A study into crown development mechanisms using a shoot-based tree model and segmented TLS data

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ABSTRACT

•Background and Aims The functional structural plant models (FSPMs) allow simulation of
tree crown development as the sum of modular (e.g. shoot level) responses triggered by the
local environmental conditions. The actual process of space filling by the crowns can be
studied. Although the FSPM simulations are at organ scale, the data for their validation have
usually been at more aggregated levels (whole crown or whole tree). Measurements made by
terrestrial laser scanning (TLS) that have been segmented to elementary units (internodes) offer a phenotyping tool to validate the FSPM predictions at comparable levels to their detail. We demonstrate in this contribution testing different formulations of crown development of Scots pine trees in LIGNUM model using segmented TLS data.

**Methods** We made TLS measurements from four sample trees growing in a forest on a relatively poor soil from a sapling size to a mature stage. The TLS data were segmented into internodes. The segmentation also produced information whether needles were present in the internode. We applied different formulations of crown development (flushing of buds and length growth of new internodes) in LIGNUM. We optimized the parameter values of each formulation using genetic algorithms to observe the best fit of LIGNUM simulations to the measured trees. The fitness function in the estimation combined both tree level characteristics (e.g. tree height and crown length) as well as measures of crown shape (e.g. spatial distribution of needle area).

**Key Results** Comparison of different formulations against the data indicates that Extended Borchert-Honda model for shoot elongation works best within LIGNUM. Control of growth by local density in the crown was important for all shoot elongation formulations. Modifying the number of lateral buds as a function of local density in crown was the best way to accomplish density control.

**Conclusions** It was demonstrated how segmented TLS data can be used in the context of a shoot-based model to select model components.

Keywords: Functional-structural model, forest stand, Scots pine, terrestrial laser scanning
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 3D structure of the tree and, consequently, (3) modification of the immediate environment, described as a three-dimensional distribution of the resource flux. The stand dynamics result from the interplay of these processes, and is primarily reflected in crown development: if the tree can lift its crown to a position that affords sufficient light in comparison to its competitors, then it will survive in the stand, otherwise it will become suppressed and is liable to die. These growth processes have been modeled in the functional structural plant models (FSPMs; Godin and Sinoquet 2005) and other modular plant models in various ways. They treat trees as modular organisms in the sense of Franco (1986): “The growth and form of a modular organism is determined by the rigid rules of iteration (branching) and the differential response of each growing point to the local conditions around it. The degree of response of each individual module is itself dependent on the degree of physiological integration of the whole organism.”

In those models, thus, individual buds are created, they develop to growth units that carry foliage and buds or die or become dormant if their local conditions are not favorable. This process has been modeled at many levels of detail and abstraction. Constraints and strategies of arborescent plant growth have been studied at abstract level e.g. by Takenaka (1994), Sterck and Schieving (2007), Palubicki et al. (2009) and Palubicki (2013). An example of a generic model that can be adjusted to specific conditions is GreenLab (e.g. Cournede et al. 2008). It applies a system of equations based on resource acquisition, distribution of resources between
sources and sinks and morphological development relying on botanical rules. It has been applied for example to beech (Letort et al. 2008) and Mongolian pine (Wang et al. 2012). There are many models that have been constructed specifically to one species. ECOPHYS for poplar (Host et al. 2008), L-PEACH (Da Silva et al. 2014) for peach and MAppleT (Costes et al. 2008) for apple trees are examples of such models.

Detailed, precise, 3D representations of individual trees are necessary for an accurate assessment of any of the above-mentioned models. The laborious destructive measurements used so far have limited the extent of validation studies severely. Terrestrial laser scanning (TLS) methods have developed quickly. They now provide some superior advantages compared to the traditional and partly manual methods to measure trees. TLS methods allow us to measure non-destructively and fast 3D characteristics of tree crowns (e.g. Raumonen et al 2013, Gatziolis et al. 2015 and Potapov et al. 2016) that were earlier very time consuming to assess. TLS’s are providing conveniently detailed data of crown structures: precise, detailed 3D representations of individual trees. TLS data are finding their way to fitting detailed tree models (e.g. Beyer et al. 2017a, 2017b).

In this paper, we make use of TLS data of trees and demonstrate their use to study different rules of development that have been proposed to govern structural organization of tree crowns. As rules of development we tested some variants of competition between buds and branches for light and space (Perttunen et al 1996, Palubicki et al. 2009), as well as growth controlled by the vigor index (Nikinmaa et al. 2003). The rules of development were implemented in the shoot-based tree growth model LIGNUM (Perttunen et al 1996, Sievänen et al. 2008). We compared the rules of development by observing how well LIGNUM equipped with the particular rule matched the actual data of growth of Scots pine trees obtained by TLS. For this
used an optimization method (Genetic algorithm) but did not aim at parameter estimation, only finding general differences between rules of development.

MATERIAL AND METHODS

THE APPROACH TO TESTING

We tested the agreement with data from Scots pine trees of rules of crown development that were implemented in LIGNUM model (Perttunen et al. 1996, Sievänen et al. 2008), Fig. 1. The agreement was measured with the aid of fit statistics (loss function). The data comprised TLS measurements of four trees at ages 8, 16, 25 and 33 years.

