ELSEVIER

Forest Ecology and Management 150 (2001) 279–291

Forest Ecology and Management

www.elsevier.com/locate/foreco

Adaptation of the LIGNUM model for simulations of growth and light response in Jack pine

Ernest Lo[a,b,*], Zhang Ming Wang[b], Martin Lechowicz[b], Christian Messier[a], Eero Nikinmaa[c], Jari Perttunen[d], Risto Sievanen[d]

[a]*Groupe de Recherche en Écologie Forestière interuniversitaire (GREFi), Université du Québec à Montréal, C.P. 8888, Succursale Centre-Ville, Montréal, Que., Canada H3C 3P8*
[b]*GREFi and Department of Biology, McGill University, 1205 Docteur Penfield Ave., Montreal, Que., Canada H3A 1B1*
[c]*Department of Forest Ecology, University of Helsinki, P.O. Box 24, 00014 Helsinki, Finland*
[d]*METLA, Vantaa Research Center, PB 18, 01301 Vantaa, Finland*

Received 22 November 1999; accepted 24 July 2000

Abstract

LIGNUM is a whole tree model, developed for *Pinus sylvestris* in Finland, that combines tree metabolism with a realistic spatial distribution of morphological parts. We hypothesize that its general concepts, which include the pipe model, functional balance, yearly carbon budget, and a set of architectural growth rules, are applicable to all trees. Adaptation of the model to *Pinus banksiana*, a widespread species of economic importance in North America, is demonstrated.

Conversion of the model to Jack pine entailed finding new values for 16 physiological and morphological parameters, and three growth functions. Calibration of the LIGNUM Jack pine model for open grown trees up to 15 years of age was achieved by matching crown appearance and structural parameters (height, foliage biomass, aboveground biomass) with those of real trees. A sensitivity study indicated that uncertainty in the photosynthesis and respiration parameters will primarily cause changes to the net annual carbon gain, which can be corrected through calibration of the growth rate. The effect of a decrease in light level on height, biomass, total tree branch length, and productivity were simulated and compared with field data. Additional studies yielded insight into branch pruning, carbon allocation patterns, crown structure, and carbon stress. We discuss the value of the LIGNUM model as a tool for understanding tree growth and survival dynamics in natural and managed forests.

Keywords: Whole-tree growth model; Tree architecture; *Pinus banksiana* Lamb.; Forest dynamics; Carbon gain; Light interception

1. Introduction

Tree growth models of crown architecture, that include both physiological and morphological processes, are useful in understanding tree growth and survival in dynamic environments (Kurth, 1994; Takenaka, 1994; Kellomaki and Strandman, 1995; Perttunen et al., 1996; de Reffye et al., 1997; Perttunen et al., 1998); these models are capable of representing the many important causal linkages between physiology, architecture, and the environment. For example, trees growing in the understory and in gaps during their establishment phase exhibit complex combinations of responses to the light environment and the

---

[*] Corresponding author: Tel: +1-514-987-3000/ext. 0278; fax: +1-514-987-4647.
E-mail address: c1344@er.uqam.ca (E. Lo).

PII: S0378-1127(00)00587-9

presence of neighboring plants. These responses include changes in biomass allocation, morphology, leaf orientation, and leaf photosynthetic capacity (Givnish, 1988; Messier et al., 1999). Greater understanding of tree growth dynamics during establishment through the use of a whole-tree growth model will lead to improved parameterization and construction of stand level models, and improved prediction of the effects of disturbance and silvicultural interventions.

As a first step towards the modeling and understanding of tree growth and survival in the boreal and temperate forests of Eastern Canada, we will adapt the model LIGNUM (Perttunen et al., 1996, 1998) to simulate Jack pine (*Pinus banksiana* Lamb.) grown in the Abitibi region of Que. (48°22′N, 79°22′W). Pines will be simulated to a maximum age of 15 years which represents their establishment phase and is a period over which the large part of the mortality caused by the dynamics of growth and competition occur. LIGNUM was originally developed for Scots pine (*Pinus sylvestris* L.) in Finland. The model combines tree metabolism with a detailed three-dimensional description of crown architecture. Foliage, sapwood, and root biomass partitioning and growth are accounted for as well. In general, process based models have large numbers of highly specific parameters and are difficult to apply to species and environments other than the ones for which they were designed (Korzukhin et al., 1996; Aber, 1997; Landsberg and Gower, 1997). We demonstrate the feasibility of converting LIGNUM to another species (albeit a closely related one), and environment. The conversion of LIGNUM entails three tasks, which define the objectives of the present paper. The first is the determination of a set of Jack pine input parameters for the model. Next, the behavior of the model must be assessed through a calibration and a sensitivity study. Finally, an initial evaluation of the Jack pine version of LIGNUM can be done through simulations of tree growth under varying light conditions.

2. Description of the LIGNUM model

Model trees consist of tree segments that each represent a year's extension growth, linked by branching points. These tree segments are composed of sapwood and heartwood, and covered with foliage. They form the basic unit of the three-dimensional crown structure. Buds are produced at the apices of segments and specify the directions for new growth. Roots are treated as an aggregate sink of carbon and have no spatial structure. The spatial structure of a model tree crown is depicted in Fig. 1a, where the tree segments are represented by line segments.

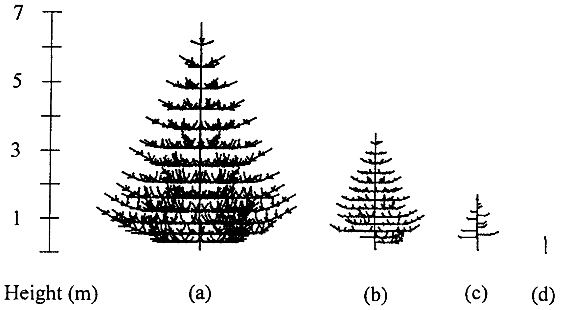

Fig. 1. Images of simulated Jack pines: (a) represents a pine simulated under open light conditions; (b–d) represent simulation results for a decreasing light level gradient. The light levels are 50, 25, and 12.5% of open light conditions, respectively.

