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Evaluation of Importance of Sapwood Senescence on Tree Growth Using the Model Lignum

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The effects of two alternative formulations of sapwood senescence on the behavior of model LIGNUM (with parameter values adjusted for Scots pine growing southern Finland) were studied. The two alternatives were: autonomous sapwood senescence assuming a maximum age for the tree ring and sapwood senescence that is controlled by the mortality of foliage. For the latter alternative two hypothetical further mechanisms were stipulated. All the formulations were implemented in LIGNUM. Simulations were made with all model variants for fertile and poor soil conditions using high, normal and low rates of foliage mortality. The simulation results were compared against of a data set consisting of 11 open grown Scots pine trees from southern Finland. Observations of heartwood proportion were used in this study. They show that heartwood starts to increase in trees from age of approximately 20 years onwards. The simulation results showed no differences between fertile and poor soil conditions as regards heartwood formation. Of the variants of foliage controlled sapwood senescence the one where death of sapwood in a tree segment induces sapwood senescence in the tree parts below only slightly was the best. This and the autonomous sapwood senescence corresponded equally well to the observations. In order to make more refined conclusions additional data and simulations are necessary.

Keywords growth model, sapwood senescence, pipe model theory, open-grown trees

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1 Introduction

Incorporation of both physiological processes driving growth and the three-dimensional structure of tree in one model (e.g. Takenaka 1994, Kellomäki and Strandman 1995, Perttunen et al. 1996, Reffye et al. 1996) has made it possible to study a wider range of problems in tree growth studies than before. The accomplished simulations deal with the effect of local light climate on tree growth and crown development, effect of branching intensity on growth and outlook of the tree, relationships of tree architecture, water relations, and growth. The simulations so far performed have been preliminary and no practical conclusions have been made yet. These preliminary studies have shown, however, the usefulness of treating tree morphology and functioning in the same model with compatible accuracy. No technical assumptions are necessary to end up with a functioning model. Examples of such assumptions are even distribution of leaf area inside the crown or treating trunk or branches as single cylinders. Such assumptions are not necessary for functional-structural models since the structure is dealt at much higher resolution.

The pipe model is frequently used as a building block of growth models (e.g. Hari et al. 1985, Valentine 1990, Mäkelä 1986). This is probably in part due of its ease of use: simple linear equations (between foliage quantity and wood cross-sectional areas) can be used in the model which then conveniently translate into relationships defining the partitioning of the growth increments (e.g. Mäkelä 1990). Cross-sectional areas of water conducting sapwood is often used instead total area since part of the pipes become disused (Shinozaki et al. 1964). It is also argued that the pipe model relationships rise from the water transport requirements (e.g. Hari et al. 1986). The pipe model has got lots of empirical evidence (see Nikinmaa 1992 for discussion) but its general validity has also been questioned and it has been shown that variations in water conductivity of wood cast simple linear relationships in doubt (Zimmermann 1983).

If the pipe model is assumed to hold true for the model tree the senescence of sapwood emerges as an important process in the model since

dying sapwood must be replaced by thickness growth to maintain the pipe relationships. Consequently, the model predictions have been sensitive to the parameter for sapwood senescence (Mäkelä 1988). The actual mechanism at cellular level that turns sapwood into heartwood is not completely understood (Saranpää 1992). Ageing and consequent loss of vitality, toxic effect of metabolic products and growth regulating substances have been proposed as the cellular level mechanisms of sapwood senescence. The outcome of these mechanisms is more or less that the sapwood rings have a maximum age that has also empirically observed (Saranpää 1992). Another line of reasoning is that since the sapwood is supporting foliage (conducting water) hence its senescence must be related to death of foliage. Kaipiainen and Hari (1985) have found indeed that dying of the whole branch whorl induces heartwood formation in sapwood rings leading to this whorl. Mechanisms proposed for sapwood senescence can be thus classified to two categories: 1) autonomous senescence (maximum age) or 2) foliage controlled senescence.