We compared alternative formulations for model components that were responsible for shoot elongation and production of new buds within crown. The parameter values of those model components were optimized for best agreement with the TLS data using genetic algorithm (Scrucca 2013). Because our focus was on the comparison of alternative rules of development we were not interested in the particular values of parameters that produced the best agreement with the data. Instead, the optimization served just to find the full potential of the rule of development. Parameter estimation would require an identifiability analysis to find out if model parameters are determined by the available TLS data. Such attempt warrants a separate study with a larger sample.

All the other crown processes included in LIGNUM were left intact and were implemented as in Sievänen et al. (2008). Altogether, we tested model components from three categories: shoot
elongation, effect of local shoot density in crown and height preference of growth allocation. This produced 18 different combinations model components, which were fitted to the data (Fig. 1). The combinations are detailed in Supplementary material. In the fitting, many functions involved in tested model components were implemented as piecewise linear curves parameterized to follow the general shape of the model functions (cf. Fig. 1). The fit statistics, that is, loss function combined both tree and shoot level characteristics of trees (Eq. 12). A genetic algorithm was used to minimize the loss function with respect of parameter values that were specific for each combination of model components. After reaching the best agreement with the data, the ranking of alternative model formulations and combinations was compared on the basis of value of the loss function.

**TARGET TREES BY TLS**

We created a pseudo growth sequence of Scots pine trees by scanning point clouds of four Scots pine trees at different ages of even aged stands growing on dryish upland sites (VT in the Finnish forest classification system; Cajander 1949) near to each other in the vicinity of Helsinki. The stands were even-aged pure Scots pine stands. The ages of forests (and thus the trees) were 8, 16, 25 and 33 years, and approximate densities 6600, 3000, 1660, and 1000 trees per hectare. The mean heights of forest stands (from youngest to oldest) were 2.5 m, 6.7 m, 10.7 m and 13.9 m. The sample trees were selected sufficiently close (subjective assessment) to average tree. The heights of scanned trees were 2.6 m, 7.2 m, 12.0 m, and 13.6 m (Fig. 9). The forests had been managed according to common forestry practices. The scanned trees can therefore be considered to present a tree in different phases of pine forest growth.
The sample trees were scanned from three locations around the tree at distances 3-5 m with Riegl VZ-400 scanner with vertical and horizontal point density 40 mdeg. The scans were co-registered; the point clouds contained 578308, 7827896, 1533189 and 5024371 points (from youngest to oldest tree). Each point cloud was first segmented into individual branches using the segmentation method presented in (Raumonen et al. 2013, Calders et al. 2015). The segmentation process randomly partitions the point cloud into small subsets whose diameters are about few centimetres and whose neighbours are defined. Starting from the bottom of the point cloud, which is the base of the stem, we use surface growing with these subsets step-by-step adding new layer of neighbours. At each step, bifurcation points are identified by checking local connectivity of the top few layers of the subsets. After the bifurcation or branching points are determined, the final segments (branches) are defined in the increasing branching order by making each segment to reach as far as possible from its base. The result is a division of the point cloud into segments (branches) that do not have any bifurcations along them and whose volume and surface can be next modelled with consecutive cylinders.

Next each branch was modelled with a number of cylinders whose relative length (length/radius) was about a user-given constant. The cylinders were fitted to data using least squares method with the aim of reconstructing the woody surface and volume. We observed that the cylinders fitted to regions with needles had a tendency to be too large in comparison to what can be expected on the basis of tapering of branches. We used this trait of segmentation to assess if there are needles in a branch. To recognize if a cylinder was too thick, we employed a loose parabola taper correction that enforces a generally decreasing taper and gives the local maximum and minimum radius for the cylinders. The parabola taper is defined based on the cylinders fitted in the first three quarters of the branch and setting the radius to 2.5 mm at the
tip of the branch. More details of the taper correction can be found in (Calders et al. 2015).

Now, if the corrected radius was at least 30% lower than the fitted radius, then we took that as an indication of existence of needles. If a branch contained cylinders with needles, then we also classified the last cylinder in the branch as containing needles. If a cylinder, that is, an internode was classified to carry needles, we estimated mass and all-sided area of needles with equations from Lintunen et al. (2011). Segmented and needle-added trees are shown in Fig. 9. We estimated the lower limit of needles (crown base) using an equation from Hynynen et al. (1994). We compared needle masses against ones computed with the aid of biomass equation (Repola et al. 2007) and the correspondence was satisfactory (Supplementary material1).

Finally, the segmented TLS trees were imported into the internal presentation of LIGNUM (see Perttunen et al. 1996). The measured trees could be processed, e.g. in the calculation of the loss function, just as the simulated trees.

**LIGNUM MODEL**

*Growth and senescence*

The LIGNUM model has been documented e.g. in publications Perttunen et al. (1996, 1998, 2001) and Sievänen et al. (2008). Here we give a brief summary of its traits relevant to this study. LIGNUM grows trees so that, in one year growth cycle, buds flush and produce a growth units with length $L$ and number of buds at distal end $N$ (Fig. 2). Both $L$ and $N$ are affected by the local conditions in tree crown (e.g. incoming light, branching order). $L$ is also
constrained by the requirement that amount of growth is equal to the available resources

(photosynthates) at tree level, represented by the global coefficient $\lambda$. $L$ and $N$ can be expressed
in general terms as

$$L = \lambda f_L(\text{local conditions}) \quad (1)$$

$$N = \lambda f_N(\text{local conditions}) \quad (2)$$

The function $f_N$ specifies the number of lateral buds, as the apical bud is always created. Any
bud, including the apical one, dies if it cannot produce a new shoot in the extension growth.

