

## A stochastic model of tree architecture and biomass partitioning: application to Mongolian Scots pines

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• **Background and Aims** Mongolian Scots pine (*Pinus sylvestris* var. *mongolica*) is one of the principal species used for windbreak and sand stabilization in arid and semi-arid areas in northern China. A model-assisted analysis of its canopy architectural development and functions is valuable for better understanding its behaviour and roles in fragile ecosystems. However, due to the intrinsic complexity and variability of trees, the parametric identification of such models is currently a major obstacle to their evaluation and their validation with respect to real data. The aim of this paper was to present the mathematical framework of a stochastic functional–structural model (GL2) and its parameterization for Mongolian Scots pines, taking into account inter-plant variability in terms of topological development and biomass partitioning.

• **Methods** In GL2, plant organogenesis is determined by the realization of random variables representing the behaviour of axillary or apical buds. The associated probabilities are calibrated for Mongolian Scots pines using experimental data including means and variances of the numbers of organs per plant in each order-based class. The functional part of the model relies on the principles of source–sink regulation and is parameterized by direct observations of living trees and the inversion method using measured data for organ mass and dimensions.

• **Key Results** The final calibration accuracy satisfies both organogenetic and morphogenetic processes. Our hypothesis for the number of organs following a binomial distribution is found to be consistent with the real data. Based on the calibrated parameters, stochastic simulations of the growth of Mongolian Scots pines in plantations are generated by the Monte Carlo method, allowing analysis of the inter-individual variability of the number of organs and biomass partitioning. Three-dimensional (3D) architectures of young Mongolian Scots pines were simulated for 4-, 6- and 8-year-old trees.

• **Conclusions** This work provides a new method for characterizing tree structures and biomass allocation that can be used to build a 3D virtual Mongolian Scots pine forest. The work paves the way for bridging the gap between a single-plant model and a stand model.

**Key words:** *Pinus sylvestris* var. *mongolica*, functional–structural plant model, canopy architecture, three-dimensional, forest canopy, virtual plant, GreenLab, parameterization.

### INTRODUCTION

The northern region of China contains arid and semi-arid areas characterized by low and unreliable precipitation, extreme temperatures, strong winds and infertile soils. Afforestation is a major way to combat desertification and to improve ecosystem service functions. Mongolian Scots pine (*Pinus sylvestris* var. *mongolica*) is one of the principal species used for windbreaks and for sand stabilization in arid and semi-arid areas in northern China (Zhu *et al.*, 2003). The natural distribution of Mongolian Scots pine is mainly in the stabilized sand dunes of the Hulun Buir sands of China. This species has high tolerance to cold, drought, soil infertility and salinity. Therefore, Mongolian Scots pines have been introduced to the

edges of other sandy areas in northern China to construct a protection system against sand dune movement.

A model-assisted analysis of the canopy architectural development and functions of Mongolian Scots pines is valuable for a better understanding of its behaviour and role in fragile ecosystems. Recently, functional–structural plant models (FSPMs) have been developed to simulate the growth and development of trees by integrating eco-physiological processes within three-dimensional (3D) architectures (Sievänen *et al.*, 2000; Eschenbach, 2005; Godin and Sinoquet, 2005; Pearcy *et al.*, 2005; Fourcaud *et al.*, 2008). Most of the recent work on FSPMs tend to include (1) fine stochastic architectural descriptions [e.g. using a hidden semi-Markov chain in Lopez *et al.* (2008) or Costes *et al.* (2008)] and (2) more

detailed physiological processes, such as light distributions [e.g. a quasi-Monte Carlo path-tracing algorithm in Cieslak *et al.* (2008) and Perttunen *et al.* (2007)], carbon reserve dynamics (e.g. Daudet *et al.*, 2002; Pallas *et al.*, 2009), transport resistance (e.g. Prusinkiewicz *et al.*, 2007), maintenance respiration, and the influence of varying environmental conditions with local effects on organ growth (e.g. Gayler *et al.* 2008). As a consequence, models have become increasingly biologically realistic but their parameterization remains weak and their increasing complexity can also create computational limitations. In this case, the duration of the growth period for simulation is usually kept very short, e.g. just 1 year for early ECOPHYS (Rauscher *et al.*, 1990), SIMWAL (Balandier *et al.*, 2000) and EMILION (Bosc, 2000). L-PEACH (Allen *et al.*, 2005) is also a spatially explicit 3D simulation model that integrates the supply/demand concepts of carbon allocation and a developmental model of tree architecture using L-systems (Prusinkiewicz and Lindenmayer, 1990; Prusinkiewicz *et al.*, 1994). These models focus more on the functioning of plant organs and less on the changes of tree structure during longer growth periods. For example, the LIGNUM model shows the growth of Scots pines with a simplified tree architecture which responds to photosynthetically active radiation with a time step of 1 year (Perttunen *et al.*, 1996, 1998; Sievänen *et al.*, 2008).

