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LIGNUM: A Tree Model Based on Simple Structural Units

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The model LIGNUM treats a tree as a collection of a large number of simple units which correspond to the organs of the tree. The model describes the three dimensional structure of the tree crown and defines the growth in terms of the metabolism taking place in these units. The activities of physiological processes can be explicitly related to the tree structures in which they are taking place. The time step is 1 year.

The crown of the model tree consists of tree segments, branching points and buds. Each pair of tree segments is separated by a branching point. The buds produce new tree segments, branching points and buds. The tree segments contain wood, bark and foliage. A model tree consisting of simple elements translates conveniently to a list structure: the computer program implementing LIGNUM treats the tree as a collection of lists.

The annual growth of the tree is driven by available photosynthetic products after respiration losses are accounted for. The photosynthetic rate of foliage depends on the amount of light. The amount of photosynthates allocated to the growth of new tree segments is controlled by the light conditions and the amount of foliage on the mother tree segment. In principle, the biomass relationships of the tree parts follow the pipe model hypothesis. The orientation of new tree segments results from the application of constant branching angles. LIGNUM has been parametrized for young Scots pine (*Pinus sylvestris* L.) trees. However, the model is generic; with a change of parameter values and minor modifications it can be applied to other species as well. © 1996 Annals of Botany Company

Key words: Growth model, photosynthesis, respiration, object-oriented modelling, tree architecture, branching structure, *Pinus sylvestris* L., developmental morphology and physiology.

INTRODUCTION

In recent years, modelling of plants has received considerable attention. Models range from simple to extremely complicated. Kurth (1994*b*) observes that plant growth has been approached roughly from two directions. First, morphological models aim at a detailed description of the plant's structure and its development in space. Second, process-based models deal with physiological processes and give a detailed account of metabolism and plant growth in terms of mass variables. The emphasis in these models dictates which aspects of plant life have attracted less attention: the morphological models ignore or simplify the metabolic processes, and the process-based models in turn make simplifications on the spatial structure. Examples of process-based models can be found e.g. in Bossel, (1994), McMurtrie, Rook and Kelliher (1990) and Mäkelä and Hari (1986). Landsberg (1986) provides an overview of the basic properties of these models. The morphological models have been based in many cases on L-systems (e.g. Prusinkiewicz and Hanan, 1989; Kurth, 1994*a*) or other descriptions of branching structure and shoot elongation (Jaeger and de Ruffye, 1992; Fisher, 1992).

Plant modelling can provide some benefit if the limitations of both morphological and process-based models can be removed or at least reduced. An obvious way to do this is to

increase both the physiological realism of the morphological models and incorporate detailed descriptions of the morphology into the process-based models (Kurth, 1994*b*). Distribution of growth is a key factor in the process-based models (Mäkelä, 1990). It serves as an example of the potential benefits improved realism in the description of the structure of trees can offer. So far, the partitioning of growth has been modelled using concepts that refer to aggregated crown geometry without any reference to the three-dimensional crown structure. This, evidently, has an effect on the distribution of growth (Ford, Avery and Ford, 1990). Hence, the process-based models would benefit from a spatial crown model in situations, e.g. competition, where spatial effects are important (Sorrensen-Cothorn, Ford and Sprugel, 1993). A realistic description of the structure of trees would allow us to build in various distribution principles for water transport, nutrient flow, etc. and test them by drawing conclusions about the reasonability of the model outputs. Moreover, a model which is based on a sufficiently detailed description of the tree structure would help us to organize the field measurements in a reasonable manner.

We have combined various points of view in the study of tree growth and development, notably process-based modelling (Nikinmaa, 1992; Sievänen, 1993), model-based reasoning in knowledge-based systems for diagnosing the

health problems of forest trees (Väkevää and Saarenmaa, 1992), and object-oriented modelling (Salminen *et al.*, 1994), to develop the model LIGNUM, which aims at combining tree metabolism with a realistic description of the spatial structure of tree crowns. In the design of LIGNUM, we have aimed at both a specific application—Scots pine (*Pinus sylvestris* L.)—and also tried to end up with as general a tree model as possible. We have done this in order to achieve properties that could make LIGNUM a modelling framework into which the results of various fields of tree research can be incorporated. We have aimed at creating both a general design and the potential ability to expand the model by applying the principles of object-oriented modelling (Salminen *et al.*, 1994). We have used concepts that should be generally applicable, and a software design that easily allows for model expansions. We believe that a general and sufficiently detailed tree model can be useful for many fields of research, e.g. process-based modelling, expert systems for diagnosing forest health problems, and studying the consequences of insect damage on crown development.

In the following section we first describe the basic structure of our model tree. The next section presents the equations defining the functioning—that is carbon metabolism—of LIGNUM. The applied branching rules are also described here. Because of our background in process-based modelling, the growth in terms of carbon is emphasised more than the generation of the spatial crown structure. The implementation of LIGNUM is described briefly and the results of the simulations of young Scots pine are presented. Finally the results are discussed.

DEFINING THE UNITS OF LIGNUM

A key to unifying the morphological and the process-based models is to consider the tree in terms of suitable units and use them to model both the metabolism and the spatial structure. The unit of modelling should be such that it allows both realism in considering the details and the ability to grasp the whole. Furthermore, it is desirable that it be possible to divide the units into parts and processes of the next hierarchical level below. The ultimate growth unit is a cell. However, morphological modelling and object-oriented programming analyses (Salminen *et al.*, 1994) led us to

define the following units for LIGNUM: the section between two branching points, hereafter called *tree segment*; the point in the tree where one or several tree segments are attached to each other, called hereafter *branching point*; and the terminal *buds* (Fig. 1). A tree segment consists of sapwood, heartwood, bark and foliage (Fig. 1). It is thus the main unit a tree consists of. It denotes here a piece of branch or stem, but it is possible that in a later application roots, for example, could also be analysed in terms of tree segments.

Geometrically, a tree segment can be thought of as a cylinder to which the foliage is attached. The branching point has, in the present application, only the task of connecting the tree segments to each other. No biological activities are assigned to branching points in the present case. However, if transport of water, for example, is considered, branching points may have an important role. Buds create new tree segments, branching points and buds. They also determine the directions of the new tree segments from the branching points. The development of tree structure is thus controlled by buds in LIGNUM. With these units the aerial parts of a tree can be described—we deal with roots only in an aggregated manner in this study. In the present application we consider Scots pine. This focus has somewhat guided our thinking in choosing the units for modelling. However, we think that the units are quite general and allow for the study of many tree species, with minor modifications. The units defined here are conceptually similar to the construct axial tree, defined by Prusinkiewicz and Hanan (1989) p. 31.

FUNCTIONING AND TREE ARCHITECTURE IN LIGNUM

The carbon balance relationships comprise the function of the tree in LIGNUM. The architectural structure of the tree is formed by simple branching rules. The main emphasis in LIGNUM is on the carbon balance formulations, and the central question is how to incorporate the carbon balance in a model tree that consists of a large number of units. This will be described extensively later in this paper. Then an account will be given of the formation of the architectural structure. But first, we will take a look at the main hypotheses used in constructing the model.