What local conditions are depends on the specific formulation applied and will be explained
below. The factor $\lambda$ is a global one and determined during each growth cycle so that the carbon
balance holds (Perttunen et al. 1996):

$$W_{\text{new}}(L) + W_{\text{second}}(L) + W_{\text{root}}(L) \leq P + M \quad (3)$$

where $W_{\text{new}}$, $W_{\text{second}}$ and $W_{\text{root}}$ are biomass needed to build new shoots (primary growth), in
secondary (thickness) growth and in growth of roots, respectively, and $P$ and $M$ are amounts of
photosynthesis and respiration during the growth cycle. Implicit in Eq. 3 is that the amounts of
primary, secondary and root growths depend on lengths of new shoots (see Sievänen et al.
2008) and thus on $\lambda$.

Part of needles of an internode are shed annually (Perttunen et al. 1996). A branch of any order
is considered dead when it has lost all its needles. Dead branches are shed.
Radiation calculations

The time step of LIGNUM is one year; we considered the photosynthetically active radiation during the growing period, 1200 MJ m\(^{-2}\) on a horizontal surface, a typical value for southern Finland (Stenberg 1996). We took into account radiation coming from different points in the upper hemisphere; we considered the radiation coming from 31 evenly distributed directions (six inclinations, five azimuths and zenith direction) (see Perttunen et al. 2001). We calculated the transparency of path from an internode to each point in the upper hemisphere separately (backward ray casting). We assumed that the radiation distribution of the sky was that of a standard overcast day (Ross 1981). The light transmission in the tree crown was calculated using a voxel space approach with 0.2 m voxel box side length. We tested this against the method of pairwise comparison of shoots (Perttunen et al. 1998) used traditionally in LIGNUM and found similarity of results satisfactory (Supplementary material1).

To speed up simulations we grew only one tree and assumed that it is surrounded by a homogeneous forest that grows in the same pace with the tree (cf. Streit et al. 2016).

The course of stand density used in simulations (Supplementary material1) was taken from measured stands. The transmission of radiation in the surrounding forest was calculated as \(\exp[-0.14 \times \text{distance travelled} \times \text{leaf area density}]\). The extinction coefficient 0.14 is that of a forest consisting of Scots pine shoots (Stenberg 1996). The absorbed radiation (driving photosynthesis) in an internode from each direction was calculated as incoming radiation \(\times\) STAR \(\times\) needle area. STAR is the shoot silhouette to total area ratio (Oker-Blom and Smolander 1988). Total incoming and absorbed radiation at an internode were summed over contributions from all directions.
THE COMPONENTS TESTED

Extension growth of new shoots

The first function (onwards LIGNUM) we tried for the length growth of new shoots is the one that was originally in LIGNUM (Perttunen et al. 1996). It combines the effects of local light (q) and branching order (g)

\[ f_L^{\text{local conditions}} \times f_q(q) f_s(g) \]  

(4)

the light effect is accounted for with the aid of relative incoming radiation, q = incoming radiation / (unshaded incoming radiation). Fig. 3 shows typical shapes of functions and the parameterization of their shape as piecewise linear curves and their parameterization.

We tried as the second option the approach by Nikinmaa et al. (2003) that replaces the effect of branching order of Eq. 4 with the strength of pathway from tree base to the shoot (onwards VIGOR). We measured the strength of pathway with vigor index (v) that uses diameters of internodes along the path in the assessment of strength (Nikinmaa et al. 2003). The strength values are relative: the strongest pathway has value 1, the others have values in the range (0, 1]. In this case the local conditions are manifested as

\[ f_L^{\text{local conditions}} \begin{cases} f_q(q) f_s(v), & \text{if apical} \\ f_q(q) f_q(q) f_s(v), & \text{if lateral} \end{cases} \]  

(5)
where \( v \) is vigor index of the mother shoot and \( f_q \) is the effect of light as in Eq. 4. Lateral shoots are somewhat shorter than apical ones, the effect depends on light conditions mediated by function \( f_q \). Typical functions with parameters used in the optimization are shown in Fig. 4.

As the third alternative, we applied extended Borchert-Honda (onwards EBH) model in the way Palubicki et al. (2009) used it. Borchert and Honda (1984) proposed the model as a mechanism to regulate the extent of branching by controlling the distribution of growth resource to buds. Palubicki et al. (2009) used the amount of light received by the buds to guide the distribution of growth resource. We considered the amount of light intercepted by the shoots, that is, the radiation that drives photosynthetic production in LIGNUM. Evaluation of the EBH operates in two passes, Fig. 5. In the first pass, information about the amount of radiation that reaches the shoots with needles flows basipetally, and its cumulative values are stored within the internodes (\( Q_1, Q_2, Q_3 \) and \( Q \) in Fig. 5). In the evaluation of path strength leading to growing shoots the strength is divided in a branching point according to radiation values of the shoots. For the internodes in Fig. 5 the strength values are

\[
S = \frac{S_1 Q}{Q_1} \frac{S_2 Q}{Q_2} \frac{S_3 Q}{Q_3} \frac{S_4 Q}{Q_4} \frac{S_5 Q}{Q_5} \frac{S_6 Q}{Q_6} \frac{S_7 Q}{Q_7} \frac{S_8 Q}{Q_8} \frac{S_9 Q}{Q_9} \frac{S_{10} Q}{Q_{10}} \frac{S_{11} Q}{Q_{11}} (6)
\]

where the parameter \( \mu \) controls whether the flow of strength (\( S_0 \) in Fig. 5) is biased towards the main axis (\( \mu > 0.5 \)) or biased towards the lateral branch (\( \mu < 0.5 \)). Other number than two lateral branches are treated analogously. The strength values of growing shoots are scaled, the largest value being equal to 1. The effect of local conditions is then directly proportional to the strength values.
We allowed that, in the first three branching orders, 1-3, $\mu$ attained different values $\mu_1, \mu_2, \mu_3$.

for orders $> 3$, $\mu = \mu_3$. In the optimization, $\mu_1, \mu_2$, and $\mu_3$ were parameters.

