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Modelling canopy growth and steady-state leaf area index in an aspen stand

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Abstract – We developed a canopy growth model to analyse the importance of different structural properties in the formation of equilibrium leaf area index in a *Populus tremula* canopy. The canopy was divided into vertical layers with the growth and structural parameters of each layer dependent on light conditions. Horizontal heterogeneity was considered through clumping parameter. The principle growth parameters considered were long shoot bifurcation ratio, number of short shoots produced by one-year-old long shoot, short shoot survival and number of leaves per shoot. Parameter values and relationships are based on field measurements of an aspen stand in Järvselja, Estonia. Depending on initial conditions, leaf area index reaches the steady state in 5–20 years. The value of initial density of long shoots affects the time needed to achieve equilibrium but has little influence on final LAI value. The most influential parameters in predicting the final LAI are thus of the relationship between long shoot bifurcation ratio and light.

canopy / growth / model / *Populus tremula* / leaf area index / shoot bifurcation

Résumé – Modélisation de la croissance et de l'indice de surface foliaire (LAI) dans un peuplement de tremble. Nous avons développé un modèle de croissance de la canopée pour analyser l'importance de différentes propriétés structurelles dans la formation de l'indice foliaire (LAI) dans une canopée de *Populus tremula*. La canopée a été divisée en couches verticales dans lesquelles la croissance et les paramètres structuraux de chaque couche dépendent des conditions lumineuses. L'hétérogénéité horizontale a été prise en compte au travers de paramètres regroupés. Les principaux paramètres de croissance pris en compte sont : rapport de fourchaison, le nombre de pousses courtes produites sur les pousses longues de l'année, le nombre de rameaux courts survivants et le nombre de feuilles par pousse. Les valeurs des paramètres et les relations sont basées sur les mesures effectuées in situ dans un peuplement de tremble à Järvselja, Estonie. Selon les conditions initiales, l'indice foliaire atteint son équilibre en 5–20 ans. La valeur de la densité initiale des pousses longues conditionne le temps nécessaire pour atteindre cet équilibre, mais a peu d'influence sur la valeur finale du LAI. Les paramètres les plus influants dans la prédiction du LAI final sont ceux qui interviennent dans la relation entre fourchaison des rameaux longs et lumière.

canopée / croissance / modèle / *Populus tremula* / LAI / fourchaison

1. INTRODUCTION

The leaf area of a tree or tree stand is a central parameter in scaling up leaf level processes of mass and heat transfer or optical properties to whole tree or stand level. As a first approximation, stand productivity is often proportional to intercepted light, which in turn is a function of the leaf area to ground area ratio (Leaf Area Index –

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LAI) [33, 41]. Tree layer LAI can also be used to predict transmission of light to lower vegetation layers, and in turn to determine ground vegetation productivity and composition [25].

Many studies have shown that productivity in an even-aged tree stand increases rapidly until canopy closure after which productivity begins to decline slowly [18, 42]. This productivity pattern is closely related to LAI dynamics. After canopy closure growth of new branches and foliage in the upper canopy equilibrates with degradation and death in the lower canopy, resulting in a relatively stable LAI. Although, the dynamics of long term productivity in tree stands is acknowledged to be the consequence of hydraulic and/or nutrient limitations [18, 42], little study has been done to reveal the mechanisms of how these limitations lead to changes in equilibrium LAI. It is evident that leaf area index of a plant canopy is predicted by mechanisms that establish the lower limit of the canopy [28]. In developing tree seedlings or coppice canopy as well as in many herbaceous species this limit is set by steady abscission of senescing leaves. Canopy growth in mature deciduous trees occurs simultaneously throughout the canopy and all leaves are approximately the same age. The lower limit of the canopy is related to limited bud development, bud break and the branching pattern at the lower canopy limit [16, 26].

Canopy growth has genetic and environmental limitations. Shoot ramification patterns, sylleptic and proleptic growth or the ratio of long and short shoots are genetically controlled and strongly species-specific [15, 19, 49]. However, within a canopy these structural parameters show clear dependence on environmental factors, mainly on light quantity or quality [3, 6, 20]. As shown by Sprugel et al. [48], branches have a high degree of autonomy and therefore development of buds and growth of new branches and leaves depend strongly on photosynthetic production of the mother branch unit. Photosynthetic production in a leaf canopy has dual dependence on light: the short term light response of CO_2 exchange, and the longer term acclimation in the amount of the leaf photosynthetic apparatus [27]. The radiation environment within a canopy is largely determined by the foliage distribution of the crowns which creates a feedback between light environment and growth parameters of the canopy.

