

# Toward extension of a single tree functional–structural model of Scots pine to stand level: effect of the canopy of randomly distributed, identical trees on development of tree structure

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**Abstract.** Functional–structural plant growth models (FSPMs) combine the description of the structure of plants and the resource acquisition and partitioning at a detailed architectural level. They offer a means to study tree and stand development on the basis of a structurally accurate description that combines resource capture at the same level of detail. We describe here how a ‘shoot-based’ individual tree model, LIGNUM of Scots pine (*Pinus sylvestris* L.) has been applied to a group of identical trees (forest). The model has been applied to isolated trees and saplings growing in forest gaps. First, we present the LIGNUM model and the changes necessary for simulation of a forest instead of individual trees. LIGNUM derives tree growth on the basis of a process-based model of tree carbon balance and the architectural development of the 3-D tree crown. The time step is 1 year. We realised the forest as consisting of individual Scots pine trees on a plot 17 × 17 m, but simplified the stand description by simulating the growth of only one tree in the middle of the plot and assumed that the other trees were identical to it at all times. The model produced results that are comparable with observations made in real Scots pine trees and tree stands in Finland. The simulations with variable values of the parameters controlling the foliage–sapwood relationship, amount of sapwood required below a point in a branch or a stem, and the senescence of sapwood showed how growth declines when the sapwood requirement in the branches and stem was high. In this case, the proportion of resources allocated to the needles became small and the needle mass was low.

**Additional keywords:** forest, *Pinus sylvestris* L.

## Introduction

The three principal interacting processes involved in the growth of a tree, and, thus, stand development, are (Ford and Sorrensen 1992): (1) resource capture as a response to the immediate environment and leading to tree growth, (2) allocation of growth to the development of the 3-D structure of the tree, and, consequently, (3) modification of the immediate environment, described as a 3-D distribution of the resource flux. Stand dynamics result from the interplay of these processes, and are primarily reflected in crown development: if the tree can lift its crown to a position that affords sufficient light in comparison to its neighbours, then it will survive in the stand, otherwise it will become suppressed and is liable to die.

The development of a tree crown is a result of morphological development: the production and flushing of buds, production of new shoots and foliage, and also from the geometrical arrangement of the new units, i.e. the plant architecture. It is,

in other words, production of metamers and growth units (Room *et al.* 1994). The extension of growth units, which determine how large they become, affects crown development. The branch length affects the amount of resources required for secondary growth because the amount of resources is proportional to the product of thickness of the new layer of growth and the length of the branch. The resource requirements of secondary growth have been modelled quite often using the so-called pipe model theory (e.g. Mäkelä 1986). Secondary growth is dependent on the availability of growth resources and their allocation along the pathway from branch tips to the roots.

The functional–structural plant growth models (FSPMs; e.g. Sievänen *et al.* 2000; Godin and Sinoquet 2005) combine the description of the structural dynamics of plants and of the ecophysiological processes governing resource acquisition and repartition. These models usually employ a very detailed

representation of the individual plant architecture (at least the aboveground part), providing a geometric description of all the organs (e.g. internodes, leaves, fruits, flowers). A detailed description of the plant architecture facilitates accurate estimation of the actual resource uptake, and, most of all, it facilitates estimation of the limits on organ growth set by resource uptake and the tree-like growth habit (Sievänen *et al.* 2000). They offer a means to study crown and tree development on the basis of a structurally accurate description that combines resource capture at the same level of detail (cf. Cournède *et al.* 2007).

Growth of plant communities has been modelled within many scientific disciplines; these include plant population biology (Harper 1977), forestry (Assmann 1970), and biomathematics (Metz and Diekmann 1986). In the simplest case, the size of the population is presented with a few variables, possibly pertaining to the mean individual combined with the total number of individuals. One of the main thrusts in modelling has been to devise methods or models to relax the assumptions of simple models and to account for differential responses of individuals in the population/plant community to their local conditions (e.g. DeAngelis and Gross 1992). In forestry models, there is a customary distinction between stand level, distance-independent, and distance-dependent models (Porté and Bartelink 2002). Distance-dependent models use spatially explicit information (often the distance to neighbouring trees) to assess the environment local to each tree, whereas distance-independent models allow trees to react individually to an environment common to all trees in the stand. Sorrensen-Cothorn *et al.* (1993) have suggested that usually the following simplifying assumptions are made in distance-dependent forestry models:

- (1) response is on the whole-plant level,
- (2) response is defined on one variable,
- (3) interaction is on the whole-plant level, and
- (4) interaction is pairwise.

Sorrensen-Cothorn *et al.* (1993) present a model of tree stands that does without these simplifying assumptions, and brings in a new level of hierarchy in the interaction of tree individuals in a stand: reaction to an environment that is local to each organ and that results in modular crown development. This is the very thing the FSPMs are apt to deal with in tree competition (stand simulation) studies: the modular interaction of individuals with the environment. Most of the FSPMs for trees have been applied to single trees (cf. conference proceedings in *Silva Fennica* vol. 31, no. 3, 1997, *Annals of Forest Science* vol. 57, no. 5/6, 2000, and *New Phytologist* vol. 166, no. 3, 2005). Only a few attempts have been made to apply FSPMs to the tree stand level. Takenaka (1994) presented a model in which growth responded to local light environment within the crown; he applied it to a group of trees. Mech and Prusinkiewicz (1996) presented an L-system-based FSPM that derives local growth from photosynthesis and that can be applied to a tree stand of individuals. They demonstrated its behaviour with competing trees. The FSPM *ECOPHYS* has been applied in scaling up studies of leaf level models of metabolism in poplar species to stand (Host *et al.* 1996; Martin *et al.* 2001) and even regional (Host *et al.* 2007) level. The growth of a patch of

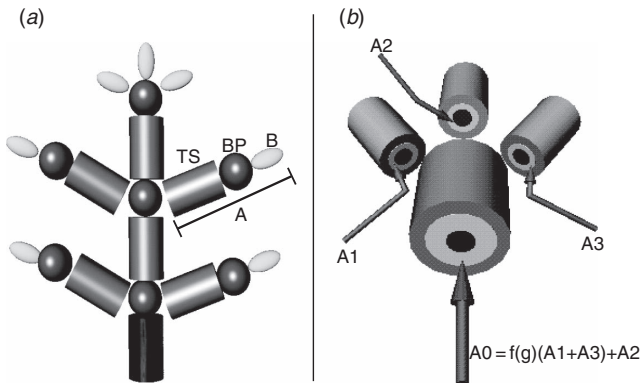
interacting (through the attenuation of radiation) individuals has been simulated and the stand has consisted of several patches. Kurth (1998) realised a tree model of light-dependent shoot growth within an L-system framework (growth grammar) and simulated the effect of different schemes of carbon allocation on the growth of a group of trees. Dzierzon (2003) studied the effect of a surrounding homogenous forest on the traits of a Scots pine (*Pinus sylvestris* L.) tree simulated by the LIGNUM model (Perttunen *et al.* 1996). Cournède *et al.* (2007) used a functional-structural tree model to build a forest stand consisting of individuals. They studied the effects of interaction between functional growth and architectural development at stand level and showed that the effects of density on tree height and radial growth that are commonly observed in real stands appear as emerging properties of the model.

The low number of (tree) stand level applications of the FSPMs is understandable because, owing to the detailed description of the plant structure, and, consequently, of the local environment of each organ, FSPMs tend to require a large number of parameters and sometimes also a detailed input. Owing to the large amount of information they contain about the plant to be modelled, they also tend to be computationally heavy. As a consequence of the amount of detail required, the model may be error-prone: an outcome may be an artefact generated by a mis-specified detail. However, despite of the difficulties of application at forest level, the FSPMs would be useful tools for studies of stand dynamics. As mentioned above, the FSPMs bring in a new level of interaction (within tree crown), and instead of assuming a predetermined geometric crown shape, they allow for simulation of the actual process of space filling by the crowns. They would be useful in studies of process-based modelling (Mäkelä 1997), biomass turnover rates in climate change studies (Körner 2004), or studies of biodiversity and ecosystem productivity (Ishii *et al.* 2004; Prentice *et al.* 2007).