Shoot growth in lower parts of crown

Shoot growth is controlled directly or indirectly by light in the above formulations. It was apparent in initial simulations that crown base rose often relatively fast. We implemented, using an \textit{ad hoc} function $f_B$, a mechanism that boosts (onwards BOOST) shoot growth in lower parts of crown by modifying the shoot length of Eq. 1 as

$$L = \lambda f_L(\text{local conditions}) \times f_B(z)$$ (8)

where $z$ is relative distance from crown base. Eq. 8 is applied only to side branches and lower order branches (Gravelius order $> 2$). This function may be thought to mimic e.g. the effect of the red to far-red ratio on shoot growth (cf. Ballaré and Pierik 2017). A typical function $f_B$ is shown in Fig. 6.

Production of buds
The number of lateral buds (Eq. 2) is determined as a function of the needle mass of the mother shoot. We estimated the parameter values of this function in all combinations of components.

The total number of buds (cf. Eq. 3) is

\[ N = 1 + f_N(W_f) \]  

where \( W_f \) is needle mass of mother shoot. A typical \( f_N \) and the parameters used in optimization are shown in Fig. 7.

Effect of local density in crown

We also tried the alternative in which the local density (needle area density or shoot density) affects the extension growth thus considering the available free growing space (cf. Runions et al. 2007). In the case of length growth we checked whether there was enough free space around the tip of a new shoot (Fig. 8A), henceforth SPACE. If there were shoot(s) closer than a certain distance (R) the new shoot was not created. The length of the new shoot in this case can be expressed as

\[ L. = f_L(\text{local conditions}) \times L_{tip} \]  

where \( L_{tip} \) equals 1 or 0 depending on closeness of other shoots to new shoots tip. In this case the radius R of the necessary circular free space around the shoot tip was optimized. As an alternative to the free space approach we modified the number of lateral buds a flushing bud
creates: the needle area density in its perception cone affects the number of new buds (onwards BUDVIEW). The perception cone is determined by its angle of aperture and height (Fig. 8b). In this case the number of buds is equal to

\[ N = 1 + f_N(W_f) \times f_c(a_f) \]  \hspace{1cm} (11)

where \( a_f \) is needle area density in the cone. A typical form of function \( f_c \) is shown in Fig. 8b. In addition to parameters p19, ..., p21 of the function \( f_c \), also the opening angle of the cone, \( \alpha \), was used in optimization. The height of the cone, was fixed to 0.5 m in the calculations.

COMPARISON OF SIMULATIONS AGAINST THE MEASURED TREES

We evaluated each of the 18 alternative formulations (Supplementary material2) by minimizing with respect to relevant parameter values the loss function that measured the distance between simulated and TLS trees. We measured the distance in terms of tree height \( H \) [m], total all-sided needle area \( A_f \) [m\(^2\)], needle area density \( d_f \) [m\(^{-1}\)], crown radius \( R_c \) [m], and relative distribution of internode lengths in different branching orders \( \rho_i \), unitless). This combination of indices defines a comprehensive metrics for comparison of 3D trees. The value of loss function was sum of height, needle area, needle area density, crown width and internode length distribution terms: \( L = LH + LA + LAD + CW + BD \). They were calculated as squared sums of differences of values from modeled \( (H_m, A_{fm}, d_{fm}, R_{cm}, \rho_{fm}) \) and measured \( (H, A_f, d_f, R_c, \rho_i) \) trees as follows:

\[ LH = w_H \times \sum_{t=8,16,25,32} (H_m(t) - H(t))^2 \]  \hspace{1cm} (12a)

15
where, $t$ is tree age (8, 16, 25 and 33 are ages of measured trees), $V_c$ is crown volume and $g$ is Gravelius order of internode (MacDonald 1983; stem = 1, branch = 2, etc.). The integral in Eq. 12c was evaluated with the aid of spatial discretization (voxel space, 0.1 m box size) as a sum, and $w_H$, $w_A$, $w_{AD}$, $w_{CW}$, and $w_{BD}$ are weights.

We applied three sets of values of the weights. First, we determined the values of them with the aid of initial runs so that each term had approximately equal contribution in the loss function. This was achieved with weight set STANDARD: $(w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.05, 0.002, 0.11, 10, 10)$. We varied the values of weights to study the sensitivity of the results obtained with the STANDARD set. The loss function consists of terms related to tree size ($LH$, $LA$ and $LCW$) and crown structure ($LAD$ and $BD$). We changed the relative importance of size-related and crown structure variables by factor 3. The weight set SIZE: $(w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.15, 0.006, 0.11, 30, 10)$ increased the importance of $LH$, $LA$ and $LW$, and weight set CROWN: $(w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.05, 0.002, 0.33, 10, 30)$ did the same for $LAD$ and $BD$.

