# An Application of Process-Based Modelling to the Development of Branchiness in Scots Pine

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A process-oriented tree and stand growth model is extended to be applicable to the analysis of timber quality, and how it is influenced by silvicultural treatments. The tree-level model is based on the carbon balance and it incorporates the dynamics of five biomass variables as well as tree height, crown base, and breast height diameter. Allocation of carbon is based on the conservation of structural relationships, in particular, the pipe model. The pipe-model relationships are extended to the whorl level, but in order to avoid a 3-dimensional model of entire crown structure, the branch module is largely stochastic and aggregated. In model construction, a top-down hierarchy is used where at each step down, the upper level sets constraints for the lower level. Some advantages of this approach are model consistency and efficiency of calculations, but probably at the cost of reduced flexibility. The detailed structure related with the branching module is preliminary and will be improved when more data becomes available. Model parameters are identified for Scots pine in Southern Finland, and example simulations are carried out to compare the development of quality characteristics in different stocking densities.

**Keywords** carbon balance, pipe model, simulation, whorl, branching, timber quality **Authors' addresses** *Mäkelä* and *Vanninen*, Department of Forest Ecology, P.O. Box 24 (Unioninkatu 40), FI-00014 University of Helsinki, Finland; *Ikonen*, Faculty of Forestry, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland **E-mail** annikki.makela@helsinki.fi **Received** 24 February 1997 **Accepted** 20 August 1997

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# **1** Introduction

The strength and appearance of a piece of timber determines its quality and end use (e.g. boards, studs, pieces of furniture). These factors largely depend on stem structure. Some of the focal indicators are the size and type of branches, the amount of heartwood and sapwood, and the distribution of annual rings inside the marketable log (Thörnqvist 1994). In order to produce good quality products, it is important for the forest manager (1) to understand how silvicultural measures affect the development of stem structure, and (2) to be able to predict the structure of a certain stem, given its outward appearance and some information concerning its growth history (Kärkkäinen 1986).

Conventionally, prediction of timber quality has been based on quality indicators, such as "the diameter of the largest live knot", "the height of the lowest dead branch", or "mean annual ring width at breast height" (e.g. Heiskanen 1954). These measurable indicators have been used in statistical analysis to produce estimates of, e.g., the general knottiness of the products, or the average wood density (e.g. Kärkkäinen 1986, Johansson 1992). Recently, the development of measuring and computing technology has vastly improved the possibilities of predicting timber quality: three-dimensional structural models are being developed where x-ray techniques and scanning of logs is used for data acquisition (Björklund 1994, Tian and Cown 1996), and the virtual logs are "sawn" by the computer in order to produce the statistics of the quality distribution of some typical logs (Usenius 1996). However, many of these methods seem to assume a given structure of the logs, while the question of growing the log is still largely unresolved (cf. Houllier et al. 1995).

The recently emerged approach of 3-dimensional structural-functional models incorporating detailed branching patterns and other structural characteristics seems an obvious tool for the analysis of the development of stem structure (Kellomäki and Kurttio 1991, Jaeger and de Reffye 1992, Kurth 1994, Perttunen et al. 1996). Some developments towards the quality application have already been initiated (Kellomäki and Strandman 1995). However, these models are still under development, and a number of questions need to be solved before efficient application. Furthermore, until now the computational capacity has constrained the approach to a few trees at a time, restricting for instance the analysis of the effects of silvicultural measures.

A more aggregated functional-structural approach is provided by the more traditional process-oriented tree and stand growth models. While these models started off as descriptions of tree growth in terms of their carbon metabolism, the need to understand tree interactions and carbon allocation has lead to an extensive analysis of the structural constraints governing tree form (Marklund 1988, Valentine 1988, Nikinmaa 1992, Sievänen 1993, West 1993, Deleuze and Houllier 1995, Valentine et al. 1994, Vanninen et al. 1996).). These include relationships such as the pipe model (Shinozaki et al. 1964) or Pressler's rule, which are apt for a detailed analvsis of sapwood and heartwood taper in both stems and branches, and models of the development of the crown base (Valentine et al. 1994, Mäkelä 1997), essential for describing the overall branchiness. Assuming that the distribution of individual branches inside the stem could be embedded in this approach, it could conceivably provide a basis for a physiologically based timber quality model readily applicable to wholestand and long-term analysis.