We describe here how a 'shoot-based' individual tree model, LIGNUM, has been extended toward the forest stand level. The model has been applied to isolated trees and saplings growing in forest gaps; here we use it to simulate a tree stand that consists of replicas of one tree and for which radiation conditions are evaluated in a detailed manner. First, we present the LIGNUM model and the changes necessary for simulation of a forest instead of individual trees. Then, we examine how the stand simulation compares with observations made in real Scots pine trees and tree stands in Finland. Finally, we show, through simulations, how pipe model relationships affect tree and stand growth.

## Materials and methods

The LIGNUM model was originally constructed to be applied to individual Scots pine (*Pinus sylvestris* L.) trees. The aboveground part of the coniferous and the deciduous trees is modelled with structural units. They are a tree segment, branching point and bud (Fig. 1a). So far, the root system has been represented only by its mass. LIGNUM combines, in one modelling framework, a process-based model of tree carbon balance and the architectural



**Fig. 1.** (a) The structural units used in LIGNUM to represent coniferous trees TS, tree segment; BP, branching point; B, bud; A, axis: it is a sequence of TS's and BP's ending with a B. (b) The sapwood cross-sectional area below a branching point ( $A_0$ ) corresponds to the sum of the cross-sectional areas ( $A_1, A_2, A_3$ ) above the branching point. The contribution of lateral branches to the sapwood area depends on their Gravelius order  $g$ .

development of the three-dimensional tree crown. The time step is one year. In the following we shortly describe the main features of the model that affect the simulations in this study. For more details, see Perttunen *et al.* (1996, 1998, 2001). The parameter values are summarised in Table 1.

*Photosynthetic production and carbon balance*

The photosynthetic production of a segment (with foliage) is directly proportional to the amount of intercepted photosynthetically active radiation (Perttunen *et al.* 1998). The production available for growth is obtained by subtracting the

respiration losses of the tree compartments and the root system from the photosynthetic production of the whole tree. The partitioning of resources to growth takes place according to the 'centralistic concept' (Kurth 1997): the photosynthetic production (after respiration) is considered to be in one pool, and all its contents (no storage considered) are distributed in primary and secondary growth according to the rules that depend on the organ position and are described in the following.

*Production of buds*

The production of new buds (at the end of new segments) determines the location in the crown to which the growth is allocated. The number of lateral buds is determined in the first place as a function of the foliage mass of the mother segment according to the function in Fig. 2a. This relationship reflects the fact that vigorous shoots produce more buds than an average shoot (Kurtio and Kellomäki 1990). This function has worked well for open-grown trees and saplings (Perttunen *et al.* 1996; Sievänen *et al.* 1997), but for forest simulation it had to be augmented by the effect of local radiation conditions such that the number of lateral buds equals:

$$\begin{cases} \# \text{ of buds from fol. mass,} & \text{if } f_L(s) \geq 0.6 \\ 0, & \text{otherwise} \end{cases}, \quad (1)$$

where

$$s = \frac{\text{incident radiation}}{\text{incident radiation at tree top}}, \quad (2)$$

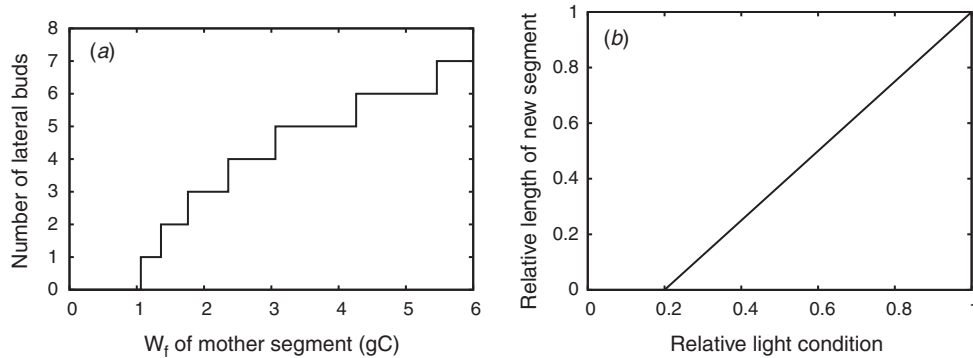
and the function  $f_L(s)$  is shown in Fig. 2b. It is the same function that controls the length of new segments; this is in accordance

**Table 1.** The parameter values applied in the simulations

Parameter	Meaning	Value and unit	Source
$a_{fol}$	Needle mass–tree segment surface area relationship	0.66 kg C m <sup>-2</sup>	P. Kaitaniemi, unpubl. data
$a_r$	Foliage–root relationship	0.5 kg C/kg C	Perttunen <i>et al.</i> (1996)
$l_R$	Radius/length of new segment	0.008 in full shade, 0.012 in full light, linear interpolation between	E. Nikinmaa, unpubl. data
$L_{min}$	Minimum length of a segment	0.02 m	This study
$m_f$	Maintenance respiration rate of needles	0.24 kg C/kg C/year	Perttunen <i>et al.</i> (1996)
$m_r$	Maintenance respiration rate of roots	0.24 kg C/kg C/year	Perttunen <i>et al.</i> (1996)
$m_s$	Maintenance respiration rate of sapwood	0.024 kg C/kg C/year	Perttunen <i>et al.</i> (1996)
$p_r$	Photosynthetic efficiency	0.6 kg C/GJ PAR <sup>A</sup>	Stenberg <i>et al.</i> (2001)
$q$	Tree segment shortening factor	0.1	This study
$s_r$	Senescence rate of roots	0.33 1/year	Perttunen <i>et al.</i> (1996)
$s_s$	Senescence rate of sapwood	0.04 1/year after tree age 15 years	E. Nikinmaa, unpubl. data
$\rho$	Density of wood	200 kg C m <sup>-3</sup>	Hakkila (1979)
$\xi$	Proportion of heartwood in new segments	0.6, increasing to 0.7 between ages 15 and 40 years	E. Nikinmaa, unpubl. data
$\alpha_{ij}$	Reduction in sapwood requirement from segment with Gravelius order $i$ to segment with Gravelius order $j$ (see Fig. 1)	$\alpha_{21} = 0.75, \alpha_{ij} = 0.79$ for all other values of $i$ and $j$ , unitless	Berninger <i>et al.</i> (2005) <sup>B</sup> for $\alpha_{21}$ , E. Nikinmaa, unpubl. data

<sup>A</sup>Contains the effect of growth respiration, corresponding approximately to the value 0.75 kg C/GJ PAR/year if growth respiration (20%) is not considered.

<sup>B</sup>These results apply to the total cross-sectional area of branches at the first living side branch. It was assumed that their result also holds for sapwood cross-sectional areas.



**Fig. 2.** (a) Number of lateral buds in Scots pine as a function of the foliage mass of a mother segment. (b) Relative length of a new segment as a function of the light conditions (function  $f_L$  in Eqn 1).

with our assumption that bud production is related with the size (represented by foliage mass; Fig. 2a) of segment. This relationship reflects the fact that bud production is low in shaded conditions ( $s < 1$ ) especially at the base of the crown. The use of relative radiation in the crown ( $s$ ) reflects the fact that trees of different sizes may produce different amount of buds at the same absolute radiation conditions. The apical bud dies if it cannot produce a new segment in the extension growth.

*Extension growth of new segments*

The buds flush and produce new segments. Their lengths are given:

$$\text{Max}[1 - q(g - 1), 0]f_L(s), \tag{3}$$

where  $q$  is a parameter,  $f_L(s)$  is the same function that is used in evaluating the number of buds (shown in Fig. 2b), and  $g$  is the Gravelius order of the segment. In the Gravelius ordering the segments in the main axis (that is trunk) are assigned order 1, segments in branches get order 2: the segments in axes forking off get a progressively higher order (MacDonald 1983; for the definition of axis, see Fig. 1). Furthermore, if the length of the new segment is less than the threshold  $L_{\text{min}}$  (a parameter of model; Table 1), then no segment is created. The segments become progressively shorter (controlled by parameter  $q$  in Eqn 3) as the branching order increases. The actual length of a new segment is determined by the availability of photosynthetic products. The radius of the new segment is directly proportional to its length. The amount of foliage in it is proportional to the surface area of the woody part, yielding the relationship between the foliage mass ( $W_{\text{fol}}$ ) and cross-sectional area of the sapwood ( $A_{\text{sw}}$ ):

$$W_{\text{fol}} = \frac{2a_{\text{fol}}}{(1 - \xi)l_R} A_{\text{sw}}, \tag{4}$$

where  $a_{\text{fol}}$  is a foliage density parameter,  $l_R$  is the ratio of the segment radius to the length, and  $\xi$  is the proportion of primary wood; see Perttunen *et al.* (1996) for more details.