We carried out the minimization with the GA package for genetic algorithms in R (Scrucca 2013). We ran the minimization until the loss function did not change noticeably any more. It

\[ LA = w_A \times \sum_{t=8,16,25,33} (A_{fm}(t) - A_f(t))^2 \]  
(12b)

\[ LAD = w_{AD} \times \sum_{t=8,16,25,33} \int_{V_c} (d_{fm}(u,t) - d_f(u,t))^2 du \]  
(12c)

\[ CW = w_{CW} \times \sum_{t=8,16,25,33} (R_{cm}(t) - R_c(t))^2 \]  
(12d)

\[ BD = w_{BD} \times \sum_{t=8,16,25,33} \sum_{g=1}^{6} (\rho_{lm}(g,t) - \rho_l(g,t))^2 \]  
(12e)
took normally one to two thousand simulation runs (20 – 40 generations with population size 50). Otherwise we used the standard settings of GA: elitism, crossover probability, and mutation probability were equal to 2, 0.8, and 0.1, respectively. The values of parameters in the minimization were restricted within plausible ranges. The parameters that were not in minimization (the set of basic parameter values of LIGNUM, Fig. 1) had always the same values taken mainly from Sievänen et al. (2008) (Supplementary material1).

We combined the model components from three baskets: shoot elongation (LIGNUM, VIGOR, or EBH), spatial control (no spatial control, SPACE or BUDVIEW) and boost of growth in lower parts of crown (BOOST or no BOOST). We ran altogether 54 minimization runs of the loss function (18 per one set of weight values). The parameters used in each minimization was a subset of all 26 parameters in fitting: $p_1, \ldots, p_{21}$ (Figs 3, 4, 6, 7, 8), $\mu_1, \mu_2, \mu_3$ (Eq. 6), $R$ (Fig. 8a), and $\alpha$ (Fig. 8b). The parameters used in minimization in each run are shown in Supplementary material2.

RESULTS

All possible combinations of components produced loss function (with weight set STANDARD) values that were not drastically different from each other. The lowest and highest loss function values were 31% apart from the mean value (loss function values are in the Supplementary material2). The lowest value of the loss function was achieved with EBH, BUDVIEW and BOOST combination (Table 1). Visualization of the simulated trees with this combination are shown in Fig. 9. EBH shoot elongation was present in all three best loss
function values (Table 1) whereas LIGNUM and VIGOR resulted in the three lowest values of it. It shows that Extended Borchert-Honda mechanism provides best fit to the data.

Evolution of tree height and needle area varied considerably between the 18 combinations of model components, Fig. 10. All combinations of components tended to produce too low needle areas at age 34 and at age 26 also too small tree heights (Fig. 10). This is probably because the target trees form only a pseudo sequence of trees from a stand: their heights may deviate from shape of height growth in one stand. The optimization of parameter values had in some cases resulted in growth trajectories with low height (Fig. 10). It happened both with LIGNUM and VIGOR shoot elongation and also with enhanced growth in lower crown (BOOST). Low height was linked with high needle area reflecting a trade-off between extension growth and needle area. The growth curves resulting from different combinations of model components show roughly similar shapes. Twists in the needle area curves are probably caused by the simplistic way, in which surrounding stand grows at the same pace with the trees (see Radiation calculations): it amplifies small fluctuations.

We take an aggregated approach in the analysis of the component combinations: we compare the mean effect of a component to values of the loss function across all component combinations in Table 2. The measure is difference of the loss function values without and with the component relative to mean loss of all combinations. EBH shoot elongation provides clearly the best fit with almost all measures: it is inferior to LIGNUM or VIGOR only in needle area density. EBH provides clearly much lower values of the loss function in other characteristics, both in the ones related to tree size and crown structure. VIGOR and LIGNUM are quite equal with some variation in parts of the loss function (Eq. 12). VIGOR is better in terms of tree height and succeeds worse with crown width than LIGNUM.
There are some trends in the mean effects of model components for assessing growing space. BUDVIEW is useful or neutral for most of the components of the loss function, only needle area is slightly negatively affected. SPACE is useful only for SIZE and tree height. SPACE enhances length growth improving the fit to height. Both BUDVIEW and SPACE decrease total needle area and they both are not useful for needle area. Overall, BUDVIEW is more useful than SPACE whereas SPACE is useful for tree height only. Promoting shoot growth, independently of radiation conditions at lower parts of the crown (BOOST) seems not to bring benefit to simulations of tree development: it is not useful for any of ALL, SIZE or CROWN. If BOOST is present, tree height does not match observations. BOOST increases allocation of resources to lower part of crown and away from growth of leader shoot. Also crown width is off target; this is because BOOST promotes growing too long branches in the lower crown.

The model components fit together in varying ways. Table 3 shows how the presence of various combinations of SPACE, BUDVIEW or BOOST affects the fit to the data of the shoot elongation formulations. LIGNUM and VIGOR benefit clearly if BUDVIEW is present. Presence of all the other combinations do not improve LIGNUM shoot elongation. VIGOR benefits also from the presence of SPACE and BUDVIEW together with BOOST, all other combinations are detrimental to the fit to the data. EBH in turn seems to benefit from BOOST in all possible combinations. On the other hand, SPACE or BUDVIEW alone do not improve the fit to the data of EBH (Table 3). The lowest values of the loss function with different shoot elongation formulations were achieved in combinations LIGNUM & BUDVIEW (0.0448), VIGOR & SPACE (0.0428), and EBH & BUDVIEW & BOOST (0.0394) showing also that the model components fit together in various way. The lowest values with LIGNUM and
VIGOR shoot extension were 13% and 9% higher than that of EBH. The combinations correspond to the highest values of usefulness in Table 3.