The present study aims at constructing a model for timber quality applications, which makes use of the tree and stand level performance of the process-oriented approach, but simultaneously, extends the structural description to characteristics necessary for the quality assessment. Predominantly, this means incorporating the population dynamics of branches in the model. The model construction starts off from a processoriented model defined at the tree level (Mäkelä 1997), then works towards greater detail by means of sub-models for whorls and branches. In order to fully utilize the tree level model, a top-down hierarchy is used where at each step down, the upper level sets constraints for the lower level.

In the extension of the model, the processoriented approach is applied down to the whorl level. Hence, in accordance with the whole-tree model (Mäkelä 1997), the description of whorl growth is based on the pipe theory. However, in order to avoid a 3-dimensional model of entire crown structure, the branch module is largely stochastic. This means that a lot of data on branching are required for model construction, in addition to the data for model testing.

The objective of this paper is to review and test the hierarchical structure of the present timber quality model, while the parameter values, especially those related with the branching module, should be regarded as preliminary. Model parameters are identified for Scots pine in Southern Finland, and example simulations are carried out to compare the development of quality characteristics in different stocking densities.

**2 Model Structure** 

The development of the present timber quality model, PipeQual, starts off from the processbased CROBAS (CROwn BASe) model developed earlier (Mäkelä 1997). CROBAS describes tree growth in terms of five biomass variables (foliage, fine roots, branch sapwood, stem sapwood, and transport root sapwood) and three dimensional variables (crown length, height of crown base, and sapwood area at crown base). The aboveground biomass variables are further divided into whorls by the submodel WHORL, and whorls are divided into branches by the submodel BRANCH. The model, therefore, employs a top-down approach where the more simple model sets the constraints for the more detailed structure (Fig. 1). In the following, the stand level model is reviewed as regards its main assumptions (those interested in the detailed model structure are referred to Mäkelä 1997), while a more profound account is given for the submodels added, and the interface between the modules.

## 2.1 CROBAS

CROBAS is a carbon balance model describing the dynamics of foliage, branches, fine roots, coarse roots, stem sapwood, and stem heartwood. It also provides the development of tree height, crown base, and breast height diameter. It is based on the growth of an individual tree, and a stand is formed of size classes of trees. Annual tree growth is computed as the difference between photosynthesis and respiration, and net growth of each biomass compartment is obtained as the difference between gross growth and senescence. The allocation of gross growth be-



Fig. 1. Structure of PipeQual.

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tween the biomass compartments is based on three structural relationships: a constant ratio between sapwood area at crown base and foliage mass (pipe model), an environment-dependent ratio between fine root and foliage mass (functional balance), and an allometric relationship between crown surface area and foliage mass (balance between self-shading and consumption of carbon in the formation of branches). Additionally, a constant ratio between crown length and average branch length is assumed.

As a result, tree structure is fixed as regards the ratio of crown length to foliage, fine roots to foliage, stem basal area to foliage, and average branch and coarse root length to crown length. The remaining structural characteristic to be determined independently is the height of the crown base, which does not seem to follow any structural rule, but is dependent on the competitive status of the tree. The dynamics of crown base are computed from the assumption that crown rise occurs when the crowns touch each other, i.e., when crown coverage is large.

In order to determine allocation of growth, the dimensional relationships have to be converted into biomass ratios. This can be done if we assume constant form factors of sapwood and heartwood in branches, coarse roots, and in the stem sections above and below crown base. Similar form factors have to be assumed for the part of sapwood that is converted into heartwood. After these conversions, the allocation coefficients are computed so as to maintain the structural relationships.

At stand level, the trees interact through shading, which affects photosynthesis, and through crown coverage, which, apart from the crown rise mentioned above, controls tree mortality: the higher the crown coverage, the faster the rate of mortality. Crown coverage is defined by size class, including all trees with crown base not below the subject tree.

## 2.2 WHORL

While CROBAS computes the development of the biomass variables and dimensional variables in continuous time, WHORL samples the state variables each year and distributes foliage biomass, sapwood area and branch length to each live whorl. The location of each whorl is obtained from the annual height growth and stored consecutively. The procedure carried out by WHORL is derived from the pipe model theory, assuming a certain shape of the vertical foliage distribution, and it follows the model by Nikinmaa (1992).

