



Application of the Functional-Structural Tree Model LIGNUM to Sugar Maple Saplings (*Acer saccharum* Marsh) Growing in Forest Gaps

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LIGNUM is a functional-structural model that represents a tree using four modelling units which closely resemble the real structure of trees: tree segments, tree axes, branching points and buds. Metabolic processes are explicitly related to the structural units in which they take place. Here we adapt earlier versions of LIGNUM designed to model growth of conifers for use with broad-leaved trees. Two primary changes are involved. First, the tree segment for broad-leaved trees consists of enclosed cylinders of heartwood, sapwood and bark. Leaves consisting of petioles and blades are attached to the segments. Secondly, axillary buds and rules governing their dormancy are included in the model. This modified version of LIGNUM is used to simulate the growth and form of sugar maple saplings in forest gaps. The annual growth of the model tree is driven by net production after respiration losses are taken into account. The production rate of each leaf depends on the amount of photosynthetically active radiation it receives. The radiation regime is tracked explicitly in different parts of the tree crown using a model of mutual shading of the leaves. Forest gaps are represented by changing the radiation intensity in different parts of the model sky. This version of LIGNUM modified for use with broad-leaf, deciduous trees and parameterized for sugar maple, yields good simulations of growth and form in saplings from different forest gap environments. © 2001 Annals of Botany Company

Key words: LIGNUM, functional-structural tree model, tree architecture, sugar maple, modelling growth and form.

INTRODUCTION

Functional-structural models (FSM) combine two traditional perspectives on the organization of plant life, one emphasizing function and the other form. Functional or process-based models treat metabolic processes in considerable detail but simplify structure and structural dynamics to the level of caricature, while structural or morphological models describe plant architecture very realistically but pay little or no attention to growth processes. Examples of process-based models can be found in Mäkelä and Hari (1986) and Landsberg (1986). The most striking models of form often use Lindenmayer or L-systems (Prusinkiewicz and Lindenmayer, 1990; Kurth, 1999), fractal geometry methods (Hearn and Baker, 1994) or other mathematical means to describe branching structures (Fisher, 1992; Jaeger and de Reffye, 1992) visualized as computer graphics.

LIGNUM is a functional-structural model which combines, in one modelling framework, a process-based model with a three-dimensional (3D) description of the tree crown. The initial implementations of LIGNUM were for Scots pine (Perttunen *et al.*, 1996) and Jack pine (Lo *et al.*, 2000). LIGNUM includes a detailed model of self-shading within

the tree crown that is based on the geometry of mutual shading (Perttunen *et al.*, 1998).

Our first objective in this study was to adapt the structural units of LIGNUM from coniferous to broad-leaved trees (i.e. from gymnosperms to angiosperms; in this paper the terms broad-leaved and hardwood are used instead of the more-correct botanical term, angiosperm). Our second objective was to apply the modified LIGNUM model to simulate the development of sugar maple saplings (*Acer saccharum* Marsh) growing in forest gaps. This involved parameterizing and implementing the functioning and the architectural development of LIGNUM to simulate the growth and survival of sugar maple saplings in different light regimes determined by openings of different sizes in the forest canopy. Measurements in four forest gaps, two at Duchesnay (46°55'N, 71°49'W) and two at Mont St. Hilaire (45°31'N, 75°08'W) in Quebec, Canada, provide the detailed data on gap light regimes used in our simulations.

Our long-term goal is to use LIGNUM as a research tool to develop new cutting guidelines for managing the natural regeneration of sugar maple, especially key features determining the size of canopy openings created during harvest and harvest frequency. At this stage in our research, it is essential that the robustness of our hardwood version of LIGNUM be evaluated.

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STRUCTURAL UNITS FOR SUGAR MAPLE

LIGNUM is intended as a generic modelling tool; different tree species can be simulated by changing the tree architecture using new branching rules, descriptions of metabolism and structural dynamics (birth, growth and senescence). The general framework of LIGNUM has been described previously (Perttunen *et al.*, 1996, 1998; Sievänen *et al.*, 1997). Presented here are the features of LIGNUM necessary to understand the modifications needed to adapt the model for broad-leaved trees. A glossary of variables is given in Table 1 and the parameters for sugar maple are summarized in Table 2.

LIGNUM represents the three-dimensional above-ground part of a tree using four structural units (Perttunen *et al.*, 1996) which are closely analogous to real tree parts: tree segment (TS), bud (B), branching point (BP) and axis (A). The root system is modelled with only one parameter denoting its mass.

The most important unit is the tree segment, the section between two branching points to which the leaves (for

broad-leaved trees) are attached. A branching point exists where one or several tree segments join. By analogy to the stem and branches of real trees, an axis is a sequence of tree segments and branching points terminating in a bud.

An axis can be implemented as a list. For example, the main axis of the model tree in Fig. 1 is:

$$[\text{TS}_0, \text{BP}_1, \text{TS}_2, \text{BP}_3, \text{TS}_4, \text{BP}_5, \text{B}_6] \quad (1)$$

Indices denote the positions of the elements in the list. Similarly, a branching point can be implemented as a list of axes. Thus the main axis in eqn (1) can be written:

$$[\text{TS}_0, [\text{A}], \text{TS}_2, [\text{A}, \text{A}], \text{TS}_4, [\text{A}, \text{A}], \text{B}_6] \quad (2)$$

By ‘unfolding’ the axes, eqn (2) becomes:

$$[\text{TS}_0, [[\text{B}]], \text{TS}_2, [[\text{TS}, \text{BP}, \text{B}], [\text{TS}, \text{BP}, \text{B},]], \text{TS}_4, [[\text{B}], [\text{B}]], \text{B}_6] \quad (3)$$

The tree segment for broad-leaved trees consists of enclosed cylinders of heartwood, sapwood and a bark layer. A leaf