In physiologically-based tree and stand level growth models, foliage is often described as a single compartment without consideration of spatial heterogeneity. Only recently has detailed spatial description of tree crown been incorporated in some functional-structural tree models and only few examples exist where the feedback between light environment and crown structure

have been successfully introduced into some single tree functional-structural models (e.g. by Takenaka [50]). In such models 3D co-ordinates of every foliage element is modelled and light conditions calculated with respect to the positions of all other elements. Application of this approach on an entire tree canopy, which involve a vast number of branch units and trees of different size and crown shape, is still impractical, owing to difficulties in parameterisation and validation of such a detailed model. Although development of rapid 3D digitising methods might soon alleviate these difficulties [46], a more simplified approach to model growth of a tree canopy is still needed. Recently, we developed a simple canopy growth model for an oak stand which considered only long shoots and where the canopy was divided into vertical layers with horizontally homogeneous distribution of shoots and leaves [26]. However, several studies, focused on the relationship between leaf area and radiation environment, have shown that majority of tree canopies cannot be described with such a "turbid medium" model, because foliage is usually substantially clumped into shoots and crowns [2, 11, 22]. Consequently, more realistic models have to incorporate spatial heterogeneity. Additionally, many tree species, especially those native to temperate climate, have distinct shoot dimorphism. Clearly, only long shoots contribute to the overall structural framework of a tree crown, and short shoots are specialised mainly for leaf display and photosynthesis [19]. Although, few studies exist where this shoot dimorphism has been investigated quantitatively (e.g. [21, 38, 51]), the consequence of dimorphism to equilibrium leaf area is unknown.

Our technique is an attempt to model stand level canopy growth on the basis of tree and shoot level mechanisms and designed to include shoot level dimorphism and canopy level spatial heterogeneity. The aim is not just to simulate the canopy growth – this task can be easily done by empirical equations – but to understand which are the most influential processes in predicting equilibrium leaf area index of a tree canopy.

2. THE MODEL

2.1. Main assumptions

1. The canopy is divided into horizontal layers whose thickness equal to the height of annual growth. Every year a new upper layer grows above the other layers and growth within other layers depends on the average radiation environment within the layer during the previous year;

2. All growth and structural parameters are functions of the radiation environment with no consideration of any particular physiological mechanism;

3. The effect of spatial foliage clumping is reflected in the radiation model by a parameter which relates actual leaf area index with effective LAI, and in the growth model by a parameter showing how much differs light intensity at the canopy element from average intensity in particular horizontal canopy layer;

4. The canopy light environment is characterised by a single parameter – the diffuse site factor [35, 39]. This is justified because the correlation between the diffuse site factor and direct site factor in this canopy was 0.98 averaging all measurements from different positions and times over the entire vegetation period. Additionally, the diffuse site factor was also highly correlated with seasonal sums of PPFD measured from 18 different locations within the canopy [34].

2.2. Diffuse site factor

The diffuse site factor above the canopy layer i is defined as integral of the diffuse sky radiation distribution, $\delta_i(\theta)$ over the entire upper hemisphere:

$$\hat{\tau}_i = \int_\theta \delta_i(\theta)\, d\theta \tag{1}$$

where θ is the zenith angle. The value of $\hat{\tau}$ represents average relative light conditions in a particular canopy layer. Foliage clumping makes the radiation field more variable resulting in a systematic difference between the average horizontal diffuse site factor and the diffuse site factor in close proximity to a canopy element, denoted here as τ. In general τ is a function of average diffuse site factor $\hat{\tau}$ and clumping index Ω:

$$\tau = \tau(\hat{\tau}, \Omega). \tag{2}$$

Within canopy layer i with ellipsoidal angular distribution of foliar elements, the extinction coefficient K for beam radiation is given by Campbell and Norman [8]:

$$K_{\mathrm{dir}}(i, \theta) = (x_i^2 + \tan^2 \theta)^{0.5} / A_i\, x_i \tag{3}$$

where x_i is the ellipsoid parameter of the leaf inclination angle distribution. A is approximated by:

$$A_i = \left[x_i + 1.774\left(x_i + 1.182\right)^{-0.733} \right] / x_i. \tag{4}$$

The radiation distribution function between layers i and $i+1$ is:

$$\delta_{i+1}(\theta) = \delta_i(\theta)\, e^{-K_{\mathrm{dir}}(i,\theta)\Omega L_i} \tag{5}$$

where L_i is the leaf area index of layer i and Ω is the clumping index.