*Secondary growth*

Secondary growth is driven by the pipe model (Shinozaki *et al.* 1964) requirement that the amount of foliage is matched by the

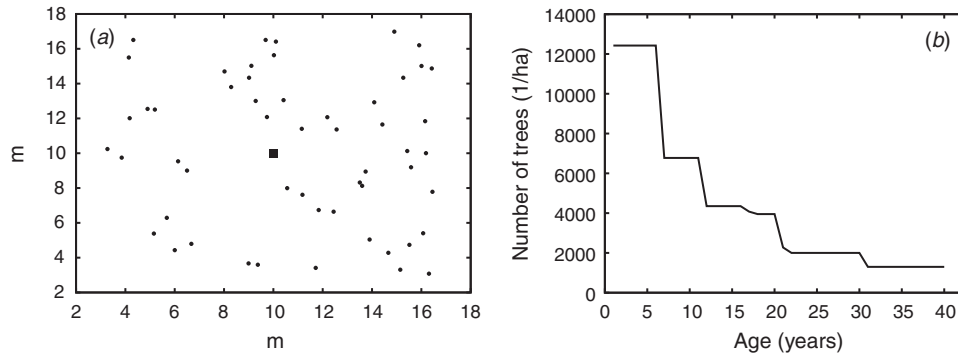
cross-sectional area of the sapwood, and that the cross-sectional area of the sapwood in a segment matches the sum of the cross-sectional areas of the sapwood in the segments distal to it (Fig. 1b). As a modification of the procedure used in previous studies, the cross-sectional sapwood areas of segments with different Gravelius orders do not match one-to-one, but have different proportions (Fig. 1b) as has been observed (e.g. Hari *et al.* 1986). The sapwood senesces such that a constant proportion of its cross-sectional area becomes heartwood each year (Perttunen *et al.* 1996). In this study it is assumed that heartwood formation takes place only after the age of 15 years (Björklund 1999). The growth of roots is proportional to that of foliage (Perttunen *et al.* 1996).

*Crown architecture*

The branching pattern of the tree is the same as that given in Perttunen *et al.* (1998) (also Perttunen and Sievänen 2005), and corresponds best to open-grown or juvenile Scots pine trees. The forking angle of the branches is 45 degrees, and for higher order branches it is 30 degrees. The orientation of new segments at the end of a branch is towards the upper hemisphere (growing downwards is avoided). During the course of the simulation, the branches bend down to produce a curved shape (cf. Fig. 5). The algorithm for bending is geometric and does not consider biomechanics (Perttunen *et al.* 1998). A branch of any order is considered dead when it has lost all its needles. Dead branches are shed.

*The forest*

The forest of individual Scots pine trees was a plot  $17 \times 17$  m (Fig. 3a). The chosen size of the plot was a compromise between reality and computational complexity. Due to the complex radiation calculations (see below), estimation of the radiation conditions for each tree on the plot would have been computationally prohibitive. We, therefore, simplified the stand description by simulating the growth of only one tree in the middle of the plot (Fig. 3a) and assumed that the other trees were identical to it at all times. These stand simulations, thus, refer to an even-aged, single species stand. We took the number of trees as the input (Fig. 3b), in which the time development corresponds approximately to the density of a naturally regenerated and



**Fig. 3.** (a) Tree locations on the plot after a 40-year simulation. The location of the tree in the middle of the plot for which radiation conditions were evaluated is marked with ■. (b) Stand density given as input in simulations.

commercially thinned Scots pine stand on a site of medium fertility. The locations of the trees on the plot were random with a minimum distance between the trees of 0.5 m (i.e. Poisson distribution with a hard core; Stoyan *et al.* 1987). Trees were periodically removed from the plot on the basis of the input function in Fig. 3b, which emulates tree removal mainly due to thinning. When the number of trees decreased according to the function, a corresponding number of trees were removed from the plot. We mimicked the increase in growing space associated with a decrease in stand density by creating an empty area around the tree that corresponded to the density. During periods when the density decreased (Fig. 3b), trees were first removed in a circle around the subject tree with a radius equal to  $\sqrt{10\,000/(\pi \times \text{trees per ha})}$  and then the rest of the thinned trees were removed randomly outside the circle.

#### The radiation regime

As the time step of LIGNUM is 1 year, we consider only the total incoming radiation (photosynthetically active radiation) during the growing period. We take into account the total radiation coming from different parts of the upper hemisphere; in this study we calculated the radiation coming from 81 evenly distributed directions (nine inclinations, nine azimuths). This number of directions has been shown to be detailed enough for LIGNUM simulations (Perttunen *et al.* 1998).

The attenuation of the beam of radiation from a point in the sky to the segment of the subject tree in the middle of the plot (Fig. 3a) was calculated on the basis of the mutual shading of the shoots, as explained in Perttunen *et al.* (1998). The method applied by Perttunen *et al.* (1998) to a single tree extends in a straightforward way to a group of trees because, in the calculations, it is determined whether there are any segments intruding between the subject segment and a point in the sky. In this study the check was performed both for segments (with foliage) in the subject tree and for those of the other trees on the plot. The calculation thus estimated the effect of both the mutual shading of trees and the self-shading of the tree. The transmittance of a shading segment  $i$  equals (Oker-Blom and Smolander 1988; Perttunen *et al.* 1998):

$$t_i = \exp[-K(\phi_i)\rho_i l_i], \quad (5)$$

where  $K$  is a function defining the light extinction in a Scots pine shoot in terms of the impact angle  $\phi_i$  (estimated by Oker-Blom and Smolander 1988),  $\rho_i$  is the needle area density of the segment (needle area divided by the volume occupied by the foliage), and  $l_i$  is the distance traversed in the needle volume. The model also checks whether the beam hits the woody part of the segment; if it does, then  $t_i = 0$ . This calculation assumes that the segments are black porous objects that let part of the radiation pass through. The amount of radiation coming to the subject segment,  $Q_{\text{seg}}$ , is then:

$$Q_{\text{seg}} = \sum_{p \in P} \left( \prod_{i \in I_p} t_i \right) Q_p, \quad (6)$$

where  $P$  is the set of sky directions,  $I_p$  is the set of the shading segments along the straight path  $p$  to the sky, and  $Q_p$  is the radiant flux coming from the sky along path  $p$ . The product is taken over all the segments along the path  $p$  and the paths are evaluated independently from each other (Perttunen *et al.* 1998). The amount of radiation from each direction  $Q_p$  was evaluated by assuming that the radiation distribution of the sky was that of a standard overcast day (Ross 1981). The total amount of incoming PAR radiation was  $1200 \text{ MJ m}^{-2}$  (on a horizontal surface) during one growing season without variation between years; this is a typical value for southern Finland (Stenberg 1996). In addition to this calculation, the plot was assumed to be surrounded by a homogeneous forest that extends to infinity and has the needle area density of the plot (between the crown base and top height of the plot). The transmission of radiation in the surrounding forest was calculated as  $\exp[-0.14 \times \text{distance traveled} \times \text{leaf area density}]$ . The extinction coefficient 0.14 is that of a forest consisting of Scots pine shoots (Stenberg 1996).

#### The data

We compare whether the predictions of LIGNUM for a forest stand are within a reasonable range of values, and not fitting any component in it. The results of empirical models accounting for the growth of Scots pine stands in Finland were used as the 'data'. We considered that comparing the simulations to results of this sort is sufficient to show whether or not the model output corresponds to average tree growth. We used the data from a yield table for conifer stands (Vuokila and Väliäho 1980) and the

simulation outcomes of an empirical model for juvenile stands of Scots pine (Varmola 1987). We used the data of a stand growing on a medium productivity site from these sources. We also used the results from Berninger *et al.* (2005), Vanninen *et al.* (1996), Mäkelä and Vanninen (2001) and Mäkinen and Colin (1998) to compare the simulation results with values that can be expected to occur in Scots pine trees growing in forests.