The GreenLab model simplifies the simulations of plant physiological processes, namely biomass production and allocation for organ morphogenesis. The deterministic version, in which the time of initiation and the position of the plant organs are fixed from the beginning of the simulation, is called GL1 (Yan *et al.*, 2004). Until now, GreenLab has been applied to crops, e.g. maize (Y. Guo *et al.*, 2006), wheat (Kang *et al.*, 2008b) and tomato (Dong *et al.*, 2008), and trees, e.g. Chinese pine saplings (H. Guo *et al.*, 2006). However, these calibration processes were based on plants having deterministic architectures that represented either specific individuals or an average topological structure derived from several samples.

Deterministic topological development is quite unrealistic bearing in mind the high variability of branching patterns observed in an actual tree stand. It is important to consider the randomness of topological development. Wang *et al.* (2007) presented a stochastic modelling method for describing a 3D canopy architecture of Mongolian Scots pine, in which the sizes of individual organs were forced, instead of resulting from eco-physiological processes within the plant. A stochastic version of GreenLab, called GL2 (Kang *et al.*, 2008a), was developed to consider the effects of random topological development on plant function. An interesting property of the GL2 model is that it is possible to calculate analytically, i.e. without explicitly computing the plant architecture, the theoretical mean and variance of the numbers of organs at any growth stage to fit the parameters driving the topological development as well as the functional processes. It implies that the model parameterization does not rely on Monte Carlo simulations, this last method inducing a high computational cost to obtain an average virtual population (to compare with observations). Monte Carlo simulations can also introduce bias if the number of individuals simulated is not large enough.

Wang *et al.* (2009) presented a procedure for parametric identification for Mongolian Scots pines by incorporating topological information in the set of target data.

In this study, we introduce a new protocol for the parameterization of the GreenLab model, by taking advantage of the simplicity of the GL2 model and its analytical solutions for calculating average plants. This work is based on both topological and organ biomass data. The model is thus used to explore the variability of organ number and biomass within Mongolian Scots pine plantations. The detailed mathematical framework of the stochastic functional and structural model GL2 is presented. The parameterization method and the results, which were first introduced in Wang *et al.* (2009), are re-used with the following results. Using the calibrated model for Mongolian Scots pine, we have analysed the range of variation of organ number and biomass of Mongolian Scots pine stands by stochastically simulating the number and biomass of their organs. Eventually, 3D views of nine young Mongolian Scots pines are presented to illustrate the opportunities of using this stochastic model for functional visualization of individual-based stand growth.

## MATERIALS AND METHODS

### Experiments

The experimental site is located in plantations affiliated with the Liaoning Sand Stabilization and Afforestation Institute in Zhanggutai (122°22'E, 42°43'N), Liaoning Province, China. The study region is on the edge of the Kerqin sands. Long-term (1953–2006) mean annual precipitation is 505.9 mm, which falls mainly between May and October. Mean annual temperature is 6.0 °C with monthly mean temperatures ranging from a low of –12.1 °C in January to a high of 24.1 °C in July. The soil type at the experimental site is classified as an aeolian sandy soil according to the Chinese Classification, or as an arenosol according to the World Soil Classification.

Two experiments to observe tree topological structure and organ biomasses were carried out in November 2006 and in August 2007. Measurements were performed for trees of different ages. At a first stage, the branching pattern of Mongolian Scots pines, i.e. monopod, and the duration of needle functioning (duration of needle photosynthesis) were determined. The number, angle and azimuth of branches of different orders were then recorded for 100 tree samples, each grouped into one of three age-groups (4-, 5- and 6-year-old trees). Samples of 1-, 2-, 3-, 5- and 6-year-old trees were also taken for destructive measurements of biomass and geometry with four replications for each tree age. To prevent water loss during measurement, plants were dug up with their roots and soil and transported to the laboratory. For 6-year-old trees, the detailed measurements for each growth unit (GU), which is the part of the stem produced during a 1-year growth cycle (GC), were the length, diameter, and fresh and dry biomass of internodes and of needles. For trees younger than 6 years, fresh biomass of internodes and needles was measured for each branching order.