Light interception of the crown is treated in detail. The solar radiation (in MJ) is calculated from all directions for each tree segment. The attenuation of the radiation by intervening segments is determined geometrically and through the use of previously developed models of light extinction (Oker-Blom and Smolander, 1988). Annual photosynthetic production by each segment is assumed to be linearly proportional to the annual intercepted radiation. The production from all the segments is summed over the entire tree. At present, the light distribution of a standard overcast sky (with no azimuthal variation) is used (Ross, 1981). The total incoming photosynthetically active solar radiation flux, for the duration of the growing season, is set to 1450 MJ/m^2 per year, based on a 15 years average taken near the Abitibi region (Environment Canada, 1984).

The main assumptions of the model are: (1) a carbon budget is determined each year that includes photosynthesis, respiration, senescence, and growth of foliage, sapwood, and root tissue. (2) The time step of the model is 1 year so that the structure of the tree is updated only at the end of each growing season. (3) Carbon produced by the tree is pooled and then redistributed to growth areas, according to their local environment. (4) The pipe model hypothesis

Table 1
LIGNUM physiological parameters

Parameter description	Symbol	Unit	Value	Source
Photosynthesis rate	P_r	kg C/MJ per year	0.0012	Stewart and Hoddinott (1993)
Maintenance respiration rate of foliage	M_f	kg C/kg C per year	0.89	Ryan (1995)
Maintenance respiration rate of sapwood	M_s	kg C/kg C per year	0.0468	Lavigne (1996)
Maintenance respiration rate of roots	M_r	kg C/kg C per year	0.24	Perttunen et al. (1996)
Senescence rate of sapwood	S_s	kg C/kg C	0.04	Yang and Hazenberg (1991)
Senescence rate of roots	S_r	kg C/kg C	0.33	Perttunen et al. (1996)
Needle mass–tree segment area ratio	A_f	kg C/m^2	0.4625	This paper
Foliage mass–root mass ratio	A_r	kg C/kg C	1.0	This paper
Fraction of heartwood in tree segments	X_i	kg C/kg C	0.16	This paper

Table 2
LIGNUM morphological parameters

Parameter description	Symbol	Units	Value	Source
Density of wood in tree segments	ρ	kg/m^3	361.7	Hegyi (1969); Gonzalez, (1990)
Initial length of seedling	L_i	m	0.075	Beaufait (1960); Rudolph and Laidly (1990)
Branch angle	A_b	°	57	This paper
Needle insertion angle	A_n	°	56	This paper
Length–radius ratio for tree segments	L_r	m/m	81.48	This paper
Tree segment shortening factor	q	–	0.4	This paper
Needle length	L_n	cm	3.24	This paper

(Shinozaki et al., 1964) and the principle of functional balance (Mäkelä, 1986) are used to describe the biomass relationships between foliage and sapwood, and foliage and roots. (5) The structure of the crowns follows from an assumption of fixed branching angles and the whorled branching architecture typical of pines. A more thorough description of the model is given by Perttunen et al. (1996, 1998). LIGNUM is implemented with the C++ programming language under the UNIX operating system. It was installed on a Silicon Graphics Indy Workstation, and run remotely from a 233 MHz Pentium PC.

3. Parameter measurement and estimation

As discussed, conversion of the model to Jack pine requires the measurement and/or estimation of its 16 parameters and three functions. These parameters and functions will be described along with the method used to determine their values. Note that the parameterization applies to, and is derived from, site environmental conditions particular to Jack pine of 1–15 years of age, growing in the boreal forest of the Abitibi region, and for climatic conditions from a representative year (1984).

The results are summarized as well in Tables 1 and 2 (where the parameters are grouped in physiological and morphological categories), and Fig. 2a–c. Note that the parameter values that were used for the final calibrated version of the model are shown. LIGNUM uses carbon mass (kg C) as its units. A conversion ratio of 0.5 is used to convert from dry biomass to carbon mass when necessary.

The parameters that follow were obtained from the existing literature on Jack pine metabolism and structure.

3.1. Net photosynthesis (P_n): 0.0012 kg C/MJ per year

The yearly photosynthetic production of a tree segment is equal to the intercepted light multiplied by the coefficient P_n which is determined from an integration over light and temperature variations for the duration of a growing season. We use an equation

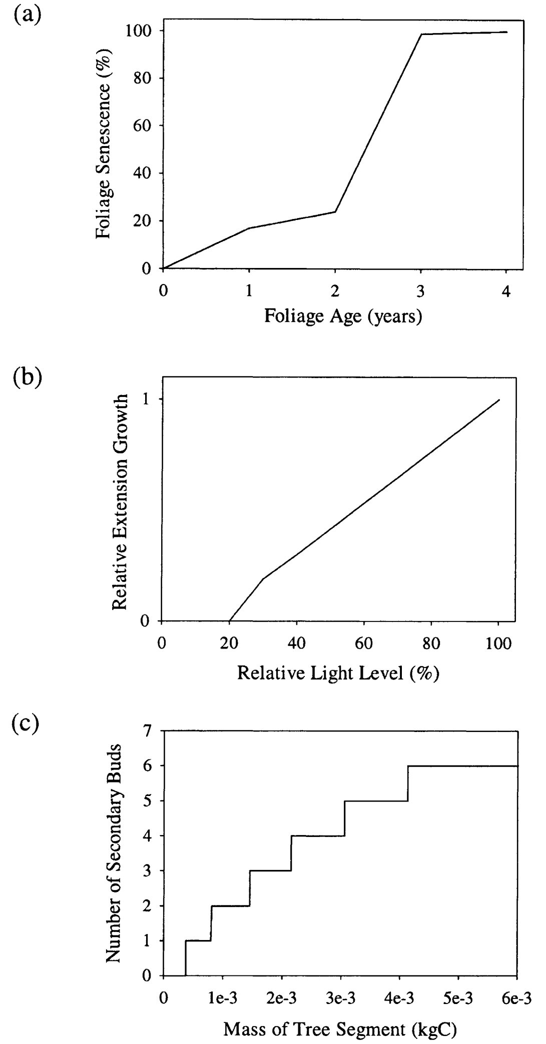

Fig. 2. Functions required by the LIGNUM model as input: (a) the amount of foliage senescence vs. age of foliage (P_f); (b) the relative extension growth of a segment vs. relative light level (f_l); (c) the number of secondary buds vs. tree segment foliage mass (f_{nb}).

