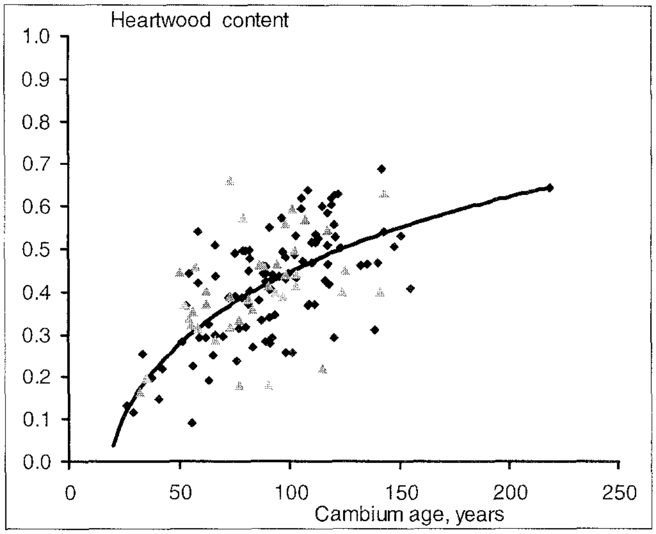

Fig. 3. Heartwood proportion of a cross-sectional area in a wood disk taken from the vicinity of the upper end of a butt log as a function of the number of annual rings in the disk. An exponential function is fitted to Dataset 1 (*diamonds*). Variation within dataset 2 (*triangles*) can be reasonably described with the same model

Heartwood content as a function of age

Heartwood content as a function of the number of annual rings in a sample disk is shown in Fig. 3. We find that cambium age explains the heartwood content less accurately than does the maturity defined in Eq. (1). An exponential function of the same type as Eq. (2), fitted to Dataset 1, provides a coefficient of determination of 0.46. Dataset 2 displays still more scatter.

Figure 4 shows that once heartwood content has been predicted in terms of cambium age, an apparent effect of growth rate remains, the normalized residuals depending on annual ring width within the sapwood. The correlation with annual ring width is negative, which agrees with findings in the literature.[8,6,11,12] We also find from Fig. 4 that at a specified age the heartwood content correlates positively with size, which also agrees with the literature.[13,14]

Heartwood content as a function of size

Heartwood content as a function of log diameter is shown in Fig. 5. We find that size explains heartwood content still less accurately than age. An exponential function of the same type as Eq. (2), fitted to Dataset 1, provides a coefficient of determination of 0.31. Dataset 2 displays at least the same amount of scatter. Figure 6 shows that once the effect of size is removed, the heartwood content has a strong negative correlation with the annual ring width and a clear positive correlation with age.

Effect of growth rate on heartwood content

Even if heartwood content at a specified maturity does not correlate with the width of annual rings (Fig. 2), it is unknown to what degree heartwood content possibly depends on the growth rate. This is because the absolute increment rate of size generally is not independent of maturity.[28–32] Thus, the eventual independent effect of growth rate on a particular property of a tree or a tissue formed by the tree must be studied in terms of a dimensionless, maturity-independent measure of the growth rate.[27]