Adjusting parameter values when tree size is important (SIZE set of weights) or crown characteristics are important (CROWN set of weights) changes the usefulnesses slightly (Table 4, loss function values are in the Supplementary material) but does alter the general picture. The order of usefulnesses for shoot elongation is EBH, VIGOR and LIGNUM with all sets of weights. The usefulness values of shoot elongation model components with SIZE set of weights are quite close to values with STANDARD weights. The usefulness of VIGOR is increased considerably with weight set CROWN whereas that of LIGNUM is much decreased. VIGOR can thus capture the development crown structure relatively well but LIGNUM does not.

The density control (SPACE or BUDVIEW) is not useful at all with SIZE set of weights. For CROWN set of weights, the result is similar to the case STANDARD: BUDVIEW is useful, SPACE is not. It seems thus that the density control is important for capturing the crown development. BOOST is not useful or only marginally useful (with weight set CROWN).

DISCUSSION

This study is an example how segmented TLS data can be readily used in the context of a shoot-based model. This is one step in the process in which improvements in data collection technology, such as TLS, make automatic acquisition of the 3D structures increasingly feasible at various spatial scales for developing FSPMs. When forest scale 3D structural data can be
easily obtained using TLS and the methods to use them in model assessment are developed accordingly, construction and testing of forest FSPMs will be more efficient than before. It was not only the 3D structure (i.e. a collection of woody internode cylinders) of trees that we used but also information about amounts of needles in the internodes. This kind information will be increasingly available from TLS when e.g. analysis of spectral characteristics of the TLS point clouds becomes commonplace (Hakala et al. 2012).

Shoot extension based on the Extended Borchert-Honda (EBH) model worked best within LIGNUM model in this study. Modifying the number of lateral buds a flushing bud creates as a function needle area density (BUDVIEW) turned out to be a useful model component too. This result comes from an aggregated analysis in which we made comparisons across all model component combinations. Promoting shoot growth in lower parts of crown independently of light conditions (BOOST) did not improve the fit to the data with original LIGNUM (LIGNUM) or vigor index (VIGOR) formulations of shoot growth. However, BOOST worked well with EBH. Density control was useful for all shoot extension formulations, BUDVIEW for EBH and LIGNUM and SPACE for VIGOR. The lowest value of the loss function was achieved with the combination EBH, BOOST and BUDVIEW. The best combinations for LIGNUM and VIGOR employed only BUDVIEW or SPACE. This shows that the components fit together in different ways. The lowest loss function values of LIGNUM and VIGOR were around ten percent higher than that of EBH. This indicates that these shoot extension formulations are also able to account for crown dynamics fairly well with suitable set of other model components.

We tested the combinations of model components against the TLS data by minimizing the loss function with respect of relevant parameters in the functions using genetic algorithms. We did
not test whether all parameters in the combinations were identifiable. It is thus possible that the minimum value of the loss function could have been reached with many combinations of values of the parameters. We ran the minimization long enough to make sure that the minimum of the loss function had been achieved. Our aim was to screen between model components on the basis of values of the loss function and we were not particularly interested in values of the parameters (the values of parameters were constrained to reasonable ranges). We therefore deemed this approach satisfactory. As the genetic algorithms are not very prone to stuck in local optima (Scrucca 2013) we trusted that the real minimum of the loss function had indeed been found. Another problem with too many parameters with respect of data can be that the model follows a peculiarity in the data (overfitting). This could be potentially dangerous for our conclusions. However, we summarize results per function (rule of development), not per combination of them, we think that the danger of false conclusions due to overfitting is minor. Further work, for example parameter estimation of a certain combination of rules of development, would warrant using a larger data set and more sophisticated methods of analysing 3D growth models (e.g. Cournède et al 2012).

Our data of four trees is rather small as a sample. However, the data was used to analyse the crown structure of the trees with fine resolution: the TLS data was segmented to branches up to sixth branching order and the amounts of needles they carry was also evaluated. This made it possible to utilize of needle area and crown structure variables as a part of loss function that measures the difference between measured and simulated trees. Due to small number of measured trees, we did not have satisfactory information about the variances and covariances of the variables that were included into the loss function. With this limited prior information at hand we deemed that a linear combination of terms as a loss function is a logical choice. The weights were determined so that each term in the loss function was approximately equally
important. We did a simple sensitivity analysis on the basis of two groups of variables in the loss function: those related to tree size and crown structure. It shows that changes in the loss function affects the usefulnesses to some degree but does not alter the main results: the order of usefulnesses for shoot elongation (EBH, VIGOR, LIGNUM), the usefulness of density control by BUDVIEW and no or only marginal usefulness of promoting growth at lower parts of crown (BOOST).

We made the evaluation for a simplified case, in which one tree was simulated but assuming that it is surrounded by a homogeneous forest. Tree height, height of crown base etc. of the forest was the same with the simulated tree. Density of the forest was the density in which the trees had grown. This simple setting may have had its effect on results but it is difficult to assess its magnitude. Furthermore, the data of comparison has been obtained from trees taken from different forest stands. Even though we tried to make sure that growing conditions (site quality, forest management etc.) of the forests had been as accurately as possible, it is not the same as measuring one tree at different points of time. This is a common problem in forest growth studies (Pretzsch 2009, p. 35). It can be managed by sampling many trees. Due to workload of detailed TLS measurements that are suitable for segmentation done in this study, sampling of many trees was not possible in our case.

