J. Perttunen, R. Sievänen, and E. Nikinmaa. 1998. LIGNUM: a model combining the structure and the functioning of trees. Ecological Modelling, volume 108, numbers 1-3, pages 189-198.

ELSEVIER

Ecological Modelling 108 (1998) 189–198

ECOLOGICAL MODELLING

LIGNUM: a model combining the structure and the functioning of trees

J. Perttunen [a,*], R. Sievänen [a], E. Nikinmaa [b]

[a] The Finnish Forest Research Institute (Metla), Unioninkatu 40 A, 00170 Helsinki, Finland

[b] University of Helsinki, Department of Forest Ecology, PB 24, 00014 University of Helsinki, Helsinki, Finland

Accepted 17 March 1998

Abstract

The model LIGNUM treats a tree as a collection of a large number of simple units that correspond to the organs of a tree. The model describes the three-dimensional structure of the tree crown and derives growth in terms of the metabolism taking place in these units. The time step is one year. The structural units are: tree segments, branching points and buds. Tree segments are separated by branching points. 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 trees as a collection of lists. The annual growth of the tree is driven by the available photosynthetic products after accounting for respiration losses. The photosynthetic rate of foliage depends on the amount of intercepted light. The amount of photosynthates allocated to the growth of new tree segments is controlled by the light conditions and the amount of foliage of the mother tree segment. The biomass relationships of the tree parts follow, e.g. from a pipe model hypothesis. The orientation of new tree segments results from application of simple branching rules. LIGNUM has been parametrized for young Scots pines *(Pinus sylvestris* L.). © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Growth model; Solar radiation interception; Tree architecture; Branching structure; *Pinus sylvestris* L.; Developmental morphology and physiology

1. Introduction

Trees are composed of numerous, rather simple basic units that form complex entities. Traditionally they have been studied in plant science analytically in a top-down fashion, starting at the level of a single organ (i.e. the tree) and working down to a level of a single cell or even in more detail. A great deal of information on local behavior of these parts has accumulated. According to Kurth (1994b) recent developments of plant sci-

* Corresponding author. Tel.: +358 857051; fax: +358 8570 5717; e-mail: jari.perttunen@metla.fi

PII S0304-3800(98)00028-3

ence and resulted models and modelling methodologies can be roughly divided into two categories.

First, the so called process-based models for tree growth and development capture a great deal of physiological detail (e.g. Hari et al., 1982; Landsberg, 1986; Mohren, 1987; Friend, 1992; Bossel, 1994). They deal with physiological processes and give a detailed account of metabolism and plant growth in terms of mass variables. Using these models and advanced measuring techniques, a great deal of plant functioning at detailed physiological level has been clarified. However, this has often been done on the expense of oversimplified structural description of trees (e.g. Kurth, 1994b).

Second, the invention of Lindenmayer systems (Lindenmeyer, 1968; Prusinkiewicz and Hanan, 1989), L-systems for short, and other mathematical descriptions of tree architecture has (Jaeger and de Reffye, 1992) brought a formal way to deal with three dimensional branching structures of trees. These methods are able to produce vivid images of plants and other branching systems. Plant images are produced even as commercial products using these methods. However, purely morphological descriptions lack the connection to physiology, i.e. the causal description of plant development.

The synthesis of these two approaches (combining tree metabolism with realistic description of tree architecture) is a tempting scientific problem. In the following, we first present shortly model LIGNUM (Salminen et al., 1994; Sievänen et al., 1995; Perttunen et al., 1996). It predicts tree growth and development with annual time step up to about 15 years of age utilizing a great number of basic tree units in terms of both functioning and architecture. We describe some predictions the model makes when used with alternative descriptions of sapwood–foliage relationship and branching habit. We also discuss the changes and improvements made in the model, in the first place the solar radiation interception in the tree crown, in comparison to the previous versions of it (Salminen et al., 1994; Perttunen et al., 1996).

2. The tree model LIGNUM

2.1. Structural units

In modelling tree growth and development the level of scrutiny should allow both realism in considering the detail and ability to grasp the whole. In LIGNUM simple structural units (Fig. 1), tree segment, branching point and bud are used to describe trees. They allow sufficiently detailed description without rendering the modelling problem too complicated. However, this approach allows us to divide the basic units into more detailed parts and processes if need arises. Described treatment of tree structure concerns only aerial parts; roots are considered simply in terms of their mass at present.