**Results**

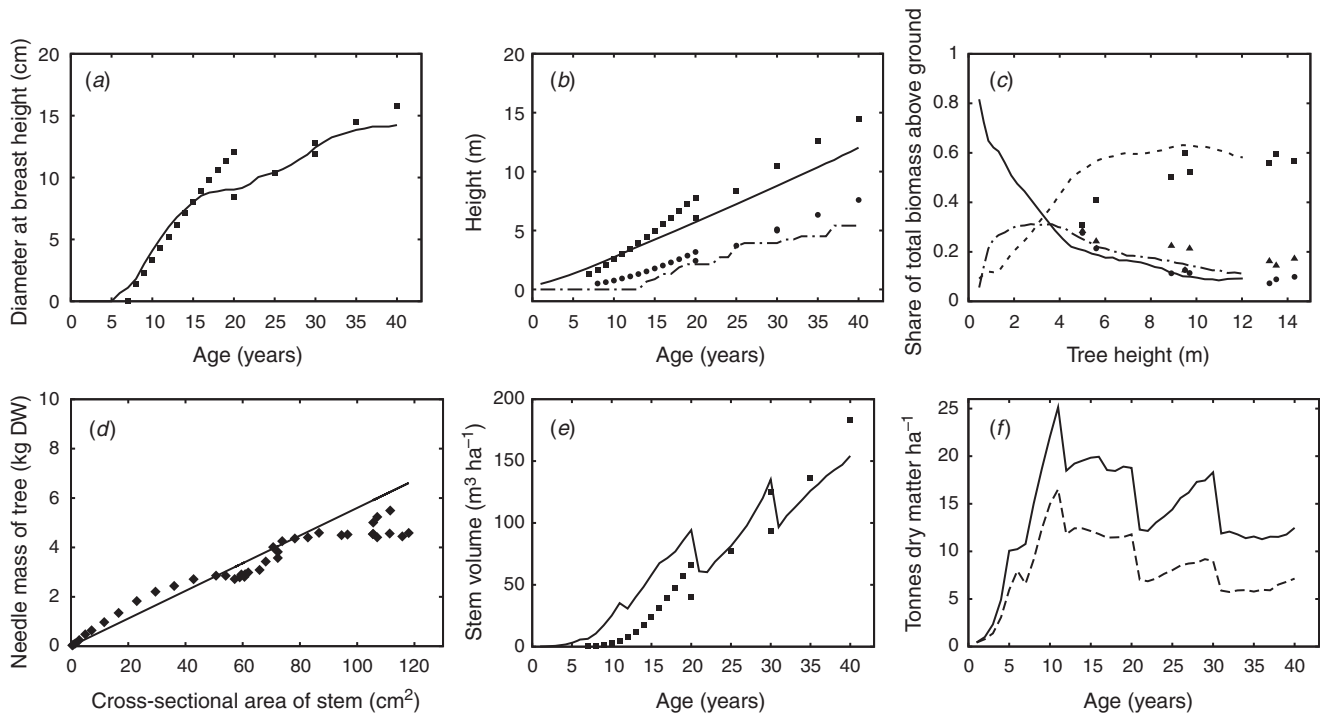
*Tree and stand simulation*

We made simulations for a period of 40 years because we had the architectural description of only juvenile trees. Furthermore, after 40 years, the trees will be large in proportion to the size of the plot used in the simulation. In such a situation, e.g. removing a tree in thinning, may have a disproportionally large effect on the subject tree. The results proved to be very sensitive to the stand density (as expected) given as input (Fig. 3b). This is because the light conditions, and thus the growth of the simulated tree, are considerably affected by stand density. Variables related to tree vigor or the degree of crowding normally regulate tree mortality and, through this, the stand density in the models (e.g. Mäkelä 1997). In the present case, this feedback link does not exist and thus the meaningfulness of the results is dependent on the prerequisite that the imposed

stand density does not present impossible growing conditions for the tree. We took this into account when specifying the stand density and tested the effect of density on results.

The diameter growth followed rather well that of the data (Fig. 4a). The height and crown height development fell below the development of an average tree in a thinned stand (Fig. 4b). The increase in height was practically linear. This is understandable on the basis of Eqn 3; the length of the new segment at the stem apex depends only on the general availability of photosynthates because both the branching order effect and radiation conditions are constant for the new segment. The availability of photosynthates did not drastically change during simulation. The crown limit was lower in the simulations, but this can be partly because the data may contain isolated branches below the limit; in the simulations it was the lowest branch with foliage.

The simulated proportions of needles, stem sapwood and branches agreed qualitatively with the observed ones (Fig. 4c), thus, demonstrating that the allocation between foliage, branches and stem sapwood was at the correct level when considering the whole compartments. The proportion of stem sapwood was too high, especially in small trees. The amount of needles per cross-sectional area of stem at the crown base corresponds well to the relationship reported for Scots pine in Finland by Berninger *et al.* (2005) (Fig. 4d). In large trees, the



**Fig. 4.** Simulated tree and stand development of Scots pine with the number of trees as in Fig. 3b, and the parameter values from Table 1. (a) Diameter at breast height (solid line), (b) tree height (solid line) and height of the crown base (dash-dotted line), (c) proportions of needles (solid line), stem sapwood (dashed line) and branches (dash-dotted line) in the aboveground biomass, (d) needle mass (◆) v. cross-sectional area of the stem at the crown base, (e) stem volume of the stand (solid line), (f) needle mass (dashed line) and annual photosynthetic production (solid line) of the stand. In (a, b, e) markers (■) depict the typical values obtained from empirical models by Varmola (1987) and Vuokila and Väliaho (1980) for Scots pine stands in commercially thinned stands on a fresh site in Finland. The height of the crown base (●) in panel b has been evaluated with a model by Hynynen *et al.* (2002). The measured shares of biomass of needles (●), branches (▲) and stem sapwood (■) have been taken from Vanninen *et al.* (1996). The solid line in (d) is the relationship reported by Berninger *et al.* (2005).

model predicts slightly lower needle mass per cross-sectional area of stem than that observed.

The simulated stand level stem volume (Fig. 4e) matches qualitatively the stem volume in a thinned stand. At the beginning, the model predicts a higher volume than in the data, whereas in year 40 the simulated volume is lower. The photosynthetic production was closely linked to the amount of foliage (Fig. 4f). The ratio of stand level photosynthetic production and foliage mass varied between 1.2 and 1.9 in the simulations. Mäkelä *et al.* (2006) reported that the GPP estimated from Eddy covariance measurements in a Scots pine stand in southern Finland varied during the period 1997–2001 in the range 19–22 tonnes dry matter ha<sup>-1</sup> year<sup>-1</sup>. The simulated photosynthetic production (after canopy closure at about year 10) was between 13 and 25 tonnes dry matter ha<sup>-1</sup> year<sup>-1</sup>, which corresponds well to the measured GPP. The estimated maximum needle mass of Scots pine stands in Finland is ~10 tonnes dry matter ha<sup>-1</sup> (Hari *et al.* 1982; Lehtonen 2005). The simulated needle masses (Fig. 4f) were relatively similar to this estimate.

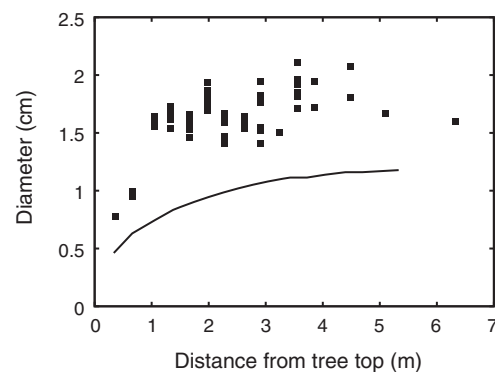
The simulated crown structure (Fig. 5) developed from a symmetrical one to an asymmetrical one in which the growth of the branches near the crown base had decreased. Development of an asymmetrical crown was the result of the non-homogeneity of the stand density (Fig. 3a). On the crowded side, there has been less light and, thus, less production of new segments. The rise of the crown base in the model resulted from a branch losing all its needles, i.e. conditions where no new



**Fig. 5.** 3D images of the simulated Scots pine tree at ages of 10, 20, 30, and 40 years (from left to right). The heights were 2.7, 5.7, 8.8, and 12.0 m, respectively. Note that the upper side in the neighbourhood of the tree (cf. Fig. 3b) was denser than on the other sides and that the crown is, therefore, unsymmetrical.

buds and segments can be created. The parameters controlling this are the functions in Fig. 2 and also the minimum segment length below which no new segments are formed. The control of crown rise is primarily at the shoot level, the only tree level factor being the availability of photosynthates that can cause the length of the new segment to remain below the minimum and to be deleted (cf. Table 1). No tree level mechanisms, which are often employed in models with an aggregated description of the crown (cf. Mäkelä 1997), are present.