Testing of these hypotheses is a matter of detailed physiological studies. However, it is also interesting to know what are their consequences to tree growth in general. Model LIGNUM (Perttunen et al 1996, 1997) offers good possibilities for studying the implications of above hypotheses on growth. Structurally and architecturally detailed models can be used to test the tree level outcome of different hypotheses concerning their parts. In this case, if the heartwood formation is primarily an age driven process, then it should be connected to the age of each particular woody segment. However, if it is driven by net growth of foliage, it would be important to know the position of those axes in tree that are supporting decreasing amount of foliage. Model LIGNUM deals with 3-D structure of the trees, i.e. the exact position of branch and stem segments between two branching points. It also keeps a track of their age and calculates the new foliage growth of shoots according to their light climate and the available carbon. These properties make it well suited to test the implications of the two hypotheses.

In the following we first shortly describe how the senescence of sapwood affects the thickness

growth of the model tree in LIGNUM, for other details of the model we refer to existing publications (Perttunen et al. 1996, 1997, Salminen et al. 1994, Sievänen et al. 1995). Then we formulate the two assumptions concerning the senescence of the sapwood. After that we present simulations made using these two alternatives and compare them with some experimental results. All parameter values, simulations and data concern Scots pine.

2 The Basic Structure of LIGNUM

The model tree in LIGNUM consists of simple basic units, tree segment, branching point and bud (Fig. 1). The growth of the tree is based on the carbon budget formulation. Therefore the central question is how to incorporate carbon balance to a model consisting of a large number of units. The key processes of carbon balance are the assimilation of carbon in photosynthesis and respiration through which carbon is lost back to atmosphere. On the long run the distribution of carbon between different parts of trees becomes a decisive factor since it determines the structure of trees. This distribution is presently solved as follows: The shoot light climate and position in trees topology determine the relative extension growth of branches and the so-called pipe model the relative thickness growth of the woody part. The shoot extension growth determine also shoot foliage growth.

According to the pipe model a tree is pictured as a bundle of pipes which extend from foliage elements to root tips (Valentine 1990). The addition of foliage requires building corresponding pipe and a certain amount of roots. Pipes that

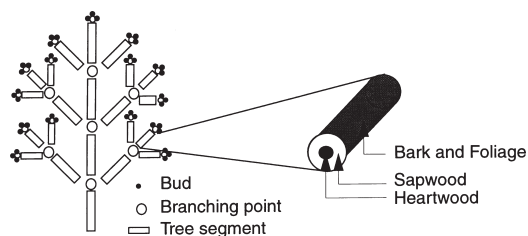


Fig. 1. The structure of the Scots pine tree in LIGNUM.

connect foliage and roots are alive and they form all together *sapwood*. Pipes that have lost the connection (e.g. foliage element has died) are dead and called *heartwood*. Application of the pipe model theory enables us to calculate the amount of wood thickness growth required below when new internode with foliage is added at the end of a branch. This relationship is demonstrated for a branching point in Fig. 2. Foliage growth also implies proportional root growth according to the functional balance ideas (e.g. Brouwer 1962). Since the relative size of new shoots in different parts of crown is known, we can evaluate the influence of adding one unit of carbon to shoot growth on total tree growth. The procedure is repeated iteratively until carbohydrates available for growth are used up.

The model works with one year time step. Its parameter values have been obtained for a Scots pine growing on fertile land in southern Finland. It has been able to reproduce the basic features of growth in young (up to 10 years) open grown trees. For other details of LIGNUM we refer to other publications (Perttunen et al. 1996, 1997).

2.1 Thickness Growth and Sapwood Senescence

The requirement to maintain sapwood area relationships (Fig. 2) in all branching points drives thickness growth in LIGNUM. We divide the cross-sectional sapwood area of the tree segment in two parts (Fig. 3): that which is fulfilling the requirement coming from above (area A_{sa}) and

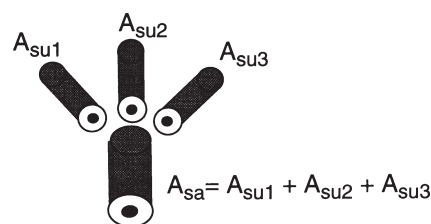


Fig. 2. Illustration of the principle of equal cross-sectional sapwood areas at branching point. The white color indicates sapwood. The sapwood area in the below segment equals the sapwood area of the segments attached to it from above (the equation).