The sky radiation distribution above the canopy is assumed to be that of standard overcast sky (SOC) [17] and that parameter x_i is a function of diffuse site factor above the layer i:

$$x_i = x(\tau_i). \tag{6}$$

2.3. Canopy growth

Every year each long shoot produces λ_1 new long shoots with N_1 leaves, and λ_s new short shoots with N_s leaves. All these parameters depend on light conditions such that:

$$\lambda_1 = \lambda_1(\tau) \tag{7}$$

$$\lambda_s = \lambda_s(\tau) \tag{8}$$

$$N_1 = N_1(\tau) \tag{9}$$

and

$$N_s = N_s(\tau). \tag{10}$$

It is assumed that a short shoot can produce only one new short shoot where

$$D_s = D_s(\tau) \tag{11}$$

is the proportion of short shoots that produces a new short shoot. Assuming that the long shoot bifurcation ratio and number of leaves per shoot in a layer are dependent on the radiation environment of the previous year, the number of new long shoots in layer $i+1$ in year j equals

$$n_{j,\,i+1} = n_{j-1,\,i}(\tau_{j-1,\,i}) \tag{12}$$

and the number of short shoots

$$s_{j,\,i+1} = s_{j-1,\,i}\, D_s(\tau_{j-1,\,i}) + n_{j-1,\,i}\, \lambda_s(\tau_{j-1,\,i}). \tag{13}$$

The total leaf area in canopy layer $i+1$ equals:

$$S_{j,\,i+1} = n_{j,\,i+1}\, N_1(\tau_{j-1,\,i})\, \sigma + s_{j,\,i+1}\, N_s(\tau_{j-1,\,i}) \tag{14}$$

where σ is the single leaf area. The total leaf area index of the canopy equals the sum of all layers:

$$S_c = \sum_i S_i. \tag{15}$$

3. MATERIALS AND METHODS

The model was parametrised for an aspen (*Populus tremula* L.) stand in Järvselja, Estonia (58°22'N, 27°20'E). The overstory (17–27 m) was dominated by

P. tremula with few *Betula pendula* Roth. trees. *Tilia cordata* Mill. was the subcanopy species (4–17 m), and *Corylus avellana* L. and the coppice of *T. cordata* dominated the understory. Trees were accessed from permanent scaffoldings (height 25 m) located at the study site. Measurements were made at four heights in the canopy: 19–20 m, 23 m, 25–26 m and 27 m (top).

The leaf inclination angle (zenith angle of the normal to the leaf blade) was measured using a protractor. A minimum of one hundred leaves was measured at each canopy level. The leaf angle distribution was fitted using an ellipsoidal function with a single parameter x [7]. Theoretical leaf angle distributions were calculated for various values of x, and the experimental data fitted by minimising the χ^2 parameter.

The branching pattern was determined by counting all current year long and short shoots on each one-year-old long shoot and each short shoot attached to two-year-old long shoots. Depending on the height, 30–100 two-year-old shoots per sampling point were analysed. Additionally, the number of leaves on each current year shoot was recorded.

The average diffuse site factor at each sample point was assessed with the hemispherical (fish-eye) canopy photographic technique [29, 35, 39]. A camera (model OM-2S, Olympus Optical Co., Ltd, Shinjuku-ku, Tokyo, Japan) with an 8 mm fish-eye lens was aligned vertically and five shots were taken at each sample point. Canopy gaps were measured with respect to zenith angle in each photograph from which the diffuse site factor (τ) was calculated.

The leaf area index was measured from litter fall using ten collectors (32 × 45 cm) positioned on the ground at random locations. Litter was collected at weekly intervals from the end of August to the beginning of November. All leaves were sorted by species and leaf area was determined using a computer graphic tablet. The overstory leaf area index, used as a reference value in this study, was calculated as the sum of *P. tremula* and *B. pendula* leaf areas.

The total canopy clumping index was calculated using the measured diffuse site factor below the overstory and the measured leaf angle distribution. Applying a horizontally homogeneous canopy model, the effective leaf area index, S_e, was calculated and the total canopy clumping index was

$$\Omega = \frac{S_e}{S_c}. \qquad (16)$$

In order to assess the contribution of leaf clumping of shoots to total canopy clumping, sixteen shoots, eight from the top and eight from the lower limit of the canopy were analysed. The zenith angle of every shoot was measured prior to cutting and repositioned at the same angle on a specially designed holder with white background screens. Photos were taken from three directions (from zenith, along the axis and perpendicularly) using a 200 mm tele-lens and black and white film. Images were scanned to create computer bitmaps from which projected shoot areas were calculated. All shoot leaves were collected and the total leaf area of the shoot was determined. The ellipsoidal parameter of every shoot was calculated as:

$$x = \frac{S_V}{S_H}. \qquad (17)$$

where S_V is the vertical projected area of the shoot and S_H average of two horizontal projections. The effective total surface area of the clump was calculated assuming ellipsoidal approximation of the shoot as:

$$L_E = S_V A \qquad (18)$$

where A is calculated according to equation (4). The shoot level clumping was determined as the ratio of shoot effective area to total leaf area of the shoot.