2.2. Functioning

LIGNUM emphasizes the formulation of carbon balance in a tree. The central processes of carbon balance are assimilation of carbon in photosynthesis and respiration through which carbon is lost back to atmosphere. A key question is how to equate the photosynthetic net production and the growth in a model that combine an individual from a large number of units. The chosen structure has key influence on functioning since it

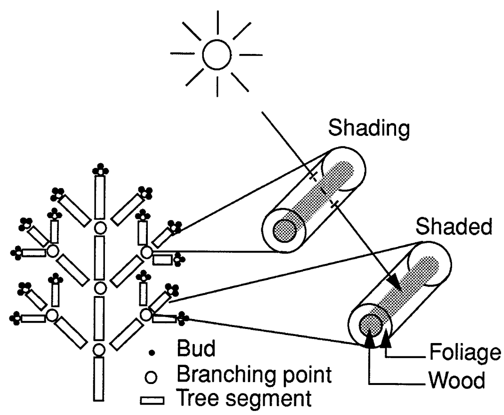

Fig. 1. Schematic presentation of a tree consisting of simple structural units in LIGNUM and the principle of the solar radiation interception model. The distance light beam traverses in foliage is marked by a dashed line.

directly affects the carbon capture of trees through determining the spatial distribution of solar radiation intercepting foliage. It also affects carbon distribution between producing and consuming organs.

Presently LIGNUM uses teleonomic arguments to distribute photosynthates. They are derived from the regularities observed to result from growth. Architectural rules based on empirical measurements (Kuitunen, 1996) determine the relative extension growth of branches and the so-called pipe model (Shinozaki et al., 1964) determine the relative thickness growth of the woody part. According to the pipe model a tree is pictured as a bundle of pipes that extend from the foliage elements to the root tips. The addition of foliage requires building corresponding pipe and a certain amount of roots. Pipes that connect foliage and roots are functional (i.e. alive) and they all together form sapwood. Pipes that have lost the connection to living foliage elements are non-functional (i.e. dead) and called heartwood. Following from this principle we can calculate the amount of thickness growth of woody axes when new tree segment with foliage is added at the terminal end of the axis.

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

$$P - M > 0 \tag{1}$$

In this case the tree extends its stem and branches by adding new tree segments and buds ($i\mathrm{W}_n$), thicken existing tree segments ($i\mathrm{W}_o$) and adds new roots ($i\mathrm{W}_r$). At the tree level the carbon balance equation reads therefore as:

$$P - M = i\mathrm{W}_n + i\mathrm{W}_o + i\mathrm{W}_r \tag{2}$$

Assume, for the time being, that the number of new tree segments is known. From the pipe model it follows that the additional sapwood area introduced by a new tree segment must be matched by tree segments below. However, it is not known at the time of its creation what is the total need of photosynthates caused by this new tree segment. It can be evaluated only by travelling from branch tips to stem base and assessing induced radial growth. Hence, finding the dimensions of the new tree segments that balance Eq. (2) must be done iteratively.

2.3. Photosynthesis and respiration

Annual photosynthesis is evaluated by calculating the amount of solar radiation each segment (that carries foliage) absorbs. The annual photosynthesis of tree segment i is then assumed to be directly proportional to the amount of intercepted radiation, I_i:

$$P_i = P_r \times I_i \tag{3}$$

where P_r is a parameter. The radiation absorption is calculated using the distribution of the radiation coming from the sky during the growing period and it is explained in the Section 2.4. The annual amount of photosynthesis (P) of the tree is obtained simply by summing up contributions of each tree segment:

$$P = \sum_{i=1}^{N_f} P_i \tag{4}$$

where N_f is the number of tree segments that carry foliage. The respiration rate (M) of the tree is obtained analogously by summing the respiration rates of all tree segments and the roots as explained in Perttunen et al. (1996).