derived by Stewart and Hoddinott (1993) for Jack pine, which describes variation with light (Q) at an optimum temperature of 28°C: $P_n = a(1 - e^{(b-cQ)})$. Q represents specifically the photosynthetically active radiation flux (PAR) with units of μmol/m^2/s. Linear interpolation between this value and a value of 0 at 0°C is used to account for variations with temperature. Hourly light variation and mean daily temperature data were obtained from Environment Canada (1984) for Normandin, Que., (48°51′N, 72°32′W) and Val d'Or (48°04′N, 77°47′W), respectively. The growing season was defined as all the days in a year with a mean daily temperature ≥5°C.

3.2. Foliage maintenance respiration (M_f): 0.89 kg C/kg C per year

We used a foliage maintenance respiration (M_f) rate of 1.7 μmol CO$_2$/kg of dry needles/s at 10°C from Ryan (1995). To correct for temperature effects, we used $Q_{10} = 2$ as in Ryan (1995) and integrated over the hourly mean temperatures for 1984 at Val d'Or, for the entire year. The respiration rate was set to 0 when the temperature was 0°C or lower.

3.3. Maintenance respiration of sapwood (M_s): 0.047 kg C/kg per year

Lavigne (1996) compared sapwood maintenance respiration (M_s) of Jack pine from southern (Nova Scotia and Maine) and northern (eastern Que.) seed sources planted in the Acadia Forest Experiment Station near Fredericton, NB, Canada. He estimated the annual total respiration measured in mature tissue and determined by theoretical methods. No differences were found between the two seed sources or the two methods. Therefore, the mean value of his estimates was used.

3.4. Root respiration rate (M_r): 0.24 kg C/kg C per year

Root respiration (M_r) includes that of both fine and coarse roots. As no references were available for Jack pine, the respiration rate for Scots pine (Perttunen et al., 1996) was used.

3.5. Sapwood mortality (S_s): 0.041

Sapwood mortality (S_s) is the proportion of sapwood that turns into heartwood in the stem each year. The mean value with age of the quantity (heartwood area)/(heartwood area + sapwood area), derived from the empirical equations of Yang and Hazenberg (1991) was used. An average was taken over the ages from 6 to 15 years, as heartwood was observed to begin to form in trees at about 6 years of age.

3.6. Root mortality (S_r): 0.33

Root mortality (S_r) is the fraction of root mass that turns over each year. No references were available for Jack pine, so the Scots pine value was used (Perttunen et al., 1996).

3.7. Wood density (ρ): 361.7 kg/m^3

Hegyi (1969) sampled 20 trees from different natural forest conditions in Wells township, Algoma district, Ont. The mean stem wood density (ρ) was 327 kg/m^3 on a green volume basis, and following Gonzalez (1990), this becomes 361.7 kg/m^3 on a dry wood volume basis.

3.8. Initial length of segment (L_i): 7.5 cm

The initial length (L_i) represents height of the tree after 1 year of growth. The value is specified from the average observed height of Jack pine seedlings ranging in age from 3 months to 1.5 years (Beaufait, 1960; Rudolph and Laidly, 1990).

The following data was collected in April 1997, from a plantation about 15-year-old in the Les Cedres area, near Montreal (45°20′N, 73°54′W). Trees in open growing conditions were chosen. Mean height and DBH of the plantation were about 6 m and 12 cm, respectively.

3.9. Branch angle (A_b): 57.0°

The angles between 1-year-old branches and the main stem were measured for 15 trees. The mean of all branch angle (A_b) measurements was used.

3.10. Needle angle (A_n): 56.6°

The mean needle angle (A_n) was calculated from measurements of needles on different branches taken from seven trees.

3.11. Foliage mortality function P_f(age)

Foliage mortality function P_f(age) describes the needle mortality rate with age. The percentage of lost (i.e. dead) needles on a given tree segment increases each year up to the fourth year, when all of the needles are lost. We counted the needle scars (without needles) and the total number of needle fascicles on different branches for different ages of seven trees. The number of needles lost divided by the total number yields the data for the function (see Fig. 2a).

The data that follow was collected from a stand located in Lac Duparquet, in the Abitibi region (48°9′N, 79°8′W). Seventeen Jack pine trees between 5 to 15-year-old were selected over a wide range of sizes and light availabilities. The mean age, height, basal diameter, and growing season percent photosynthetic flux density (PPFD) were 12 years, 83.6 cm, 10 cm, and 51%, respectively.

3.12. Tree segment shortening factor (q): 0.4

The shortening factor determines the degree of apical dominance in the crown. Branches with higher (Gravelius) order are increasingly shortened by an amount determined by the value of q. The shortening factor was measured from the ratio between the length of current year apical extension growth at the tops of crowns and their immediate side branches.

3.13. Needle mass–tree segment area relationship (A_f): 0.4625 kg C/m^2

The ratio between needle (or foliage) mass and sapwood cross section is assumed to be constant according to the pipe model theory and in agreement with previous field studies (Nikinmaa, 1992; Mäkelä, 1997). Dry needles from the leaders of each tree were weighed to the nearest 0.01 g. To compute the tree segment area, the leader was treated as a cylinder. Diameter measurements were taken at the base of the leader and at the base of the terminal buds, and the mean value was used. The heartwood fraction was accounted for (see Section 3.17 below).

3.14. Foliage–root relationship (A_r): 1.0

The ratio of carbon allocated to roots to that allocated to foliage is assumed to be constant according to the principle of functional balance and supported by experimental measurements (Brouwer, 1962; Santantonio et al., 1977; Brouwer, 1983). Our estimate was made from measurements of three trees <1 m in height.