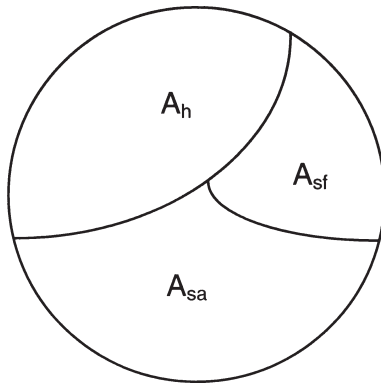


Fig. 3. A schematic presentation of tree segment cross-section as consisting of sapwood that corresponds to sapwood cross-sectional area above (A_{sa}), that serves the foliage of the segment itself (A_{sf}), and heartwood (A_h).

Table 1. Definition of the main variables.

Name	Definition
A_h	Cross-sectional area of heartwood in a tree segment
A_{hu}	Heartwood area requirement coming from above
A_s	Cross-sectional area of sapwood in a tree segment
A_{sa}	Cross-sectional area of sapwood serving above sapwood requirement
A_{sf}	Cross-sectional area of sapwood supporting foliage of segment
A_{sR}	Growth of area necessary to match sapwood requirement
A_{su}	Sapwood area requirement coming from above
dA_h	Increase of heartwood cross-sectional area
dA_{sf}	Sapwood cross-sectional area released from dead foliage in the segment

that supporting the foliage of the segment itself (area A_{sf}), making together the total sapwood area A_s : $A_s = A_{sa} + A_{sf}$. Variables are defined in Table 1. Rest of the cross-sectional area is occupied by heartwood (area A_h). The changes in these cross-sectional areas drive the thickness growth. The thickness growth is governed in LIGNUM by the requirement that the additional sapwood area introduced by new tree segments must be matched by tree segments below as indicated in Fig. 2. The senescence of sapwood affects the areas in equation of Fig. 2 and thus also thickness growth. Every time new segments (and sapwood area) are formed at the distal parts of the crown the induced radial growth can be evaluated only by traveling from branch tips to stem base and assessing induced radial growth, which is also affected by amount of dying sapwood in each segment. In the following we describe how this is accomplished both for autonomous senescence (maximum age) and foliage controlled senescence of sapwood.

2.1.1 Autonomous Senescence

We assume that each year a fraction (s_s) of existing sapwood area turns into heartwood. The de-

crease in sapwood area (equals increase of heartwood area, denoted by dA_h) is thus given by

$$dA_h = s_s A_s \quad (1)$$

This way of dealing with sapwood senescence only approximates the case when sapwood rings have a maximum age. In the case when formation of new sapwood area and heartwood formation are in balance the equation holds exactly. When the growth rate varies this relationship holds only approximately. We have used as the nominal value for parameter s_s value 0.07 which means that the maximum age of a tree ring is $1/0.07 \approx 15$ years (Perttunen et al. 1996). If the assumption of maximum age of sapwood rings was implemented exactly the model should keep track of all tree rings. Tracking of annual growth is, however, not implemented in LIGNUM at the moment.

We consider now a junction at branching point (Fig. 2) and denote the total sapwood cross-sectional area of tree segments above it by A_{su} . The sapwood area of the segment must be at least equal to this (A_{sa} , Figs 2, 3). In addition, if there is foliage attached to the segment, it requires supporting sapwood (A_{sf} , Fig. 3). The senescing foliage of the segment that dies during

the time step releases sapwood area, we denote it by dA_{sf} . Hence the sapwood area required to support the foliage of the segment itself is equal to $A_{sf} - dA_{sf}$ at the end of the time step. This formulation means that sapwood area released by dying foliage can be reused. Other areas the segment must incorporate are the heartwood area A_h , and new heartwood formed during the time step dA_h . The new radius with these area components is given by

$$R_{new} = \sqrt{\frac{A_{su} + A_h + dA_h + A_{sf} - dA_{sf}}{\pi}} \quad (2)$$

This is Eq. 16 in Perttunen et al. (1996), the symbols are only a bit different. The sapwood area that this segment passes to the segment below is obtained as

$$A_{su} + A_{sf} - dA_{sf}. \quad (3)$$

2.1.2 Foliage Related Senescence

This alternative assumes that the foliage and sapwood are closely tied together. Hence, the death of foliage controls the senescence of sapwood. In this case we assume that excess sapwood dies. Excess sapwood exists if the segment has a larger sapwood area than matching above sapwood area and supporting own foliage requires. It is also assumed, as previously, that the sapwood area released by the dying foliage can be reused to match the sapwood requirement coming above. Faithful to the pipe model which regards trees consisting of bundles of pipes it is assumed that when a certain area of sapwood turns into heartwood, the same area of sapwood in each segment on the path down to trunk base dies also. This mimics the phenomenon when whole pipes die out.