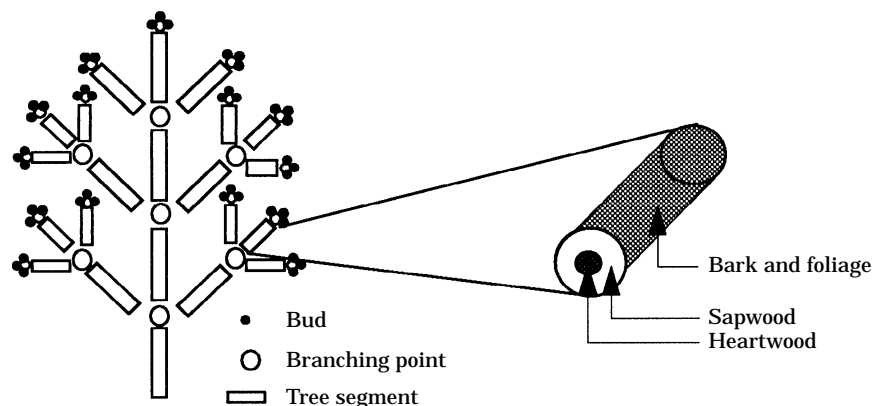


FIG. 1. Schematic presentation of a tree consisting of structural units of LIGNUM. Also shown is the structure of a tree segment.

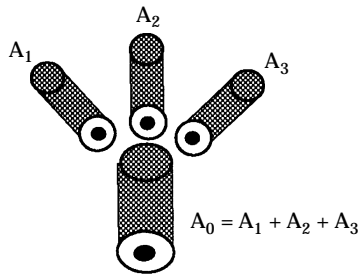


FIG. 2. Illustration of the pipe model principle in a junction of tree segments.

Basic assumptions

The main approach to the production and allocation of carbon in a tree is taken from Nikinmaa (1992). The tree growth model implemented by LIGNUM has the following main characteristics: (1) the time step is 1 year. The carbon balance is considered on an annual basis. (2) Photosynthesis, respiration, senescence and growth are included in the carbon budget of the tree. The carbon budget drives tree growth. (3) The allocation of growth to new and existing parts of the tree is modelled at the tree level; that is, the distribution of available photosynthates is assumed to take place so that the carbon acquired by the tree is distributed to the growing areas according to the local environment of the parts of the tree. (4) The pipe model hypothesis and the principle of functional balance (Nikinmaa, 1992) are used to describe the relationships of biomass and dimensions in the tree. (5) The architecture of the tree follows from an assumption of fixed branching angles and from simple heuristics, which prevents buds pointing unnaturally downwards.

According to the pipe model hypothesis, a tree can be pictured as consisting of foliage, fine roots and a bundle of pipes (Valentine, 1990). The active pipes extend from the root tips to the foliage elements, and the disused pipes no longer connect the roots and the foliage elements. A cross-sectional area of the active pipes corresponds to the cross-sectional area of sapwood. Accordingly, the heartwood consists of disused pipes. The original pipe model idea was further modified to allow for the observed dynamics of the active pipes that the dying foliage releases for reuse (Nikinmaa, 1992). We assume that the foliage biomass is associated with a certain cross-sectional area of sapwood below the foliage. Thus, the new wood growth is proportional to the net change of foliage above the tree segment in question. In our case, it means that the cross-sectional area of sapwood in a tree segment just below a branching point is equal to the sum of the cross-sectional areas of sapwood in the tree segments going upwards from that branching point (Fig. 2). We also assume that the foliage density on the surface of a new tree segment is constant. This leads to a linear relationship between the cross-sectional area of the sapwood and the foliage mass in a new tree segment. The functional balance hypothesis states that in cases where the soil conditions remain constant, the amount of foliage and roots in a tree are linearly related (Nikinmaa, 1992).

Annual growth of the tree

The net production of the tree is used in the growth of new tree segments and their foliage, in adding a new layer of sapwood to the existing tree segments, and in root growth. Part of the roots dies annually, as well as part of the sapwood and the foliage in each tree segment. These events drive the growth dynamics of the model.

In evaluating the annual growth increment, the balance of photosynthesis and respiration is first summed for the whole tree and then allocated to the growth of the different parts of the tree. New growth is possible if the photosynthetic production (P) exceeds the respiration demands of the foliage, the sapwood and the roots (M):

$$P - M > 0 \quad (1)$$

In this case the tree adds new tree segments and buds (iW_n), thickens the existing tree segments (iW_o) and adds new roots (iW_r). At the tree level the carbon balance equation therefore reads

$$P - M = iW_n + iW_o + iW_r \quad (2)$$

Assume for the moment that the number of new tree segments is known. Since the additional sapwood area introduced by a new tree segment must be matched by the tree segments below (Fig. 2), the total need of photosynthates caused by this new tree segment at the time of its creation is not known. It can be evaluated only by travelling from each branch tip to the stem base and assessing induced radial growth. Thus, given certain sizes of new tree segments, there is no guarantee that eqn (2) will hold. Hence, the balancing of eqn (2) must be done iteratively. We define a parameter λ which affects the size of all new tree segments. Say, when $\lambda = 0$, the sizes of the tree segments are equal to 0, and with increasing λ they increase. In this case the right-hand side of the photosynthate balance equation [eqn (2)] depends on λ and can be written

$$P - M = iW_n(\lambda) + iW_o(\lambda) + iW_r(\lambda) \quad (3)$$

Also root growth iW_r is a function of new foliage (as will be explained below) and therefore a function of λ . We solve this equation for λ iteratively using the Van Wijngaarden-Dekker-Brent method (Press *et al.*, 1992).

The number of new tree segments is determined by the conditions of the mother tree segments. During each time step, the number of new tree segments is first calculated and then the solution of eqn (3) for λ is sought. The realized growth is obtained using the solved value of λ . In the following section we specify the relationships which produce the values of the terms P and M in eqn (3). We also describe how growth takes place in tree segments and roots, which determines the values of the terms $iW_n(\lambda)$, $iW_o(\lambda)$ and $iW_r(\lambda)$.