4. RESULTS

4.1. Parameterisation of the model

Leaf inclination angle distribution in the *Populus tremula* canopy was best approximated with a prolate ellipsoid with acute inclination angles dominating in the top of the canopy and almost spherical distribution in the lower part of the canopy (*figure 1*). An average value for parameter x, 0.83 (*figure 1D*), was used in the model calculations.

The most variable branching parameter was the long shoot bifurcation ratio λ_1 (*figure 2A*), which was almost two at the canopy peak and decreased below one in the lower part of the canopy. Based on our measurements on other species [26] we used a non-rectangular hyperbola to describe the relationship between long shoot bifurcation ratio and diffuse site factor:

$$\lambda_1 = \frac{\lambda_{max} + k_\lambda \tau - \left(\left(\lambda_{max} + k_\lambda \tau\right)^2 - 4 k_\lambda \theta \lambda_{max} \tau\right)^{0.5}}{2\theta} + R \qquad (19)$$

where λ_{max} is maximal value of long shoot bifurcation, k_λ is the initial slope of the relationship, θ is convexity and R is the intercept. The values of these parameters are
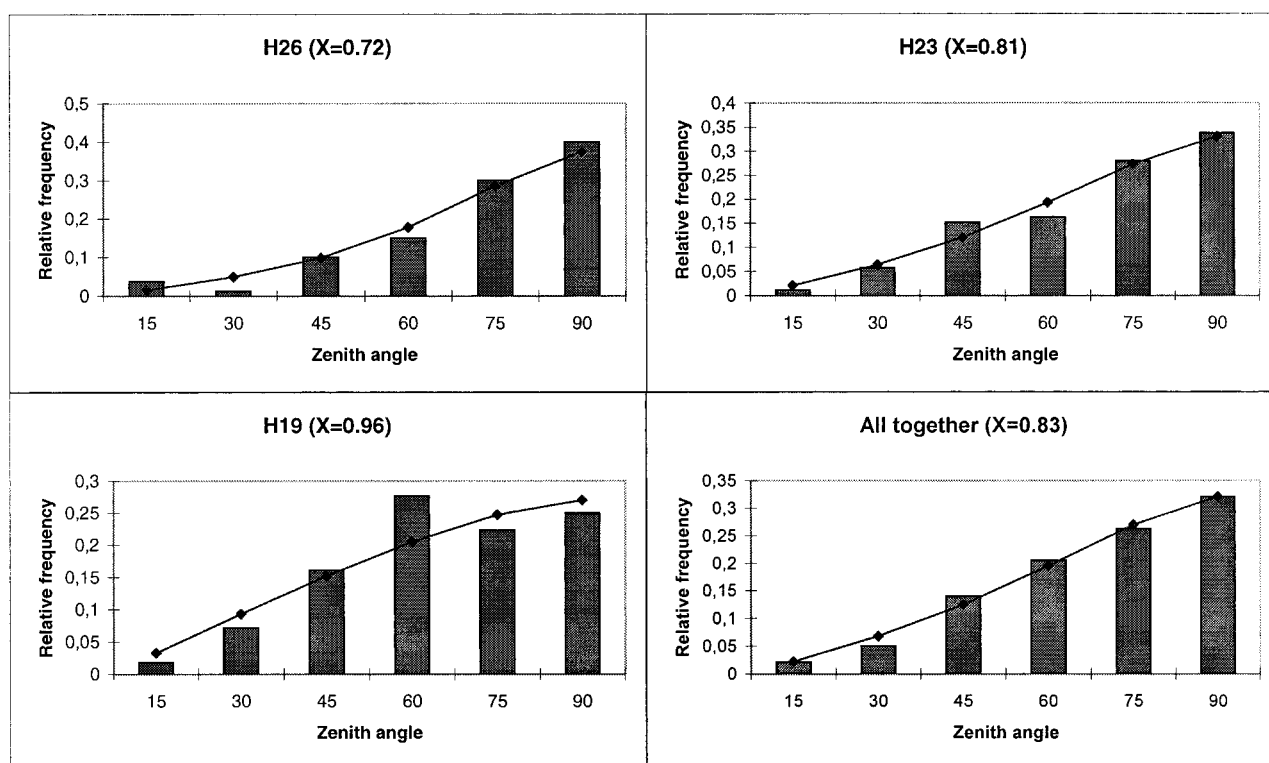
Figure 1. Leaf inclination angle distributions at three heights of *Populus tremula* canopy and for bulk data (bars). Lines present best-fit ellipsoidal distributions with ellipsoidal parameter × values shown on each graph.

given in *table II*. For the long to short shoot bifurcation, λ_{s}, and short shoot survival, D_{s}, we used linear regression to establish the parameter relationships with the diffuse site factor (*figures 2 B* and *C*):

$$\lambda_{s} = 0.915\, \tau + 1.06 \qquad (20)$$

$$D_{s} = -0.473\, \tau + 0.622. \qquad (21)$$

Mechanical damage due to wind in the upper part of the canopy seem to account for decreased short shoot survival and production in upper sections of the canopy.