We consider a junction again (Fig. 2). The available sapwood area in the tree segment equals existing sapwood that serves the above needs (A_{sa} , Fig. 3) with that released from dying foliage (dA_{sf}):

$$A_{sa} + dA_{sf} \quad (4)$$

The amount of segment growth necessary to match the sapwood requirement from above (A_{su}) is thus

$$A_{sR} = A_{su} - A_{sa} - dA_{sf} \quad (5)$$

Depending whether the existing sapwood area can match the sapwood requirement two alternatives arises:

- A) In the case the above sapwood requirement is larger than the available sapwood ($A_{sR} > 0$) increase in sapwood area of the segment occurs. Further to this let us denote the accumulated area of heartwood (pipe area that has died above) by A_{hu} . That requires growth of heartwood with the corresponding amount. The new cross-sectional area of the stem segment is obtained as the sum of sapwood requirement (A_{sR}) and existing area ($A_{sa} + A_{sf} + A_h$) and heartwood increase (A_{hu}) yielding after rearrangement

$$A_{su} + A_{sf} + A_h + A_{hu} - dA_{sf} \quad (6)$$

This gives for the new radius

$$R_{new} = \sqrt{\frac{A_{su} + A_{sf} + A_h + A_{hu} - dA_{sf}}{\pi}} \quad (7)$$

and there is no senescence of the sapwood in the segment ($dA_h = 0$). Note that the equation for the new radius is the same as in the case of autonomous sapwood senescence, with two exceptions: the term for sapwood senescence is missing here and heartwood divides into the existing heartwood of the segment and the heartwood formation initiated above the segment. The sapwood requirement passed to the segment below equals now

$$A_{su} + A_{sf} - dA_{sf} \quad (8)$$

and the area of cumulated heartwood (A_{hu}) does not change.

- B) In the case the sapwood requirement is lower than the existing sapwood area, that is $A_{sR} < 0$, no increase in sapwood area is necessary and only A_{hu} has to match with growth, hence the new radius is obtained as (old cross-sectional area plus A_{hu})

$$R_{new} = \sqrt{\frac{A_{sa} + A_{sf} + A_h + A_{hu}}{\pi}} \quad (9)$$

and the surplus sapwood area of the segment turns into heartwood:

$$dA_h = A_{sa} + dA_{sf} - A_{su}.$$

The sapwood area requirement that is passed to the segment below is

$$A_{su} + A_{sf} - dA_{sf} \quad (10)$$

which consists of sapwood serving the above requirement together with area serving own foliage. The accumulated heartwood area equals

$$A_{hu} + dA_h \quad (11)$$

after this segment.

2.1.3 Modifications to Foliage Related Sapwood Senescence

It turned out that the assumption that if heartwood was formed in segment the heartwood area increased with the corresponding amount in all segments below (Eqs 7, 9, and 11, mimicking the death of whole pipes) had marked effects on the behavior of the model. Therefore some alternative formulations of foliage related sapwood mortality was tested as well. Two modifications was coined to further to study this matter: first, *half of the formed heartwood area* was passed down. Second, we used a *threshold* value that the heartwood formation in the segment needs to surpass before any new heartwood requirement was passed down. These modifications were accomplished as follows.

The accumulated heartwood is passed down according to Eq. 11. This equation was modified in these alternative formulations. In the case *half of the formed heartwood area* were passed, it reads

$$A_{hu} + \frac{dA_h}{2} \quad (12)$$

and the case the *threshold* was applied only heartwood that exceeds a certain share (p) of the total sapwood area was passed down. In this case the equation reads

$$A_{hu} + \begin{cases} 0, & \text{if } dA_h \leq p \cdot A_s \\ dA_h - p \cdot A_s, & \text{if } dA_h > p \cdot A_s \end{cases} \quad (13)$$

Several values of threshold p were tested. Small values of p did not change the results much. Here the results which were obtained by using

threshold value $p = 0.05$ are shown.