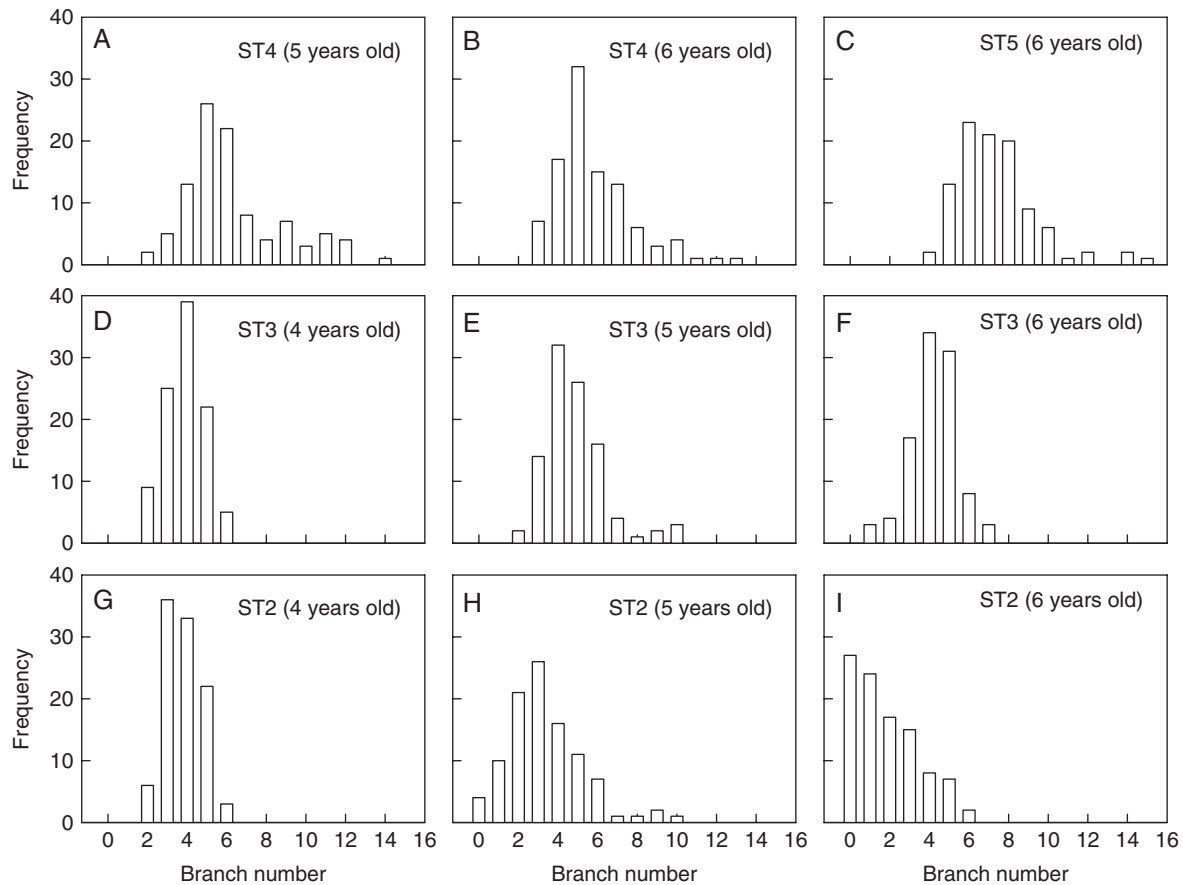


FIG. 1. Frequency distribution of first-order branch numbers at the different node positions of Mongolian Scots pines. Note: ST2, ST3, ST4 and ST5 refer to the second, third, fourth and fifth nodes counting from the bottom of the trunk.

### Stochastic organogenesis model

The GL2 model is a stochastic functional–structural model, in which plant organogenesis depends on the probabilities of bud state. In general, a bud may die, or remain dormant, or give rise to a different number of metamers at each developmental stage. For Mongolian Scots pine, each year an apical bud can develop into a growth unit (arbitrarily regarded as a single metamer), so growth probability is always 1. Based on our observations, the probabilities of death or dormancy are negligible in young trees. The variability of tree architecture is represented mainly by the number of branches arising at different nodes. Thus, only the branching probabilities are taken into consideration.

In the GreenLab model, biomass computation is based on knowledge of the number of sink and source organs. Mean and standard deviation of the numbers of organs for each tree in a stand were chosen as input variables. In GreenLab, the plant architectural description is hierarchically organized using the botanical notion of physiological age (PA) (Barthélémy and Caraglio, 2007). In this case, PA is equivalent to branching order: 1 for the trunk, 2 for first-order branches, 3 for second-order branches and 4 for third-order branches, which is the maximum PA for the trees in this study. An assumption inherent to GreenLab is that organs of a given type (internode or leaves) or PA that appear in the same year have the same biomass regardless of their position

in the plant's architecture. Making this assumption, although the actual branching probability evolved with node rank (Fig. 1), an average branching probability for each PA is proposed and the criterion is that the number of organs from the sampled trees can be satisfactorily fitted by the organogenesis model.

### Theoretical computation of stochastic organogenesis model

To fit the number of organs from the observations, we use the theoretical mean and variance of organ numbers as a function of their branching probability. These are calculated in an analytical way (Kang et al., 2008a), which is more efficient than a Monte Carlo simulation, making the iterations in the fitting process more affordable.