The average number of leaves per long shoot (≈ 8) was almost twice the number of leaves on short shoots (≈ 4)

and these numbers were unrelated to the vertical position in the canopy (*figure 2D*).

Based on litter analysis, the total leaf area index of the principle tree layer was 4.22 m^2/m^2. The average diffuse site factor measured below the crowns of the trees 17–19 m above the ground was 0.216 ± 0.032. Inversion of the radiation model using $x = 0.83$ yields an effective leaf area index of 2.30 m^2/m^2 and, consequently, the total clumping in the canopy was estimated to be $\Omega = 0.55$. We estimated the effect of shoot level clumping to be negligible (*table I*). This surprising result my have been due to underestimation of the total leaf area, the result of measuring the individual leaves after drying.

Table I. Total leaf area and projected leaf area of *Populus tremula* shoots from two heights in the canopy ($n = 8$).

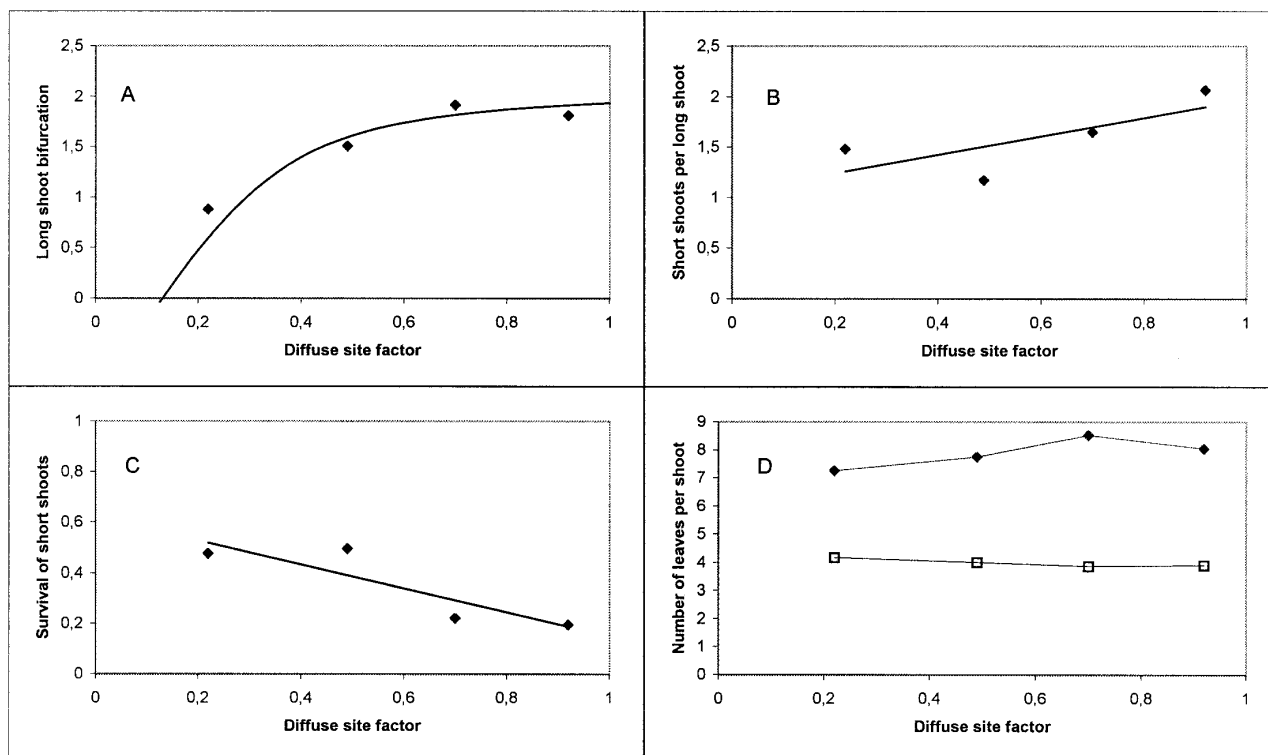| Height	Total leaf area of shoot, S_{T}, $cm^2 \pm STD$	Vertical projected area, S_{V}, $cm^2 \pm STD$	Average horizontal projected area, S_{H}, $cm^2 \pm STD$	Shoot effective leaf area (Eq. 18), L_{E}, $cm^2 \pm STD$	L_{E}/S_{T}
26 m	183 ± 81	68 ± 30	106 ± 23	202 ± 66	1.02 ± 0.08
20 m	175 ± 36	80 ± 25	102 ± 23	188 ± 45	1.09 ± 0.14

Figure 2. **A** – Long shoot bifurcation ratio, λ_l, *versus* diffuse site factor. Data are fitted with hyperbola (Eq. 19) with parameters given in *table II*. **B** – Number of short shoots per long shoot, λ_s, versus diffuse site factor. Regression line is given by equation (20). **C** – Survival of short shoots, D_s, *versus* diffuse site factor. Regression line is given by equation (21). **D** – Number of leaves per long shoot ($\blacklozenge$) and short shoot ($\square$) *versus* diffuse site factor.