#### 2.2.1 Foliage and Sapwood Area

On the basis of empirical findings (e.g. Hari et al. 1982), the vertical foliage biomass distribution can be described using the  $\beta$ -function, with 2 parameters determining the shape. Foliage density at relative crown depth *x*,  $w_f(x)$ , is given as

$$w_f(x) = w_0 x^p (1-x)^q \tag{1}$$

where  $w_0$  is a scaling factor. It is calculated by requiring that the integral of the distribution equals total foliage mass, input from the treelevel module. Foliage mass in each individual whorl is computed by integrating the vertical distribution from the top to the base of the whorl.

It is assumed that in each whorl, *i*, branch sapwood area,  $A_{bi}$ , is proportional to the foliage mass,  $W_{fi}$ , in that whorl. In accordance with empirical observation, the coefficient of proportionality,  $a_b$ , is allowed to vary with whorl age, *i*:

$$A_{bi} = a_b(i) \ W_{fi} \tag{2}$$

Similarly, the sapwood area of the stem at the base of whorl i,  $A_{si}$ , is assumed to be proportional to the foliage mass above the whorl:

$$A_{si} = a_s(i) \sum_{k=1}^{i} W_{fi} \tag{3}$$

Again, the coefficient of proportionality is allowed to vary with whorl age. The following functional form was used for both  $a_b$  and  $a_s$ :

$$a(i) = \frac{i_0 + i}{a_0 i} \tag{4}$$

The parameters were such that in the top whorl, the ratio of sapwood to foliage was about twice as large as its minimum value, then reduced rapidly.

#### 2.2.2 Branch Length

Based on empirical analysis, the ratio of branch length to canopy depth at the branch base is largest in the top of the crown, and gradually levels off deeper in the canopy. This is consistent with the observation that branch growth slows down exponentially with time (Kellomäki and Kurttio, 1991, Deleuze et al. 1996). The following equation is used for branch length at whorl *i*,  $h_b(i)$ :

$$h_{b}(i) = \gamma_{b0} \left( 1 - \frac{a_{1}i}{a_{2} + i} \right) h_{c}(i)$$
(5)

where  $\gamma_{b0}$ ,  $a_1$ , and  $a_2$  are parameters and  $h_c(i)$  is canopy depth at whorl *i*.

### 2.2.3 Formation of Heartwood

Sapwood turnover in each whorl is driven by (1)aging and (2) foliage shedding. Aging is simply assumed to cause the turnover of a fixed percentage of sapwood each year. Turnover caused by foliage shedding occurs when current sapwood area is smaller than the previous year's sapwood area in a whorl. In the model, this is a consequence of the crown moving upwards. In the top of the crown, sapwood area increases, while in the lower part, foliage and sapwood in each whorl decrease from year to year. This is reflected in the stem, such that a corresponding heartwood turnover occurs from the subject whorl down to the base of the stem. In the pipe model terminology, this turnover represents the disused pipes that become disconnected from the foliage.

### 2.3 Interface between Tree and Whorl Calculations

In CROBAS, part of tree structure is described through constant form parameters, such as the ratio of average branch length to crown length. Owing to its more detailed structure, WHORL provides a means for calculating these parameters explicitly. Furthermore, because some aspects of the structure are dynamic, these form parameters are not necessarily constant from year to year. For consistency between the two modules, the combined PipeQual model uses WHORL to update the form parameters required by CROBAS each year, then applies the updated parameter set for the calculations of the subsequent growing season.

The interactive parameters are related to (1) the ratio of foliage mass to sapwood area at crown base, (2) average branch length, (3) sapwood form in the woody parts, (4) form of senescent sapwood, and (5) sapwood senescence rate due to the rise of the crown. The method of updating the parameters is the same for each parameter, and it involves calculating the "true" value of the parameter in WHORL, then estimating it in terms of the equations used by CRO-BAS. For example, the volume of sapwood in the stem above the crown base,  $V_c^c$ , is defined in CROBAS as the product of crown length,  $H_c$ , sapwood area at crown base,  $A_s$ , and the form coefficient,  $\varphi_c$ .

 $V_c{}^C = \varphi_c H_c A_s \tag{6}$ 

In WHORL, the corresponding volume of sapwood,  $V_c^w$ , is computed whorl by whorl, and  $\varphi_c$ is evaluated from this using the state variables of CROBAS:

$$\varphi_c = \frac{V_c^W}{H_c A_s} \tag{7}$$

The interaction of the two modules causes a slight discontinuity in CROBAS at the beginning of each year. However, it turns out that all the parameters determined in this way are very conservative, and the use of the method outlined above, therefore, seems justified.