Let  $p_k$ , the probability that a lateral bud of PA  $k$  can develop into a branch, be called the branching probability of PA  $k$ , for  $k$  ranging from 2 to 4. Suppose that there are potentially  $n_k$  lateral buds at each node with bud of PA  $k$ . The number of branches that actually appears at a node then follows a binomial law  $(n_k, p_k)$ . The mean  $M_B^k$  and variance  $V_B^k$  of the numbers of branches at such a node are:

$$\begin{cases} M_B^k = n_k p_k \\ V_B^k = n_k p_k (1 - p_k) \end{cases} \quad (1)$$

We define a substructure of PA  $p$  as the whole branch originating from a bud of PA  $k$ . Let  $S_n^{k,p}$  be the number of GUs of a given PA  $p$  in a substructure of PA  $k$  and of chronological age (CA)  $n$ .  $S_n^{k,p}$  is a function of the branching probabilities of different orders. When  $k = 1$ ,  $S_n^{1,p}$  refers to the number of GUs of PA  $p$  in the whole plant structure. Using compound law formulae, their mean and variance,  $M_{S_n^{k,p}}$  and  $V_{S_n^{k,p}}$ , can be computed recurrently from the highest PA value (Kang et al., 2008a):

$$\begin{cases} M_{S_n^{k,p}} = M_G^{k+1} M_X^{k+1'} \\ V_{S_n^{k,p}} = V_G^{k+1} M_X^{k+1'} + M_G^{k+1} V_X^{k+1} M_G^{k+1'} \end{cases} \quad p > k \quad (2)$$

In eqn (2),  $M_G^{k+1}$  and  $V_G^{k+1}$  are the mean vector and covariance matrix of the number of branches along the axis of substructure  $k$ , and their elements are computed from eqn (1); for example:

$$\begin{cases} M_G^{k+1} = [M_B^{k+1} & M_B^{k+1} & \dots & M_B^{k+1}] \\ V_G^k = \begin{bmatrix} V_B^{k+1} & & & 0 \\ & V_B^{k+1} & & \\ 0 & & \dots & \\ & & & V_B^{k+1} \end{bmatrix} \end{cases} \quad (3)$$

Remember that, for a pine, axes of PA  $k$  bear branches of PA  $k + 1$ . For  $V_G$ , their non-diagonal elements are zeros based on the hypothesis that the numbers of branches per node are independent of each other.  $M_X$  and  $V_X$  are the mean vector and covariance matrix of the number of GUs in branches along the axis, i.e.

$$\begin{cases} M_X^{k+1} = [M_{S_n^{k+1,p}} & M_{S_{n-1}^{k+1,p}} & \dots & M_{S_1^{k+1,p}}] \\ V_X^{k+1} = \begin{bmatrix} V_{S_n^{k+1,p}} & & & 0 \\ & V_{S_{n-1}^{k+1,p}} & & \\ 0 & & \dots & \\ & & & V_{S_1^{k+1,p}} \end{bmatrix} \end{cases} \quad (4)$$

The recursive computation as in eqn (2) starts with the maximum PA, which has no branches. The number of GUs in a branch with the maximum PA is simply the total number of GUs in its axis, which is a deterministic variable for a young pine as each year a new GU is formed, i.e.  $M_{S_n^{p,p}} = n$ ;  $V_{S_n^{p,p}} = 0$ . This equation holds for the number of GUs in the axis of any PA. The number of GUs in a substructure of PA  $p - 1$ ,  $S_n^{p-1,p}$  is dependent on the branching probability of a bud of PA  $p$  (eqn 3). Equation (2) gives recursively the mean and variance of the number of GUs in a plant (with PA 1), which follows a binomial distribution as a compound of binomial laws. As the number of organs per GU is regarded as a deterministic value (all needles in a GU are regarded as one leaf), the number of organs of any age is known. Once the mean number of organs is calculated for each cycle of plant growth, it is possible to compute the dynamics of average plant production and demand throughout its growth using the sink–source model that was developed in GL1.

#### Simulation of stochastic trees

Simulation of the stochastic tree consists of three parts: simulation of bud events, computation of organ biomass and size (see

below), and construction of tree geometrical structure. The history of bud behaviour (being dormant or active) is recorded so that once the tree structure is given in the next cycle, the same tree continues growing. The stochastic substructure algorithm (Kang et al., 2003) is applied to increase the efficiency of the Monte Carlo simulation: a small sample of stochastic branches is re-used in building the branches of a lower PA. The biomass computation is based on the number of organs of a sample tree. As a consequence, the biomass varies between individual trees. By simulating a population of trees, the mean and variance of both the numbers of organs and the biomasses can be obtained for the population.