However, according to our estimate, shrinkage of aspen leaves is limited to 10%. Therefore, shoot leaves pack efficiently with minimal shelf-shading, and most of the clumping in the canopy is caused by heterogeneity at the higher branch and crown scales.

The relationship between average light conditions at a given height in the canopy and "effective" light conditions close to a leaf clump should depend on character of heterogeneity and location and character of the light sensing mechanism. We assume, that intercepted light per unit of leaf area is important for bifurcation and consequently equation (2) takes the simplest form:

$$\tau = \Omega \hat{t}. \tag{22}$$

The only parameter in the model requiring an initial value for the topmost canopy layer is n_0, he number of long shoots per square meter of ground area. We used $n_0 = 0.1$ m^{-2} as a standard value in the model, but as discussed later, the steady-state LAI depends little on this value.

4.2. Steady-state LAI

According to the model, steady growth in upper canopy is soon compensated by degradation in the lower canopy (*figure 3*). Depending on the initial conditions, LAI achieves a steady state in 5–20 years. The value of initial density of long shoots, n_0, affects the time needed to achieve the steady state but has little influence on the final LAI. A small increase in LAI with a very high shoot density (*figure 4*), is mainly caused by increased integration errors, because the errors depend on leaf area and light gradient in a single canopy layer.

The value of LAI (5.15 m^2/m^2) calculated from the model using the standard parameters (*table II*) is higher than measured from litter fall (4.22 m^2/m^2), although, a slight decrease in the intercept value (R) of equation (19) alleviates this discrepancy (*figure 5*). This indicates that direct measurements of long shoot bifurcation at the lower crown limit may be biased. An overestimation of
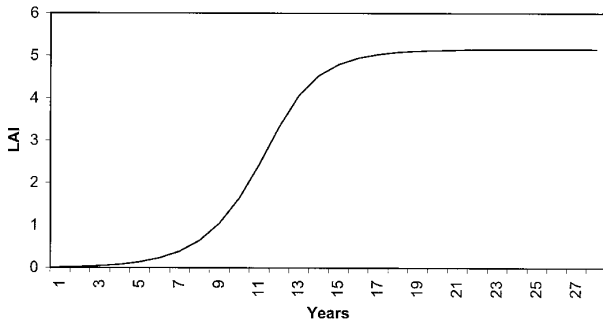
Figure 3. Time course of LAI in *Populus tremula* canopy calculated by the model with standard parameter set (*table II*).

actual bifurcation coefficient is likely if larger branches at the lower crown limit die.

4.3. Sensitivity analysis

Sensitivity of the steady state LAI was calculated using the 10 per cent parameter increment of Thornley and Johnson [52]:

$$S(P_i) = \frac{\Delta \text{LAI}}{\text{LAI}} \times 10 \tag{23}$$

where LAI is the steady state value for the standard parameter set and ΔLAI is the change in steady-state in response to an increase in parameter P_i. The most influential relationship in predicting the steady state LAI is the relationship between diffuse site factor and long

Table II. Standard values of parameters and sensitivity of equilibrium LAI (Eq. 23).

Parameter		Standard value	Sensitivity of LAI
Number of leaves on long shoot	N_1	8	–0.17
Number of leaves on short shoot	N_s	4	0.19
Parameters of long shoot bifurcation, λ_1 *versus* τ relationship (Eq. 19)	λ_{max}	3.1	2.32
	k_λ	8	2.32
	θ	0.9	8.35
	R	–1	–2.01
Long to short shoot bifurcation, λ_s, (Eq. 20)	slope	0.915	0.01
	intercept	1.056	0.18
Short to short shoot bifurcation, D_s, (Eq. 21)	slope	–0.473	–0.06
	intercept	0.622	0.73
Ellipsoid parameter	X	0.83	–0.19
Single leaf area	σ	0.005	0.01
Clumping index	W	0.55	1.17

shoot bifurcation, incompassed in equation (19), whose four parameters are among the most effective parameters (*table II*). Among other parameters only the clumping parameter, Ω, noticably influences the value of steady state LAI.