TABLE 1. Glossary of symbols

Symbol	Meaning	Unit
A_e	Area of leaf ellipse	m^2
A_f	True area of leaves in a tree segment	m^2
A_h	Heartwood area	m^2
A_l	Area of a leaf	m^2
A_{sf}	Sapwood requirement—foliage	m^2
A_{su}	Sapwood requirement—diameter growth	m^2
A_{ts}^{new}	New cross-sectional area of a tree segment	m^2
A_{ts}	Cross-sectional area of a tree segment	m^2
A_s	Sapwood area	m^2
dA_s	Sapwood senescence	m^2
I_{PAR}	Annual photosynthetically active incoming radiation	MJ m^{-2} per year
I_b^a	Total radiation absorbed by a bud	MJ per year
I_{REL}	Relative light climate of a bud	—
I_{0c}	Radiant intensity of radiation beam from sector c	$\text{MJ m}^{-2} \text{sr}^{-1}$ per year
I_{lc}	Radiant energy coming from sector c that reaches leaf l	$\text{MJ m}^{-2} \text{sr}^{-1}$ per year
I_{lc}^a	Total radiation absorbed by a leaf l from sector c	MJ per year
I_l^a	Total radiation absorbed by a leaf	MJ per year
I_{ts}^a	Total radiation absorbed by a tree segment	MJ per year
L	Length of a tree segment	m
L_p	Length of a petiole	m
λ	Parameter to balance carbon balance equation	—
M_{ts}	Respiration of a tree segment	kgC per year
M	Respiration of a tree	kgC per year
μ	Transmission of radiation through leaf ellipse	—
N_s	Number of sectors in the sky	—
N_{sf}	Number of shading leaves	—
N_f	Number of leaves in a tree segment	—
P_{ts}	Photosynthetic production of a tree segment	kgC per year
P	Photosynthetic production of a tree	kgC per year
V_{lc}	Attenuation of radiant energy from sector c	—
v	Vigour index	—
ΔW_f	Mass of new leaves	kgC
W_l	Mass of a leaf	kgC
iW_d	Diameter growth	kgC per year
iW_n	Growth of new tree segments	kgC per year
iW_{rn}	Growth of roots	kgC per year
W_s	Mass of sapwood in a tree segment	kgC
W_{ts}	Mass of a tree segment	kgC
$W_{r\text{new}}$	Living root mass after a growing period	kgC
W_r	Root mass	kgC

TABLE 2. Parameters, their definitions and normal values

Symbol	Meaning	Value	Unit	Reference
A_l^{\max}	Maximum size of leaf	0.0045	m ²	Beaudet and Messier (1998)
a_r	Foliage-root relationship	1.0	kg kg ⁻¹	Walters and Reich (1996)
d_f	Degree of filling of a leaf	0.80	—	This study
m_f	Respiration rate of a leaf	0.20	kgC kg ⁻¹ C per year	See text
m_s	Respiration rate of sapwood	0.03	kgC kg ⁻¹ C per year	See text
m_r	Respiration rate of roots	0.9	kgC kg ⁻¹ C y ⁻¹	See text
p_0	Radiation conversion efficiency	0.00075	kgC MJ ⁻¹	Beaudet <i>et al.</i> (2000)
ρ_c	Density of wood	280	kgC m ⁻³	DeLucia <i>et al.</i> (1996)
SLA_c	Specific leaf area	30	m ² kg ⁻¹ C	Reich <i>et al.</i> (1998)
s_r	Root senescence	0.33	kgC kg ⁻¹ C per year	—
s_s	Sapwood senescence	0.04	kgC kg ⁻¹ C per year	—
ν	Attenuation coefficient of a leaf	0.94	—	From transmission coefficient of mean green leaf. Ross (1981)
Y_c	Foliage mass supported by 1 m ² of foliage	123.8	kgC m ⁻²	This study

Carbon concentration is assumed to be 50 % dry weight.

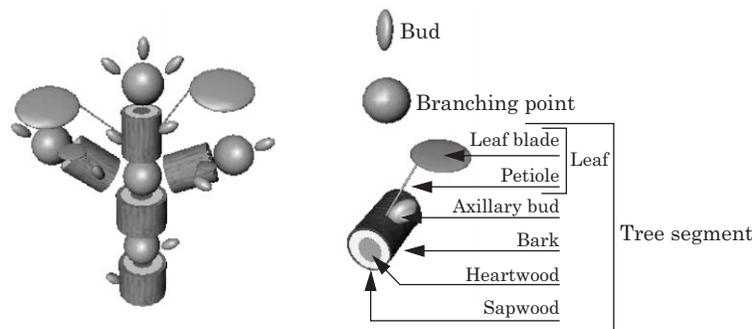


FIG. 1. Schematic presentation of a broad-leaved tree using structural units of LIGNUM. Also shown is the structure of the tree segment.

consists of a petiole connecting to a tree segment and bearing a leaf blade (Fig. 1). The leaf blades are presented as ellipses which are, in fact, only partly covered by the leaf lamina (parameter d_f ; see below). This simplifies computations of irradiance.

The presence of buds at the axil of each leaf completes the structure of a tree segment for broad-leaved trees (Fig. 1). These axillary buds are initially dormant but once they become active and begin to develop into a new shoot then the parent tree segment is cut into two segments at that point, and a new branching point with the flushed bud is inserted between the two segments. This maintains the structural integrity of the model.

LIGNUM was implemented with C++ programming language under the UNIX operating system. Visualization was done with the OpenGL graphics library.

PRODUCTION OF PHOTOSYNTHATES AND RESPIRATION

The models for photosynthesis and respiration are largely as in Perttunen *et al.* (1996, 1998). The time step of the sugar maple simulations is 1 year, as in previous applications (Perttunen *et al.*, 1996, 1998; Sievänen *et al.*, 1997). The length of the time step affects the parameter values (Table 2) and the radiation submodel.

Incoming radiation

LIGNUM uses the amount of incoming photosynthetically active radiation during the growing period, I_{PAR} , as its critical environmental input. Radiation is summed for all sectors of sky divided into 326 sectors. Since the real distribution of sky irradiance was not available, we simply assigned the relative brightnesses of sky sectors according to standard overcast sky (Ross, 1981). In this case, sky radiance depends only on inclination (Fig. 2). The total amount of unshaded incoming radiant energy of PAR during the growing season is about 1450 MJ m⁻² per year including both direct and diffuse radiation (Lo *et al.*, 2000). This value is based on a 15-year average of growing season irradiance near Abitibi (48°22'N, 79°22'W) in Quebec, Canada.