Photosynthesis and respiration

The annual photosynthetic production of a tree is the sum of the photosynthetic productions of the tree segments:

$$P = \sum_{i=1}^{N_f} P_i \quad (4)$$

where N_f is the total number of tree segments which carry

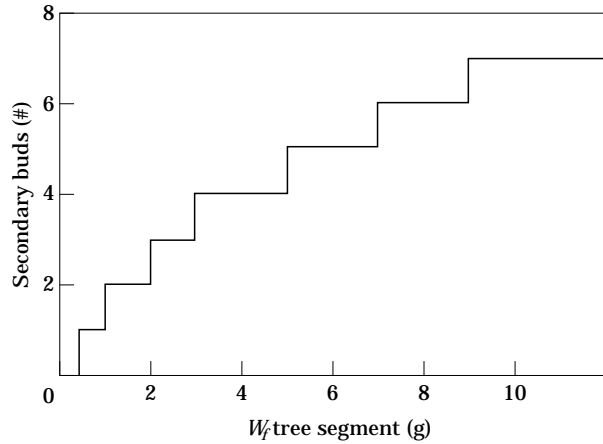


FIG. 3. Number of secondary buds as a function of the foliage mass of the mother tree segment as applied in LIGNUM. The function has been determined on the basis of an unpublished empirical study by Kuitunen and Nikinmaa.

foliage. The photosynthetic production of each tree segment is obtained by applying a model for photosynthesis in a Scots pine stand by Hari *et al.* (1982). According to their model, the annual photosynthetic production of a unit mass of foliage within a pine stand equals $P_0 i_p(b)$, where P_0 is the photosynthetic production in unshaded conditions and $i_p(b)$ is the so-called photosynthetic light ratio. The latter depends on the needle biomass (b) above each location. The function i_p has been determined empirically for a Scots pine stand (Hari *et al.*, 1982) and is given as

$$i_p(b) = \frac{1}{1 + 5.43b^{0.58}} \quad (5)$$

where the dimension of b is kg m^{-2} . In LIGNUM the shading foliage mass for a tree segment is calculated as

$$W_{fu}/A_c \quad (6)$$

where W_{fu} is the foliage mass of the tree above the particular tree segment and A_c is the vertical projection area of the crown. The annual photosynthetic production of a tree segment i with foliage mass W_{fi} in LIGNUM is obtained as

$$P_i = P_0 i_p(W_{fu}/A_c) W_{fi} \quad (7)$$

This simple model mimics the shading experienced by the lower branches.

Maintenance respiration takes place in the needles, in the sapwood of tree segments and in the roots. The annual amount of maintenance respiration (M) of a tree is obtained as the sum of the respiration of the tree segments and roots:

$$M = \sum_{i=1}^N (m_f W_{fi} + m_s W_{si}) + m_r W_r \quad (8)$$

where N is the total number of tree segments, W_{fi} and W_{si} are the foliage and sapwood masses in tree segment i , and m_f , m_s and m_r are the respiration parameters. The amount of maintenance respiration of the roots is assumed to be proportional to their total weight W_r . The respiration of the bark is included in the sapwood respiration.

Extension growth and architecture

Number of new buds. The number of new buds which are created at the apex of a tree segment and which fork away from its direction (N_{ns}) depends on the foliage weight W_f of the mother tree segment as

$$N_{ns} = f_{nb}(W_f) \quad (9)$$

The function f_{nb} is shown in Fig. 3.

New tree segments. The length of a new tree segment depends on the shading. The amount of shading is measured by the photosynthetic light ratio i_p , which is used in calculating photosynthesis [eqns (5) and (7)]. In addition to light, the relative position of the mother tree segment in the tree affects the length of the new tree segment. When the Gravelius order of the tree segment (ω) increases by 1, its length decreases linearly according to a factor $q \in [0, 1]$ (which is a parameter). The Gravelius order of the main stem is 1, that of a main branch is 2, and so on (MacDonald, 1983). In addition to this, the carbon balance adjustment parameter λ [eqn (3)] controls the length of the tree segment. With all these factors, the length of the new tree segment is given by

$$L = \begin{cases} \lambda[1 - (\omega - 1)q]f_L(i_p), & \text{if } 1 - (\omega - 1)q > 0 \\ 0, & \text{otherwise} \end{cases} \quad (10)$$

where the function f_L is depicted in Fig. 4. The radius and length of the new tree segment are related by parameter l_R .

$$L = l_R R \quad (11)$$

Part of the cross-sectional area of the new tree segment is primary wood—i.e. non-conducting wood—present from the very beginning. In LIGNUM it is treated as heartwood. Let ξ denote the proportion of primary wood in the initial cross-sectional area. The radius of heartwood of a newly formed tree segment is then given by

$$R_h = \sqrt{\xi} R \quad (12)$$

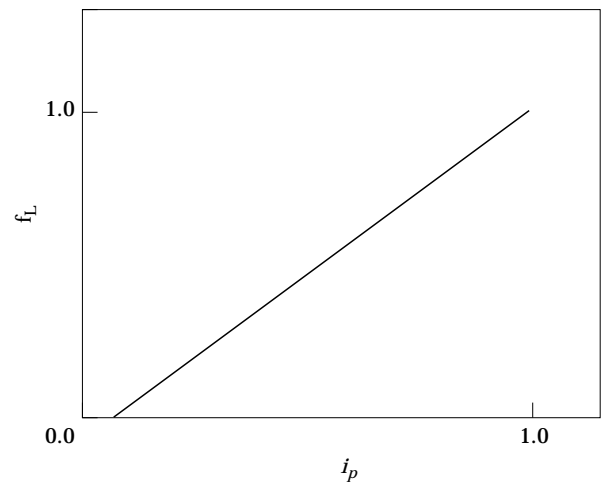


FIG. 4. Relative length of a new tree segment as a function of the light conditions of the mother tree segment, which are represented by the value of function i_p [eqn (5)]. The function has been determined on the basis of an unpublished empirical study by Kuitunen and Nikinmaa.

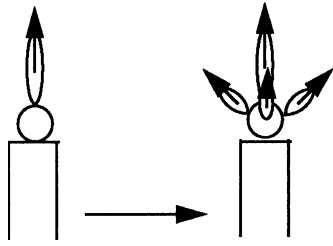


FIG. 5. Branching structure applied in LIGNUM viewed from the side. The branching angle is 45°. The buds are distributed evenly around the branching point.

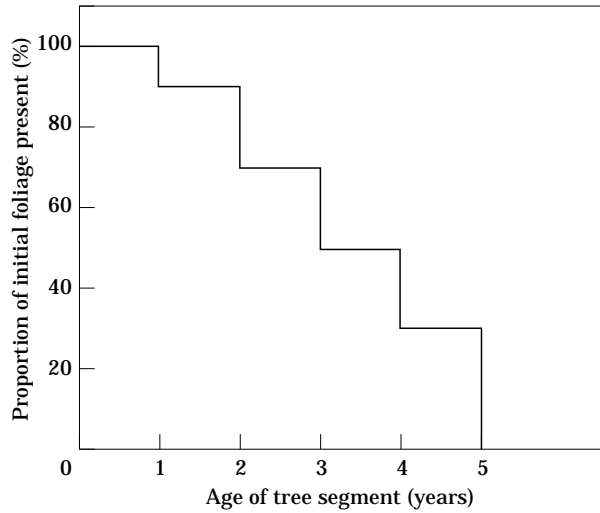


FIG. 6. Proportion of initial foliage present in the tree segment as a function of its age (p_f). The function has been determined on the basis of an unpublished empirical study by Kuitunen and Nikinmaa.

Branch orientation. In the present application of LIGNUM, the main emphasis has been on carbon balance formulations. The development of the architectural structure is therefore treated in a simplified manner. At present, a constant branching angle is applied; the inclination is 45° with respect to the axis of the terminal bud, and the azimuth orientation is symmetric (Fig. 5). Simple heuristics prevents unnatural directions (e.g. buds are not allowed to point downwards). This allows us to model a young Scots pine up to about 15 years of age.