Although the proportion of biomass in the branches seemed to be approximately in agreement with the observations at tree level (Fig. 4d), the characteristics of the simulated individual branches did not match the observed values very well (Fig. 6). The diameter of the top branch was higher than that of the empirical model. The difference remained on moving down towards the crown base. Despite the different level, the shape of the simulated branch diameter curve approximately corresponded to the observed one. The simulated branch lengths (not shown) were also larger than would be expected in Scots pine trees in Finland. Apparently, how the length of the new segments was calculated (Eqn 3) did not sufficiently reduce the length growth of the branches. The way the reductions were calculated was due to the branching order (parameter  $q$ ) and radiation conditions (function  $f_L$ ), the same for all the branching orders. They should have had a stronger effect on the branches (Gravelius order equal to two). The simulated number of branches at the age of 20 years was 80. Kellomäki and Väisänen (1988) reported an average of 50 branches in young (up to 20 years old) Scots pine trees. However, their data represented a slightly less fertile site than the present case. Nevertheless, the simulated number of branches appeared to be somewhat higher than the observed number. As a result, Eqn 1 apparently predicted too many lateral buds in the stem apex. The equation was the same for all the apices, irrespective of their order. Another reason for the higher number of simulated branches may be that branch mortality inside the living crown in the model did not correspond to the situation in real trees, where branches start to die from about the fourth whorl down from the tree top (Kellomäki and Väisänen 1988). In the model, branch mortality only occurred close to the crown base where the radiation conditions (Eqn 1) prevented the production



**Fig. 6.** Simulated (■) branch diameters *v.* position on the stem of Scots pines. The solid line is the prediction given by the empirical branch diameter model by Mäkinen and Colin (1998).

of new buds. In the upper parts of the crown, the radiation conditions were such that all the branches survived. Even though the dimensions of the simulated branches were larger than the observed values, the proportion of branch biomass corresponded to that of the observed values (Fig. 4d). This is because a constant wood density (Table 1) was used in the model. The density of wood in branches is generally higher (Hakkila 1989), but this was not taken into account in this version of the model.

The simulated distribution of the vertical needle mass appeared to be concentrated relatively close to the tree top compared with the observed distribution (Fig. 7). It would appear that the production of new segments was too high or their sizes were too large (the initial amount of foliage was proportional to the segment size) in the upper part of the crown. The production of buds is controlled by the foliage mass and light conditions of the mother segment (Eqns 1, 2), and the segment size by the light conditions (Eqn 3). The steep distribution of the simulated vertical needle mass may also be an artefact caused by the fact that all the trees were of equal size: if the trees had different heights, then the vertical radiation distribution in the stand would obviously be different and might allow for flatter vertical needle mass distributions in the trees.

#### Effect of stand density and neighbouring trees

We studied the effect of the stand density by making simulations with densities differing from that of Fig. 3b. The results did not change much with varying density. The slenderness of the trees increased with increasing density (Fig. 8) whereas tree height was less sensitive to density (the heights differed less than 3% from that of Fig. 4b). This is a common feature observed in thinning trials of forestry (Assmann 1970). We also varied sizes of neighbouring trees so that some (up to 80%) were 5 years older or younger than the subject tree. In these simulations (data not shown), the results were also logical: the tree with large neighbours developed a slender stem, and the tree with small neighbours increased in diameter; height growth was not

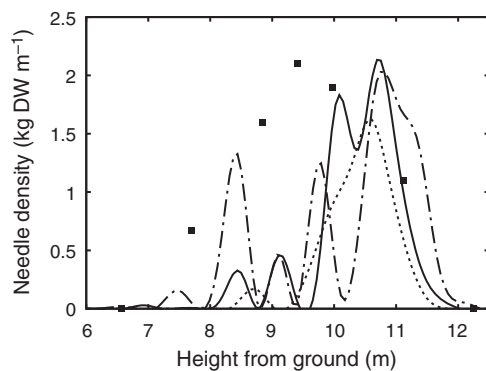
affected much. This is again as expected on the basis of empirical studies (Assmann 1970). The crown length was larger in the sparser stand (Fig. 7), whereas increased density produced short crowns and narrow vertical needle distributions.

#### Effect of some parameters of the needle mass–wood relationships

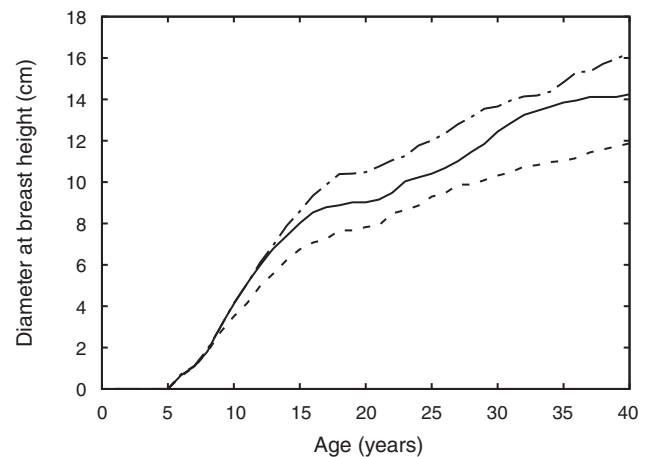
The parameters of the model that control foliage–wood relationships at the shoot level are parameters  $a_f$ ,  $l_R$ , and  $\xi$  of Eqn 4. Furthermore, the amount of wood required in the branches and stem per unit of needle mass is affected by the parameters of the sapwood requirement  $\alpha_s$  (Fig. 1b; Table 1) and the rate of senescence of the sapwood,  $s_s$  (Table 1).

Changing the value of parameter  $a_f$  had an opposite effect on tree growth, as was anticipated: a larger value of  $a_f$  (i.e. more needles v. cross-sectional area of sapwood) decreased growth and *vice versa* (Fig. 9a); only at very low values the growth ceased. The reason for this is that an increased needle mass causes crowding and lower photosynthesis per unit of needle mass. Extension growth was stronger with a low value of  $a_f$ , which, in turn, enhanced photosynthetic production (by decreasing crowding) and the production of woody material at the same time. The parameter  $a_f$  strongly affects the share of resources that are allocated to needles (Fig. 9b).

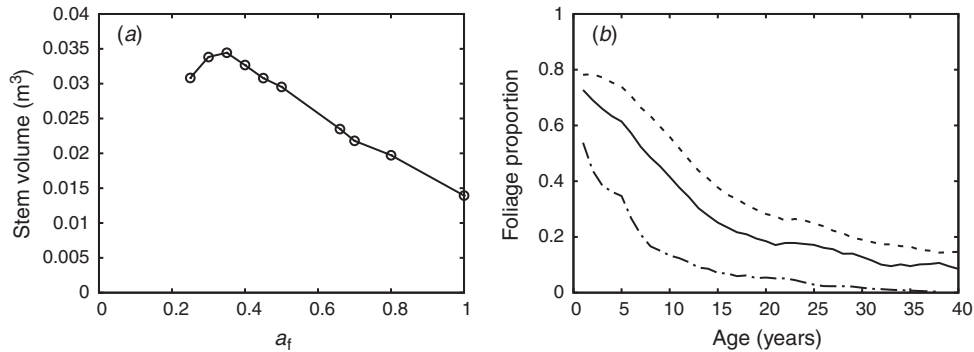
The simulations with the values of parameters controlling the foliage–sapwood relationship, amount of sapwood required below a point in a branch or a stem, and the senescence of sapwood showed allocation changed when the sapwood requirement in the branches and stem was high (Fig. 10). In this case, the proportion of resources allocated to the needles became small and the needle mass was low. After the crown rise started (after 12 years; Fig. 4b), there was a lack of resources, the tree could not sustain any more high allocation to sapwood either and the high rate of sapwood senescence cause the proportion to decline.