## 2.4 BRANCH

The submodel BRANCH is the next step down in the hierarchy of models incorporated in Pipe-Qual. BRANCH takes the whorl-based information from WHORL as input, then proceeds to calculate information concerning individual branches in each whorl. BRANCH is a statistical model based on empirical results. In the current version of PipeQual, the components of

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BRANCH are preliminary. Extensive data on branch dynamics in Scots pine are being collected, and the submodel will be improved as more empirical measurements become available.

The procedure for calculations in the BRANCH module is divided into new branches, which are added to the top of the tree, and updating old branches, which can either grow or die. These procedures are described below.

#### 2.4.1 Emergence of New Branches

For the formation of new branches, the BRANCH module uses input information from WHORL concerning foliage mass, sapwood area and internode length in the top whorl. The output produced by BRANCH comprises the number of branches, their size distribution, and their compass angles and insertion angles.

In the current version, the number of new branches is based on leader length,  $\Delta h$ , with a random component. In a statistical analysis of the number of branches attached to a whorl, it is important to note that the number of branches is always positive, excluding the use of methods based on the normal distribution. In this study, a logistic function was used for computing the probability that the number of branches in a new whorl is greater than n:

$$P\{n_{br} > n\} = f_n(\Delta h) = 1/(1 + \exp(a_n + b \,\Delta h))$$
(8)

The parameters  $a_n$  and b (n = 0,...,10) were preliminarily estimated from the 10 topmost whorls (where branch death was assumed negligible) in 8 dominant trees of different ages. The trees have been previously described by Vanninen et al. (1996).

In accordance with this model,  $f_n$  is evaluated for each n, a random number x is drawn from a uniform distribution between 0 and 1, and the value of  $f_n$  is compared with this. Branch number  $n_{br}$  is chosen such that  $f_{nbr} < x < f_{nbr-1}$ .

The size distribution of the new branches is generated assuming that the standard deviation of branch cross-sectional area  $(s_A)$  is a function of the mean cross-sectional area  $(A_m)$ . Based on the same data set as above, the following preliminary model was used

(9)

$$s_A = A_m^{1.07}$$

Branch sizes are drawn from a normal distribution with mean  $A_m$  and standard deviation  $s_A$ , and the final sizes are adjusted to give the correct total size with the proportions as drawn at random.

The branches are located at compass angles with even intervals over the cross-section of the stem, with a shift of 30° clockwise between the first branches of each consecutive year. Branch insertion angle of branch *j* is initially set to  $45^{\circ} + \delta_j$ , where  $\delta_j$  is a normally distributed random variable with mean 0 and standard deviation of 5°.

#### 2.4.2 Development of Branches

The development of whorl branches comprises individual branch growth, the possible death and shedding of branches, and the change of the insertion angle. These processes are accounted for once a year when the state of the branches is updated. The input from the WHORL level to the older branches consists of information on total sapwood and heartwood area of each whorl.

First, the number of branches in each whorl is updated using a stochastic model for branch death. This assumes that the probability of death, k (yr<sup>-1</sup>), is independent of branch age. This parameter was estimated from the 8 trees mentioned above through the model

$$N_i = N_0(\Delta h) \ e^{-ki} \tag{10}$$

where  $N_i$  is the number of branches in a whorl of age *i* and  $N_0(\Delta h)$  is that in a new whorl with leader length  $\Delta h$ . A linear model was used for the dependence of  $N_0$  on  $\Delta h$ . Based on the statistical analysis, the value k = 0.015 was used in the model runs. Further, within each whorl, the probability of branch death was set proportional to branch size, with the constraint that the total probability of death in the whorl is 0.015N.

The whole whorl dies when the crown base (from CROBAS) rises above it. Dead branches are shed after a certain time below the live crown. As young trees seem to shed dead branches as early as after about 8 years (Kellomäki et al. 1992), but older trees seem to retain theirs for a longer time, a preliminary model was used where the time before shedding depends linearly on tree age. No branch shedding is assumed to occur inside the crown.

The insertion angle (the angle from branch to stem *above* the whorl) of branches is assumed to increase with whorl age, *i*, following a saturating function  $\alpha(i)$ :

$$\alpha(i) = 45^{\circ} + \frac{90^{\circ}(i-1)}{30^{\circ} + (i-1)}$$
(11)

The initial random component remains throughout the life of the branch, such that the actual insertion angle is  $\alpha(i) + \delta_i$ .