Mass growth

Foliage weight of new tree segments. The foliage weight of a new tree segment (W_{f0}) is evaluated using the assumption that the foliage is distributed evenly on its surface. Excluding the end disks from the surface area, this gives

$$W_{f0} = a_f 2\pi LR \quad (13)$$

where a_f is the foliage density parameter. Note that a simple calculation with eqns (11–13) yields the following relationship between foliage mass and cross-sectional area of sapwood (A_{s0}) in a new tree segment:

$$W_{f0} = \frac{2a_f l_R}{1-\xi} A_{s0} \quad (14)$$

This foliage mass—sapwood area relationship has been

subject to numerous empirical studies at tree level (cf. Nikinmaa, 1992).

Secondary wood thickening. New tree segments add sapwood area in the distal parts of the model tree that must be matched by the sapwood area of the tree segments below (Fig. 2). This induces radial growth. In addition, two further factors affect radial growth. First, sapwood dies, that is, turns into heartwood. This loss must be counteracted by radial growth. Second, when foliage in a tree segment dies, the corresponding part of the original sapwood area is released for reuse, that is, to match the sapwood area of the tree segments above. Let p_f denote the proportion of initial foliage present in the tree segment (Fig. 6). Then the sapwood area requirement of the remaining foliage of the tree segment (A_{sr}) is given in terms of the original sapwood area of the tree segment (A_{s0}) as

$$A_{sr} = p_f A_{s0} \quad (15)$$

Assume that the changes have already been realized above the present tree segment and denote the sum of the cross-sectional areas of sapwood above it by A_{su} . Denote the loss of sapwood area by dA_s (specified later in the section on Senescence). The new radius, R_{new} , of the tree segment follows from the requirements that the sapwood area of the tree segment must correspond to A_{su} , the sapwood loss must be counteracted, the remaining foliage must be matched by sapwood area, while the tree segment contains existing heartwood area (equal to πR_h^2). All this results in a new radius according to the following formula:

$$R_{new} = \max \left[\sqrt{\frac{A_{su} + R_h^2 + dA_s + A_{sr}}{\pi}}, R \right] \quad (16)$$

where the max-operation prevents the reduction of the diameter in case the sapwood area above the tree segment has decreased strongly. Note that when a tree segment has no foliage left, $A_{sr} = 0$, the radial growth of the tree segment is controlled by the senescence of its sapwood and the growth above. Further, the new radius of the heartwood is

$$R_{h_{new}} = \sqrt{\frac{R_h^2 + dA_s}{\pi}} \quad (17)$$

The above equations specify the changes in the dimensions of the tree segments. These changes are converted to changes in dry-weight by calculating volumes with the aid of dimensions and changed further to mass using wood density ρ .

Root growth. Roots are taken into consideration in LIGNUM in an aggregated manner. Following the principle of functional balance (Mäkelä, 1990), new growth of foliage iW_f (the sum of the foliage mass of all new tree segments) requires a corresponding addition of new roots iW_r :

$$iW_r = a_r iW_f \quad (18)$$

where a_r is a parameter. A portion of s_r of the root mass (W_r) dies annually:

$$dW_r = s_r W_r \quad (19)$$

Annual changes in the root mass result from increase and senescence. The root mass of the following year $W_{r_{new}}$ is

$$W_{r_{new}} = W_r - dW_r + iW_r \quad (20)$$

Senescence

Foliage is shed annually as shown in Fig. 6. A certain proportion of the sapwood turns into heartwood annually. The sapwood cross-sectional area is given as

$$A_s = \pi(R^2 - R_h^2) \quad (21)$$

A portion of it, given by the parameter of sapwood senescence (s_s), turns annually into heartwood:

$$dA_s = s_s A_s \quad (22)$$

THE IMPLEMENTATION OF LIGNUM

LIGNUM is implemented with the C++ programming language and the X Window System (OSF/Motif) under the UNIX operating system. An object-oriented language suits well our approach, which is to match the structure of a tree closely to its function. We wanted to leave the door open for future extensions to be made in the model, and a language that supports modular design is essential to that. A knowledge of Object Modeling Technique (OMT, Rumbaugh *et al.*, 1991) and C/C++ is helpful, but not necessary, for understanding the description of the implementation.

Program architecture

The implementation of any computer program involves two activities. First, one identifies and creates data types to describe the concepts of interest. Second, one describes real world entities with data objects as examples of the data types. The final step is the construction of the necessary algorithms.

In ‘Defining the units of LIGNUM’, we defined the tree as a collection of tree segments (*TS*), branching points (*BP*) and buds (*B*). For the implementation we introduce a new tree compartment called *axis* (*A*). The axis binds the basic units into a main stem and into branches. An axis can be represented as a list. With the list notation employed here, the main stem of the tree in Fig. 1 is

$$[TS_0, BP_1, TS_2, BP_3, TS_4, BP_5, TS_6, BP_7, B_8] \quad (23)$$

The indices denote the position of the element in the list. Tree segments are at even positions and branching points at odd positions on the axis. The last element in the axis is a bud. A branching point connects a set of axes to the tree. We can continue the use of lists in our design by defining a branching point as a list of axes. For example, using our notation for lists, the main stem in Fig. 1 can be written as

$$[TS, [A, A], TS, [A, A], TS, [A, A], TS, [[B], [B]], B] \quad (24)$$

The branching points in eqn (23) are ‘unfolded’ as lists of axes (*A*). The axes in the last branching point are also unfolded showing the buds as the only list members.

The tree and the axis are dynamic units where new tree compartments are created and old ones that don’t perform any growth processes (like dead branches) can be deleted during the simulation. The order of the tree and axis parts

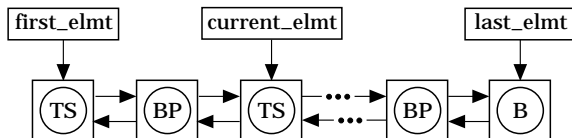


FIG. 7. Presentation of a stem with the aid of a two-way list (TS, tree segment; BP, branching point; B, bud).

remains the same during the flow of development, although some parts are added and some deleted.

The bud is a concept of interest in our design for two reasons. First, buds create new tree segments, branching points and buds during the simulation. Suppose that each of the three buds in eqn (24) creates one tree segment and one branching point with two axes consisting of only one bud. The list would then appear as

$$[TS, [A, A], TS, [A, A], TS, [A, A], TS, [[TS, [[B], [B]], B], [TS, [[B], [B]], B]] \quad (25)$$

Second, buds determine the three dimensional shape of the tree during the growth process. In order to do that, the position and the direction of each bud must be known. The position of the bud is a point in three dimensional space, and the direction of the bud is determined by the direction cosines of a unit vector \vec{U} of length 1:

$$\vec{U} = (\cos \alpha, \cos \beta, \cos \gamma) \quad (26)$$

α , β and γ are the angles between \vec{U} and the positive x , y , and z axes, respectively. When the length of the new tree segment is known, the terminal bud can be given a new position in space.