3.15. Length/radius ratio for a new tree segment (L_r): 81

New tree segments have a fixed length-to-radius ratio. This ratio was calculated from the lengths and basal radii of the 17 tree leaders.

3.16. Needle length (L_n): 32 mm

Needles were scanned with a flatbed scanner and their lengths determined using commercial software (MacNEEDLE, Régent Instruments Inc., Québec, Canada). The mean value of samples taken from the leaders of all the 17 trees was used.

3.17. Fraction of heartwood in a new tree segment (X_i): 0.16

This fraction is the area of pith divided by the total area, at the base of a new tree segment. Diameters of tree segments taken from the trees were measured to the nearest 0.01 mm with a micrometer (Disc Instrument, USA). The mean value was used to determine the area fraction.

3.18. Degree of interaction function $f_l(I_p)$

This function describes the relationship between extension growth and relative light level (I_p). It was determined from measurements of current year leader growth and light level. The function is shown in Fig. 2b.

3.19. Bud number function $f_{nb}(W_s)$

The number of secondary buds produced at an apical meristem is a function of the tree segment foliage mass (W_f). There is always at least one bud (the apical bud). Buds on the leaders of the 17 trees were counted, and their needle dry masses were obtained to get the data for this function, which is shown in Fig. 2c.

4. Model calibration

Calibration of the Jack pine version of LIGNUM, consisted of a qualitative assessment of crown shape and structure, and a quantitative fitting of tree height, foliage biomass, and total aboveground biomass, with field data. The process entailed the refinement and re-evaluation of the model input parameters from the original values for Scots pine to the current values listed above. Fig. 1a depicts the calibrated simulation result for an open grown Jack pine of 15 years. Features that are typical of Jack pine are reproduced by the model: the layered appearance of the crown (each layer originates from a whorl on the main stem), the apical dominance of the main stem, and the overall crown shape. The density, orientation, and spacing of higher order branches also has a realistic appearance, as confirmed qualitatively by field ecologists from two tree ecology laboratories. Note that the images in Fig. 1 show only the branches of the tree (as straight lines of fixed diameter) and so are indicative of branching architecture only.

The shortening factor q has the greatest effect on the crown appearance. The initial estimate of this value (0.47) may have been obscured by a bias in crown position, i.e. measurement at the leader may not reflect the average apical dominance throughout the entire tree. A reduction in the value of q to 0.4 yielded crowns that were qualitatively satisfying.

Graphs of height versus age for simulated and real trees are shown in Fig. 3. The field data were obtained from several data sets and include a height measurement data set Sheedy, 1990; Sheedy, 1996a,b) and an empirical height regression equation (Longpré et al., 1994, p. 30), but all taken from Jack pine growing in the Abitibi region. The results depicted in Fig. 3 show

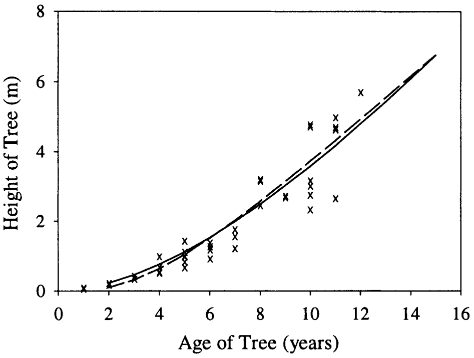

Fig. 3. Jack pine height curves. Solid line denotes simulation results. Crosses denote height measurements obtained from the field. Dashed line denotes results of the stand height regression equation derived by Longpré et al. (1994).

a satisfactory match between the simulated trees and those measured in the field. Both the height achieved after 15 years of growth as well as the curvature of the growth curve are in agreement. An accelerating growth rate occurs in the first few years of growth; the acceleration then decreases past the 8th year. By the 15th year, the height curve is almost linear. This growth trend is likely caused by the increase in proportion of non-photosynthetic biomass (sapwood and root) that occurs in simulated trees and which has also been reported in field studies.

In order to quantify the comparison between model simulation results and field data, the two were plotted against each other and a linear regression was performed. The goodness of fit (R^2) is a measure of how closely the two data sets match in terms of their curvature and/or trend. The slope value (β) is a measure of the numerical closeness of the data, with a value of 1 indicating that the values are the same. For the comparison of model with field data, $R^2 = 0.962$, and $\beta = 1.2$; for the comparison of model with regression equation, $R^2 = 0.999$, and $\beta = 0.96$. These results as well as those of subsequent regressions which were done for each of the calibration and evaluation data sets, are also summarized in Table 3. Ter-Mikaelian and Korzukhin (1997) present a comprehensive review of biomass regression equations for 65 North American tree species including Jack pine. All of the equations use DBH as the single dependent variable in a power law expression, and describe the growth of trees in stands. The simulated Jack pine foliage, and total aboveground biomass versus DBH produced by LIGNUM are compared to the results obtained using these regression equations. Foliage biomass versus diameter is shown in Fig. 4a and total above-ground biomass versus diameter is shown in Fig. 4b. The general growth trend in the biomass values match well between the model and the regression equations, as can be seen from the Fig. 4a and b and indicated by the R^2 values of the regression results (Table 3). Some variations in the absolute numerical values between the simulation and equations are indicated by Fig. 5 and by the β values of the regression, as would be expected from differences in site conditions. This is evident from the significant differences between the equations themselves.