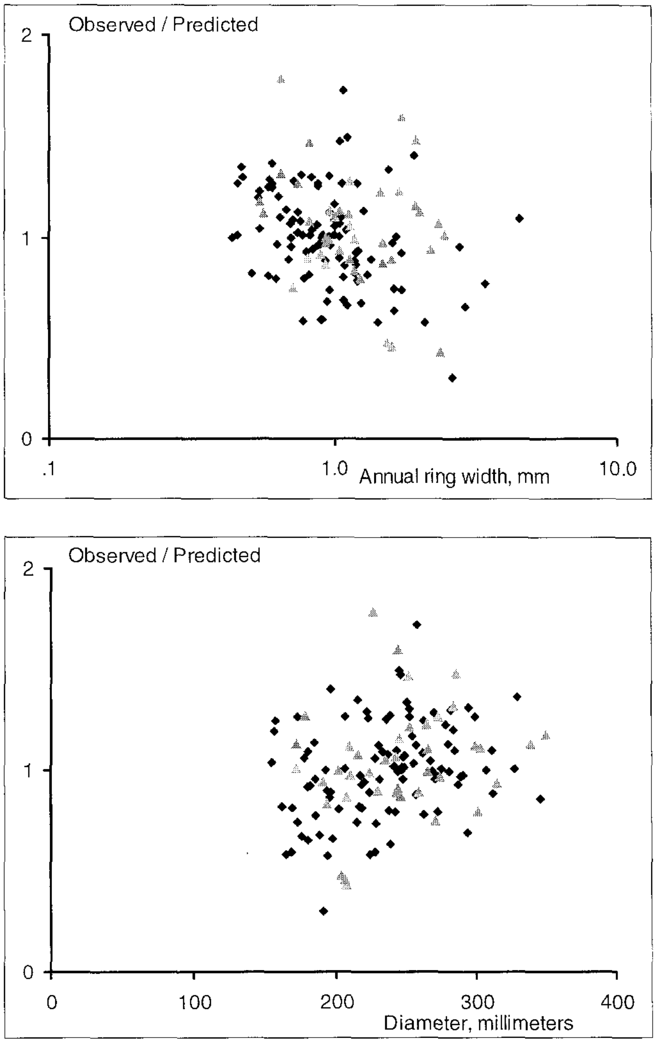

Fig. 4. Normalized residual variation of heartwood proportion as a function of the sapwood annual ring width (**top**) and as a function of log diameter (**bottom**)

A dimensionless, maturity-independent growth rate can be produced by normalizing an absolute increment rate of size by the increment rate of size that is statistically typical for that particular maturity.[20,27] In the present case, with maturity being defined as in Eq. (1), the growth rate is:

$$\text{Growth rate} = \frac{{}^{\mathrm{d}r}\!/_{\mathrm{d}t}}{\overline{\left({}^{\mathrm{d}r}\!/_{\mathrm{d}t}\right)}_{\mathrm{M}}} = \frac{r}{\overline{r}_{\mathrm{M}}} \tag{3}$$

where $\overline{(\mathrm{d}r/\mathrm{d}t)}_{\mathrm{M}}$ is a typical (mean) value for the incremental rate of radial growth at maturity M, and $\overline{r}_{\mathrm{M}}$ is the typical (mean) bole radius at maturity M. The equality of the two expressions in Eq. (3) results from the definition of maturity in Eq. (1).

In terms of practice, Eq. (3) implies that either the annual ring width or the bole radius must be modeled as a function of maturity to determine the dimensionless growth rate. It is somewhat easier to model the bole radius; and so we intend to determine the dimensionless growth rate using the right-hand side of Eq. (3). Once maturity approaches zero, the bole radius also approaches zero. On the other hand, once maturity approaches infinity, the bole radius approaches a finite limit. Such a function is represented by

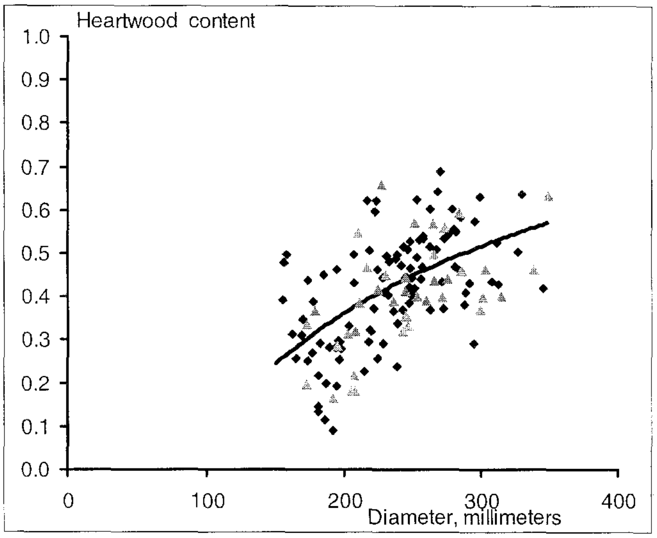

Fig. 5. Heartwood proportion of a cross-sectional area in a wood disk taken from the vicinity of the upper end of a butt log as a function of the diameter of the disk. An exponential function is fitted to Dataset 1 (*diamonds*). Variation within Dataset 2 (*triangles*) can be reasonably described with the same model

$$\overline{r}_{\mathrm{M}} = c\left[1 - \exp\left(-\left(\frac{\text{maturity}}{d}\right)^{e}\right)\right] \tag{4}$$

where c, d, and e are constants, the constant c having the physical interpretation of the size limit. Eq. (4), fitted to Dataset 1, is shown in Fig. 7. Observations from Datasets 1 and 2 are also plotted in Fig. 7. On average, the growth rate in Fig. 7 is somewhat higher in Dataset 2 than in Dataset 1.