The design of the tree as a collection of lists makes the program a consistent, easily comprehended and robust structure. Further, the various growth processes described above can be implemented using well-known list functionals (Paulson, 1993). For example, photosynthesis [eqn (7)] is performed using the list functional *map*: the tree (i.e. each axis) is traversed, and the operation for this metabolic function is applied to each tree compartment. The annual photosynthetic production of the tree [eqn (4)] can be obtained using *list reduction*: the tree is traversed, and the photosynthates in the tree compartments are summed.

The two-way list

We use a two-way list (Meyer, 1988) as the list structure (Fig. 7). The list (called *DList*) is a sequence of list elements in which each element is connected both to the previous and to the next element. The *first_elmt* and the *last_elmt* mark the boundaries of the list. Each list element can store data, in our case information describing the tree compartment (i.e. tree segment, branching point or bud). The status of the list is defined not only by the contents of the list but also by the position of the *current_elmt*.

This choice enables us to construct an efficient operational interface for the list. The first and the last list element can be found at constant time and the ubiquitous, usually recursive list operations, like *map* and *reduce*, can be used effectively.

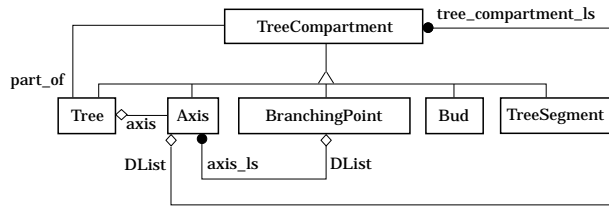


FIG. 8. Object model (cf. Rumbaugh *et al.*, 1991) for LIGNUM.

Once the operations for this list are implemented, the result is a verified reusable C++ class.

The tree compartments

The object model for those tree compartments described in previous sections uses OMT-notation (Rumbaugh *et al.*, 1991) to present relationships between the classes that constitute the structure of the tree (Fig. 8). An outline for a detailed object model of a tree may be found in Salminen *et al.* (1994).

Axis and *BranchingPoint* establish the basic structure of the implementation with their list structures. *TreeSegment* is responsible for the metabolic functioning of the tree, and *Bud* has methods to create new tree compartments. The class *Tree* provides interface to manipulate and query the status of the structure of embedded lists of tree compartments. The common association *part_of* to all tree compartments is used to access tree level information. For example to compute shadiness in various parts of the tree, the foliage mass at different height levels must be known [eqn (6)].

An *abstract class* is a class that has no direct instances. It is used to organize features common to several classes. The abstract class *TreeCompartment* organizes common features of its subclasses *Axis*, *BranchingPoint*, *TreeSegment*, *Bud* and *Tree* by defining only the signatures of the methods, like photosynthesis. The class-specific behaviour is implemented in the subclasses. The same operation takes on different forms in different classes. This is called *polymorphism*. In practice polymorphism presumes *dynamic binding*. The actual piece of program code to be executed is determined at the time the method is called.

The use of dynamic binding allows us to deal with the tree compartments in a uniform manner when computing e.g. metabolic functioning. When the annual photosynthesis is about to be evaluated in the tree, the *map*-operation can be applied straightforwardly. Each axis, plant segment, branching point and the last bud can all be viewed as instances of *TreeCompartment* [eqn (23)]. Dynamic binding guarantees that the correct method is evaluated in each object.

SIMULATIONS OF YOUNG SCOTS PINE

The parameter values shown in Table 1 apply approximately to the conditions in southern Finland. They do not correspond to any particular stand and have not been adjusted to obtain a good fit to data. The sources of the values are studies by Nikinmaa (1992), Mäkelä (pers. comm.) and a presently still unpublished study by Kuitunen and Nikinmaa. The initial tree in the simulations was one tree segment, the size of which could be varied.

Simulation with normal parameters and comparisons

The general look of the simulated forest-grown tree is realistic (Fig. 9). The decreasing irradiation in the lower part of the crown is reflected as slower growth of branches.

The height growth pattern that LIGNUM produces was compared against seedling growth data available from northern Finland. In simulations, the photosynthetic pro-

TABLE 1. Parameters of LIGNUM with values for young Scots pine trees growing in southern Finland. The sources of values are Nikinmaa (1992), Mäkelä (pers. comm.) and an unpublished study by Kuitunen and Nikinmaa

| Parameter | Meaning | Unit | Value |
|-----------|--|--|-------|
| a_f | Needle mass—tree segment area relationship | kg m ⁻² | 1.3 |
| a_r | Foliage—root relationship | kg kg ⁻¹ | 0.5 |
| l_R | L/R for a new tree segment | — | 100 |
| m_f | Maintenance respiration rate of needles | kgC kgC ⁻¹ year ⁻¹ | 0.2 |
| m_r | Maintenance respiration rate of roots | kgC kgC ⁻¹ year ⁻¹ | 0.24 |
| m_s | Maintenance respiration rate of sapwood | kgC kgC ⁻¹ year ⁻¹ | 0.024 |
| P_0 | Photosynthetic production in unshaded conditions | kgC kgC ⁻¹ year ⁻¹ | 4.6 |
| q | Tree segment shortening factor | — | 0.1 |
| s_r | Senescence rate of roots | 1 year ⁻¹ | 0.33 |
| s_s | Senescence rate of sapwood | 1 year ⁻¹ | 0.07 |
| ρ | Density of wood | kg m ⁻³ | 400 |
| ξ | Fraction of heartwood in new tree segments | — | 0.6 |

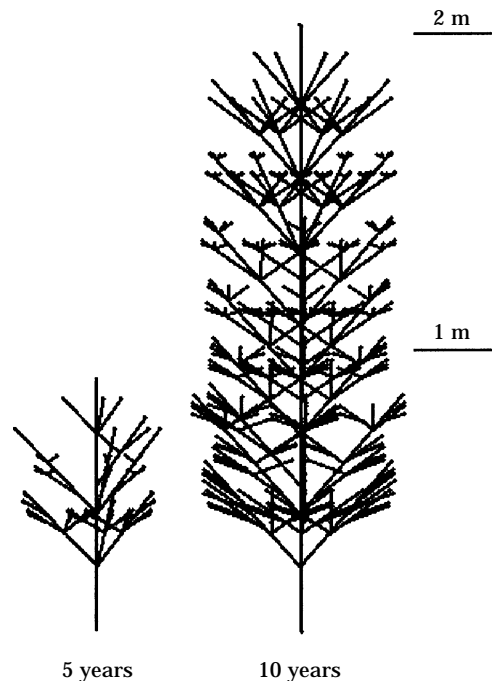


FIG. 9. Images of the tree produced by LIGNUM at two ages viewed from the side. The parameter values are according to Table 1. Stem and branch thickening is not visualized.