5. DISCUSSION

During tree canopy development, leaf area index usually increases rapidly to a maximum value, and then
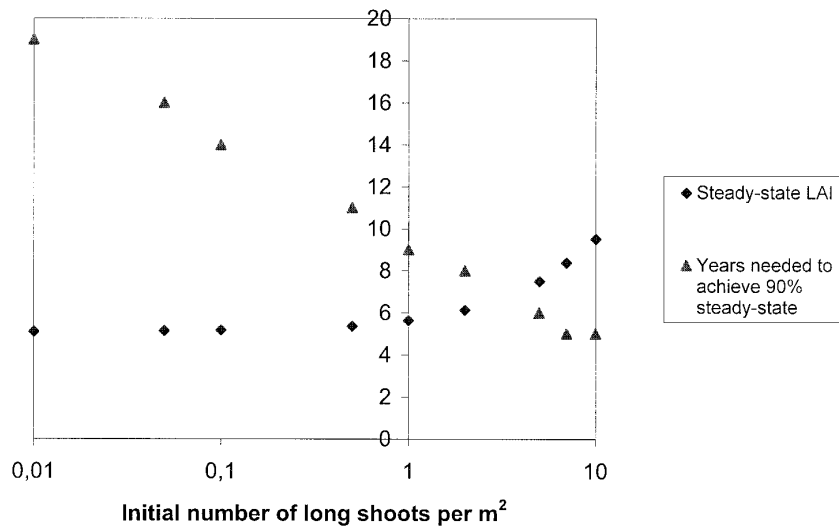

Figure 4. Dependence of equilibrium LAI and time needed to achieve 90% of this equilibrium value on initial density of long shoots.
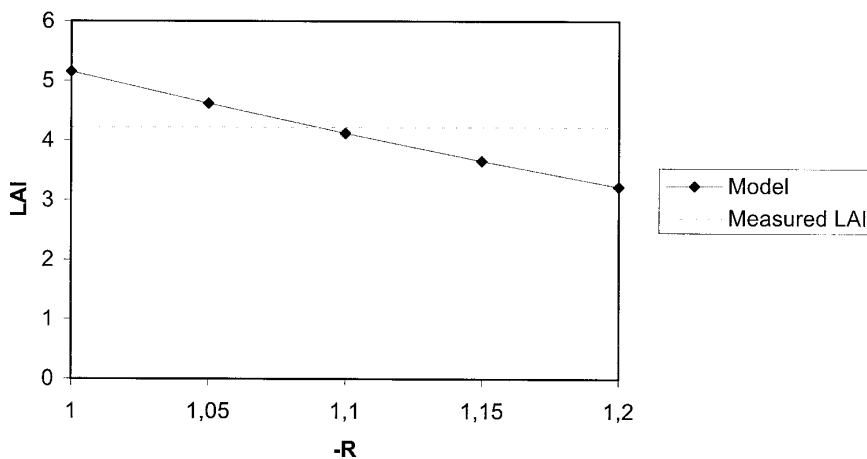
Figure 5. Dependence of equilibrium LAI on intercept value of parameter *R* in equation (19) in comparison with actually measured LAI in *Populus tremula* canopy.

remains relatively stable for a long period or slowly decreases with stand age [18, 22, 36, 42]. Leaf area of a single tree increases longer than LAI of a stand, because some thinning occurs in the stand. Hence, the quasi-steady-state LAI is a stand level rather than a single tree level phenomenon. This fact serves as additional support to use a canopy level model instead of a single tree model to understand the formation of canopy LAI. Thinning or pruning in the canopy temporarily changes the number of branch units in the canopy and may affect clumping, and consequently alter the time required to achieve the steady-state, but as shown by our model, the maximum LAI value is much less affected.

Although there is little data available on stand LAI development, the estimated time required to achieve maximum or equilibrium LAI during stand development is 5–40 years depending on species and growing conditions [1, 4, 22, 36, 40, 53]. Ruark and Bockheim [40] showed that *Populus tremuloides* requires 20 years to reach maximum LAI and production, whereas Johansson [23] found that LAI in young stand of *Populus tremula* depends heavily on tree spacing density. Consequently, our model result on the dependence of the time needed to achieve steady-state LAI on the initial shoot density seems realistic. However, the self-thinning that occurs in a stand over time is not considered in our model and consequently, the actual LAI increase is probably somewhat slower.