Some variations in value are expected between the simulation and equations, and also between equations themselves due to differences in site conditions. The discrepancy near the origin in Fig. 4a is caused by the artificial constraint that the regression equation pass through the origin. The simulated total above-ground biomass (Fig. 4b) is significantly higher than all of the regression curves. This is likely caused by a lack of pruning in model trees, especially of the heavy lower branches (this issue is discussed below). Adjustments to the model were required to bring simulated height and biomass into agreement with field data, as initial simulations produced trees that were taller and with significantly higher biomass. The starting tree height represented by the parameter L_i was reduced from 0.15 to 0.075 m, to match field measurements of seedlings; this parameter was at first a fixed number within the model. The value for the root:foliage allocation ratio, A_r,

Table 3
Linear regression results for the model calibration and evaluation

	Regression description	R^2	Slope
Fig. 3	Height: model vs. field measurements	0.962	1.21
Fig. 3	Height: model vs. regression equation	0.999	0.96
Fig. 4a	Foliage mass: model vs. data set 1	0.994	1.27
Fig. 4a	Foliage mass: model vs. data set 2	0.977	1.45
Fig. 4a	Foliage mass: model vs. data set 3	0.994	0.98
Fig. 4b	Above-ground biomass: model vs. data set 1	0.994	1.44
Fig. 4b	Above-ground biomass: model vs. data set 2	0.996	1.53
Fig. 4b	Above-ground biomass: model vs. data set 3	0.999	1.32
Fig. 4b	Above-ground biomass: model vs. data set 4	0.997	1.17
Fig. 5a	Height: model vs. field measurements	0.923	1.14
Fig. 5b	Above-ground biomass: model vs. data at age of 4 years[a]	0.917	1.46
Fig. 5b	Above-ground biomass: model vs. data at age of 6 years[a]	0.969	1.81

[a] Regressions for these cases were done on a log–log scale.

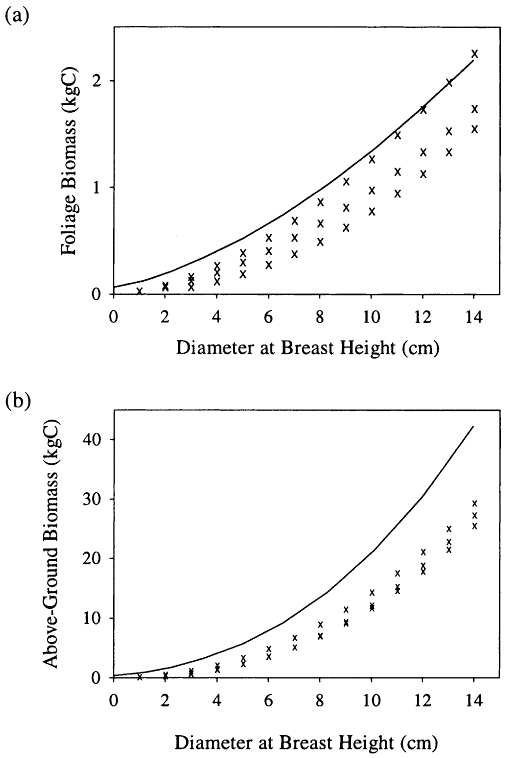

Fig. 4. Calibration curves for (a) Jack pine foliage biomass vs. DBH and (b) Jack pine total above-round biomass vs. DBH. Lines denote the simulation results; (×) indicates data generated by empirical biomass regression equations taken from Ter-Mikaelian and Korzukhin (1997).

was increased from 0.76 to 1.0, to more accurately reflect sandy (poor) soil conditions and root turnover effects.

The qualitative crown appearance and three structural parameters have been examined for model Jack pines and matched to those of trees growing in the field. For the structural parameters, the degree of fit between model and data as measured by linear regression yields R^2 values from 0.994 to 0.999. Each calibration component reflects a different aspect of tree growth and form, and together comprise an adequate calibration for initial simulation studies of growth and survival dynamics.

5. Sensitivity analysis

Sensitivity analyses of the model input parameters were done by varying the value of the parameter by ±25% of its original value. The corresponding degree of variation in height, above-ground biomass, and total branch length in simulated trees were then measured. The total branch length of a tree is a quantity readily

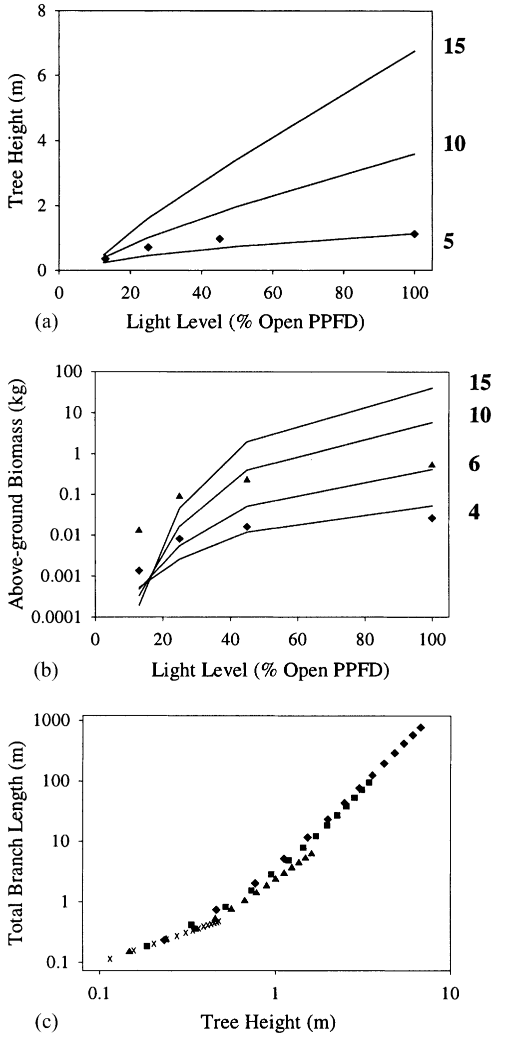

Fig. 5. (a) Simulated and measured variation in tree height with light level. Lines indicate LIGNUM simulation results. Each line is marked with a boldface number that represents the age of the tree; (◆) indicates data taken from Logan (1966) for 5-year-old trees. (b) Simulated and measured variation in tree above-ground biomass with light level. The lines indicate LIGNUM simulation results. Boldface numbers represent the age of the tree. Symbols indicate data taken from Logan (1966): (◆) represents 4-year-old Jack pines; (▲) represents 6-year-old Jack pines. (c) Variation in total branch length vs. height for varying light levels: (◆) PPFD = 100%; (■) PPFD = 50%; (▲) PPFD = 25%; (×) PPFD = 12.5%.