Both these alternatives limit the propagation of the effect of heartwood formation downwards to other segments. It means that the sapwood senescence is a more local phenomenon here than in the above formulations.

3 Material and Simulations

We compared the simulation results against of a data set consisting of 11 open-grown Scots pine trees from southern Finland collected by Lukkarinen (1992, Table 2). The trees were often found at forest edges, agricultural field boundaries etc., so they formed a rather heterogeneous group as regards to their site conditions. The trees were felled and a number of measurements were made (Lukkarinen 1992), including taking stem discs at several heights. The heights were different for different trees. The heartwood diameter was measured by holding a thin disc against the sky and marking the contour of translucent wood boundary that approximates that between sapwood and heartwood with a pen. The total and the heartwood diameter were recorded as the mean of measurements in two perpendicular directions. The measured heartwood proportions are shown in Fig. 4.

The model LIGNUM was used to simulate tree growth in otherwise identical simulation runs with exception of using the four different types

Table 2. The open-grown trees of the present study (measured by Lukkarinen 1992).

Tree	Age, a	Height, m	Growth site
2	21	3.7	Abandoned sand pit
4	25	9.7	Seed orchard for pine
5	26	8.7	Seed orchard for pine
6	14	5.5	Railway bank
7	14	4.1	Under powerline
9	22	6.4	Seed orchard for spruce
10	21	6.8	Seed orchard for spruce
12	20	6.8	Abandoned field
13	30	11.4	Edge of field
14	–	4.8	Seed plantation
17	19	5.6	Roadside

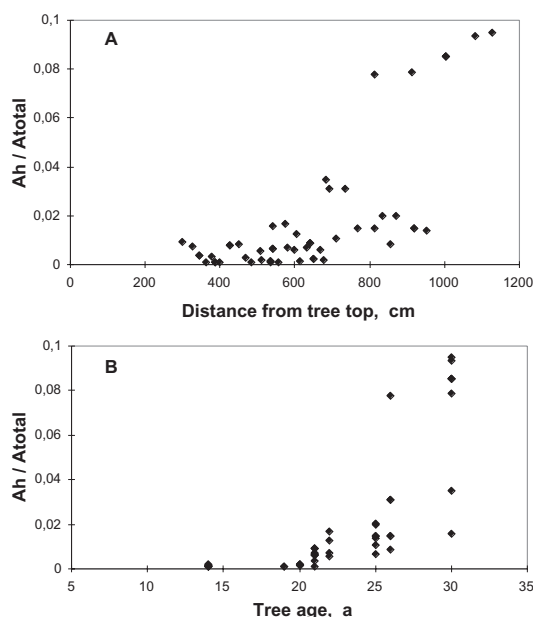


Fig. 4. Proportion of heartwood along the stem in the data (11 trees) collected by Lukkarinen (1992), Table 2, as a function of the distance from the top of the tree (A), and as a function of tree age (B). Several disks per tree were taken, data of all of them is shown. The heights of the disks were different in different trees. The distance from the top of the tree correlates with the age of the disk quite well.



Fig. 5. Outlook of a 10 years old open-grown Scots pine tree simulated by LIGNUM (autonomous sapwood senescence, fertile soil, and normal foliage mortality).

of models for sapwood senescence to heartwood. The trees were grown for 10 years assuming no year to year variation in weather. Save the sapwood senescence equations the parameter values were the same as in Perttunen et al. (1997). The autonomous sapwood senescence case was exactly the model of Perttunen et al. (1997). The conditions of solar radiation corresponded those of an isolated tree, hence the simulations are for an open-grown tree (Fig. 5) as the available data also was. The simulation runs were made for both fertile and poor soils and for high, low, and medium rate of foliage mortality (Fig. 6). The parameter values of Perttunen et al. (1996, 1997) correspond to fertile soil conditions. The poor soil conditions were mimicked by increasing the proportion of roots (doubled from fertile conditions) which slowed down growth.

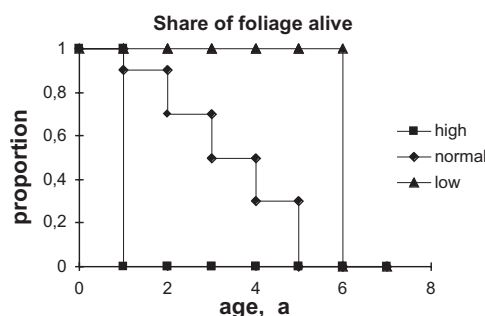


Fig. 6. The proportion of initial amount of needles present as a function of age for three alternatives of needle mortality used in simulations: high, normal, and low. The normal needle mortality is the same as used by Perttunen et al. (1996, 1997).