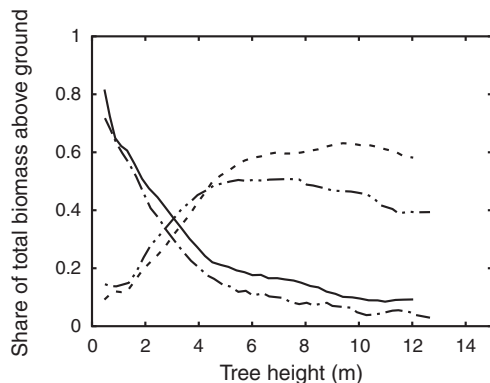
**Fig. 7.** Simulated vertical needle density at the age of 40 years in one Scots pine tree (solid line) and observations (■) made on a 41-year-old dominant tree growing on a fertile site by Mäkelä and Vanninen (2001). Shown are also simulated vertical needle densities at age 40 years when density was 30% higher (dashed line) and 30% lower (dash-dotted line) than that in Fig. 3b.



**Fig. 8.** Simulated diameter at breast height with three densities. In Fig. 3b (solid line), density was 30% higher (dashed line), and 30% lower (dash-dotted line).



**Fig. 9.** (a) Stem volume of Scots pines at age 20 years with different values of parameter  $a_f$ . (b) Proportion of photosynthetic production allocated to needles with three values of parameter  $a_{f0i}$ : 0.66 (solid line), 1.0 (dashed line), and 0.25 (dash-dotted line).



**Fig. 10.** The proportion of needles (solid line) and stem sapwood (dashed line) of Scots pines with the parameter values in Table 1. The proportion of needles (dash-dotted line) and stem sapwood (double dot-dashed line) with parameter values changed for increased sapwood requirement:  $s_s=0.07$ , sapwood senescence takes place from year 1;  $\xi=0.6$ ; and  $\alpha_i=1$  in all junctions.

## Discussion

We applied a functional–structural tree model of Scots pine for simulating a tree stand. The model derived growth on the basis of shoot level relationships taking into account how the resources are distributed in the network of shoots. The model applies no explicit tree-level control, such as modification of the rise in the crown or allocation of resources inside the crown, which would be affected by the condition of the whole tree (e.g. measure of dominance by neighbours). In other words, we aimed to explore the question posed by Sorrensen-Cothorn *et al.* (1993) ‘Can rules for tree growth under a spatially varied resource also fully describe competition between trees?’, to which they gave an affirmative answer on the basis of their modular tree and stand model. On the basis of our results, it is also obvious that stand growth phenomena can be understood from interaction of shoots with their local environment (cf. Nikinmaa *et al.* 2003). However, in our approach the shoot growth is constrained by their position in the crown but also by the whole tree level requirement of balanced growth. Our results thus partially agree with the idea that the plastic growth of whole plants is the sum of modular

(e.g. shoot level) responses triggered by local environmental conditions (de Kroon *et al.* 2005). The simulations produced results that are comparable with observations made in real Scots pine trees and tree stands in Finland. The simulations produced reasonable values for tree variables in the forest simulation, and also reasonable values for stand variables. The parameters of the model were not optimised for the best fit, but their values were chosen on the basis of available information.

However, because we employed some simplifications due to the computational complexity or lack of data, there is scope for further improvement of the model and, thus, a possibility for even more accurate predictions. First, the stand did not consist of individually growing trees, but of replicas of a single growing tree and the stand density was given as input. As a result, the two-way interaction between neighbours that exists in real forest stands is missing. In our case, if the subject tree grows rapidly, then the neighbouring trees also grow rapidly. In reality, however, at least some of the neighbours would grow less rapidly. However, simulations with changed input density and sizes of neighbouring trees showed that the results do not change much. The changes with density were logical and as could be expected on the basis of knowledge about silviculture. We have employed some further simplifications in the models, such as a constant wood density in all parts of the tree, and neglected other factors (such as requirements of stability, e.g. King and Loucks 1978) than the pipe model in the regulation of diameter growth. These factors may have caused some discrepancies between the simulation results and real observations. The characteristics of the branch system (branch diameters and lengths, vertical distribution of needle mass) do not match the observations well, although the tree level proportion of the branch mass is at the correct level. We simulated only the first 40 years of a stand. Scots pine trees can attain an age of several hundreds years and the rotation time in Finnish forestry practice is also often more than 100 years. We did not have the necessary information concerning parameter values, which most probably change over the whole life span of Scots pine, to cover such an extended time period.

The first obvious future improvement is that the stand should consist of individual trees instead of replicas of one tree. In order to be able to make this improvement, we will either have to reduce the computational complexity of the calculations in estimating the radiation conditions in a stand or to use parallel computing. With

the present geometrical approach, in which all segments are checked to ensure that the beam of radiation is not obstructed by another segment, simulation of a plot of the size used here ( $17 \times 17$  m) and consisting of individual trees, would be computationally prohibitive. We tested the discretation of the crown space (voxel space approach), but it would appear that the architectural development of a tree is very sensitive to the spatial averaging that the discretation of the crown space introduces. We, therefore, used a geometrical approach in this study. The problem of matching the detailed account of the tree (plant) structure that the FSPMs employ and estimation of the radiation conditions in a computationally feasible way is a challenge for the application of the FSPMs to plant communities that have a complicated structure, like forests. If the radiation conditions are evaluated with rough spatial averaging, there is not much point in using a plant model that is capable of utilising information about the local environment of a plant organ on a very fine scale. Cournède *et al.* (2007) pointed out that 'there is a real need to study the extension of individual-based functional-structural models to plant populations, especially in terms of competition for light'.

The current simulations were made for Scots pine, which simplifies the description of the bud formation and extension of buds. Unlike many broadleaved trees and even conifers such as Norway spruce, new pine buds are formed at the apex of existing shoots. This greatly facilitates the description of the impact of shoot position and shoot environment on the bud formation as all the buds formed are positioned at the same place and they are morphologically identical. However, there are clear size differences between the shoots produced by lateral and apical buds. We have considered this in the model: the lateral buds produce shorter segments than the apical ones (Eqn 3). We assume that the segments produced by lateral buds have the same size but point in different directions. At the next time step they will be in a different light climate and develop differently. The lack of initial size differences in the lateral segments may influence our results, as in reality there may be initial size differences that rapidly lead to differences in branch size as well. The simulated tree crowns may suffer from too little differentiation between the sizes of branches, which could partially explain the simulation results. However, our purpose was to use as simple relationships in the model as possible (see next paragraph) and we did not consider the size distribution of segments in this study. Initial size difference in forest stands leads to differentiation of trees into canopy classes and prevents stagnation of tree stands (Huston *et al.* 1988; Oliver and Larson 1996), but it has been shown that individual shoots and branches obey a similar relationship between their size and density as the self thinning rule predicts for vegetation (Kellomäki 1986). The question of how initial size differences of shoots (growth potential of buds) affects stand dynamics and crown development clearly warrants its own (simulation) study.

There are many factors that are absent or have a small impact on single tree applications but which may be important for stand simulations. We have intentionally excluded stochastic elements in the model (except location of trees on the plot). We believe that it is informative to see how far it is possible to go with deterministic formulations. There are many places where

stochastic elements could be used. They include sizes and properties of new shoots, annual and inter-annual variation of environmental conditions (radiation primarily), and bud and branch mortality. An interesting possibility in including stochastic elements in the model is that they may change the dynamics in comparison to using mean values, as has been shown to be the case with accumulating errors on long-term growth predictions of forestry models (Kangas 1997). Including stochastic elements in an FSPM-based stand model is challenging, since they can be considered on several hierarchical levels: organ, tree and stand. We consider that it would be better to evaluate the effect of including stochastic elements in a separate, comprehensive study. A matter that should also be investigated in this context is whether or not it is possible to explain tree death (i.e. loss of all foliage) on the basis of the productivity and respiration relationships of the model, or is it necessary to include (stochastic) agents – like herbivores – that facilitate mortality.