The effect of growth rate, as defined in Eq. (3), on the heartwood content is shown in Fig. 8. The heartwood content is not dependent on the growth rate.

Discussion

Rapidly grown trees have a lower heartwood content only when they are compared with more slowly grown trees of the same size.[13,14] When the age is the same, trees of large diameter appear to have a higher heartwood content.[13,14] Up to now, chronological age being considered the primary measure of the maturity of pine trees, the authors have had significant difficulty interpreting such observations. They appear to be contrary to findings according to which the proportion of heartwood increases with age,[6,8–11] and is negatively correlated with the growth rate of the tree.[6,8,11,12]

Retarded maturation of trees grown on poor soil and in a cold climate[21–24] indicates that at a specified maturity, trees from regions and sites of inferior growth are older than trees that experienced more favorable growth conditions. In

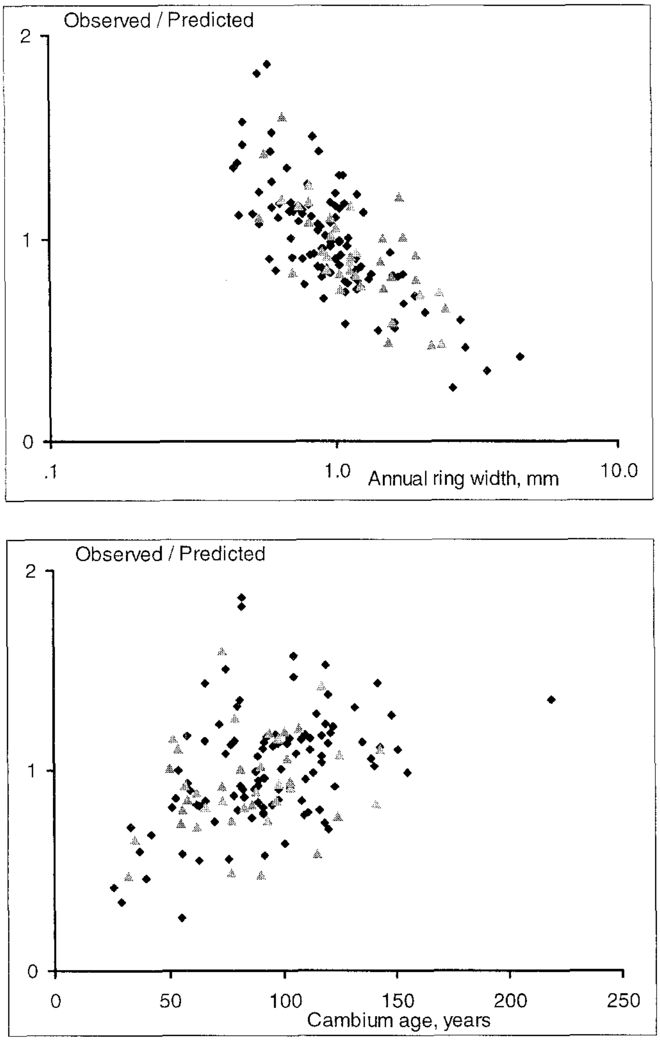

Fig. 6. Normalized residual variation of the heartwood proportion as a function of the sapwood annual ring width (**top**) and as a function of cambium age (**bottom**)

other words, at a specified chronological age trees from areas with favorable growth conditions are more mature than trees from areas of poor growth conditions. This appears to explain the observation that large trees have a larger heartwood content than small trees at the same chronological age.[13,14] Werberg's[13] data were gained with significant soil fertility variation, and Tamminen's[14] data were obtained with significant climatic variation; both of these factors obviously induce a change in the time scale of the tree maturation process.[21–24]

The present approach to tree maturity appears to have at least one complication. The increment rate of size fluctuates owing to variations in environmental conditions, and so the relative increment rate of size does not decline steadily. This problem can be avoided by determining the increment rate of size over such an extended period of time that the fluctuations in the growth rate due to the variation in climate are averaged.