In order to facilitate comparison of simulations and model variants they are labeled as follows:

Autonomous (Eq. 2): A, Foliage related (Eqs 7 and 9): F, Foliage related, half of formed heartwood passed down (Eqs 12, 7, 9): F-H, and Foliage related, threshold in formed heartwood passed down (Eq. 13, 7, 9): F-T.

4 Results

4.1 Simulations

The results in all simulations between the alternatives of heartwood formation are clear: foliage related (F) produces most heartwood and the variants (F–H, F–T) less (Fig. 7) as can be expected. In the case of threshold its ranking depends of course on the value of the threshold. In the case of low foliage mortality all foliage related heartwood formation alternatives (F, F–H, F–T) give only little heartwood (Fig. 7c), less than the autonomous one (A). Autonomous heartwood formation is independent foliage mortality and hence it is not affected by foliage mortality whereas the foliage controlled heartwood formation (F) produces much more heartwood (Fig. 7a, b) in these cases. The modified versions (F–H, F–T) produce less than or at most equal amount of heartwood in all cases than the autonomous version (A).

The stem profiles that these four alternatives of heartwood formation produce are almost identical in each level of foliage mortality (Fig. 8). In the case of high foliage mortality, foliage mortality controlled heartwood formation produces a more bulky stem (Fig. 8a). The simulated stems become increasingly slimmer with increasing rate of foliage mortality although the difference between normal and low mortality is very small. The height growth is only affected with high foliage mortality, whereas varying the foliage mortality from normal to low increased only thickness growth. This is in accordance with results of earlier simulations (Perttunen et al 1996, Fig. 15) in which height growth was less affected than other characteristics when parameter values were varied.

The simulations with parameter values corresponding to poor soil fertility were almost identical to the results shown. No qualitative differences between these two sets of results exist. Apart the size differences (smaller trees for poor soil) also the quantitative results are very similar to the shown results. Therefore the results of these simulations are not shown.

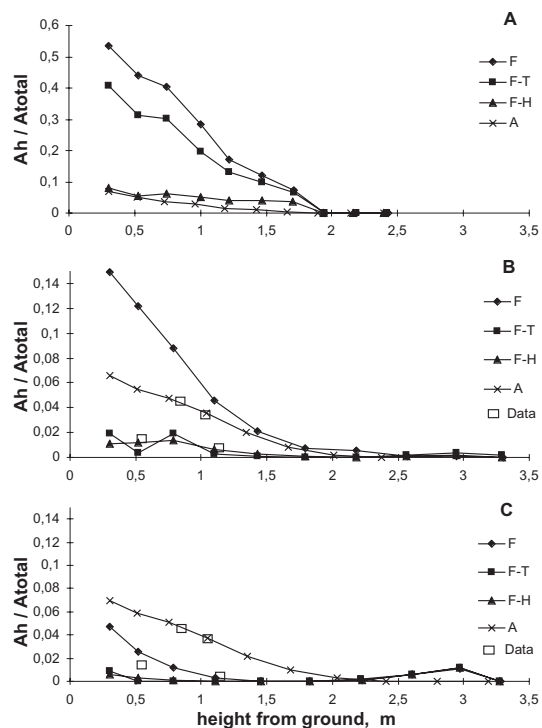


Fig. 7. Simulated proportion of heartwood as function of height along the stem for three modes (Fig. 6) of foliage mortality: high (panel A), normal (panel B), and low (panel C). In each panel the results for four alternatives of heartwood formation are shown. The curves are labeled as follows, A: autonomous sapwood mortality (Eqs 1, 2), F: foliage related sapwood mortality (Eqs 7 and 9), F–H: foliage related sapwood mortality, half of formed heartwood passed down (Eq. 12), and F–T: foliage related sapwood mortality, threshold in passing formed heartwood down (Eq. 13). Superimposed on panels B and C are mean heartwood proportions of the data at distances 2.2, 2.3, 2.5, and 2.8 m from the tree top.