Extended Borchert-Honda model derives shoot growth on the basis of amount of light the shoots along the path from the growing shoot to tree base have intercepted. In a junction, apical and lateral branches (and shoots) are differentiated with a parameter ($\mu$ in Eq. 6). Also VIGOR shoot elongation is based on the strength of path from tree base to the shoot but the strength is evaluated with the aid of relative thicknesses of the branches. VIGOR method thus relies on past performance (accumulated growth) in evaluating the path strength whereas EBH method
uses the current condition (light) in assessing the strength. Our results indicate that the growth based on current conditions is more suitable. The original LIGNUM shoot elongation considers only the branching order as the “path strength” factor. It is therefore understandable that it did not stand out. Both VIGOR and LIGNUM methods make use also of the local light conditions (Eqs 3 and 4). The EBH method lumps both effects of light and crown structure along the path to one factor (function) that uses only one parameter — dependent on axis order in our case — that determines relative priorities of apical and lateral directions. It could be that this difference in the effect of light (local vs along a path) caused that promoting shoot growth in the lower parts of crown (BOOST) was useful for EBH but neither for LIGNUM nor VIGOR. Attractive is that EBH employs a low number of parameters, three versus five in LIGNUM and eight in VIGOR. In the best fit case, the values of the EBH parameters were 0.614, 0.615 and 0.517 for branches, side branches and higher order branches, respectively. These values correspond to a rather strong apical preference in the first two orders a lower one in the higher order branches.

We demonstrated how segmented TLS data can be used in the context of a shoot-based model to select model components. We could sort out the importance of the components for the model. Due to the small size of the data as a pseudo growth sequence, applying the distance metric between data and simulations as a simple linear combination and the limited sensitivity analysis, the results need to be regarded as preliminary. The study demonstrates the applicability of TLS data as a phenotyping tool that can readily operate in model evaluation for structural characteristics such as tree height, total needle area, spatial distribution of needle area, crown width, and shoot lengths of different branching orders at different tree age.

595 LITERATURE CITED


FIGURE CAPTIONS

Figure 1. Principle of testing of different combinations of model components. The minimization of the loss function (Eq. 12) revealed how well the combination of the components fits the data. It was defined as a linear combination of squared error terms between simulated trees and those segmented from TLS data (Eq. 12). On the right side, it is shown as an example how the functions of shoot elongation of the original LIGNUM formulation
(Perttunen et al. 1996) (Fig. 2) were parameterized (as piecewise linear curves) for minimization: parameters p1, ..., p5. Other functions were parameterized in a similar manner.

Figure 2. The principle of growth in LIGNUM model: a bud (at the end of a shoot) produces a new growth unit consisting of a shoot with length L and three buds (apical one and two lateral ones) during one growth cycle.

Figure 3. Typical shapes of functions $f_q$ (left panel) and $f_g$ (right panel) of Eq. 4 controlling shoot length in the formulation according to Perttunen et al. (1996). $q$ is relative incoming radiation = incoming radiation / (unshaded value), $g$ is Gravelius order of the mother shoot (MacDonald 1983; stem = 1, branch = 2, etc.). Shown are the parameters p1, ..., p5 that control the shape of the functions and were used in the optimization.

Figure 4. Typical vigor index ($f_v$) and apical ($f_a$) functions. $v$ is vigor index (Nikinmaa et al. 2003) and $q$ is relative incoming radiation = incoming radiation / (unshaded value). Indicated are the parameters p6, ..., p11 that were used in the optimization.

Figure 5. The principle of EBH calculation. The intercepted radiation (Q values) are first accumulated basipetally, thus $Q = Q_1 + Q_2 + Q_3$. The strength values (S) flow acropetally according to Eq. 6.

Figure 6. A typical shape of function $f_0$ of Eq. 8. It is determined by parameters p12, p13, and p14 that were used in the optimization.
Figure 7. A typical function \( f_N (W_f) \) for number of lateral buds as a function of needle mass of mother shoot, \( W_f \). Shown are also parameters \( p15, \ldots, p18 \) that determine its shape and were used in the optimization.

Figure 8. A: Requirement of free growing space of radius R around the tip of a new shoot: this one cannot grow (\( \chi_{tip} = 0 \)) since other shoot is inside the growing space, B: Evaluation of needle area density in a cone with \( \alpha/2 \) half angle with maximum distance D, and C: a typical function reducing the number of lateral buds (Eq. 11) as a function needle area density in the cone of perception of a bud (c). D was fixed to 0.5 m the optimizations.

Figure 9. Scanned (left) and best fit trees (right) (combination EBH & BUDVIEW & BOOST) at ages 8, 16, 25 and 33 years, heights are those of the scanned trees.

Figure 10. A: Tree heights (solid lines) and heights of crown base (dashed lines) of best fit runs of all component combinations versus values of target trees (lines with circles). B: The same for needle area. Red (LIGNUM & BOOST), blue (VIGOR & BOOST), green (VIGOR & SPACE & BOOST) and cyan (VIGOR & BUDVIEW) colors mark runs that have distinctively different evolutions of height or needle area in comparison to the rest of runs.
Table 1. The combinations that produce three lowest and highest values of the loss function with weight set STANDARD: \((w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.05, 0.002, 0.11, 10, 10)\).