2.4. Interception of solar radiation

The sky is divided into sectors (like a shell of a turtle) and the amount of radiation coming from each sector during the growing period is assumed to be known. In the present simulations we used the zonal brightness of standard overcast sky (independent of the azimuth) as defined by Ross (1981) (p. 163) to evaluate the amount of radiation coming from the sectors of the sky. We used value of 1200 MJ/m^2 per growing period for the total incoming photosynthetically active solar radiation which is a typical value for southern Finland (P. Stenberg, personal communication, 1996). The radiation received by the subject tree segment depends on the brightness of the sector and shading caused by the other tree segments of the tree. In the case the light beam coming from the sector collides with a woody part of any of the shading tree segment the sector is blocked and the subject tree segment does not receive any radiation from that direction. This is analyzed as a (rather simple) geometrical problem (Fig. 1). The radiation received by the subject tree segment is the sum of the radiation coming from all sectors of the sky and shaded (or blocked) by the other tree segments.

In calculation of the amount of shading the tree segments exercise, we use the results of Oker-Blom and Smolander (1988) on solar radiation absorption by Scots pine shoots much in the way Kellomäki and Strandman (1995) did in their model. First, suppose the light beam from the sector of the sky has traversed distance l_i in the foliage of a shading tree segment *i*. On the basis of the results of Oker-Blom and Smolander (1988) the transmission h_i through segment *i* is:

$$h_i = \exp[-K(\phi_i)\rho_{fi} l_i] \tag{5}$$

where ρ_{fi} *is* the foliage area density of the tree segment (area of the foliage divided by the volume occupied by the foliage), ϕ_i is the angle between the axis of the segment and the direction of the light beam, and K is a function defining the light extinction coefficient of a Scots pine shoot as a function of its inclination angle. It has been empirically determined by Oker-Blom and Smolander (1988). Whether the light beam hits the tree segment (c.f. Fig. 1), whether it hits the woody part of the segment and the distance the light beam possibly travels inside the volume of the segment that is occupied by foliage can be analyzed with the aid of analytical geometry. For this analysis tree segment is treated consisting of a wood cylinder surrounded by a mantle of foliage (Fig. 1). We do not report those calculations here but refer to textbooks of analytical geometry (e.g. Anton 1987).

The transmission through all segments that are on the way of the light beam to the subject segment is

$$H = \Pi h_i \tag{6}$$

where the product is taken over all shading segments. When the amount of radiation coming from the sector s of the sky is I_s^c, the subject segment that is shaded by others is receiving radiation the amount

$$I_s^0 = H I_s^c \tag{7}$$

from the sector s of the sky. In the case the light beam hits the woody part of a shading segment, it is blocked and the subject segment does not get any radiation from this sector of the sky and in this case I_s^0 equals 0. Finally, the amount the subject segment intercepts from the coming radiation I_s^0 is given by (c.f. Kellomäki and Strandman, 1995)

$$I_s = (1 - \mathrm{e}^{-K(\phi)A_N/A_C})A_C I_\mathrm{s}^0 \tag{8}$$

where A_N is the foliage area of the segment, ϕ is the angle between the axis of the subject tree segment and the direction of the light beam (analogous to ϕ_i in Eq. (5)), K is the function explained in conjunction of Eq. (5) and A_C is the projection area of the tree segment cylinder in the direction of the light beam (depends thus on angle ϕ given by (Oker-Blom and Smolander, 1988)

$$A_C = 2LR\cos(\phi) + \pi R^2 \sin(\phi) \tag{9}$$

where L is the length of the tree segment and R is the radius (including the foliage) of it.

The amount of radiation the subject segment is intercepting is then given by

$$I = \Sigma I_s \tag{10}$$

where the summation is taken over all segments s of the sky.