To model the light conditions of sugar maple saplings growing in the understorey of forest gaps, open sky radiation was transformed. Radiation was assessed in selected forest gaps in two regions, Mont St. Hilaire and Duchesnay, using hemispheric photographs to calculate attenuation of the open sky radiation as a function of solar inclination (Fig. 4). Each photograph gives a template that can be superimposed on the open sky radiation field to estimate the distribution of incoming radiation in the forest gap. Two gap models (G1 and G2) were constructed for Mont St. Hilaire and three (G3, G4 and G5) for

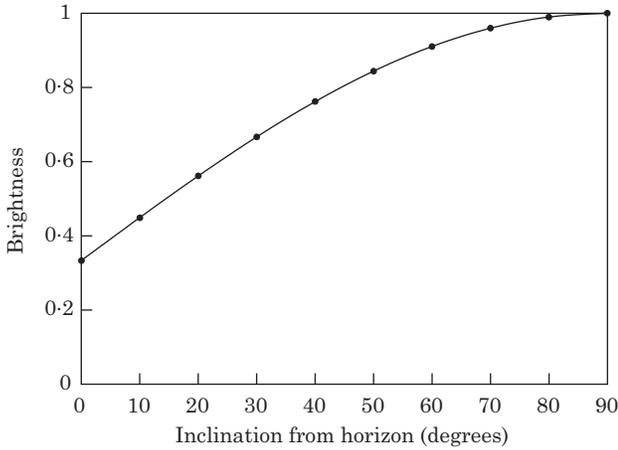


FIG. 2. Relative sky brightness of standard overcast sky (Ross, 1981) that was applied in this study as a function of inclination. The sky was divided into 326 sectors each with an approximately solid angle ($\approx 2\pi/326$); any two sectors with equal inclination had the same brightness.

Duchesnay; the fraction of incoming radiation reaching the understorey in the gap varied from 5.6 to 26.6 % (Fig. 4). Gap G5 is not real but is constructed from G3 so that the total amount of light is approximately the same as in gaps G2 and G4 but comes only from directly overhead.

Absorption of radiation by leaves

Computation of the photosynthetic irradiance for a leaf is adapted from our previous work for Scots pine (Perttunen *et al.*, 1998). Radiation received by a Scots pine segment from a sky sector depends on the brightness of the sky sector and the shading caused by the other segments of the crown. This is evaluated by tracing a ray from the centre of the segment towards the sky sector and testing whether upper segments are in the ray's path. This leads to pairwise comparison of all segments in the crown.

For sugar maple, the principle behind the calculation is the same, but the shading elements are leaf ellipses instead of segment cylinders. The shading effect of the woody parts is neglected (Ross, 1981). The ellipse dimensions are fitted to frame the leaf blade perimeter. This leads to an ellipse larger than the blade area, i.e. the areas of the leaf, A_l , and the corresponding ellipse, A_e , are related by $A_l = d_f A_e$, where d_f is a parameter ($d_f < 1$). To determine whether a leaf ellipse is on a ray path requires only elementary linear algebra (see e.g. Anton, 1987). Neither reflected nor scattered radiation is considered in the computations.

When the radiation beam hits the leaf ellipse, the transmission of radiation through the leaf (in the direction of the beam) is equal to:

$$\mu = 1 - d_f + d_f(1 - \nu) \quad (4)$$

where ν is the attenuation coefficient. The term $1 - d_f$ allows for the part of the ellipse that is not covered by the blade. Both d_f and ν are constant for all leaves (cf. Table 2). If there are N_{sf} shading leaves (each having transmission μ_i) in the path of a ray from sky sector c to subject leaf l , then

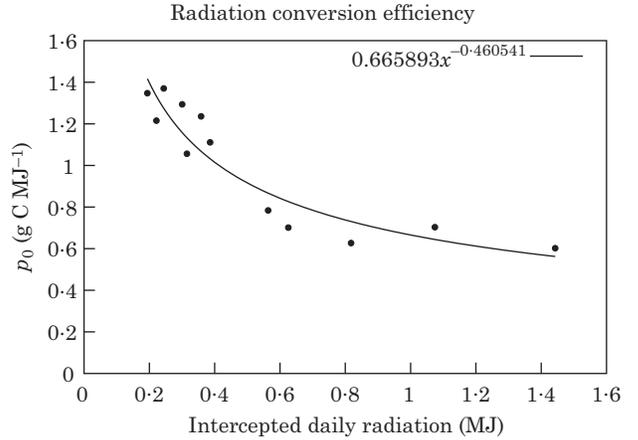


FIG. 3. Radiation conversion efficiency parameter p_0 (daily photosynthesis divided by intercepted radiation) of sugar maple seedlings in different light climates. Intercepted daily radiation indicates the light climate of the seedling. The data cover 3 d in July in Duchesnay and Mont St. Hilaire (Beaudet *et al.*, 2000). For the fitted curve with Marquardt method root mean square of residuals = 0.111941.

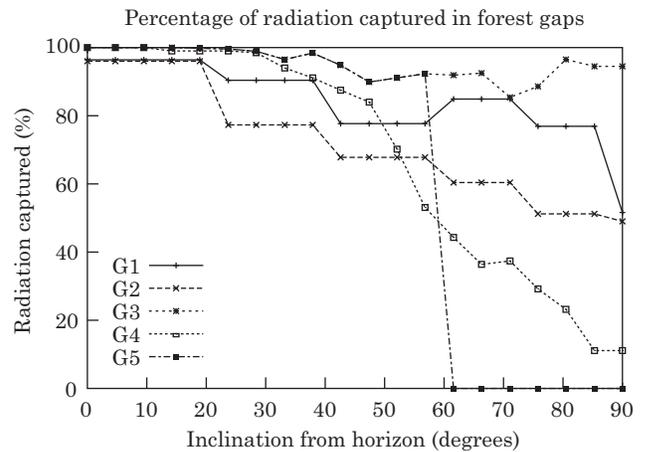


FIG. 4. Percentage of radiation captured by the surrounding trees as a function of inclination measured in forest gaps G1-G5 (100 = no light, 0 = full light). Amount of incoming radiation (PAR) above the trees was 1450 MJ m^{-2} . The percentage of radiation coming through the gap was 14.5 % (G1), 26.6 % (G2), 5.6 % (G3), 24.0 % (G4) and 26.0 % (G5).