There is abundant information showing that wood density is different in branches than in stems, and that it varies along and within branches (Hakkila 1989). Despite this, we chose to use a uniform value of wood density (Table 1) because other factors like stability requirements (King and Loucks 1978) and branch mortality, should also be taken into consideration when improving the details of branch growth in the model. In addition, because we employed a central pool of growth resources (see below), using a different density of branch wood would only affect (through the cost of construction) the tree level growth resources, and not only the branches. Here, we consider only the effects of the pipe model in more detail. It is probably this simple treatment of branches that primarily results in the characteristics of the branches not corresponding very well to the observations. Kellomäki and Väisänen (1988) showed that branch mortality starts from the third whorl down from the tree top in Scots pine stands. In our model branches die only at the crown base. This is because all the branches of the whorl are of about the same size – they are identical at the beginning, and there are no such major differences in radiation inside the crown that would cause a branch to die before the crown base reaches this point. Note, however, that the height of the crown base can vary on different sides of the crown as a result of the varying radiation conditions. A combination of stability requirements and the pipe model and a mechanism for branch death will be implemented in a future version of the model.

Although the model contains no explicit tree level control that would modify shoot level phenomena, the partitioning of resources to growth itself exerts a form of implicit tree level control. The growth resources (photosynthetic production minus respiration losses) are considered to be in one pool, and all its contents are distributed into primary and secondary growth. If the growth resources are low, then all the growing segments grow less (modified by their local conditions), and *vice versa*. This means that a branch, which produces less than it consumes in respiration, decreases the growth of segments that produce a surplus. However, this may not be the case in reality (Sprugel *et al.* 1991). There are several other possible mechanisms than the one applied in this study for the distribution of growth in the tree crown (Lacointe 2000), and different degrees of branch autonomy

may be observed depending on the influence of specific factors on growth (Kaitaniemi and Ruohomäki 2006). It is possible that the local partitioning of growth resources would allow for more flexible adjustment of the tree crown in a heterogeneous environment – and maybe a more accurate prediction. More flexible crown development may require that the growth be decentralised in the model. This would require that growth of each shoot is determined by its local conditions but also by how well it is able to attract resources from other parts of the tree. In our previous papers, we examined how this kind of mechanism could be achieved using Thornley's transport resistance principle (Berninger *et al.* 2000). We have also tried to emulate its impacts in a central allocation scheme using shoot positional information within the crown transport structure along with the shoot light climate as growth determining factors (Nikinmaa *et al.* 2003). This type of approach would result clearly into very different crown structures but, owing to complexity of the forest simulations, we used more simple approach here.

In our model, the distribution of growth along the paths from the branch apices down to the base of the trunk is controlled by the pipe model (Fig. 1b) associated with the senescence of sapwood. In applying the pipe model, different relationships across the junctions between different branching orders have been taken into account as shown (partly) by means of empirical measurements. The tree level distribution of mass in the foliage, branches and stem sapwood is at approximately the correct level. This indicates that the pipe model, as it has been applied here, can explain the distribution of matter in the tree. However, the dimensions of the branches differ from the observed ones. As the radiation conditions also affect (through bud production and length of growth units) the development of the branches, it is not possible to conclude whether the reason for the observed discrepancies is the pipe model, the effect of radiation, or both. If the production and size of new segments was affected to a lesser degree by radiation conditions than at the present, it would probably lead to more even vertical distribution of needle mass. However, it would then slow down crown rise that is already a bit slower than in the observations (Fig. 4b). The sharp simulated vertical needle mass distribution may also be an artefact of all trees being equal size: if trees had different heights, the vertical radiation distribution in the stand would obviously be different and might allow for flatter vertical needle mass distributions in trees. In any case, more attention should be paid to branch growth in future applications.

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## References

- Assmann E (1970) 'The principles of forest yield study.' (Pergamon Press: Oxford)
- Berninger F, Nikinmaa E, Sievänen R, Nygren P (2000) Modelling of reserve carbohydrate dynamics, regrowth and nodulation in a N<sub>2</sub>-fixing tree managed by periodic prunings. *Plant, Cell & Environment* **23**, 1025–1040. doi: 10.1046/j.1365-3040.2000.00624.x
- Berninger F, Coll L, Vanninen P, Mäkelä A, Palmroth S, Nikinmaa E (2005) Effects of tree size and position on pipe model ratios in Scots pine. *Canadian Journal of Forest Research* **35**, 1294–1304. doi: 10.1139/x05-055
- Björklund L (1999) Identifying heartwood-rich stands or stems of *Pinus sylvestris* by using inventory data. *Silva Fennica* **33**, 119–129.
- Courmède P-H, Mathieu A, Houllier F, Barthélémy D, de Reffye P (2007) Computing competition for light in the GREENLAB model of plant growth: a contribution to the study of the effects of density on resource acquisition and architectural development. *Annals of Botany* **101**, 1207–1219. doi: 10.1093/aob/mcm272
- de Kroon H, Huber H, Stuefer JF, van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants. *New Phytologist* **166**, 73–82. doi: 10.1111/j.1469-8137.2004.01310.x
- DeAngelis DL, Gross LJ (1992) 'Individual-based models and approaches in ecology. Populations, communities and ecosystems.' (Chapman & Hall: London)
- Dzierzon H (2003) Development of methods for characterizing plant and stand architecture and of model comparisons. Institute of Forest Biometry and Informatics, Faculty of Forest Sciences and Forest Ecology, University of Göttingen. Available at <http://webdoc.sub.gwdg.de/diss/2003/dzierzon/> [Verified 4 August 2008]
- Ford ED, Sorrensen KA (1992) Theory and models of inter-plant competition as a spatial process. In 'Individual-based models and approaches in ecology'. (Eds DL DeAngelis, LJ Gross) pp. 363–407. (Chapman & Hall: New York)
- Godin C, Sinoquet H (2005) Functional–structural plant modelling. *New Phytologist* **166**, 705–708. doi: 10.1111/j.1469-8137.2005.01445.x
- Hakkila P (1979) 'Wood density survey and dry weight tables for pine, spruce and birch stems in Finland.' (Communicationes Instituti Forestalis Fenniae: Helsinki, Finland)
- Hakkila P (1989) 'Utilization of residual forest biomass.' (Springer-Verlag: Berlin)
- Hari P, Kellomäki S, Mäkelä A, Ilonen P, Kanninen M, Korpilahti E, Nygrén M (1982) Metsikön varhaiskehityksen dynamiikka. *Acta Forestalia Fennica* **177**, 1–39. [In Finnish, with English summary: Dynamics of early development of tree stand].
- Hari P, Heikinheimo P, Mäkelä A, Kaipainen L, Korpilahti E, Salmela J (1986) Trees as water transport system. *Silva Fennica* **20**, 205–210.
- Harper J (1977) 'Population biology of plants.' (Academic Press: London)
- Host GE, Isebrands JG, Thesiera GW, Kiniry JR, Graham RL (1996) Temporal and spatial scaling from individual trees to plantations: a modeling strategy. *Biomass and Bioenergy* **11**, 233–243. doi: 10.1016/0961-9534(96)00012-8
- Host GE, Stech H, Lenz KE, Roskoski K, Mather R, Donahue M (2007) Leaves to landscapes: using high performance computing to assess patch-scale forest response to regional temperature and trace gas gradients. In 'Proceedings of the 5th international workshop on functional–structural plant models'. (Eds P Prusinkiewicz, J Hanan, B Lane) pp. 46–1 to 46–4. Available at <http://algorithmicbotany.org/FSPM07/proceedings.html> [Verified 4 August 2008]
- Huston MA, DeAngelis D, Post W (1988) New computer models unify ecological theory. *Bioscience* **38**, 682–691. doi: 10.2307/1310870
- Hynynen J, Ojansuu R, Hökkä H, Siipilehto J, Salminen H, Haapala P (2002) 'Models for predicting stand development in MELA system. Research papers no. 835'. (Finnish Forest Research Institute: Vantaa, Finland).
- Ishii HT, Tanabe S, Hiura T (2004) Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science* **50**, 342–355.
- Kaitaniemi P, Ruohomäki K (2006) Uncaged larvae elicit a combination of local and integrated growth responses within mountain birch crown. *Oikos* **115**, 537–548. doi: 10.1111/j.2006.0030-1299.14878.x