Table 4
Results of the sensitivity study in metabolic parameters[a]

	Foliage respiration[b] (%)	Photosynthesis[b] (%)	Foliage respiration[c] (%)
Height (+)	−2.5	+26.0	−7.0
Height (−)	+2.1	−25.3	+10.3
Biomass (+)	−7.5	+130.6	−38.8
Biomass (−)	+8.7	−70.3	+38.4
Branch length (+)	−4.0	+57.4	−26.5
Branch length (−)	+5.4	−55.4	+12.5

[a] (+) Denotes the change in a tree structural parameter that results from a 25% increase in a metabolic parameter (column headers), whereas (−) denotes the change corresponding to a 25% reduction.

[b] Values pertain to 15-year-old Jack pines simulated under open conditions.

[c] Results for a simulation using 25% PPFD.

calculated by the model from the tree data structure, and when plotted against tree height, is an indicator of crown density, apical dominance, and degree of self-shading.

The variables chosen for the sensitivity analysis were the physiological parameters of respiration and photosynthetic production, also referred to as the metabolic parameters of the tree. These parameters are the most difficult to measure accurately due to dependence on the environment (temperature, light, moisture) and the practical issues of in vivo measurement. A partial table of results is shown in Table 4, for the foliage respiration and photosynthetic production, for simulated open grown trees of 15 years.

The model is insensitive to variation in the foliage respiration — the variations produced in simulated trees are proportionately much smaller than the variations in the input parameter, over the three morphological indices. This result is explained by the fact that foliage respiration (and actually the total respiration as well), represents a relatively small fraction of the total carbon budget (see also the 100% PPFD case in Fig. 6). The model was also found to be even less sensitive to the sapwood and root respiration — these represent smaller contributions to the total respiration.

Variation in the rate of photosynthetic production (P_n) has a significantly larger impact on simulated trees. Biomass and branch length variations are >25%.

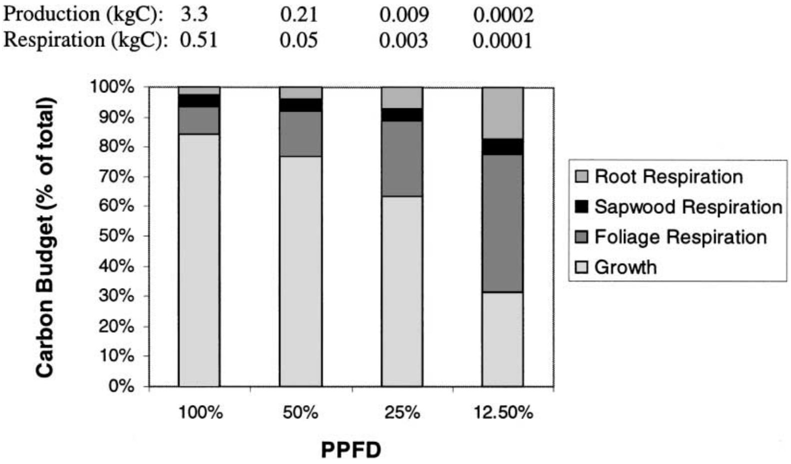

Fig. 6. Yearly carbon budget for a 10-year-old model Jack pine for four light levels. The amounts are expressed as percentages of the total photosynthetic carbon production of the tree. Absolute annual amounts of carbon (in kg) for total respiration and photosynthetic production are listed above the graph.

Photosynthetic production is significantly greater than respiration costs (see the 100% PPFD case in Fig. 6); the annual increment in both biomass and branch length depend directly (linearly) on the net carbon production rate per year. Annual differences are then compounded over the 15 years of tree growth.

Analysis of the model has shown that variation in all of the metabolic parameters can be understood in terms of their effect on increasing or reducing the net carbon production rate per year. Pronounced instabilities or discontinuities in the model were not observed. The model is also expected to be robust towards uncertainty in the metabolic parameters, as these uncertainties should cancel to a degree. The overall carbon budget of the tree can be set correctly through the calibration process.

The parameters that determine crown architecture (q, $f_l(I_p)$) were investigated as well. Sensitivity in crown form with q was observed. However, deviations in the value of q are readily correctable, as the crown quickly assumes an unrealistic looking branching architecture.

6. Model evaluation and the effect of varying light level

The calibrated model was tested under a new set of conditions represented by varying the light level. A simulation experiment was done where Jack pine were grown under four light levels: 100, 50, 25 and 12.5% of the total PPFD of open conditions, respectively. The distribution of light was unchanged. The crown appearance, height, biomass, and total branch length were monitored. Images of the resulting tree crowns at 15 years of age are shown in Fig. 1a–d. The response of the model is initially satisfying as a reduction in light level over an order of magnitude, leads to a continuous reduction in growth, and in tree crowns that look realistic. Jack pine crowns observed in the field however, especially under low light conditions (i.e. in the understory), tend to be more cylindrical in shape and less triangular. This is a consequence of the pines' ability to prune branches, typically those that are lower on the crown and have reduced productivity due to self-shading. It is likely that the lower branches in the model Jack pines are non-productive in that their respiration costs exceed their production capacity. Both crown efficiency and realism of form would likely be improved by a pruning algorithm that removes unproductive branches.

The variation in tree height with light level is shown in Fig. 5a for three different ages. The responses are all approximately linear. A comparison is made with a light level study performed by Logan (1966) on 5-year-old Jack pine seedlings (data points are shown in the figure). These seedlings were grown in the open and in light-screening shelters, in well irrigated sandy loam near Petawawa, Ont. (48°9′N, 79°8′W). Height variation matches those of the model well overall, with the linear regression yielding $R^2 = 0.966$ and $\beta = 0.838$. The decrease in height with light level of the measured seedlings however is slower overall.