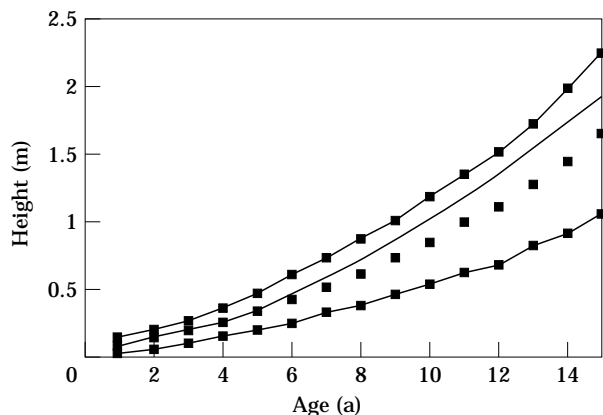


FIG. 10. Comparison of height according to LIGNUM (continuous line) with average height of seedlings (■) vs. age. The source of data was a subset of permanent sample plot material from Northern Finland described by Gustavsen, Roiko-Jokela and Varmola (1988). Lines with markers (■) denote one standard deviation around the average. The parameter P_0 (Table 1) was decreased by 30% to correspond to the less favourable growing conditions in northern Finland as suggested by Nikinmaa (1992).

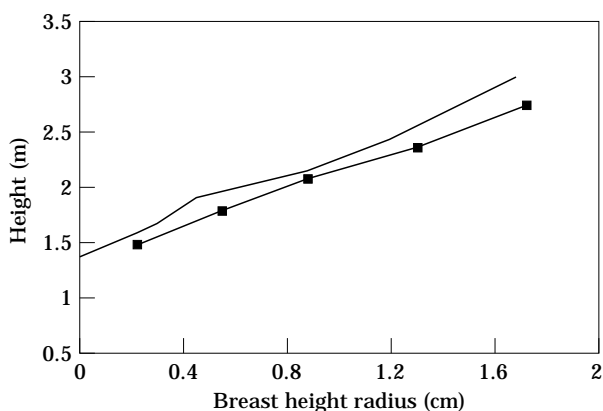


FIG. 11. Tree height as a function of breast height radius simulated by LIGNUM (—) the corresponding relationship analysed from a tree which has grown in a sapling stand (—■—). The data are from Lukkarinen (1992), tree no. 16. Its age was 14 years; the LIGNUM curve corresponds to a 15-year simulation.

duction parameter determined in southern Finland was decreased to account for the effect of the less favourable growing conditions in northern Finland (by 30%, cf. Nikinmaa, 1992). The pattern of the growth curve mimics well the observed one (Fig. 10). LIGNUM generates the similar accelerating height growth that is observed in seedlings. The acceleration of growth is caused by the slow processes of supplying the crown with the necessary amount of needles. This was also shown in the simulations: when the size of the initial tree segment was increased, the growth was generally faster.

The height-diameter relationship of the tree follows from tree segment level dependences in LIGNUM [eqns (10) and (16)]. Observing whether this relationship corresponds to that obtained in tree level observations is thus a test for the model (Fig. 11). The model prediction coincides qualitatively

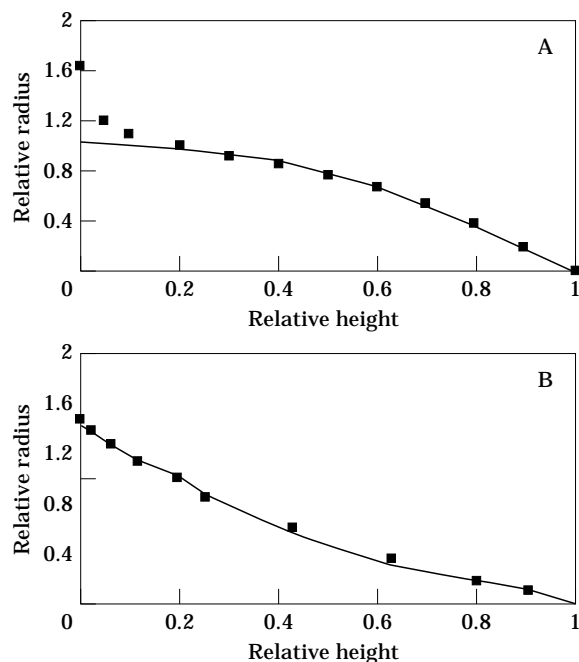


FIG. 12. Taper curves produced by LIGNUM (solid line) for a tree growing in a stand (A) and in isolation (B). The curve in graph A was obtained with normal parameter values (Table 1). The curve in graph B was obtained by constraining $f_L(i_p) \equiv 1$, which mimics open-growing conditions. The simulated period was 15 years. Displayed observations (■) are: (A) average taper curve for Finnish Scots pines (Laasasenaho, 1982), (B) observations of Lukkarinen (1992) of an isolated tree (tree no. 6, age 14 years).

well with the observations, indicating that in this respect LIGNUM works properly.

The taper curves produced reflect the pipe model relationships built into LIGNUM. The simulation with the normal parameter values produces a taper curve that is fairly similar to the average taper curve of Finnish Scots pines (Fig. 12A). The butt swell is lacking in LIGNUM's taper curve. This is understandable since the pipe model does not consider that phenomenon. Another taper curve (Fig. 12B) was simulated for isolated trees. The isolation was—somewhat deliberately—mimicked by modifying function f_L (Fig. 4) so that $f_L(i_p) \equiv 1$, that is, light conditions have no effect on relative shoot elongation. This results in a small branchy tree. The shape of the taper curve produced by LIGNUM has a similar shape to the measured one (Fig. 12B).

The tree level relationship between foliage mass and cross-sectional area of sapwood follows in LIGNUM from the tree segment level relationship of eqn (14). In addition to this, the senescence of foliage and sapwood affects the tree level relationship. According to the pipe model hypothesis (Nikinmaa, 1992), the relationship between the cross-sectional area of sapwood at the crown base and the foliage mass should be a straight line. The relationship simulated by LIGNUM is not a completely straight line but a somewhat curved one (Fig. 13). However, the curvature is so slight that it can be approximated with a straight line. It should be noted that LIGNUM's predictions concern one tree over a

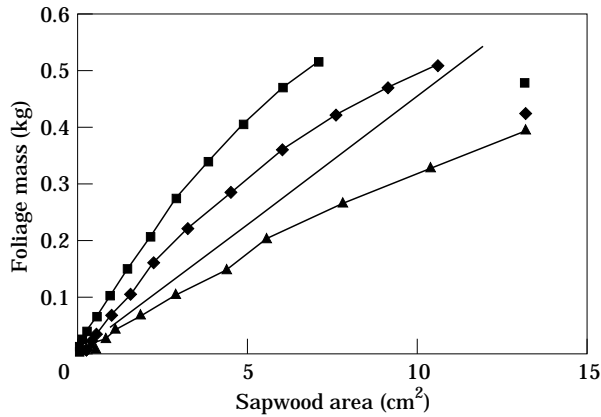


FIG. 13. Foliage mass vs. sapwood area at crown base with values 0.5 (\blacktriangle), 1.3 (\blacklozenge), and 2.1 (\blacksquare) of parameter a_f [eqn (13)]. The normal value of a_f is 1.3 (Table 1). Superimposed is a line which has the measured average slope for Southern Finland (450 kg m², Kaipiainen and Hari, 1985).