2.5. New tree segments and tree architecture

The length *(L)* of a new tree segment (which determines also the radius and hence the size) is obtained as a product of four factors:

$$L = \begin{cases} \lambda[1-(\omega-1)q f_L(i_\mathrm{p}), & \text{if } 1-(\omega-1)q > 0 \\ 0, & \text{otherwise} \end{cases} \tag{11}$$

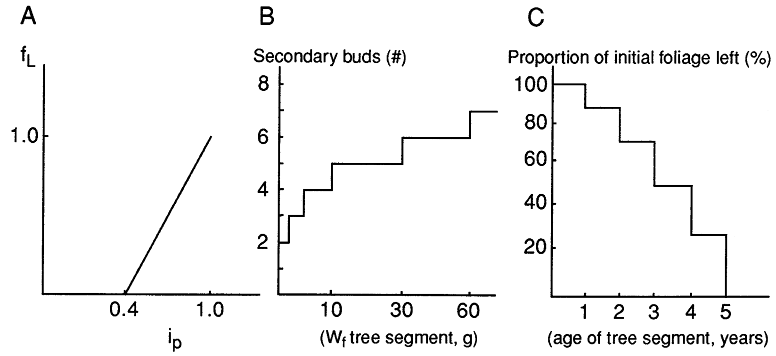

Fig. 2. Functions affecting the growth of LIGNUM. A, relative length of a new tree segment as a function of the light conditions of the bud that will create it. B, number of secondary buds as a foliage mass of the mother tree segment. C, foliage mortality of a tree segment as a function of its age.

where λ is a parameter reflecting availability of photosynthates, ω is the gravelius order of a tree segment, q *is* the tree segment shortening factor and f_L, accounts for light condition of the mother tree segment (Fig. 2A). The function f_L, λ, ω and q are as defined in Perttunen et al. (1996) but due to new solar radiation interception model the definition of i_p (the photosynthetic light ratio) has been changed to:

$$i_p = I/B_s \tag{12}$$

where the B_s is the sum of the incoming radiation from all sectors of the sky (measured perpendicular to the direction of the sector). The value of i_p is equal to maximum relative interception if the tree segment is in unshaded conditions (e.g. at the top of the tree) and it equals 0 if the tree segment does not receive any radiation at all. The photosynthetic light ratio in the terminal buds is defined to be the same as in the mother tree segment.

The branching order factor ω accounts for the fact that the new tree segments forking away from the direction of mother tree segment are shorter than the new tree segment continuing in direction of the mother tree segment. The length of the new tree segments increases with improving light conditions of the mother tree segment.

The number of new buds at the end of each distal tree segment depends on the amount of foliage of the mother tree segment (Fig. 2B).

At present, the architectural development of tree is treated as follows. First, a constant branching angle is applied: the new buds are inclined 45° away from the direction of terminal bud. One of the new buds is chosen as the first secondary bud and the other secondary buds are rotated evenly around the branching point. Simple heuristic prevents unaccepted growing directions (e.g. buds are not allowed to point downwards).

The first secondary buds are rotated 144° relative to each other in subsequent branching points. As a result of this, every 6th year first secondary buds leaving from the same axis (i.e. stem) point to the same direction.

New tree segments in a secondary branch bring about the gradual bending of the branch due to its own increased weight as it ages. This requires the revision of the coordinates of all the tree compartments in the branch and the algorithm implementing this procedure operates as follows (see also Fig. 3). The foremost tree segment connected to the main stem is first turned downwards. The next branch whorl will be assigned the end point of the bent tree segment and the new position is propagated to the succeeding tree segments connected to the branch whorl as their new base coordinates. This procedure is repeated up to the branch tip. Curved branch is achieved by turning downwards tree segments further away from the main stem less than the tree segments closer to the main stem.

Maximum angle from the vertical straight line of a branch segment is limited to 90°.

The algorithmic framework implementing the gradual bending of the secondary branches is currently only for visualization purposes. It does not include physiological processes, tenacity calculations or empirical measurements of any kind related to branch bending yet.

3. The implementation of LIGNUM as a computer program

The implementation of any computer program involves two activities. First we need to identify and create data types to describe the concepts of interest and then with the data objects as examples of the data types we describe the real world entities. Construction of suitable algorithms follows those steps.