A suppressed tree may have a low growth rate over an extended period of time, and its growth can be significantly enhanced if the suppressing trees are removed. Even if the rate of size increment were averaged to exclude fluctuations in climate, the inverse of the relative incremental rate of growth within such a suppressed tree may decrease with time. Such a behavior obviously is physical and so it must be accepted that *maturation may be partly reversible*. The suppressed tree actually may have been not far from death in its suppressed state, but it may have a significant amount of life ahead after removing the suppressing trees.

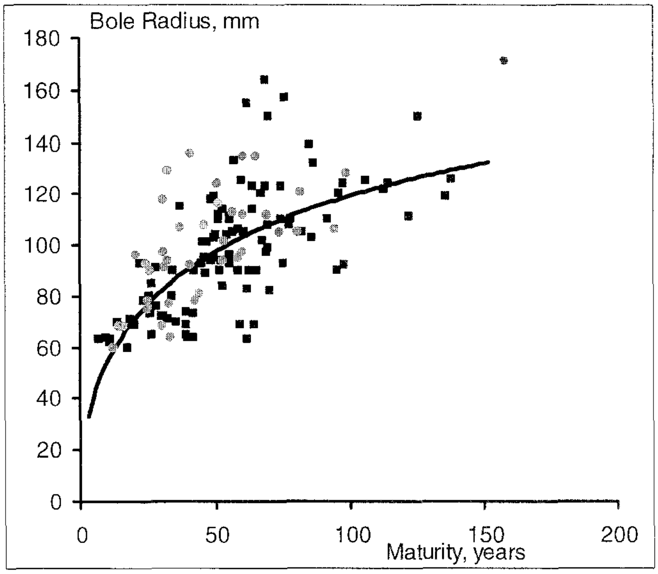

Fig. 7. Bole radius as a function of maturity. Eq. (4) is fitted to Dataset 1 (*squares*). Logs of Dataset 2 (*circles*) are somewhat larger at any specified maturity than logs of Dataset 1

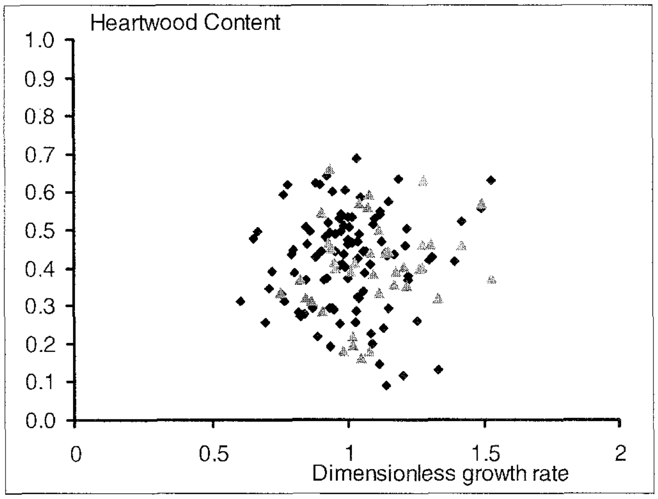

Fig. 8. Heartwood content as a function of dimensionless growth rate in Dataset 1 (*diamonds*) and Dataset 2 (*triangles*)

Acknowledgments The authors are obliged to Mr. Petri Hallikainen for his contributions regarding the measurements, and to their industrial collaborators for their technical and financial assistance.