4.2 Empirical Results

The results show clearly that there is very little heartwood inside the crown (Fig. 4). The amount of heartwood starts to increase only at long distance from the tree top. It seems that in first 2.5 meters from the tree top there is virtually no

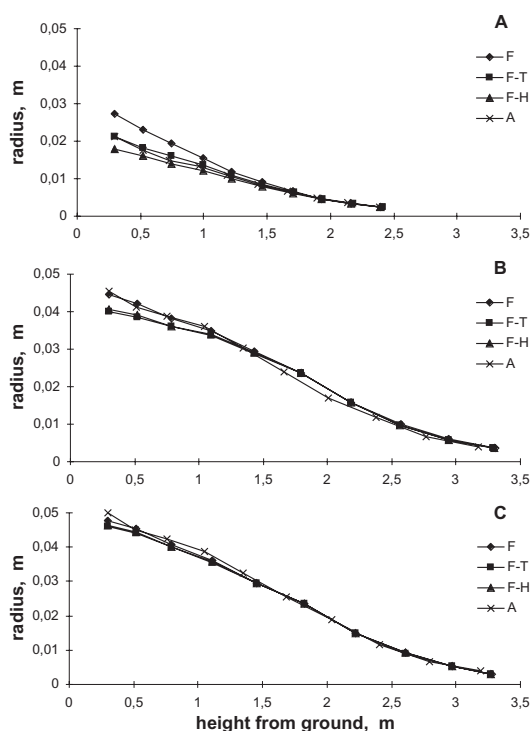


Fig. 8. Simulated radius of the stem (m) as a function height for the same cases as in Fig. 7. Legends are also the same.

heartwood. When results are arranged according to the age of the tree (Fig. 4b) it is obvious that there is not much heartwood formation below the age 20 a. After that the heartwood proportions increase quite rapidly.

The data is variable as regards growing conditions. It is possible that those differences reflect in variability in the heartwood proportions. The results of the tallest tree are markedly different. This tree was also the oldest.

5. Discussion

The turnover of sapwood into heartwood has received minor attention in the ecophysiological research. This neglect can be said to be ill-justified. Modeling studies that use pipe-model principle to distribute resources between foliage and

wood have shown the results to be very sensitive to sapwood senescence parameters (Mäkelä 1988, 1990, Nikinmaa 1992). Even though it can be argued that pipe model might not be an undisputed presentation between foliage and wood growth, the intimate connection between sapwood quantity, its conductivity and the above foliage quantity and its gas-exchange capacity can hardly be questioned (e.g. Tyree and Sperry 1989).

Sapwood represents a major support cost for trees. A favorite theory for tree mortality is based on trees carbon balance becoming negative as the relationship between the productive and non-productive tissue becomes gradually more unfavorable as tree size increases (e.g. Waring 1987, Givnish 1988). A major proportion of the living biomass of a large tree is in wood (e.g. Vanninen et al. 1996). Although the specific activity of wood is lower than other living tissues (Mohren 1987) the large proportion makes it a major source of respiratory losses in trees. Gerrish (1990) has hypothesized that the frequently observed collapses of metrosideros forest stands might be caused by too large quantities of sapwood in comparison to foliage mass.

Despite of the significance of heartwood formation on tree functions and growth, we know surprisingly little about the processes bringing it about (Saranpää 1992). Observations on heartwood proportions show that it is rarely observed in young stems and that the heartwood proportion is lower in slow growing or northern stand for the same size trees (Saranpää 1992). There is also evidence that heartwood proportion is higher in trees suffering from needle-loss than in healthy trees (Konsenkranus, unpublished results). Kaipiainen and Hari (1985) have noticed an intimate linkage between non-conducting tree-rings and senesced branch whorls. Sapwood also seem to become non-conducting upon pruning lower branches (Nikinmaa et al. 1996).

There seem to be experimental evidence supporting hypotheses of sapwood turnover to heartwood being an age driven process or connected to crown dynamics. In this study we examined the implications of both hypotheses on tree growth in a modeling study. Apart from trying to clarify an interesting question we wanted to study the utility of structurally detailed model in iden-

tifying tree level behavior that results from functioning of its parts. A further motivation for this study was to improve the presentation of heartwood formation in the model LIGNUM.