Total above-ground biomass is shown in Fig. 5b, where the biomass is plotted against light level for 4 and 6-year-old seedlings Logan (1966). The regression statistics for this case indicate significant deviation between model and field data. For the 4-year-old pines, $R^2 = 0.917$ and $\beta = 1.464$; for the 6-year-old pines, $R^2 = 0.969$ and $\beta = 1.808$. As the regressions in this case were done on log–log scales, the slopes indicate that the shape of the biomass growth curves are significantly different. As was observed in the height data, the deviation between model and data occurs mainly as a reduced decrease in biomass with light for the real seedlings (as evidenced in Fig. 5b), though here the effect is much more pronounced. In simulated crowns, the rapid and nonlinear decrease in tree size with light level, is caused by the exponential nature of tree growth — increased biomass feeds back on itself through increased photosynthetic capacity. Therefore, we find that the growth rate of real seedlings is not completely explained by the exponential growth mechanism represented in the model. Real seedlings likely also change their shoot 'structure, specific leaf area and photosynthesic response to acclimatize to low light conditions (Messier and Nikinmaa, 2000).

The total crown branch length plotted against tree height is depicted in Fig. 5c. It is interesting to note that the relative growth rates between branch length and height are approximately equal over varying light levels, as indicated by the almost superimposed data points. Under reduced light, the model is expected to produce shorter segments (the $f_l(I_p)$ response to light) and, hence, fewer buds per segment (the f_{nb} response to segment size). However, this is offset by reduced yearly height increments that brings successive whorls or crown layers closer together. Prediction of crown branchiness variation with environment is of silvicultural interest (Raulier et al., 1998). Our results suggest that the ratio of branch length-to-tree height is fairly independent of light. This result is somewhat surprising and may reflect the linear dependence of growth from intercepted light in the model.

Model trees are found to regulate their above-ground biomass and architecture effectively. Decreased light levels result in lower production capacities, however, the total biomass is also reduced so that respiration requirements are lower as well, and there is a net carbon gain each year for allocation to new growth. The effect is presented in Fig. 6 which shows the carbon budget of the tree. Even at 12.5% light, the photosynthetic production exceeds respiratory losses by 20–30% despite extremely low absolute carbon production. It is expected, however, that further reductions in the light level would eventually drive the budget towards zero growth and, hence, tree death.

The growth of model trees is also expected to be more sensitive to variation in the respiration costs (or any other carbon sink) when grown under reduced light. This is indicated by the values of the third column of Table 4 which shows a repetition of the foliage respiration sensitivity study described earlier, but under shade conditions of 25% light. The resulting increased sensitivities can be explained by the increased significance of respiration costs to the carbon budget (see Fig. 6). In real trees, the same process may produce increased sensitivity under low light conditions to any kind of carbon stress (Givnish, 1988; Messier et al., 1999).

7. Conclusions

The LIGNUM model has been calibrated for Jack pine. This process was accomplished in the time span of one field season (the work amounted to about four person-months). It is believed that this would likely be the case for any of the common and commercially important tree species of eastern Canada which we are interested in modeling. The development of a more general set of rules for crown structure and branching would first be required, however, for deciduous hardwoods, and represents ongoing work (Landsberg and Gower, 1997; Aber, 1997).

Simulation of Jack pine for different sites would require calibration of the model against field data specific to those sites. Note that limitation of the model to the first 1–15 years of growth does eliminate some of the inherent variability in these parameters. The simulation of year-to-year climate variation for a given site is readily done by varying the value of the total light radiation and recalculation of photosynthesis and respiration rates from the temperature- and light-dependent equations (see Section 3). These studies are beyond the scope of the present paper but could be carried forth wherever growth, mortality, and management analyses involving Jack pine are being done. Work towards a more general version of the model that responds to climate change is also currently being developed (Berninger et al., 2000).

A sensitivity study indicates that the effect of uncertainties and errors in the model parameters can be minimized through the calibration process. In addition, the behavior of simulated trees varies continuously as the input parameters are varied, which indicates that the model operates in a stable regime in the vicinity of the chosen parameter values. Evaluation of the model through the light level study reveals several insights into Jack pine growth and development. Comparison of the results with field data also reveals shortcomings in the model and suggests areas where the model should be improved. These modifications can be readily added to the model due to its object oriented construction (Salminen et al., 1994; Perttunen et al., 1996).

The success in the present conversion of LIGNUM to Jack pine is a promising result for applying detailed process-based models for silvicultural purposes. Jack pine is a light demanding tree species whose abundance may be negatively influenced by reduction in light availability. The three-dimensional tree crown simulation and detailed light model in LIGNUM allows estimation of how variation in the seedling light environment influences its energy capture, resource allocation, and growth. The model, therefore, has direct implications towards the management of tree density in Jack pine stands by clarifying the mechanisms that produce desired individual tree growth rates, tree quality, and stand productivity.

The exact tracking of each tree segment allows us to follow, how different growing environments influence the size and distribution of the branches on the trunk. The model could also describe the influence of the growing environment on tree ring width distribution in the trunk cross section with tree height. Thus, there is the possibility to simulate the influence of environmental conditions on two of the most important timber quality indicators (i.e. branchiness and ring width).

Trees in the presented simulation studies were grown solitary, and in open or artificially decreased light climates. This undoubtedly influenced the crown shape development. In the real world, trees are always surrounded by other vegetation which produces a heterogeneous light field for the tree, where there is more shading from the sides than from above. The relative ease of parameterizing the model for different species, potentially allows us to simulate tree stand development with different species and size combinations. Such usage of the model would also make it an invaluable tool for estimating the influence of gap size and tree seedling species combination on the relative success of different species.

Acknowledgements

We would like to thank Yves Claveau for the collection and interpretation of the field data and for reviewing an earlier draft of the manuscript, Cynthia Claveau and Sylvain Parent for additional help with the field data collection, and Marc-Olivier D'Astous for work in the laboratory. Financial support for this work was provided by NSERC (National Sciences and Research Council of Canada), the NCE-SFM (Network Centres of Excellence in Sustainable Forest Management Network), GREFi, and The Academy of Finland, Research Grant No. 37090. This is University of Idaho, College of Natural Resources Experiment Station publications 916.

References

Aber, J., 1997. Why don't we believe in models? Bull. Ecol. Soc. Am. 78 (3), 232–233.