the proportion of radiant energy coming from that sky sector to the subject leaf is given by:

$$V_{lc} = \prod_{i=1}^{N_{sf}} \mu_i \quad (5)$$

As it is assumed that the ray represents the whole sector, radiant energy from sector c reaching leaf l is given by:

$$I_{lc} = V_{lc} I_{0c} \quad (6)$$

where I_{0c} is the unshaded radiant energy from sky sector c . The amount of radiation I_{lc}^a absorbed by leaf l from sky sector c depends on its area and the angle of incidence of the radiation beam, giving:

$$I_{lc}^a = I_{lc} \cos(\alpha) A_l \quad (7)$$

where α is the angle between leaf normal, \vec{n} , and the direction, \vec{v} , of the sky sector c given by $\alpha = \arccos(|\vec{n} \cdot \vec{v}|)$. The total radiation I_l^a absorbed by leaf l is the summation of the irradiances over the N_s sectors of the sky:

$$I_l^a = \sum_{c=1}^{N_s} I_{lc}^a \quad (8)$$

The total radiation I_{ts}^a absorbed by a tree segment, ts , is then:

$$I_{ts}^a = \sum_{l=1}^{n_f} I_l^a \quad (9)$$

where n_f is the number of leaves in the segment.

Photosynthesis

The photosynthetic production of a single leaf l is proportional to absorbed radiation. Photosynthetic production of a tree segment, P_{ts} , is the sum of production in all n_f leaves:

$$P_{ts} = p_0 \sum_{l=1}^{n_f} I_l^a \quad (10)$$

where the parameter p_0 is the radiation conversion efficiency (photosynthetic production per unit of absorbed radiation). Photosynthetic production, P , of the tree is the sum of production in the N_{ts} segments:

$$P = \sum_{ts=1}^{N_{ts}} P_{ts} \quad (11)$$

Respiration

Respiration of a tree is the sum of respiration of the tree segments and of the root system. First, respiration in a single tree segment consists of sapwood respiration and respiration in leaves:

$$M_{ts} = m_s W_s + \sum_{l=1}^{n_f} m_f W_l \quad (12)$$

where m_s and m_f are the respiration parameters, and W_s and W_l are the weights of the sapwood and a single leaf respectively.

The respiration, M , of the tree is then obtained simply by summing respiration in the segments and roots:

$$M = \sum_{ts=1}^{N_{ts}} M_{ts} + m_r W_r \quad (13)$$

The root system is modelled in an aggregated manner with a single variable W_r for root mass and m_r as its respiration parameter.

THE STRUCTURAL DYNAMICS

The carbon balance

New growth is possible if photosynthetic production (P) exceeds respiration (M): $P - M > 0$; otherwise the tree is considered dead. The photosynthates used in growth are consumed in adding new tree segments and leaves, iW_n , in

diameter growth, iW_d , and in growth of roots, iW_r . Production of new tree parts at branch tips requires diameter growth in the segments below (see below) and also induces root growth. The amount of photosynthates used in growth depends on the sizes of the new parts. We use a parameter λ to control the sizes of new segments. We assume that all net production is allocated, i.e. there is no storage pool for a proportion of photosynthates, hence we require that:

$$P - M = iW_n(\lambda) + iW_d(\lambda) + iW_r(\lambda) \quad (14)$$

The right-hand side of eqn (14) is a non-linear function of λ . It was solved using the iterative method of van Wijngaarden, Dekker and Brent (Press *et al.*, 1992), a general one-dimensional root finding method where the values of the function are known, but its functional form and the derivative are not.

During the iteration, λ alternately elongates and shortens the new tree segments [see below, eqn (17)] and consequently induces a requirement for diameter growth throughout the tree. The new cross-sectional areas for the tree segments are calculated according to a pipe model defined for sugar maple [see below, eqns (18) and (20)], and the new root mass according to eqn (22).

Crown architecture

There is currently no formal, general definition for the architecture of different tree species in LIGNUM. We implemented the morphological development of a young sugar maple with the following ad hoc heuristics. The time step of the architectural development is the same as the metabolic part of the model: 1 year. Sugar maple has some capacity for indeterminate growth, but representing the annual growth as a single flush is adequate for our present purposes.

Any new tree segments will maintain the growth directions of the buds that create them (see below). Thus, the architecture of the tree can be defined by the trajectories of its buds in 3D space during tree growth and development. The initial axis that starts growing upright is called the main stem. It is assumed that there is a terminal bud at the end of the main stem. Table 3, taken from Goulet (1999), defines the number of leaf pairs (and thus the number of axillary buds) as a function of segment length. The axillary buds fork off at 45° from the direction of the main stem on the opposite sides of the main stem. Each subsequent pair of axillary buds is consecutively rotated through 90°. Thus, when viewed from above, the pairs of buds are arranged in a crosswise manner. At the tip of the branches (and subsequently in sub-branches), the axillary buds are simply created to rest in the same plane so that the angle between the terminating bud is 45°. The direction of a leaf petiole is that of the axillary bud. The orientation of the leaf blade (i.e. leaf normal) is random but the leaf normal is not allowed to point downwards.

The vigour index

The extension growth of new segments depends on their local light conditions and their position within the crown

TABLE 3. Number of leaf pairs as a function of segment length (Goulet, 1999)

Segment length (m)		Leaf pairs			
0	≤	L	<	0.03	0
0.03	≤	L	<	0.06	1
0.06	≤	L	<	0.2	2
0.2	≤	L	<	0.3	3
0.3	≤	L	<	∞	4

[see eqn (17)]. In previous studies for Scots pine (Perttunen et al., 1996) and Jack pine (Lo et al., 2000), the influence of position on branching was mainly controlled by a constant defining the shortening of lateral segments relative to the apical one. In this work, we replaced the shortening factor with an empirically determined vigour index, V (Goulet et al., 2000).