The growth of the individual branches is based on the whorl level information. If no branches die in a whorl, the new sizes are obtained by distributing the new total sapwood and heartwood in the same proportions as previously. If a branch dies, the new total sapwood is distributed between the remaining branches, again, in the same proportions as the branches were before, but the dying branch is subtracted from the heartwood of the whorl.

## **2.5 Acclimations**

Tree structure acclimatizes to different local environments. At present, PipeQual incorporates three acclimations of structure, two of them with respect to light climate and one with respect to the nutrient balance. Firstly, the parameters of the foliage distribution function change according to the local light climate, measured as the crown coverage (specific to each size class). In full light, maximum foliage mass occurs at a lower level than in shade. The allometric ratio between foliage mass and crown surface area also changes with light conditions, the crowns being denser in full light and sparser in shade (Mäkelä and Vanninen, unpublished data). Thirdly, the ratio of foliage to fine roots is regulated by the nutrient requirement when recycling of nutrients from senescent material is taken into account. This leads to larger root: foliage ratios in young trees growing fast, and respectively, lower ratios in established, old trees.

# **3 Model Runs**

The parameters of the model have been estimated for Scots pine growing in Southern Finland on the fairly fertile Myrtillus type (Cajander 1949) growth site (Mäkelä 1997, Vanninen et al. 1996, Kellomäki et al. 1992). The parameters were chosen based on their biological/physical definition, some of them through guesswork, but no model fitting against data was carried out. A comprehensive list of the parameter values in CROBAS is given by Mäkelä (1997). There are some changes to these due to the inclusion of vertical variation in the parameters related to crown structure (Section 2.2), the parameters related to the branching module (Section 2.3), and the parameters due to the adaptation processes (Section 2.4).

Model runs were designed to compare differences between (1) stocking densities and (2) tree size classes in one stand. Because of the structural relationships, the initial state can be computed from tree height and crown ratio only. In addition, initial age has to be provided for determining the initial number of whorls. For stand level calculations, the number of size classes and the stocking of each size class must be provided. Three different initial densities were studied, with no thinnings. Stand configurations were such that the densest stand had the most variety (5 size classes), and the sparsest stand had the least variety (3 size classes). In each case, the tallest trees were initially at breast height (Table 1).

The CROBAS model has previously been tested against tree and stand growth data (Mäkelä 1997). No data has yet been available for testing the WHORL and BRANCH modules. The following describes some model results involving the new detailed structure.

Table 1. Initial state.

Density (1/ha)	Nr size classes	Smallest trees, height (m)
2000	3	0.8
4000	4	0.5
7500	5	0.2



**Fig. 2.** Comparison of branch biomass development in dominant (medium line) and suppressed (thin line) trees of the dense stand and dominant (thick line) trees of the sparse stand.



Fig. 3. Comparison of the total number of live branches (a) and the diameter of thickest live branch (b) in dominant trees of the sparse stand (thick line) and dominant (medium line) and suppressed (thin line) trees of the dense stand.

# 3.1 Comparison of Simulated Stands and Trees

Perhaps due to the stand configurations chosen, the largest tree classes, or dominant trees, developed in a very similar manner in all the simulated stands, and the differences between the stands were due to the smaller size classes. In the densest stand, the smallest size class was completely eliminated by stand age 40 years. As a rule, mortality was largest in the smallest tree classes. The sparsest stand developed slightly more foliage and branches but less stem volume than the other stands, due to larger crowns and marginally slower height growth than in the denser stands.

The greatest differences between the different tree classes were found in variables describing branchiness. Expectedly, total branch biomass



Fig. 4. Comparison of taper curves of stem and heartwood in dominant trees of the sparse (thick line) and the dense stand (dashed line).

was greatest in the dominant trees of the sparse stand and smallest in the suppressed trees of the dense stand (Fig. 2). Dominant height growth was largely unaffected by stand density, but reduced by suppressed social position, while the opposite was true of the height of the crown base. The total number of live branches was closely related to the lenght of the live crown, being largest in the dominant trees of the sparse stand and smallest in the suppressed trees of the dense stand (Fig. 3a). The diameter of the largest live branch followed a similar pattern (3b). The non-smooth development of the branch characteristics is due to the random effects in branch growth and mortality.