- Kangas A (1997) On the prediction bias and variance in long-term growth projections. *Forest Ecology and Management* **96**, 207–216. doi: 10.1016/S0378-1127(97)00056-X
- Kellomäki S (1986) A model for the relationship between branch number and biomass in *Pinus sylvestris* crowns and the effect of crown shape and stand density on branch and stem biomass. *Scandinavian Journal of Forest Research* **1**, 455–472.
- Kellomäki S, Väisänen H (1988) Dynamics of branch population in the canopy of young Scots pine stands. *Forest Ecology and Management* **24**, 67–83. doi: 10.1016/0378-1127(88)90025-4
- King D, Loucks OL (1978) The theory of tree bole and branch form. *Radiation and Environmental Biophysics* **15**, 141–165. doi: 10.1007/BF01323263
- Körner C (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society. Biological Sciences* **359**, 493–498. doi: 10.1098/rstb.2003.1429
- Kurth W (1997) Growth grammars simulating trees – an extension of L-systems incorporating local variables and sensitivity. *Silva Fennica* **31**, 285–295.
- Kurth W (1998) Some new form for modelling the interactions between plant architecture, competition and ca allocation. *Bayreuther Forum Ökologie* **52**, 53–98.
- Kurtio O, Kellomäki S (1990) Structure of young *Pinus sylvestris*: branching and its dependence on tree size. *Scandinavian Journal of Forest Research* **5**, 169–175.
- Lacointe A (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional–structural tree models. *Annals of Forest Science* **57**, 521–533. doi: 10.1051/forest:2000139
- Lehtonen A (2005) Estimating foliage biomass in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plots. *Tree Physiology* **25**, 803–811.
- MacDonald N (1983) 'Trees and networks in biological models.' (John Wiley & Sons: Avon)
- Mäkelä A (1986) Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology* **123**, 103–120. doi: 10.1016/S0022-5193(86)80238-7
- Mäkelä A (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science* **43**, 7–24.
- Mäkelä A, Vanninen P (2001) Vertical structure of Scots pine crowns in different age and size classes. *Trees* **15**, 385–392. doi: 10.1007/s004680100118
- Mäkelä A, Kolari P, Karimäki J, Nikinmaa E, Perämäki M, Hari P (2006) Modelling five years of weather driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology* **139**, 382–398. doi: 10.1016/j.agrformet.2006.08.017
- Mäkinen H, Colin F (1998) Predicting branch angle and branch diameter of Scots pine from usual measurements and stand structural information. *Canadian Journal of Forest Research* **28**, 1686–1696. doi: 10.1139/cjfr-28-11-1686
- Martin MJ, Host GE, Lenz KE, Isebrands JG (2001) Simulating the growth response of aspen to elevated ozone: a mechanistic approach to scaling a leaf-level model of ozone effects on photosynthesis to a complex canopy architecture. *Environmental Pollution* **115**, 425–436. doi: 10.1016/S0269-7491(01)00232-9
- Mech R, Prusinkiewicz P (1996) Visual models of plants interacting with their environment. In 'Computer graphics proceedings, annual conference series, SIGGRAPH 96'. pp. 397–410. (ACM SIGGRAPH: New York)
- Metz JAJ, Diekmann O (1986) 'The dynamics of physiological structured populations. Lecture Notes in Biomathematics 68'. (Springer-Verlag: Berlin)
- Nikinmaa E, Messier C, Sievänen R, Perttunen J, Lehtonen M (2003) Shoot growth and crown development: effect of crown position in three-dimensional simulations. *Tree Physiology* **23**, 129–136.
- Oker-Blom P, Smolander H (1988) The ratio of shoot silhouette area to total needle area in Scots pine. *Forest Science* **34**, 894–906.
- Oliver CD, Larson BC (1996) 'Forest stand dynamics.' (John Wiley & Sons: New York)
- Perttunen J, Sievänen R (2005) Incorporating Lindenmayer systems for architectural development in a functional–structural tree model. *Ecological Modelling* **181**, 479–491. doi: 10.1016/j.ecolmodel.2004.06.034
- Perttunen J, Sievänen R, Nikinmaa E, Salminen H, Saarenmaa H, Väkevä J (1996) LIGNUM: A tree model based on simple structural units. *Annals of Botany* **77**, 87–98. doi: 10.1006/ambo.1996.0011
- Perttunen J, Sievänen R, Nikinmaa E (1998) LIGNUM: A model combining the structure and functioning of trees. *Ecological Modelling* **108**, 189–198. doi: 10.1016/S0304-3800(98)00028-3
- Perttunen J, Nikinmaa E, Lechowicz MJ, Sievänen R, Messier C (2001) Application of the functional–structural tree model LIGNUM to sugar maple saplings (*Acer saccharum* Marsh) growing in forest gaps. *Annals of Botany* **88**, 471–481.
- Porté A, Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling* **150**, 141–180. doi: 10.1016/S0304-3800(01)00476-8
- Prentice IC, Bondeau A, Cramer W, Harrison SP, Hickler T, Lucht W, Sitch S, Smith B, Sykes MT (2007) Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In 'Terrestrial ecosystems in a changing world'. (Eds JP Canadell, D Pataki, LF Pitelka) pp. 175–192. (Springer-Verlag: New York)
- Room PM, Maillette L, Hanan JS (1994) Module and metamer dynamics and virtual plants. *Advances in Ecological Research* **25**, 105–157. doi: 10.1016/S0065-2504(08)60214-7
- Ross J (1981) 'The radiation regime and architecture of plant stands'. (Dr W. Junk Publishers: The Hague, The Netherlands).
- Shinozaki K, Yoda K, Hozumi K, Kira TA (1964) A quantitative analysis of plant form – the pipe model theory. I. Basic analysis. *Japanese Journal of Ecology* **14**, 97–105.
- Sievänen R, Nikinmaa E, Perttunen J (1997) Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. *Silva Fennica* **31**, 329–340.
- Sievänen R, Nikinmaa E, Nygren P, Ozier-Lafontaine H, Perttunen J, Hakula H (2000) Components of functional–structural tree models. *Annals of Forest Science* **57**, 399–412. doi: 10.1051/forest:2000131
- Sorensen-Cothorn KA, Ford ED, Sprugel DG (1993) A model of competition incorporating plasticity through modular foliage and crown development. *Ecological Monographs* **63**, 277–304. doi: 10.2307/2937102
- Sprugel DG, Hinckley TM, Schaap W (1991) The theory and practice of branch autonomy. *Annual Review of Ecology and Systematics* **22**, 309–334. doi: 10.1146/annurev.es.22.110191.001521
- Stenberg P (1996) Metsikön rakenne, säteilyolot ja tuotos. University of Helsinki, Department of Forest Ecology Publications no. 15. [in Finnish].
- Stenberg P, Palmroth S, Bond B, Sprugel DG, Smolander H (2001) Shoot structure and photosynthetic efficiency along the light gradient in a Scots pine canopy. *Tree Physiology* **21**, 805–814.
- Stoyan D, Kendall WS, Mecke J (1987) 'Stochastic geometry and its applications.' (John Wiley & Sons: New York)
- Takenaka A (1994) A simulation model of tree architecture development based on growth response to local light environment. *Journal of Plant Research* **107**, 321–330. doi: 10.1007/BF02344260
- Vanninen P, Ylitalo H, Sievänen R, Mäkelä A (1996) Effects of age and site quality on the distribution of biomass in Scots pine. *Trees (Berlin)* **10**, 231–238.
- Varmola M (1987) Männyn viljelytaimikoiden kasvumalli. Lic. For & Agric. Thesis, Department of Forest Mensuration, University of Helsinki, 89 p. [in Finnish].
- Vuokila Y, Väliaho H (1980) Viljeltyjen havumetsiköiden kasvatusmallit. *Communications Instituti Forestalis Fenniae* **99**, 271. [In Finnish with English summary: Growth and yield models for conifer cultures in Finland].