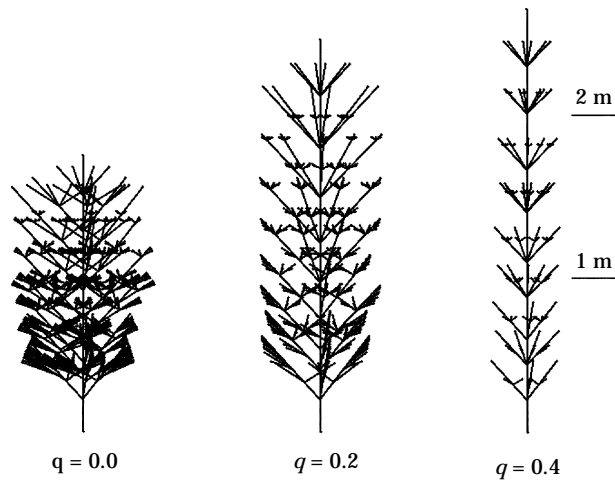


FIG. 14. Simulation of 10-year-old trees with three values of parameter q that determines the shortening of tree segments as a function of branching order [eqn (10)]. Trees are viewed from the side. Stem and branch thickening is not visualized.

period of time, whereas the empirical observations for this relationship of the pipe model hypothesis have been made from many trees at one time. The curve with the normal value of the a_f parameter (Table 1) corresponds qualitatively to the line with the empirically determined slope (Fig. 13).

Simulations depicting the effects of branching and sapwood senescence

The most important factors that control tree growth in LIGNUM are the relative length growth function f_L , the number of secondary buds f_{nb} , and the parameter q , which controls the decreasing of tree segment length with increasing Gravelius order [eqn (10)]. All these factors contribute to the growth which takes place at the ends of the branches. The common feature in the effect of these factors is that with increasing evenness of the growth pattern (i.e. growth is the same, regardless of the conditions of the

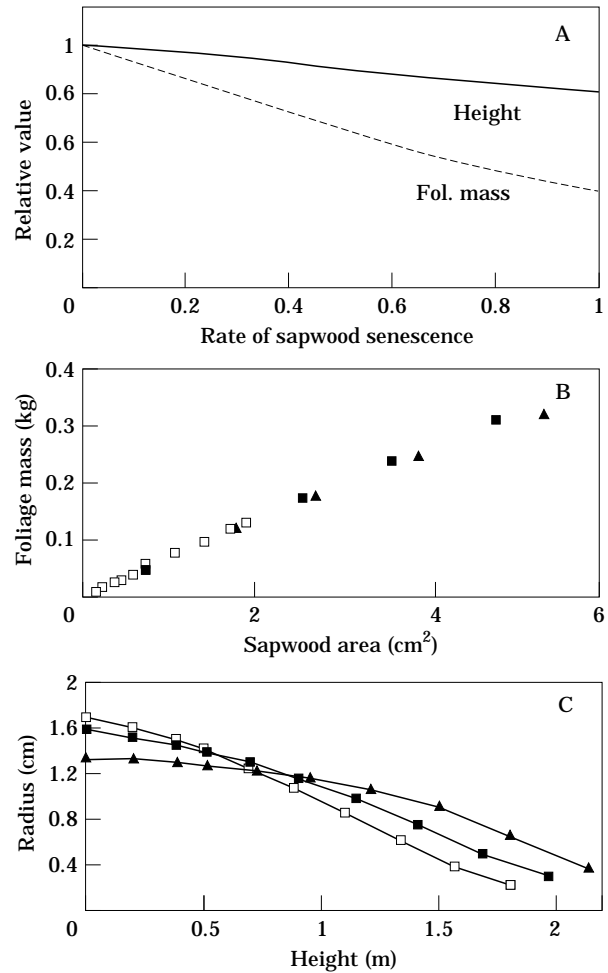


FIG. 15. Effect of the rate of sapwood senescence (s_s) on tree growth. A, height and foliage mass. B, Foliage mass vs. cross-sectional area of sapwood at crown base with values 0 (\blacktriangle), 0.07 (nominal value, Table 1) (\blacklozenge) and 1 (\square) of s_s , and taper curves with values 0 (\blacktriangle), 0.5 (\blacksquare), and 1 (\square) of s_s (C).

mother tree segment) the tree form becomes more bushy and height growth is slower. This effect is clearly shown with varying values of parameter q (Fig. 14). The relationship between the length growth of the secondary and main axes has a clear effect on the shape and height growth of the tree. The shorter the secondary axes are, relative to the main axis, the longer and slimmer the tree becomes. A similar pattern is also observed when the function f_L (cf. Fig. 12) and f_{nb} are changed so that growth is less dependent on the conditions of the mother tree segment. If the growth conditions of the real tree change, it is likely that all these factors should be changed in the model.

The senescence of the sapwood is a factor which clearly affects the structural relationships of tree growth, but which is rather poorly known and understood (e.g. Saranpää, 1990). The likely effect of sapwood senescence was demonstrated with simulations in which the senescence parameter s_s varied between 0 (no sapwood senescence) and 1 (all current year sapwood turns into heartwood during the time step) (Fig. 15). Increasing sapwood senescence means

increasing consumption of assimilates in maintaining the sapwood cross-sectional area relationships [eqn (16)], which diminishes growth (Fig. 15A). The relative change is remarkably larger in foliage growth than in the height growth. This indicates that the increase in sapwood senescence may not be reflected in the first place in the size of the tree but in the foliage density. The rate of sapwood senescence seems not to affect the pipe model relationship (Fig. 15B). With all values of s_s , the relationship follows the same line (actual curve, cf. Fig. 13); only the maximum amounts of foliage and sapwood differ. Increasing the rate of sapwood senescence makes the tree thicker (Fig. 15C). Although increasing s_s promotes diameter growth, volume growth of the stem is largest with $s_s = 0$ (calculated from the taper curves of Fig. 15C).

DISCUSSION

We have constructed a model that deals both with the three-dimensional structure of tree crowns and with carbon metabolism, which produces material for growth. The unification of the two aspects—structural and functional—of plant existence was achieved by composing the model tree with the aid of a few basic units. By combining these units and observing their co-ordinates, the three-dimensional structure of a tree crown can be described. When submodels for carbon gain, loss and consumption in growth are confined to the basic units, the mass balance driving growth can be formulated. The distribution of growth to the construction of new units was arranged so that the local conditions influence the size and number of new growth units, constrained by the requirement that the photosynthate balance be met at tree level.