The simulations have shown how different alternatives of sapwood senescence result in clear differences in heartwood proportions. The differences in diameter and height are less pronounced. These results lend themselves well to comparison with experimental results. The empirical results show virtually no heartwood at distance 2.5 m from the tree top in open-grown Scots pine trees of southern Finland. This is in contrast to (most) simulated results where heartwood formation occurs almost along all the stem. However, the measured open-grown trees should be compared to normal or low foliage mortality (Fig. 7b, c). There the differences are not that large. Especially low foliage mortality gives heartwood proportions that are comparable to data. Looking at heartwood proportion as a function of age in the data (Fig. 4b) shows that heartwood formation seems to start approximately at age 20 yr. This suggests the parameter for autonomous sapwood senescence has a bit too high value (corresponding approximately to 15 years) right now.

The results of the study also show that the pipe model assumption that pipes become disused as they are in excess (F) results into too high rate of sapwood turnover into heartwood (e.g. Fig. 7b). It seems that even if there is excess sapwood at some distal part of the crown it does not trigger its turnover from that point downward into heartwood, at least immediately. Kaipainen and Hari (1985) argued that such a process would take place if the whole of a branch whorl was dying. We approximated this by assuming that only a part of the excess sapwood would trigger its turnover (F-H) into heartwood or assumed that certain accumulation of excess sapwood was necessary before it would trigger heartwood formation from that point below (F-T). The simulations using the latter modifications gave heartwood proportions well comparable to with the observed values in the case of normal or low mortality (Fig. 7b, c). In the case of high foliage mortality (Fig. 7a) only the alternative with half of formed heartwood passed down (F-H) gives heartwood proportions that are comparable with

observations and the autonomous sapwood senescence (A). The two other alternatives (F and F-T) are a way above.

Exact correspondence between simulations and observed values could not be made. First of all the heartwood in model and that which is observed may be slightly different due to difficulties in determining the heartwood in the field. The model assumes sapwood to be sapwood and heartwood to include the real heartwood and the transition zone between heartwood and sapwood, which is often included in sapwood in field determinations. This would mean that the simulated heartwood should be slightly higher than the observations would indicate. On the other hand, the open grown trees against which we compared our simulation values came from variety of conditions the growth history of which we do not know exactly (Lukkarinen 1992). The comparison is also confounded by the fact that empirical data is from older and larger trees than the simulations. The best basis for comparison is to compare the results in terms of distance from tree top (cf. Fig. 7b, c).

No decisive conclusions could be made between the sapwood senescence methods. It seems that after some modifications they both would be able to describe heartwood formation equally well in standard conditions. In this respect the simpler, age driven approach may seem more attractive. Further, the observations indicate that heartwood can be found only after age of approximately 20 years. This observation suggests that age related sapwood senescence with tracking of individual tree rings would be a good description in a model. Such a mechanism has not been realized in LIGNUM yet. On the other hand, the insensitivity of age related sapwood senescence to foliage mortality would suggest that it may not be able to predict observed variation as a function of tree growth rate or needle-loss. The alternative where half of the formed heartwood is passed down (F-H) gives reasonable values for all rates of foliage mortality and therefore seems more appropriate than the other one (F-T). The simulations with different growth rate did not produce differences in heartwood formation in any approach. This is likely because simulated trees were growing in open and it would require a very big difference in tree size

to see any major difference in their light climate and thus foliage growth dynamics. The heartwood differences between slow growing and fast growing trees have been observed with stand grown trees in which growth rate translates to more rapid pruning of lower branches that Kaipainen and Hari (1985) claim to be connected with heartwood formation.

The present study depicts potential of LIGNUM in studying the tree level implications of the phenomena affected by the architecture and functioning of the tree. The fact that different processes can be translated into measurable quantities facilitates new kind of testing of various hypotheses. In this particular case the results fell a bit short from our initial aims. First, making a definite distinction between the age related and the sapwood related heartwood formation would have required data from conditions where foliage mortality is high (cf. Fig. 7a). Second, due to the simple presentation of branching architecture (cf. Perttunen et al. 1997) and computer resource requirements in the light climate calculation we extended the simulations only to age of ten years. As a result of this the major part of available data is outside the simulated range. However, even the present results are able to rule out some alternative hypotheses on sapwood turnover mechanisms.

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Total of 28 references