Computation of the vigour index is based on the relative thickness of axes forking away from a branching point. The thicker the axis the more growth potency it has. The vigour index is formulated as follows (c.f. Goulet et al., 2000):

$$V_{\text{base}} = 1$$

$$V_n = \left(\frac{A_{\text{ts}_n}}{\max[A_{\text{ts}_i}]} \right)^{V_{\text{below}}} \quad (15)$$

where V_{below} is the vigour index of the segment below the branching point, A_{ts_n} is the cross-sectional area of segment n , and the maximum A_{ts_i} is taken over all segments forking away from the branching point towards the apexes. The recursion starts at the base with a value of 1. The logical consequence of this definition is that the vigour index is in the open interval (0...1) and there is at least one continuous sequence of the thickest segments from the base of the tree to some bud retaining the index value 1 describing the apical control.

Tree segments

The length L of a new tree segment is assumed to depend only on the vigour index V and the local relative light climate I_b^{REL} of bud b at the end of an axis:

$$I_b^{\text{REL}} = \frac{I_b^{\text{a}}}{I_{\text{PAR}}} \quad (16)$$

where I_b^{a} is simply the intercepted radiation I_{ts}^{a} of the mother segment. The length of the new segments depends in a multiplicative way on V and I_b^{REL} given by:

$$L = \begin{cases} \lambda v I_b^{\text{REL}} & \lambda v I_b^{\text{REL}} > 0.03 \\ 0 & \text{otherwise} \end{cases} \quad (17)$$

where the threshold prevents the creation of very short segments in different parts of the tree (as discussed previously).

Diameter growth

To define diameter growth of sugar maple trees, we firstly assume that one unit area of sapwood can support a certain mass of leaves specified by a parameter. Given a leaf area, A_{f} , in a segment, the sapwood requirement A_{sf} in the segment is given by:

$$A_{\text{sf}} = \frac{A_{\text{f}}}{SLA_c Y_c} \quad (18)$$

where SLA_c is the specific leaf area. Equation (18) defines the pipe model for newly created segments that have foliage.

The diameter growth for other segments is more complicated due to senescence and interaction with neighbouring segments connected to the same branch whorl. The first requirement is that a segment with cross-sectional area A_{ts} must match the sapwood requirement A_{su} from the segments connected to it at the next immediate branching point above. Secondly, some of the sapwood given by the parameter s_s (sapwood senescence) is assumed to die annually:

$$dA_s = s_s A_s \quad (19)$$

Determining the value of parameter s_s for sugar maple is an open research problem. The value used in this study ($s_s = 0.04$) is based on our studies of conifers (Sievänen et al., 1997; Perttunen et al., 1998).

The new wood area $A_{\text{ts}}^{\text{new}}$ including sapwood and heartwood of the segment is then:

$$A_{\text{ts}}^{\text{new}} = \max[A_{\text{su}} + dA_s + A_{\text{h}}, A_{\text{ts}}] \quad (20)$$

where A_{h} is the existing heartwood. There is no sapwood requirement for foliage in the older segments because leaves persist for only one growth period, i.e. only new segments have leaves. Equation (20), defining the pipe model for older segments, prevents the segment from shrinking if A_{su} required is already supported by the segment.

Given the wood density ρ_c , the mass W_{ts} of a segment is:

$$W_{\text{ts}} = \rho_c A_{\text{ts}} L \quad (21)$$

New roots

The root system is modelled with a single variable for its mass. With regards to the dynamics of the root system, we assume that a unit amount of new foliage requires a certain amount (parameter a_r) of roots to be produced following the principle of functional balance (Mäkelä, 1990). A proportion of the root mass (parameter s_r) is assumed to die annually. The living root mass after the growing period is given by:

$$W_{\text{r}_{\text{new}}} = W_{\text{r}} - s_r W_{\text{r}} + a_r \Delta W_{\text{f}} \quad (22)$$

where ΔW_{f} is the amount of new leaf material produced.

In determining the value for s_r ($= 0.33$), we assumed that about 15% of all roots are fine roots having a turnover rate of 2 and that coarse root senescence is negligible.

Leaves

To adapt the general leaf model in LIGNUM for sugar maple, the shape of the leaf ellipse, the size of the leaves and the length of the leaf petioles were determined.

Regarding shape, we set the ratio between the minor and major axes of the leaf ellipse for sugar maple to 10:11. The parameter d_f for degree of filling is 0.80. The size of the leaf is assumed to decrease from the predefined maximum size A_1^{\max} , Table 2) along the segment so that the smallest leaves are located at the end of the segment. The length of the petiole is assumed to be related to leaf size according to Messier and Nikinmaa (2000):

$$L_p = 0.0215 + 6.9 A_1 \tag{23}$$

Finally, the weight of a leaf is:

$$W_1 = A_1/SLA_C \tag{24}$$

BUDS

We recognize that for broad-leaved trees the retention or activation of dormant axillary buds is an important behavioural response allowing adaptation to changes in the ambient environment and to structural damage in the crown, but for the moment a rudimentary approach to bud dormancy and release was adopted, namely, the first two pairs of axillary buds in the new segments flush. A more sophisticated implementation of LIGNUM for hardwood trees will require modelling of the adaptive release of dormant buds, but the empirical data on which such an implementation might be grounded are not yet available.

DETERMINING RADIATION CONVERSION EFFICIENCY AND RESPIRATION RATES

We estimated the radiation conversion efficiency p_0 from reported values of daily photosynthetic production and light attenuation in the crowns of sugar maple seedlings (Beaudet et al., 2000). The parameter p_0 decreases as light conditions improve (Fig. 3).