In addition to tree segment *(TS)*, branching point *(BP)* and bud *(B)* we introduce for the implementation one additional data type axis (*A*). Axis collects the basic units to main stem and branches. Axis is represented as a list. With the list notation employed here the main stem of the tree in Fig. 1 can be written

$$[TS_0, BP_1, TS_2, BP_3, TS_4, BP_5, TS_6, BP_7, B_8] \quad (13)$$

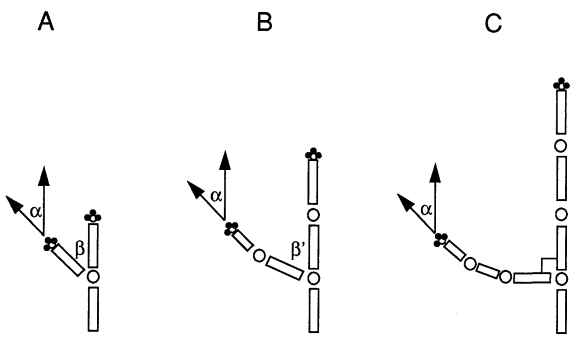

Fig. 3. Schematic view from the side showing the modelling of the gradual bending of a secondary branch (A, the initial state; B and C, after gradual bending). New tree segments cause the branch to incline requiring the revision of the coordinates of all the tree compartments in the branch. The growth direction (α) of the terminating bud remains the same. The maximum bending of a branch is limited to 90° from the vertical straight line.

The square brackets denote the beginning and the end of the list, the commas separate the list elements and the (optional) indices denote the positions of the elements in the list. In an axis, tree segments are on even positions and branching points on odd positions. The last element in an axis is a bud and there is at most one bud in an axis.

We continue the use of lists in our design by defining a branching point to be a list of axes. For example, using our notation for lists the main stem in Fig. 1 can be written as:

$$[I, [A, A], I, [A, A], I, [A, A], I, [[B], [B]], B] \quad (14)$$

The branching points in Eq. (14) are ‘folded out’ as lists of axes. The axes in the last branching point are also folded out showing the buds as the only list members.

The order of the tree units remains the same during the development of the tree. However, tree and axis are dynamic units where new tree compartments are created and old ones that do not perform any growth processes (like dead branches) can be deleted in the simulation. The design of the tree as a collection of lists renders the program a consistent, easily comprehended and robust structure.

LIGNUM has been implemented with C + +. The program compiles under several UNIX platforms (Sun Solaris, Hewlett–Packard HP-UX, Silicon Graphics IRIX). The scientific visualization (Figs. 4–6) has been done using OpenGL (Neider et al., 1993) application programming interface. For a more detailed explanation of the implementation of LIGNUM we refer to Perttunen et al. (1996).

4. Simulation examples

We parameterized LIGNUM for a young Scots pine growing in southern Finland. Simulations and comparisons with some observations indicate that LIGNUM is able to reproduce several features of growth in young Scots pines (Perttunen et al., 1996).

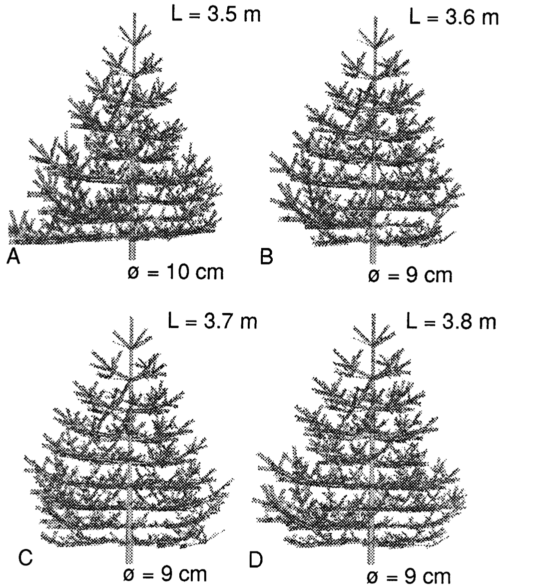

Fig. 4. The effect of the number of sectors in the sky on the appearance of tree simulated with LIGNUM (A, 2×2, B, 4×4; C, 6×6 and D, $10x \times 10$ sectors). Also the length of the tree (L) and the diameter at base ($ø$) are presented.