#### Biomass production and allocation

The component of GL2 for biomass production and allocation follows the same principles as for GL1 so we refer to Yan et al. (2004) for a more detailed description. Note that only above-ground growth is modelled in this study. The biomass production per growth cycle is assumed to be proportional to leaf area per unit ground area and to plant transpiration. In GreenLab, the effects of light, water and temperature are accounted for in a function  $E(n)$ .  $E(n)$  is the average potential of biomass production during growth cycle  $n$ , which is the potential evapotranspiration in this study, but can be adjusted to other environmental variables if required. Hence, the assimilates available for a plant in growth cycle  $n$ ,  $Q(n)$  [g] is calculated using the Beer–Lambert law to account for a diminishing contribution per unit leaf area as the latter increases, as in eqn (5):

$$Q(n) = \frac{E(n)S_p}{R} \left\{ 1 - \exp \left[ -k \frac{S(n)}{S_p} \right] \right\} \quad (5)$$

where  $S_p$  [m<sup>2</sup>] is the ground area available to a plant, computed as the inverse of the population density.  $R$  is an empirical parameter to be estimated with the inversion method. The value of  $k$  is 1, which is analogous to the extinction coefficient in the Beer–Lambert law.  $S(n)$  [m<sup>2</sup>] is the total functioning leaf area of a plant, being the sum of the individual leaf areas at tree age  $n$ .

At each growth cycle, the assimilates available for growth are considered to be located in a virtual common pool (Heuvelink, 1995). From the common pool, biomass is allocated dynamically among individual organs according to organ number, age and relative sink strength (Lacointe, 2000). The relative sink strength for organs of given type  $o$  and PA  $p$  is a dimensionless variable indicating the ability of that organ to compete for biomass. The sink strength of needles in the top GU of the trunk is set to 1 as a reference value. Hence, the overall demand  $D(n)$  at tree age  $n$  is the sum of the sink strengths of all growing organs appearing in the above-ground parts of the plant, as expressed in eqn (6):

$$D(n) = \sum_{o=a,e} \sum_{k=1}^M p_o(k) N_o(k, n) + p_c \quad (6)$$

where  $o$  represents organ type,  $a$  stands for needles (all needles on one GU are treated as a single entity),  $e$  stands for internode



and  $p_c$  stands for the sink strength for secondary growth;  $M$  is the maximum PA of the tree (4 in our study);  $N_o(k, n)$  represents the number of organs of type  $o$  and PA  $k$  appearing in growth cycle  $n$ ; and  $p_o(k)$  represents the relative sink strength of organs of type  $o$  and PA  $k$ .

A new organ  $o$  (leaf or internode) with PA  $k$  gains biomass in proportion to its sink strength and the ratio between the biomass supply from the previous cycle and current demand at tree age  $n$ , as shown in eqn (7):

$$q_o(k, n) = \frac{p_o(k)}{D(n)} Q(n-1) \quad (7)$$

The biomass of internodes comes from their primary growth (corresponding to internode elongation) and from secondary growth (corresponding to the annual growth-ring increment). Primary growth takes place exclusively during the first year while secondary growth does not stop until the branch is dead. Simulation of secondary growth proceeds in two steps. First, biomass is allocated globally to the ring compartment  $\Delta Q_c(n)$ , which is calculated according to the biomass production  $Q(n-1)$  and relative sink strength of secondary growth  $p_c$ . In the second step,  $\Delta Q_c(n)$  is distributed to each metamer according to two different rules: a uniform allocation rule and the Pressler rule (Deleuze and Houllier, 2002), as shown in eqn (8). In the uniform mode, all needles contribute to the cambial growth of each metamer, independent of their position, and thus the biomass for the annual ring is allocated to each internode according to a coefficient of secondary growth for each PA  $R_p(k)$  and the length of the internode. In the Pressler mode, the allocation of biomass for the annual ring is dependent on the number of living needles above the internode in the architecture. As a result, the internodes in the lower positions can have more secondary growth than the internodes in the upper positions. These two modes can be mixed with a proportion coefficient  $\lambda$  in  $[0, 1]$ , which can be used to assess the effects of numbers of leaves and their positions on the partitioning of ring biomass (Letort et al., 2008).

$$\begin{cases} D_g(n) = \sum_{k=1}^M \sum_{m=1}^{n-1} N_e(k, m, n-1) l(k, m-n+1) R_p(k) \\ D_p(n) = \sum_{k=1}^M \sum_{m=1}^{n-1} N_a(k, m, n-1) N_e(k, m, n-1) \\ \quad l(k, m-n+1) R_p(k) \\ \Delta q_c(k, m, n) = \left( \frac{1-\lambda}{D_g(n)} + \frac{\lambda N_a(k, m-1, n-1)}{D_p(n)} \right) \\ \quad l(k, m-n+1) R_p(k) \Delta Q_c(n) \end{cases} \quad (8)$$