Light-dependent branching is one possible mechanism which allows trees to actively forage for light resources and to effectively fill canopy caps [6, 45]. The light dependence of growth is most likely mediated by photosynthesis. The main source of carbohydrates for the developing bud is the closest leaf, while branch units are known to be relatively autonomous and do not import assimilates from the rest of the tree [48]. Consequently,

the ability of leaves to export carbohydrates to buds may be the mechanism responsible for light dependent-branching. Takenaka [50] explored an analogous mechanism based on photosynthetic control of branching in his model. In a recent study which compared model analysis and measured data [28] we showed that the canopy lower limit is most likely established by the conditions where export from a leaf ceases. This study adds additional support to our hypothesis and indicates that the decline in long shoot bifurcation ratio is the direct mechanism which links the lack of export from leaves with degradation of the lower canopy.

Because distinct short and long shoots are characteristic only for some deciduous temperate trees and are rare in evergreens and tropical trees [15, 51], few structural models of tree growth have included dimorphism (e.g. model by Remphrey, Powell [38]). As shown, consideration of shoot dimorphism is important because of the completely different demography of long and short shoots. Birth and death rates of short shoots are insensitive to radiation climate, whereas the ramification pattern of long shoots is the most important factor to predict canopy growth and equilibrium LAI. This difference in behaviour explains the variations in the frequency of long shoots versus short shoots with crown position observed by Isebrands and Neilson [21]. Like *Populus tremula*, species with such shoot dimorphism tend to be early successional with great extensional growth and are more adapted to foraging new space than producing an efficient photosynthetic area [43].

Most tree canopies are clumped to some extent [13, 14, 22, 44], often involving several types of clumping (e.g. shoot, branch, crown) [10]. For instance, Smith et al. [47] showed that in a *Pseudotsuga menziesii* canopy, with a total clumping index of 0.38, 74% was due to needle clumping within shoots and 26% due to

non-random spacing of branches. The unexpected, almost negligible shoot level clumping in the *Populus tremula* canopy simplifies spatial heterogeneity in canopy radiation models. Although, models where several scales of heterogeneity are involved are still in stage of development (e.g. model by Cescatti [9]). However, non-random spacing of canopy elements makes the average value of radiation characteristics useless for physiological approaches, because light intensity on leaves is always less than the average at the same height in the canopy. Clumping leads to better light transmission through the canopy, but decreases average absorbance and photosynthesis per unit of leaf area [12]. Application of a simple relationship (Eq. 22) to describe physiological effect of radiation is justified only if average intercepted light is appropriate. Incorporating all spatial heterogeneity in the model is possible only when real 3D models can include the entire forest canopy.

A steady-state LAI appears when equilibrium is reached between growth in the upper canopy and degradation in the lower canopy. In functional-structural tree models the degradation in the lower crown has been handled in several ways. Reffye et al. [37] defined the maximal life span of branch units, whereas Mäkela et al. [32] calculated the dynamics of the crown base from the empirical assumption that crown rise occurs when the crowns touch each other. In other models direct [30] or indirect [31] dependence of bud-brake and shoot development on radiation intensity is involved. However, data for parameterisation of this relationship are scarce. We have investigated shoot bifurcation ratio with respect to light conditions in a *Quercus robur* canopy and found a similar relationship, with bifurcation being relatively constant in upper canopy and rapidly declining in the lower part. Koike [24] has described similar results for *Castanopsis cuspidata*. In the majority of tree branching pattern studies the Strahler system of ordering has been used, which has mechanical rather than biological or chronological implications [19]. Bifurcation ratios based of two different ordering methods differs if an individual shoot subtends fewer than two shoots, by which the system may appear to be unbranched according to the Strahler system, although developmentally, several orders of branching may be involved. This difference renders Strahler notation data inapropriate for canopy growth models.

The relationship between long shoot bifurcation and light makes canopy LAI very sensitive to small variations in parameters, implying that precise measurements are required. In contrast, small fluctuations in annual global radiation should have a strong influence on canopy LAI. Little data on time-series of LAI is available to show considerable variability. For instance,

Burton et al. [5] measured intra-annual variability in LAI in an *Acer saccharum* stand as large as 34%. The steady decrease in shoot propagation is possibly not the ultimate mechanism causing degradation in lower crown. The tendency of the model to overestimate LAI indicates that our methods may be unable to detect the total shoot loss, perhaps due to the abrupt loss of some larger branches as could occur when foliage mass per branch mass drops below some critical limit. If there is some additional loss of branches then the crown net degradation may occur in conditions when shoot bifurcation ratio is greater than one. Continuous monitoring of shoot demography should provide better insight to the phenomenon.

The analysis based on the canopy growth model developed here points clearly to two aspects that require additional study in order to understand the formation of equilibrium LAI in tree canopies. *A priori,* it is clear that processes at the lower limit of the canopy are the most influential in predicting total leaf area, but the model shows that the relationship between long shoot *versus* light and its mechanisms that are the most important. The analysis also shows that spatial heterogeneity, which exists to some extent in all tree canopies, should not be ignored in a canopy growth model.

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