<table>
<thead>
<tr>
<th></th>
<th>Three lowest values</th>
<th>Three highest values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loss function value</td>
<td>0.0394, 0.0396, 0.0427</td>
<td>0.0572, 0.0647, 0.0703</td>
</tr>
<tr>
<td>Combination</td>
<td>EBH, BUDVIEW, BOOST</td>
<td>EBH, SPACE, BOOST</td>
</tr>
<tr>
<td></td>
<td>EBH, VIGOR, LIGNUM, BOOST</td>
<td>EBH, VIGOR, SPACE, BOOST</td>
</tr>
</tbody>
</table>

Table 2. Usefulness of model components in percent values for the combined loss function (ALL), combination of terms related to tree size (SIZE) and crown characteristics (CROWN) as well as for all components of Eq. 12. Positive values mean that loss function values are smaller on average when the component is in use and negative values the opposite. LIGNUM, VIGOR, EBH and BOOST affect shoot elongation and SPACE and BOOST affect growth through local density. Weight set STANDARD was used in the loss function \((w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.05, 0.002, 0.11, 10, 10)\).

<table>
<thead>
<tr>
<th></th>
<th>Shoot elongation</th>
<th>Density control</th>
<th>Growth of lower crown</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LIGNUM</td>
<td>VIGOR</td>
<td>EBH</td>
</tr>
<tr>
<td>ALL²</td>
<td>-12</td>
<td>-7</td>
<td>19</td>
</tr>
<tr>
<td>SIZE²</td>
<td>-22</td>
<td>-11</td>
<td>33</td>
</tr>
</tbody>
</table>
Table 3. Usefulness\(^1\) of combinations of SPACE, BUDVIEW and BOOST in per cent values in conjunction with shoot elongation formulations LIGNUM, VIGOR and EBH. Note that usefulness is defined here other way than in Table 2. Weight set STANDARD was used in the loss function \(((w_H, w_A, w_{AD}, w_{CW}, w_{BD}) = (0.05, 0.002, 0.11, 10, 10))\).

<table>
<thead>
<tr>
<th>Combination</th>
<th>LIGNUM</th>
<th>VIGOR</th>
<th>EBH</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPACE</td>
<td>-20</td>
<td>21</td>
<td>-15</td>
</tr>
<tr>
<td>BUDVIEW</td>
<td>19</td>
<td>17</td>
<td>-11</td>
</tr>
<tr>
<td>BOOST</td>
<td>-20</td>
<td>-7</td>
<td>8</td>
</tr>
<tr>
<td>SPACE &amp; BOOST</td>
<td>-1</td>
<td>-33</td>
<td>2</td>
</tr>
<tr>
<td>BUDVIEW &amp; BOOST</td>
<td>-2</td>
<td>9</td>
<td>8</td>
</tr>
</tbody>
</table>

\(^1\) Defined as \((\text{mean loss without component} - \text{mean loss with component}) / \text{mean loss of all combinations}\)

\(^2\) \text{ALL} = LH + LA + LAD + CW + BD (Eq. 12)

\(^3\) \text{SIZE} = LH + LA (Eq. 12)

\(^4\) \text{CROWN} = LAD + CW + BD (Eq. 12)
Defined as (loss with LIGNUM, VIGOR or EBH only - loss with combination) / mean loss of all combinations

Table 4. Usefulness of model components in percent values for the combined loss function (ALL = LH + LA + LAD + BD + CW) with weight sets SIZE and CROWN. See Table 2 for explanation of symbols.

<table>
<thead>
<tr>
<th>Shoot elongation</th>
<th>Density control</th>
<th>Growth of lower crown</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIGNUM</td>
<td>VIGOR</td>
<td>EBH</td>
</tr>
<tr>
<td>Weight set SIZE: ($w_{H}$, $w_{A}$, $w_{AD}$, $w_{CW}$, $w_{BD}$) = (0.15, 0.006, 0.11, 30, 10)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>-14</td>
<td>-7</td>
</tr>
<tr>
<td>Weight set CROWN: ($w_{H}$, $w_{A}$, $w_{AD}$, $w_{CW}$, $w_{BD}$) = (0.05, 0.002, 0.33, 10, 30)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>-32</td>
<td>13</td>
</tr>
</tbody>
</table>

SUPPLEMENTARY MATERIAL

File1: Supplementary material1

Comparison of foliage mass to biomass equation

The main parameter values applied in the simulations

Comparison of voxel-based and pairwise light calculation

Stand density in simulations
Table 1. Summary of tested model components and parameters in the optimization runs. STANDARD set of weights

Table 2. Values of loss function (TOTAL) and its components in the minimization runs. STANDARD set of weights

Table 3. Values of loss function (TOTAL) and its components in the minimization runs. SIZE set of weights

Table 4. Values of loss function (TOTAL) and its components in the minimization runs. CROWN set of weights
LIGNUM
Unmodified with basic parameter values

Modified LIGNUM, parameters only of tested model components in estimation:
$p_1, \ldots, p_n$

TLS Data

Genetic algorithm:
minimization of loss function using
$p_1, \ldots, p_n$

Parameters in tested model components

$fg(q)$

$q$, rad. rel. to unshaded

$p_1$, $p_2$

Example functions

$fg(g)$

$g$, Grav. order (stem = 1)

$p_3$, $p_4$, $p_5$

Other parameters, functions ...

Result: loss function value with best fit parameter values
= how well these components work,
altogether 18 combinations of components tested