To avoid unnecessary computations the first step in verifying the solar radiation interception model is to decide how many sectors will be needed in the sky in order to get reliable results. Fig. 4 shows the results of the simulations of LIGNUM up to 10 years of age with parameter values shown in Table 1 and functions in Fig. 2 (c.f. Perttunen et al., 1996) with the number of azimuths (compass directions) and inclinations (sextant directions) in the sky varying. As we can see in Fig. 4, there is no qualitative difference neither in the outlook nor in the length and diameter at base of the trees using either 4×4 sectors (four azimuths, four inclinations) or 10×10 sectors. Thus, the simulations for this article with LIGNUM were made with the sky divided into 6×6 sectors and functions in Fig. 2. The parameter values are as in Table 1 unless otherwise stated. Notice that the parameter for photosynthetic production in unshaded conditions, P_0 (Perttunen et al., 1996), has become obsolete due to the new solar radiation interception model.

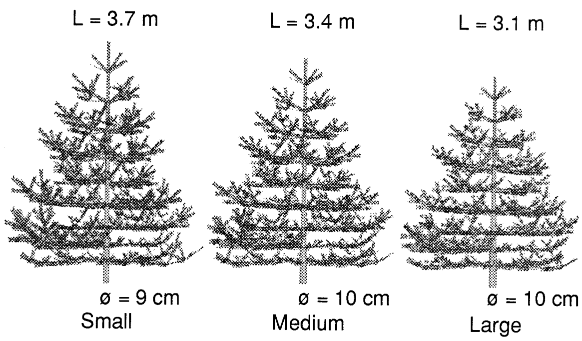

Fig. 5. Simulation of the effect of the rate of sapwood senescence ($S_s = 0.2$, small; $S_s = 0.6$, medium; $S_s = 1.0$, large) on growth for a 10 year old tree. The length of the tree (L) and the diameter at base ($ø$) are also presented.

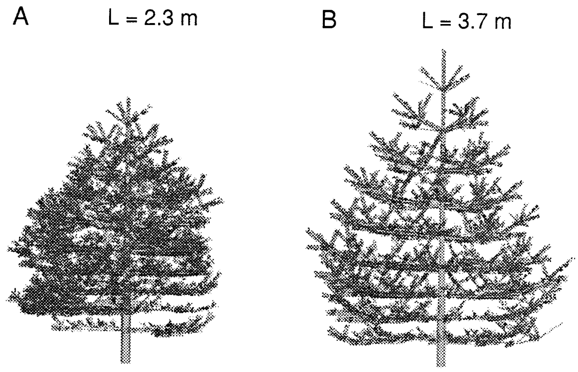

Fig. 6. The effect of branching habit (A, $q = 0$, branch order does not affect the length of laterals; B: $q = 0.2$, it affects) on outlook and height of the tree (L) at the age of 10 years. Diameter at base is in both cases 8 cm.

The present use of pipe model and empirical rules for extension growth makes the model naturally very sensitive to parameter values in those relationships. The application of pipe-model principle for carbon allocation has also been shown to be very sensitive to the rate of sapwood transition to heartwood (e.g. Mäkelä, 1988; Nikinmaa, 1992). It can be argued that such sensitivity is an artifact of the model but it may reveal an important mechanism in trees that has been largely overlooked in plant science. The frequent observations of pipe model relationships with a large number of species would suggest that also those processes that the sapwood senescence may be important process also in the real world.

In LIGNUM heartwood formation is either an age dependent process or the sapwood turnover

Table 1
Parameters for young Scots pine growing in southern Finland

Parameter	Meaning	Unit	Value
a_f	Foliage (needle) mass-tree segment area relationship	kg/m^2	1.3
a_r	Foliage (needle)-root relationship	kg/kg	0.5
l_R	L/R for a new tree segment		100
m_f	Maintenance respiration rate of needles	kgC/kgC per year	0.2
m_r	Maintenance respiration rate of roots	kgC/kgC per year	0.24
m_s	Maintenance respiration rate of sapwood	kgC/kgC per year	0.024
q	Tree segment shortening factor	–	0.1
S_r	Senescence rate of roots	1/year	0.33
S_s	Senescence rate of sapwood	1/year	0.07
ρ_w	Density of wood	kg/m^3	400
ξ	Fraction of heartwood in new tree segments	–	0.6
P_r	Proportion of bound solar radiation that is used in photosynthesis	–	0.001

to heartwood is connected to whole tree crown dynamics. Fig. 5 shows the drastic effect that different rates of heartwood formation (by changing the value of the parameter S_s, the parameter q set at 0.2 in all three cases) had on the initial development of young Scots pines. The effect is very clear on the thickness versus height growth which has strong effect on the performance of trees when grown in stands.