The simulated stem taper was largest in the dominant trees of the sparse stand, while the suppressed trees were clearly more slender than the more dominant ones. The simulated heartwood content was greatest in the suppressed trees of the dense stand and smallest in the dominant trees of the sparse stand (Fig. 4). According to Fig. 4, the model probably overestimates the amount of heartwood proportion to some extent.

### 3.2 Three-dimensional Stem Structure

In order to demonstrate the simulated three-dimensional structure of the stem, the model has been linked to a sawing simulator which cuts up the simulated log into boards according to specifications given by the user, and computes the value of the boards on the basis of the occurrence and size of dead and live knots (Väisänen et al. 1989). This connection is illustrated in a dominant tree from the medium stand (Fig. 5).

# **4** Discussion

The process-based approach utilized in this study has been motivated by the idea of causality in model structure (e.g. Sharpe 1990); a model presenting the biological entities and their connections as they are in the real system is supposed to represent the behaviour of the system in a more general way than a statistical model. However, no model can be entirely causal, but empirical elements and aggregation are necessary in some structures or parameters (e.g. Korzukhin et al. 1996). The causality of the present model is due to its carbon balance structure, allowing for the analysis of growth through the effects of environmental factors on the physiological processes affecting the carbon metabolism. In the present version of the model, this is demonstrated in the differences in growth pattern between tree size classes and stands of different stocking, but the



Fig. 5. An example of the application of the model in a sawing simulator. The left-hand picture shows the stem of a simulated dominant tree from the medium stand at the age of 100 years. The zones of sound and dry knots and the knotless zone are shown. The middle part of the picture shows a sawing of the butt log into boards of standard size, and the right-hand picture illustrates two indvidual pieces. Piece 6 from the outer part of the log is shorter but knotless, while piece 7 near the pith has mainly sound knots.

model structure could easily incorporate other effects, such as inter-seasonal variation.

However, the causal structure only goes down to the level of whorls, while the branch module considers the probable distribution of the branches in one whorl of given size. This means that we cannot causally follow the development of an individual branch in the tree. The only way to overcome this would be to look at the individual branches in the 3-dimensional space and their interactions with other branches and trees, such that their growth and senescence would be regulated by their metabolic balance in competion with other branches. This was not considered practical at this stage, because of two reasons. Firstly, the application to timber quality only directly requires stem structure instead of crown structure. Secondly, from the point of view of model construction and computational limits,

there seems to be a trade-off between individualtree and stand level complexity. A previous quality model that started off from individual branches only considered the mean tree of a stand (Väisänen et al. 1989), and the shoot-level models only simulate a few trees at a time (Kurth 1994, Perttunen et al. 1996, Kellomäki and Strandman 1995).

The aggregated approach means that variation – which is large in real logs – has to be genererated through stochastic processes. In the present model, the stochastic component is essential for the number of new shoots in the leader, the size distribution of the branches, and the death of branches inside the live crown. It would be an interesting question to study with the aid of the 3-dimensional shoot-level tree models how much of this variation could be produced simply through inter-branch interactions in a deterministic approach. Intuitively, it would seem unlikely that stochastic elements could be entirely avoided, at least as regards the emergence and initial size distribution of new shoots.

The aim of the present preliminary version of PipeQual was to complete the structure of the model, such that more empirical information can be fed in as soon as it becomes available. The main task in the near future will be the improvement of the BRANCH module. One of the most challenging questions is probably the development of the size distribution of the branches in a whorl, such that the temporal development of the individual branches remains consistent. Measurements are being taken on all the compartments included in BRANCH in a number of stocking trials of different ages.

Allthough the model includes different size classes and seems to produce reasonable size distributions, there are unresolved questions as regards the competition between trees. The main driving force of competition in the present version of PipeQual is crown coverage, i.e. the average spacing between the trees. It would be desirable to connect the competition for space closer to competition for light. This calls for an improvement of the shading and photosynthesis models of PipeQual.

It has become apparent from the simulations that the acclimation processes are crucial for model behaviour. One impact of all the acclimations has been to slow down height growth in full light, and similarly, to enhance it in low light. The results seem to be consistent with observation. However, only a few acclimations have been included in the present version. The measurements will be utilized in order to analyse the acclimation processes more thoroughly from the perspective of model building.

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nted through stochastic processes. In the present nodel, the stochastic component is essential for he number of new shorts in the leader, the size listribution of the branches, and the death of tranches inside the live grown. It would be an interesting question to study with the aid of the i-dimensional short-level tree models how much of this variation could be produced simply brough inter-branch interactions in a determin-





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