The realization of LIGNUM was accomplished with a C++ program that treats the model tree as a collection of lists consisting of basic units. This enables us to make use of existing algorithms for list manipulation and leads to an efficient design. The implementation is also open for adding or changing model components. Modularity and relative ease in incorporating new model components was one of the goals in the construction of the model. The object-oriented approach offers very good possibilities for construction of such simulation models (Sequeira *et al.*, 1991). LIGNUM is aimed at being a framework which can incorporate (sub)models taken from various fields of tree research. Often programs for simulation purposes have been written with one purpose in mind, used once or twice to test the model at hand, and then discarded. The consequence is that it has been easier to write *ad hoc* applications than utilize previous work. It is important for us to develop the current implementation of LIGNUM so that it can become a useful tool for forest ecologists, growth and yield researchers, and tree physiologists. Modellers should be able to express growth processes by reusing the components and structure of LIGNUM.

Our definition of tree units (tree segment, branching point and bud) allows us to deal with basic features of tree growth. If more complicated phenomena are going to be studied, a more versatile set of units must be defined. However, due to the object-oriented design of LIGNUM,

the basic units can be divided into processes and units on the next hierarchical level below with no need to change the basic structure of the existing model. This makes it possible to refine the units when the need arises. The ultimate aim of the LIGNUM model is to be generic. Therefore the structure should be such that different crown types can be simulated with it. In a botanical sense, certain anatomically similar structures are repeated throughout the trees, forming the crown (e.g. Hallé, Oldeman and Tomlinson, 1978). At present the model considers only vegetative organs. However, consideration of reproductive parts will be necessary eventually.

The present description of the tree architecture is very simple. It was, however, quite adequate for modelling the growth of young Scots pine trees. The AMAP model (Jaeger and de Reffye, 1992), in which images of all kinds of plants are produced, is based on considering plant organization on many levels, e.g. internodes, growth units, plant axes and architectural units. Such detailed division is lacking in the present version of LIGNUM, but it is possible that similar concepts can be introduced in the future to improve the efficiency of the program. Such a division would also be reasonable to account for the hierarchical nature of the function of a tree. Changes take place rapidly at the leaf level, and the communication is mainly with the atmosphere and with the branch to which the leaves are attached. On the other hand, a branch as a whole competes for water and nutrients with other branches, while they as a whole supply the stem and roots with energy for their functions. Also, the time constant of these 'partitioning' reactions is much slower than those at the leaf level.

The pipe model hypothesis is used in the present case to describe the relationships between biomass and tree dimensions. This hypothesis has been frequently used for describing tree structure (cf. Nikinmaa, 1992). There exist alternatives to the pipe model hypothesis, e.g. the theory of mechanical strength (Assmann, 1970; Morgan and Cannell, 1988). LIGNUM is not tied to any one theory of secondary growth in trees. On the contrary, it offers a framework to study the consequences of partitioning principles at tree level.

The L-systems (Prusinkiewicz and Hanan, 1989) offer a well-established means to achieve an advanced description of branching. Kurth (1994a) has introduced the software tool GROGRA for the interpretation of stochastic, context-sensitive growth grammars (i.e. L-systems). Using such a system in conjunction with LIGNUM might possibly improve the present description of the branching. Intuitively thinking, we should be able to simplify the growth grammars significantly for our purposes, because most of the growth factors (e.g. length of tree segments, number of new buds, etc.) described in the replacement rules of the L-systems are defined in our equations for the carbon budget of the tree.

Simulations and comparisons with some observations indicate that LIGNUM is able to reproduce several features of growth in young Scots pine trees. It was interesting that some tree level relationships were reproduced by LIGNUM, although the modelling was made at the level of tree parts. On the other hand, consideration of the pipe model at a detailed level did not reproduce it exactly at tree level. The

performed comparison was not intended to be a comprehensive test. It would require more data about conditions than we had at our disposal. We also feel that such a test would not be appropriate at the present, i.e. early, stage of model development. However, even the present, fairly simple treatment of growth showed the importance of a correct description of architectural design and the processes that affect wood growth in tree segments. The simulations also hint at a relationship between foliage density in the crown and the sapwood turnover rate. Such a result is interesting, e.g. from the point of view of foliage loss studies.

As mentioned, the present version of the model treats trees in a centralized manner as regards to carbon balance. To describe trees as modular organisms (e.g. Sprugel, Hinckley and Schaap, 1991), the growth of each new tree segment (i.e. shoot) should take place in an independent manner based on the local photosynthetic production. Then the growth should be balanced so that it could consider the structural requirements of the other parts of the tree (e.g. Ford *et al.*, 1990). Such description needs to be coupled with a more detailed description of the light climate. The study by Sorrensen-Cothorn *et al.* (1993) demonstrated the potential improvements that could be expected at tree level growth if spatial heterogeneity of shoot-level light climate is considered. Such improvements are fairly easy to introduce into LIGNUM.

The exact control of axis elongation and secondary growth of xylem are still somewhat poorly understood (see review by Nikinmaa, 1992). Hormonal control has a major role to play (e.g. Aloni, 1987, 1991; Savidge, 1991), but other substances are most likely also involved (e.g. Savidge and Wareing, 1981). However, whatever the method of the control of growth, a realistic description of tree architecture offers possibilities to study the effects of different growth-controlling principles and mechanisms on the structure. A more physiologically-based control of growth implies description of the relevant material flows with the tree—such as water and nutrients, assimilates and perhaps even hormones. Such a description may require a further division of the basic morphological units of the model into their components such as phloem, cambium and xylem. As mentioned, this division is compatible with the present program architecture.

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APPENDIX
Glossary of symbols

| Variable | Meaning | Units |
|-------------|--|----------------|
| A_c | Vertical projection area of tree crown | m ² |
| A_s | Cross-sectional area of sapwood in a tree segment | m ² |
| A_{su} | Sum of cross-sectional areas of sapwood in tree segments just above the tree segment in question | m ² |
| A_{s0} | Cross-sectional area of sapwood in a new tree segment | m ² |
| A_{sr} | Sapwood area requirement of the remaining foliage of tree segment | m ² |
| dA_s | Cross-sectional area of sapwood turning into heartwood during one year in a tree segment | m ² |
| dW_r | Amount of roots dying in one year | kgC |
| iW_f | Sum of foliage masses of all new tree segments | kgC |
| iW_n | Annual amount of carbon required to build new tree segments | kgC |
| iW_o | Annual amount of carbon required in secondary wood thickening | kgC |
| iW_r | Annual amount of carbon required for root growth | kgC |
| L | Length of tree segment | m |
| M | Annual amount of carbon used for respiration | kgC |
| N | Number of tree segments | — |
| N_{ns} | Number of new secondary buds at the end of mother tree segment | — |
| P | Annual amount of photosynthetic production | kgC |
| p_f | Share of initial foliage mass present in a tree segment | — |
| R | Radius of tree segment | m |
| R_h | Radius of heartwood in tree segment | m |
| R_{new} | New radius of tree segment | m |
| W_f | Foliage mass of tree segment | kgC |
| W_{f0} | Foliage mass of new tree segment | kgC |
| W_{fu} | Foliage mass above a tree segment in the tree | kgC |
| W_r | Root mass | kgC |
| W_r^{new} | New root mass | kgC |
| W_s | Mass of sapwood in a tree segment | kgC |
| λ | Parameter to balance carbon balance equation | — |
| ω | Gravelius order of tree segment | — |