Various other models have shown earlier on how small differences in the branching parameters may influence the long term growth very drastically (e.g. Ford et al., 1990; Fisher, 1992). When the pipe model principle is used to derive the relationship between foliage and wood growth the influence is even stronger (Nikinmaa, 1992). Fig. 6 shows how the stem curve of trees clearly changes with the changing values in branching model parameter q. The change is coupled with clearly different outlook of plants; the shorter but thicker tree has a bushy appearance while the slimmer tree has clearly a layered branch whorl structure. Thus the simulation results support the importance of studying varying tree architecture as one determinant of their success in the nature.

5. Discussion

The detailed light model allows more direct linking between the crown architecture and the tree photosynthetic performance. The main challenge in improving the model at the moment is to aggregate the calculation of light climate without losing too much information in order to facilitate calculation of growth of older trees. Simultaneously we are paying effort to bring the problem down to parallel computing, which may be able to handle the present computational complexity.

LIGNUM represents a paradigm shift in process-based modelling of tree growth and development. The interdisciplinary workshop on the synthesis and simulation of living systems held in Los Alamos, 1987 is now considered to be the emergence of a new scientific paradigm called artificial life (a-life in short). According to Langton (1989) a-life complements traditional biological sciences by viewing an organism as a large aggregate of simple interacting objects. The basic idea in a-life is to build models of life phenomena (i.e. behavior in a broad sense) from some biological or physical ‘basic laws’ and utilize computers to scale up to a higher level of organization. By viewing the growth and the development of a tree as a synthesis of distributed and interacting simple structural units as a methodological approach, LIGNUM can be very well subsumed under this paradigm.

Traditionally the shift between levels of hierarchy in plant modelling has been accomplished by making simplifying assumptions. These, however, tend to obscure the effects that lower level phenomena exercise on the higher level. If simplifying assumptions for scaling up are not needed, the models and their parameters can be more closely tied to the phenomenon and therefore they are also biologically more meaningful. We believe that the design of LIGNUM allows us to redefine both the structure and the functioning of a tree in more detail when necessary and still maintain the same aggregated realism that is described at the moment, without any need for simplifying assumptions.

With the new improvements in the local performance of tree parts, also a more localized control of growth (modular growth) is another future challenge to develop LIGNUM. Although pipe model principle is able to produce realistic looking trees and can be useful for many purposes it still is only a gross approximation what results from the growth processes. Our intention is to develop the next version of LIGNUM so that it would derive growth and senescence of the structural units from the resource supply and tree level hormonal control signals. However, even at its present stage LIGNUM is a very promising tool for many ecological, forestry and horticultural purposes.

Acknowledgements

We acknowledge the work of Matti Lehtonen (Systems Analysis Laboratory, Helsinki University of Technology) on the scientific visualization of LIGNUM.

Appendix A. Glossary of symbols

Variable	Meaning	Units
A_C	Projection area of the treesegment cylinder in the direction of the light beam	m^2
A_N	Foliage (needle) area of tree segment	m^2
B_S	Sum of the incoming radiation from all the sectors of the sky	MJ
H	Shading caused by all tree segments	–
I	Amount of radiation tree segment intercepts from all the sectors of the sky	MJ
L	Length of tree segment	m
l_i	Distance light beamtraverses in the foliage (needles) of shading tree segment i	m
M	Annual amount of carbon used for respiration	kgC
P	Annual amount of photosynthetic production	kgC
R	Radius of a tree segment	m
$i\mathrm{W}_n$	Annual amount of carbon required to build new tree segments	kgC
$i\mathrm{W}_o$	Annual amount of carbon required in secondary wood thickening	kgC
$i\mathrm{W}_r$	Annual amount of carbon required in root growth	kgC
λ	Parameter to balance carbon balance equation	–
ρ_{fi}	Foliage (needle) area density of tree segment i	m^2/m^3
ϕ_i	Angle between the axis of the segment i and the direction of the light beam	–
ω	Gravelius order of tree segment	–

References

Anton, H., 1987. Elementary Linear Algebra 5e. John Wiley, New York.