Beaufait, W.R., 1960. Influences of shade level and site treatment, including fire, on germination and early survival of *Pinus banksiana*. Michigan Department of Conservation, Forestry Division Technical publication no. 1.

Berninger, F., Nikinmaa, E., Sievänen, R., Nygren, P.A., 2000. Modelling of reserve carbohydrate dynamics, regrowth and nodulation in a N_2-fixing tree managed by periodic printings. Plant Cell Environ. 23 (10), 1025–1040.

Brouwer, R., 1962. Distribution of dry matter in the plant. Neth. J. Agric. Sci. 10, 361–376.

Brouwer, R., 1983. Functional equilibrium: sense or nonsense? Neth. J. Agric. Sci. 31, 335–348.

de Reffye, P., Fourcaud, T., Blaise, F., Barthélémy, D., Houllier, F., 1997. A functional model of tree growth and tree architecture. Silva Fennica 31 (3), 297–311.

Environment Canada, 1984. Monthly Radiation Summary 25.

Givnish, T.J., 1988. Adaptation to sun and shade: a whole plant perspective. Aust. J. Plant Physiol. 15, 63–92.

Gonzalez, J.S., 1990. Wood density of Canadian tree species. Forestry Canada Informational Report NORX-315.

Hegyi, F., 1969. A study of basic density variation in Jack pine. Can. Dep. Fish. For., Can. For. Serv., For. Res. Lab., Sault Ste. Marie, Ont., Intern. Rep, pp. 0–17.

Kellomaki, S., Strandman, H., 1995. A model for the structural growth of young Scots pine crowns based on light interception by shoots. Ecol. Model. 80, 237–250.

Korzukhin, M.D., Ter-Mikaelian, M.T., Wagner, R.G., 1996. Process versus empirical models: which approach for forest ecosystem management? Can. J. For. Res. 26, 879–887.

Kurth, W., 1994. Morphological models of plant growth: possibilities and ecological relevance. Ecol. Model. 75/76, 299–308.

Landsberg, J.J., Gower, S.T., 1997. Applications of Physiological Ecology to Forest Management. Academic Press, Toronto.

Lavigne, M.B., 1996. Comparing stem respiration and growth of Jack pine provenances from northern and southern locations. Tree Physiol. 16, 847–852.

Logan, K.T., 1966. Growth of tree seedlings as affected by light intensity. II. Red pine, White pine, Jack pine and Eastern larch. Department of Forestry Publication no. 1160, Canada.

Longpré, M.-H., Bergeron, Y., Paré, D., 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can. J. For. Res. 24, 1846–1853.

Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., Lechowicz, M., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29, 812–823.

Mäkelä, A., 1986. Stand growth model based on carbon uptake and allocation in individual trees. Ecol. Model. 33, 205–229.

Mäkelä, A., 1997. Structural-functional relationships in whole tree growth: resource allocation. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A., Warren, W.G. (Eds.), Process Modeling of Forest Growth Responses to Environmental Stress. Timber Press, Portland, OR, pp. 81–95.

Messier, C., Nikinmaa, E., 2000. Effects of light availability and sapling size on the growth, biomass allocation and crown morphology of understory sugar maple, yellow birch and american beech. Ecoscience 7 (3), 345–356.

Nikinmaa, E., 1992. Analyses of the growth of Scots pine; matching structure with function. AFF. 235, 1–68.

Oker-Blom, P., Smolander, H., 1988. The ratio of shoot silhouette area to total needle area in Scots pine. For. Sci. 34 (4), 894–906.

Perttunen, J., Sievanen, R., Nikinmaa, E., 1998. LIGNUM: a model combining the structure and the functioning of trees. Ecol. Model. 108, 189–198.

Perttunen, J., Sievanen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., Vakeva, J., 1996. LIGNUM: a tree model based on simple structural units. Ann. Bot. 77, 87–98.

Raulier, F., Ung, C.-H., Begin, J., 1998. Analytical estimation of branchwood volume in sugar maple linked to branchiness. Trees 12, 395–405.

Ross, J., 1981. The Radiation Regime and Architecture of Plant Stands. Dr. W. Junk Publishers, The Hague.

Rudolph, T.D., Laidly, P.R., 1990. Jack Pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, Vol. 1, Conifers. USDA Forest Service, Washington DC, pp 280–293.

Ryan, M.G., 1995. Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. Plant Cell Environ. 18, 765–772.

Salminen, H., Saarenmaa, H., Perttunen, J., Sievänen, R., Väkevä, J., Nikinmaa, E., 1994. Modeling trees using an object-oriented scheme. Math. Comput. Model. 20 (8), 49–64.

Santantonio, D., Germann, R.K., Overton, W.S., 1977. Root biomass studies in forest ecosystems. Pedobiologia 17, 1–31.

Sheedy, G., 1990. Résultats de l'enquête de 1989 sur la stabilité des plants de diverses plantations de pin gris et d'épinette noire. Ministère de l'énergie et des ressources (forêt). Note de recherche forestière 69.

Sheedy, G., 1996a. Quelques résultats préliminaires de croissance d'une plantation de pins gris traitée avec des boues de station d'épuration. Ministère des ressources naturelles. Note de recherche forestière 72.

Sheedy, G., 1996b. La stabilité des plantations: résultats des évaluations réalisées en 1989 et en 1994 dans six plantations de pin gris en Abitibi. Ministère des ressources naturelles. Note de recherche forestière 69.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitative analysis of plant form — the pipe model theory I. Basic analyses. Jap. J. Ecol. 14, 97–105.

Stewart, J.D., Hoddinott, J., 1993. Photosynthetic acclimation to elevated atmospheric carbon dioxide and UV irradiation in *Pinus banksiana*. Physiol. Plants 88 (3), 493–500.

Takenaka, A., 1994. A simulation model of tree architecture development based on response to local light environment. J. Plant Res. 107, 321–330.

Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manage. 97, 1–24.

Yang, K.C., Hazenberg, G., 1991. Sapwood and heartwood width relationship to tree age in *Pinus banksiana*. Can. J. For. Res. 21, 521–525.