To assess respiration of a tree in the model LIGNUM, the rates for sapwood respiration m_s , foliage respiration m_f and root respiration m_r must be determined. To estimate the growth respiration rate we assumed that 25% of growth is lost in respiration (Mohren, 1987). For maintenance

respiration we used the specific respiration rates reported by Reich et al. (1998) for above-ground parts, assuming a doubling of the rate with each 10 °C rise in temperature, and by Zogg et al. (1996) for fine root respiration using the temperature dependence they reported. Annual maintenance respiration rate was integrated using daily temperature data from the region for which the simulations were made (Canadian Climate Normals 1961–1990, Duchesnay station, Environment Canada). We assumed that the rate of wood respiration was 5% of leaf respiration, given that roughly 10% of the wood biomass is alive but that it is less active than leaves. Furthermore, for m_f we used only the night-time value (about 30% of total leaf respiration) since p_0 gives net daytime photosynthetic production. Thus, the actual calculated annual maintenance respiration rates were 0.26 for m_f , 0.04 for m_s and 0.95 for m_r . The parameters used and appropriate references are summarized in Table 2. We refer to the values presented and used in the simulations as normal values. Changes to the parameter values in different canopy gap models are explicitly stated in Table 4.

SIMULATIONS OF SUGAR MAPLE SAPLINGS

The purpose of the simulations with LIGNUM was to produce realistic sugar maple saplings based on observations and measurements made in our field experiments. To verify the results we can, in the first instance, use computer graphics to examine the appearance and the general shape of the simulated trees. As a second line of evaluation, we can collect numerical data during and after simulations. For this study, Figs 5 and 6 present simulated sugar maple saplings. Table 4 and Figs 7–9 introduce data describing the general shape and dimensions of the saplings.

Simulations with saplings growing in a forest gap started with two similar growing conditions in open gaps G2 and G4 in Mount St. Hilaire and in Duchesnay respectively (Fig. 5B and C). The trees produced are similar in appearance and no significant differences in growth were observed, but the sapling in G2 appears more vigorous due to slightly better radiation conditions. The third simulation in a closed gap, G1, in Mont St. Hilaire shows less growth due to decreased light (Fig. 5A). The fourth simulation in a closed gap (G3) in Duchesnay is interesting because it models fairly low light conditions (Fig. 6A). It was not sufficient to

TABLE 4. Simulated sugar maples in gaps G1-G5

Location	Gap	Age (years)	L (m)	LBP (m)	TLA (m ²)	WRB (m)
Duchesnay	G3 ^a	10	1.52	0.41	0.10	0.004
	G4	10	3.69	1.66	1.01	0.013
	G5	10	3.50	2.88	3.73	0.023
Mont St. Hilaire	G1 ^b	10	2.86	1.06	0.13	0.012
	G2	10	3.57	2.00	1.43	0.016

L, Length; LBP, longest projection length of the branches; TLA, total area of the leaves; WRB, wood radius at base.

^a $p_0 = 0.0018$, $m_f = 0.16$, $m_r = 0.400$, $m_s = 0.02$.

^b $p_0 = 0.0009$.

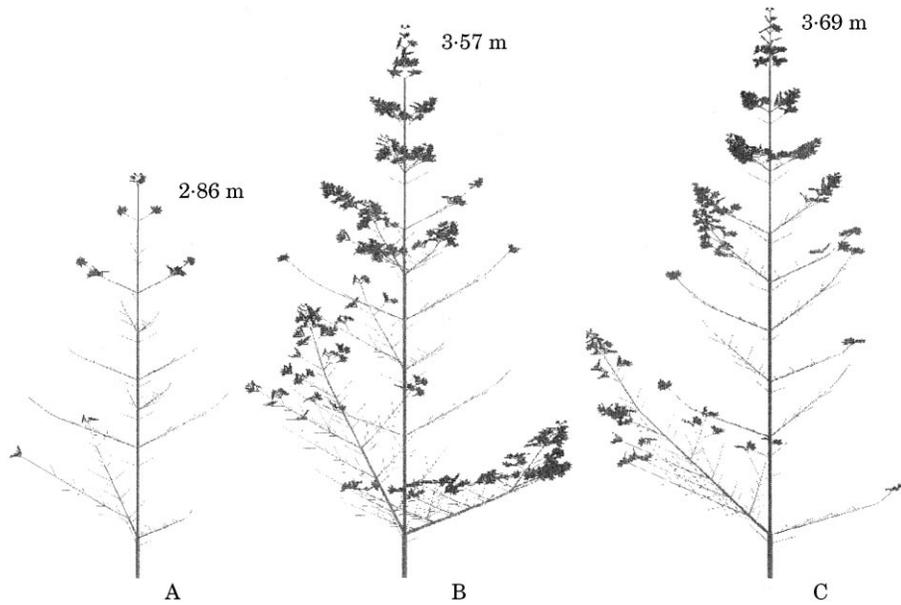


FIG. 5. Three 10-year-old sugar maple saplings. A, Mont St. Hilaire G1. B, Mont St. Hilaire G2. C, Duchesnay G4.