Bossel, H., 1994. TREEDYN3 Forest simulation model. Ecol. Model. 90 (2), 187–227.

Fisher, J.B., 1992. How predictive are computer simulations of tree architecture? Int. J. Plant Sci. 153 (3), 137–146.

Ford, E.D., Avery, A., Ford, R., 1990. Simulation of branch growth in the Pinaceae: Interactions of morphology, phenology, foliage productivity, and the requirement of structural support, on the export of carbon. J. Theor. Biol. 146, 15–36.

Friend, A.D., 1992. A physiology-based model of forest dynamics. Ecology 74, 792–797.

Hari, P., Kellomäki, S., Mäkelä, A., Ilonen, P., Kanninen, M., Korpilahti, E., Nygren, M., 1982. Dynamics of early development of tree stand. Acta Forestalia Fennica 177.

Jaeger, M., de Reffye, Ph., 1992. Basic concepts of computer simulation of plant growth. J. Biosci. 17, 275–291.

Kellomäki, S., Strandman, H., 1995. A model for structural growth of young Scots pine crowns based on light interception by shoots. Ecol. Model. 80, 237–250.

Kuitunen, P., 1996. The impact of the size of shoots, number of forking daughter shoots, the shoot position and the geographical location of the stand on the allometric relationships of Scots pine (*Pinus sylvestris* L.) shoots. M.Sc. Thesis, University of Helsinki, Department of Forest Ecology. p. 41, (In Finnish).

Kurth, W., 1994b. Morphological models of plant growth: possibilities and ecological relevance. Ecol. Model. 75–76, 299–308.

Landsberg, J.J., 1986. Physiological Ecology of Forest Production. Academic Press, London.

Langton, C.G., 1989. Artificial life. In: Langton, C.G. (Ed.), Artificial Life, The Proceedings of an Interdisciplinary Workshop on the Synthesis and Simulation of Living Systems. Addison-Wesley, Redwood City, CA, pp. 1–47.

Lindenmeyer, A., 1968. Mathematical models for cellular interaction in development, parts I and II. J. Theor. Biol. 18, 280–315.

Mohren, G.M.J., 1987. Simulation of forest growth, applied to Douglas fir stands in The Netherlands. Pudoc, Wageningen, The Netherlands.

Mäkelä, A., 1988. Models of pine stand development: An ecophysiological systems analysis. University of Helsinki, Department of Silviculture. Research Notes 62, 1267.

Neider, J., Davis, T., Woo, M., 1993. OpenGL Programming Guide. Addison-Wesley, Reading.

Nikinmaa, E., 1992. Analysis of the growth of scots pine; matching structure with function (Seloste: Analyysi mannyn kasvusta; rakenteen sopeutumista aineenvaihduntaan). Acta Forestalia Fennica 235.

Perttunen, J., Sievanen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., Vakeva, J., 1996. Lignum: A tree model based on simple structural units. Ann. Bot. 77, 8798.

Oker-Blom, P., Smolander, H., 1988. The ratio of shoot silhouette area to total needle area in Scots pine. For. Sci. 34 (4), 894–906.

Prusinkiewicz, P., Hanan, J., 1989 Lindenmayer Systems, Fractals and Plants. Lecture Notes in Biomathematics 79, Springer-Verlag, Berlin.

Ross, J., 1981. The radiation regime and architecture of plant stands. W. Junk, The Hague-Boston-London, p. 391.

Salminen, H., Saarenmaa, H., Perttunen, J., Sievanen, R., Nikinmaa, E., Vakeva, J., 1994. Modelling trees with an object-oriented scheme. Math. Comput. Model. 20 (8), 49–64.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitative analysis of plant form-the pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14, 97105.

Sievänen, R., Nikinmaa, E., Hakula, H., Perttunen, J., Salminen, H., Saarenmaa, H., Vakeva, J., 1995. LIGNUM-modelling trees with simple structural units. CSC NEWS June 7 1995 (2), 20–24.