In this equation  $M$  is the maximal physiological age;  $N_e(k, m, n-1)$  represents the number of GUs of PA  $k$ , and CA  $m$  at tree age  $n-1$ ;  $l(k, m-n+1)$  represents the length of the GU of PA  $k$  that appears at GC  $m-n+1$ ;  $R_p(k)$  is a repartition coefficient for biomass allocation to cambial growth of the GU of PA  $k$  [ $m^{-1}$ ] – it is a relative value, with its reference being the GU of PA 1;  $N_a(k, m, n-1)$  is the number of living needles above a GU of PA  $k$  and CA  $m$  at tree age  $n-1$ ;  $D_g(n)$  and  $D_p(n)$  represent the plant demand for ring growth at tree age

$i$  with the uniform and Pressler modes, respectively; and  $\Delta q_c(k, m, n)$  is the ring biomass increment of the GU of PA  $k$  and CA  $m$  at tree age  $n$ .

#### Model calibration

Some parameters in the model, namely the number of branches, leaf functioning time and plant density, were obtained directly from observations in the experimental plot. Specific leaf weight  $\varepsilon$ , organ scale coefficient  $b$  and shape coefficient  $\beta$  were calculated according to plant organ fresh biomass and organ (needle and internode) lengths and diameters.

The other parameters in the model were estimated by the generalized least square method, which is used to find a set of parameters that minimize the difference between the model output and the measured data. The accuracy of fitting is expressed in the root-mean-squared error (RMSE) between the target data and the corresponding model output. Compared with the classical fitting protocols of GreenLab, the novelty of this approach is that the measured data include the mean and variances of number and biomass of organs. Therefore, the fitting process has to be carried out in two steps in the GL2 model. The first step concerns plant topology and includes fitting the branching probabilities for branches of each order so that the organogenesis model produced the closest number of organs to the observations. During the observations, the numbers of branches were counted, from which the numbers of GUs were calculated. By fitting the observed and calculated number of GUs from eqn (2), the branching probabilities were estimated. Note that the aim of fitting was to find the average bud probabilities that gave the closest organ numbers to the real data. The numbers of branches of 5- and 6-year-old trees were used to estimate the branching probabilities.

The second step was to solve for the sink–source parameters by fitting the organ biomasses of an average plant. As the numbers of internodes and needles (considering all the needles in one metamer as a single entity) can be calculated from that of the GUs, the number of sink and source organs of a plant is known. The sink–source parameters were identified using the GreenScilab toolbox (<http://liama.ia.ac.cn/greenscilab>) for GL2. After calibration, the architecture and biomass of these Mongolian Scots pines were stochastically simulated using the GreenScilab software.

## RESULTS

#### Model parameters from direct observations

The maximum branching order of young trees was three on 6-year-old trees. The number of branches per node varied significantly between the different orders. The maximum number of branches per node was 15 for the first-order branch ( $n_2 = 15$ , Fig. 1C), six for the second-order branch ( $n_2 = 6$ ) and four for the third-order branch ( $n_3 = 4$ ). The maximum number of branches on the whorl reduced with increasing branching order. Average specific leaf weight ( $SLW = 0.035 \text{ g cm}^{-2}$ ) and internode allometry scale ratio were used to calculate organ dimensions from their biomasses. The

TABLE 1. The descriptions and values of the main parameters used in the GL2 model for Mongolian Scots pines

Parameter	Description (units)	Value
Observation		
$n_l$	Needles functioning time	3
$n_k$	Maximum number of branches per node (PA = 2, 3, 4)	15, 6, 4
$\varepsilon$	Specific leaf weight ( $\text{g cm}^{-2}$ )	0.035
$b$	Scale coefficient of single internodes (PA = 1, 2, 3, 4)	76.4, 163.3, 197.7, 358.0
$\beta$	Shape coefficient of single internodes (PA = 1, 2, 3, 4)	-0.24, -0.30, -0.20, 0.14
Fitting		
$p_k$	Branching probabilities (PA = 2, 3, 4)	0.27, 0.22, 0.13
$r_p$	Biomass production resistance	0.92
$p_c$	Relative sink strength of 'internode' (PA = 1, 2, 3, 4)	0.45, 0.24, 0.07, 0.02
$p_a$	Relative sink strength of needles (PA = 2, 3, 4)	0.46, 0.17, 0.05
$p_c$	Relative sink strength of ring demand	7.16
$R_p$	Secondary sink for ring repartition (PA = 2, 3, 4) ( $\text{cm}^{-1}$ )	0.05, 0.01, 0.001
$\lambda$	Coefficient for blade influence on ring partitioning	0.03

descriptions and values of the main parameters used in the model are listed in Table 1.