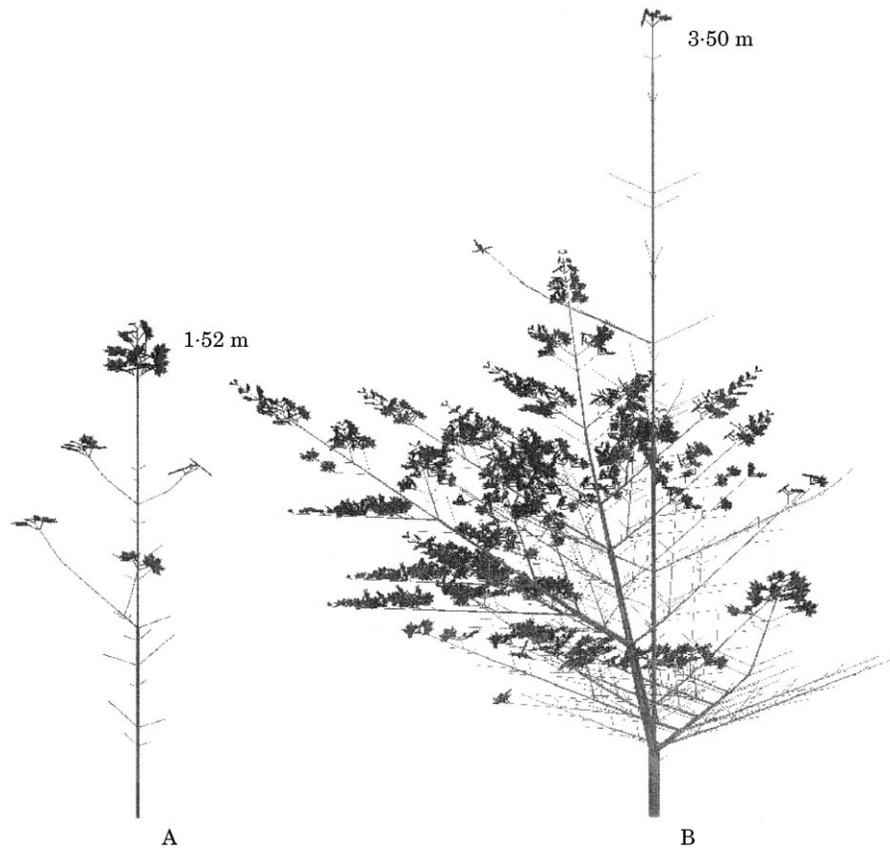


FIG. 6. Two 10-year-old sugar maple saplings. A, Duchesnay G3. B, Duchesnay G5.

increase the photosynthetic efficiency alone; we also had to decrease the respiration rates noticeably to simulate sapling survival for 10 years in such a radiation regime.

To compare simulated and real trees, we utilized data reported by [Messier and Nikinmaa\(2000\)](#). In this study,

approx. 80 sugar maple saplings growing in a variety of light regimes in an old-growth stand at Duchesnay were measured. To assess the taper curve relationship we selected two trees M1 and M2 ([Fig. 7](#)) that grew in less than 30 % light and were 10 years old. The larger sapling M1 currently

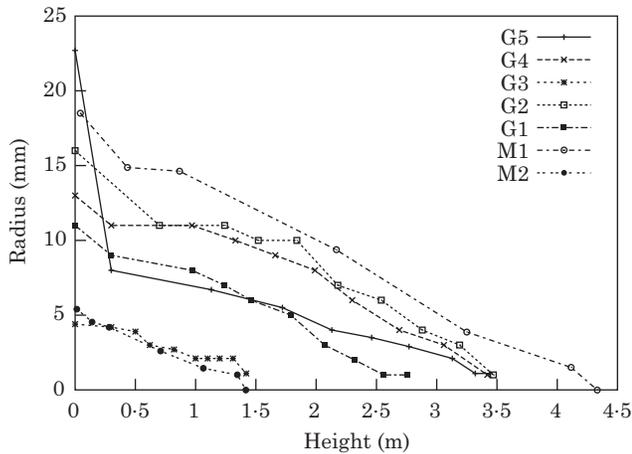


FIG. 7. Taper curves for two measured (M1 and M2) and five simulated sugar maple saplings in gaps G1–G5. M1, Duchesnay, 6% light at the time of measurement, age 10 years. M2, Duchesnay, germinated and grown in 5% light, age 10 years.

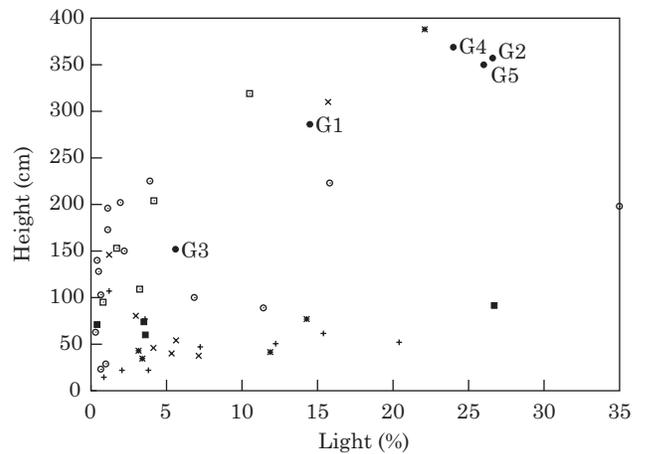


FIG. 8. Height of the 46 measured (Duchesnay) and the five simulated (G1–G5) sugar maple saplings in different light conditions. The age of the measured saplings was: < 9 years (+), 9 years (x), 10 years (*), 11 years (□), 12 years (■) and > 12 years (○).

received only 6% light, but it had developed in a gap created some years prior to our measurements; presumably the present light regime was more shaded than had been the case during initial growth for sapling M1. The taper curves for sapling M2 and the sapling simulated in gap G3 agree well.

Data from Messier and Nikinmaa (2000) and other unpublished data at Duchesnay include height variation from 0.2 m to 4 m for 9- to 12-year-old sugar maples in less than 5% light up to 25% light (Fig. 8). The simulated trees are within the observed size variation, but they tend towards the upper limit.

Common to sugar maple simulations in gaps G1–G4 is that saplings suffer from lack of light. The fifth simulation in gap G5 at Duchesnay demonstrates how LIGNUM could be used to consider ‘what if’ questions in studying the survival of sugar maple saplings in forest gaps. Notice that the growth of the sapling is remarkably different in G5 (Fig. 6B) compared to cases G2 and G4. There is only a small difference in height growth but the gap opening has led to a much bushier sapling in G5. The growth of the lower branches has also caused a butt swell which is clearly visible in Fig. 7. Thus, the model suggests that not only the total amount of light but also the directional distribution of the light affects sugar maple growth.

Finally, total leaf areas for the saplings were also available (Messier and Nikinmaa, 2000) to compare simulated saplings to measured ones (Fig. 9). In these comparisons, the sum of the areas of leaves correlates well for the simulated and real saplings, except in G5.