References

1. Johansson S (1977) Moisture-repelling treatment for wood (in Swedish). Swedish Wood Research Institute [Svenska träforskningsinstitutet], Report A 467
2. Koponen HR (1983) Moisture transport in wood and wood plates 4 (in Finnish). Helsinki University of Technology, Laboratory of Wood Technology, Report 7
3. Grönlund A, Karlsson G, Karlsson L (1979) Pine wood with high proportion of heartwood for window joineries (in Swedish). Swedish Wood Research Institute (Svenska träforskningsinstitutet), Report A 553
4. Rennerfelt E (1947) Some investigations regarding the cabability of rot fungi to assault pine heartwood and sapwood (in Swedish). State Forest Research Institute Report [Meddelanden från statens skogsforskningsinstitut] 36(9):1–24
5. Erdtman H, Frank A, Lindstedt G (1951) Constituents of pine heartwood 27: the content of pinosylvin phenols in Swedish pines. Svensk Papperstidning 54:275–279
6. Trendelenburg R (1939) Wood as raw material (in German). J. F. Lehmanns Verlag, Munich
7. Kärkkäinen M (1985) Wood science (In Finnish). ISBN 951-99628-2-4
8. Schwappach A (1892) Investigations regarding the quality of pine wood (in German). Z Jagdwesen 14(1):75–88
9. Pilz (1907) About pine heartwood formation (in German). Allg Forst Jagdztg 83:265–272
10. Eneroth O (1922) Wood structure. In: Forest technology handbook (in Swedish). Viktor Petterssons Bokindustriaktiebolag, Stockholm, pp 5–33.
11. Lappi-Seppälä M (1952) About the heartwood and stem form of pine (in Finnish). Comm Inst For Fenn 40(25): 26
12. Kuylenstierna F (1964) Why is there heartwood formation (in Swedish)? Skogen 54:312–313
13. Werberg K (1930) Pine heartwood and sapwood (in Estonian, with German summary). Tartu Ulikooli Metsaosakonna Toimetused 17:1-184 + 1-19
14. Tamminen Z (1964) Moisture content, density and other properties of wood and bark. II. Norway spruce. Swedish Royal College of Forestry, Department Forest Products. Research note 47
15. Longman KA, Wareing PF (1959) Early induction of flowering in birch seedlings. Nature 184:2037–2038
16. Robinson LW, Wareing PF (1969) Experiments on the juvenile-adult phase change in some woody species. New Phytol 68:67–78
17. Hackett WP (1976) Control of phase change in woody plants. Acta Hort 56:143–154
18. Wareing PF, Frydman WM (1976) General aspects of phase change, with special reference to *Hedera helix* L. Acta Hort 56:57–69
19. Olesen PO (1978) On cyclophysis and topophysis. Silvae Genet 27:173–178
20. Kärenlampi PP, Riekkinen M (2002) Maturity and growth rate effects on Scots pine basic density. Wood Sci Technol (in press)
21. Ilvessalo Y (1930) The forests of Suomi (Finland) described by areas fertility: results of the general survey of the forests of the country carried out during the years 1921–1924. Comm Inst For Fenn 15.4. p 96
22. Vuokila Y (1956) On the development of managed spruce stands in southern Finland. Comm Inst For Fenn 48.1. p 138
23. Vuokila Y, Väliaho H (1980) Growth and yield models for conifer cultures in Finland. Comm Inst For Fenn 99.2. p 271
24. Vanninen P, Ylitalo H, Sievänen R, Mäkelä A (1996) Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees 10:223–239
25. Michajlow J (1952) Mathematical formulation of the growth of trees and stands (in German). Schweitzer Z Forstwesen 103:368–380
26. Kucera B (1994) A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood Fiber Sci 26(1):152–167
27. Sirviö J, Kärenlampi P (2001) The effects of maturity and growth rate on the properties of spruce wood tracheids. Wood Sci Technol 35:541–554
28. Volkert E (1941) Investigations regarding the level and variation of wood density in softwood (in German). Schriften Hermann Göring Akad Dtsch Forstwissenschaft 2:1–133
29. Hiley WE (1955) Quality in softwoods. Q J For 49:159–164
30. Rendle BJ, Phillips EWJ (1958) The effect of rate of growth (ring width) on the density of softwoods. Forestry 31(2):113–120
31. Hakkila P (1967) Variation patterns of bark weight and bark percentage by weight. Comm Inst For Fenn 62.5. p 37
32. Uusvaara O (1974) Wood quality in plantation-grown Scots pine. Comm Inst For Fenn 80.2. p 105