Fitting results

The values of bud probabilities and sink–source parameters are shown in Table 1. Both the mean and the variance of the number of GUs, for the trunk and different order branches, were satisfactorily simultaneously fitted by the model. This result supported the hypothesis that the number of GUs follows a binomial distribution (Fig. 2). The trunk of a Mongolian Scots pine grows by one GU each year. As a result, the number of GUs of the trunk increases linearly with tree age and the variance is zero. The mean number of GUs in a second-order branch (PA3) increases rapidly with tree age, as does its variance. Because a 6-year-old Mongolian Scots pine is still very young, the number of GUs in a third-order branch (PA4) remains at a low level. Taking a 6-year-old tree as example, the simulated mean and variance of the total numbers of GUs are 112.2 and 28.3 % respectively. The mean and variance of GUs of first-order branches are 39.2 and 27.6 % for measured values, while their simulated values are 39.8 and 23.6 %. The maximum number of GUs is for second-order branches, of which the mean and variance are 51.3 and 35.9 % for measured values and 52.7 and 33.9 % for simulated values. The minimum number of GUs is for third-order branches, of which the measured and simulated values are 11.3 and 13.7, but the variance is large. The bud probabilities identified are given in Table 1. It can be seen that these decrease with higher branching orders. The mean numbers of branches per node for first-, second- and third-order branches were 3.98, 1.33 and 0.52, respectively, from eqn (1).

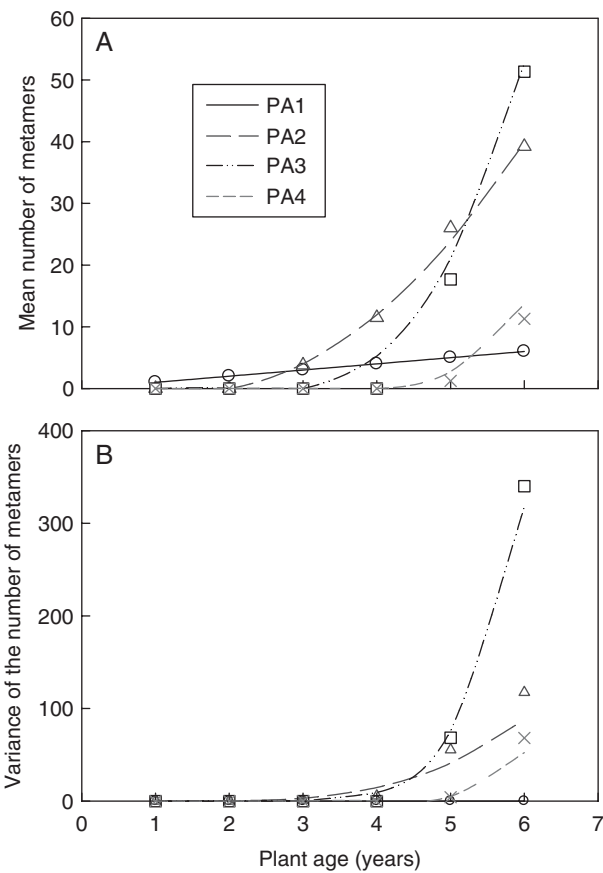


FIG. 2. Means and variances of the number of GUs in the trunk and branches of different orders of Mongolian Scots pines. PA1, trunk; PA2, first-order branch; PA3, second-order branch; PA4, third-order branch: from measured data (symbols) and from the model output (lines).

The measured data and fitting results can be used to investigate the trends in biomass partitioning among the different branching orders throughout growth of the plant from 1 to 6 years. Figure 3A and B show the fitting results on the length and diameter of each GU in the 6-year-old trees. From these results, we can obtain tree height and stem diameter at the base, which are 82.9 and 3.1 cm, respectively. Compared with the fitting results on fresh biomass of GUs of trunk (Fig. 3C), the results for internode length and diameter were less accurate. This may be due to the continuing growth of internodes when the measurements were taken in August. Figure 4A shows the observed and simulated values for fresh biomass (including internodes and needles) of branches of different orders, i.e. the sum of internodes and needle biomass for all branches of the same order. For trees less than 6 years old, the fresh biomass of the trunk is the largest and this decreases with at higher orders. This trend is reversed when tree age reaches 6 years: the fresh biomass of first-order branches overtakes that of the trunk. The fresh biomass of the third-order branches is the lowest because the number of branches is very low. From Fig. 4B we can obtain the above-ground fresh biomass of the reconstructed plants, which are 2.4, 16.2, 39.3, 123.6, 411.8 and 924.7 g, respectively, for trees from 1 to 6 years old. The corresponding relative errors with reference to these measurements (except for the 4-year-old trees for which