DISCUSSION

LIGNUM has been previously implemented for Scots pine (Perttunen et al., 1996) and Jack pine (Lo et al., 2000). The former study established the basic model structure for coniferous trees and the latter showed the generality of the conifer version of the model by successfully redefining the parameter values for Jack pine. This study has defined the basic model structure for broad-leaved trees and shown

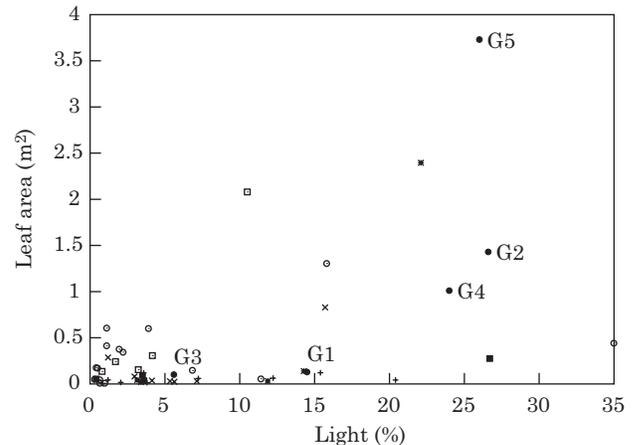


FIG. 9. Leaf area of 46 measured (Duchesnay) and five simulated (G1–G5) sugar maple saplings in different light conditions. The age of the measured saplings was: < 9 years (+), 9 years (x), 10 years (*), 11 years (□), 12 years (■) and > 12 years (○).

its utility by calibrating the model specifically for understorey sugar maple saplings.

As functional-structural models (FSM) are applied to new species, it is important to capture simultaneously the essential features of structural development and the main physiological functions producing the material for growth. Our results showed that the structural description originally designed for conifers is general enough to be applied to broad-leaved species. It was generally possible to use existing literature to parameterize the model (Mohren, 1987; Zogg et al., 1996; Reich et al., 1998; Goulcet, 1999; Beaudet et al., 2000), although sapwood senescence is poorly understood for sugar maple. There are some estimates for fine root senescence (Nadelhoffer and Reich, 1992; Hendrick and Preitzer, 1993, 1996) but to take advantage of these we need to refine our description of the root dynamics to include at least the division between fine and coarse roots. Despite the problems mentioned, tree

growth estimates based on reported physiological parameters, empirical shoot growth rules and allometric relationships between shoot growth and growth in other parts of tree were within the range observed in similar conditions (Messier and Nikinmaa, 2000). The crown architecture also responded to variation in the light climate in a logical manner.

The main attraction of FSM in studying sapling behaviour in scenarios involving gap regeneration is that these models are, in principle, capable of capturing subtle differences in resource allocation to structural growth and their consequences for future seedling performance (Sievänen *et al.*, 2000). Differences in resource allocation may be more important determinants of seedling survival than production differences *per se* (Körner, 1991; Küppers, 1994; Sims *et al.*, 1994). Functional-structural models also represent the spatial distribution of plant organs realistically, which is an important aspect in whole-plant resource uptake (Kellomäki *et al.*, 1985). An FSM can also fully capture the limitations set by, for example, the bud bank on the response of a tree to changing environmental conditions. Accounting for this type of small variation in tree response is particularly important when trees are growing close to their survival limit (Beaudet and Messier, 1998; Messier and Nikinmaa, 2000).

Architectural development in LIGNUM presently arises in a set of empirically determined rules that give the (relative) growth of new segments restricted by the whole tree carbon balance. The number of tree segments that potentially develop is determined by the bud population. The number of axillary buds formed on each segment depends on segment size (Goulet, 1999). The segment growth rules give relative growth as a function of the segment light conditions and position within the crown (Goulet *et al.*, 2000). Although the growth rules are empirical regressions, functional aspects were considered in their derivation (Goulet *et al.*, 2000). Results of the simulation show that the approach is flexible enough to be applied to broad-leaved trees and conifers. A great deal of crown plasticity can be captured with the approach while the requirement for carbon balance guarantees that growth remains within feasible limits.

Although the allocation of photosynthates is controlled centrally in LIGNUM [eqn (14)], the vigour index introduces a positive feedback mechanism in branch growth [eqn (17)] that leads to development of only a few major branches and suppression of smaller ones. Such development has been observed by Room *et al.* (1994). The factors influencing the initial development of dormant buds into segments also have a fundamental influence on the shape of the crown. In this sense our simulations were very rigid since we allowed no variation in bud release. The rather regular crown forms obtained reflect our working rule that only the two uppermost, opposite buds on a segment would develop. More variable functions allowing more variable bud release, including some element of stochasticity, could improve the model for studies of seedling behaviour in diverse understorey environments. The possibility of splitting growth into deterministic and stochastic components is especially desirable since this could allow investigation of

how overall growth potential interacts with different degrees of browsing or with other direct damage in influencing seedling performance.

LIGNUM is one of the first models to attempt to link detailed tree architecture development with tree physiology. The improvement of our approach over strictly architectural models lies in the fact that the growth of the simulated tree results from measurable physiological processes. The rich field of ecophysiological studies then becomes available to estimate seedling responses to a variety of environments, as was also preliminarily demonstrated in this work. The improvement in comparison to traditional process-based models is that tree architecture and ontological development are explicitly considered. For example, different formulations of flushing of buds or number and orientation of leaves along the shoots (the terminal tree segments) will eventually lead to very different growth patterns at the whole tree level. These types of interactions cannot be appreciated using very simple structural representations of the tree.

It is clear that our present application of LIGNUM for sugar maple growth and architecture development has deficiencies. There are still rather crucial shortcomings in our understanding of, for example, factors determining the activation of buds. However, the model offers opportunities to analyse the influence of various formulations of bud release on the overall development of the tree. For the sake of simplicity, and due to rather limited understanding of factors influencing the source-sink dynamics, we used empirical rules governing carbon allocation that attempt to mimic the maintenance of functional balance within the tree. This is an over-simplification and rigorous testing needs to be carried out to ascertain under which conditions the assumption is justified. However, the explicit structural description of a tree facilitates linking of the developmental processes to resource uptake and transport within tree and needs to be pursued further.

Various options for modelling the tree in an FSM-framework exist, but all are based on similar principles derived from botanical knowledge including LIGNUM. The L-system formalism is probably the strongest method for describing the structural development of trees in particular. However, whether L-systems can handle effectively the functional features of large saplings and mature trees remains to be tested. The parallel semantics of the L-systems may be computationally too costly when describing, for example, nutrient flows in a tree. The present representation of a tree in LIGNUM allows efficient (linear time), species-specific implementations in modelling metabolic processes, and this may in fact be the most beneficial approach to modelling trees in the long run.

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