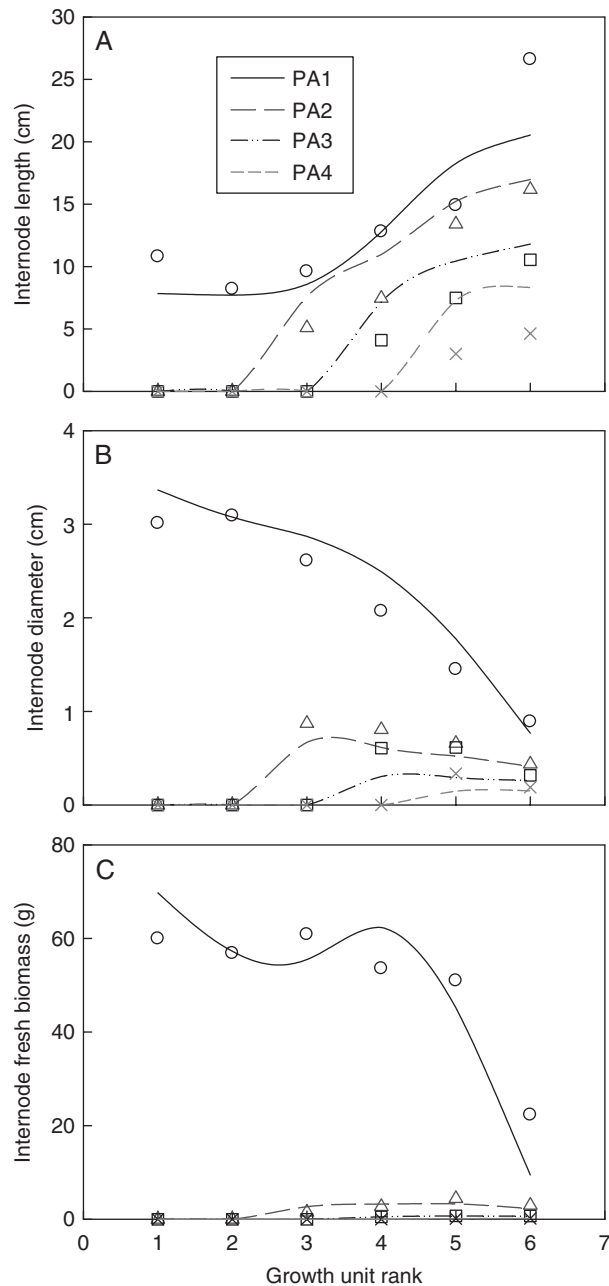


FIG. 3. Fitted results. Length, diameter and fresh biomass of internodes of the trunk of 6-year-old Mongolian Scots pines. PA1, trunk; PA2, first-order branch; PA3, second-order branch; PA4, third-order branch: from measured data (symbols) and from the model output (lines).

there were no data) are 50.8, 43.7, -44, -11.3 and -3.7 %. The relative error is lowest for the 6-year-old trees because its detailed measurement data were included in the fitted file while only compartment data (total biomass of internodes and needle) were included for the trees of other ages.

#### Stochastic simulation of plant growth

Tree growth was stochastically simulated with 50 replications using the calibrated model. The simulation results of

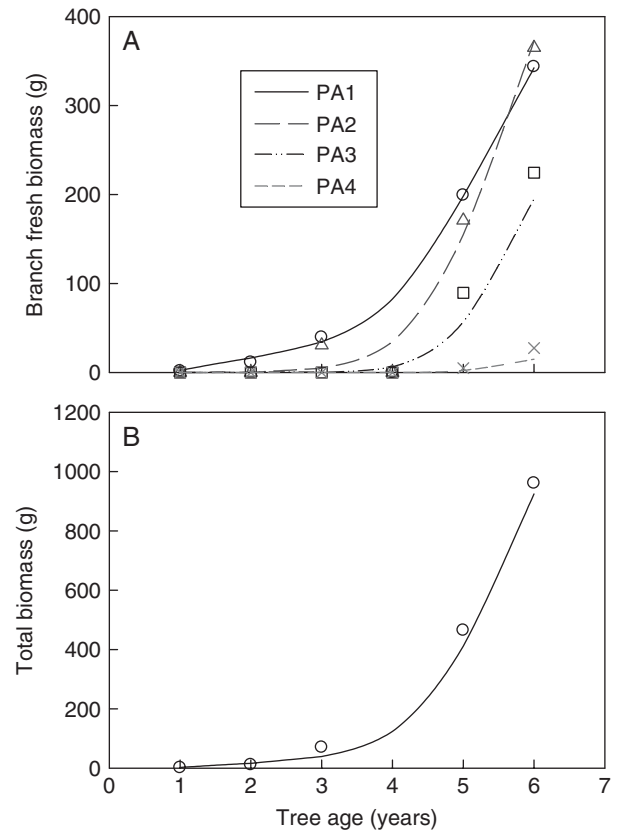


FIG. 4. Fitted results. Fresh biomasses of branches (including internodes and needles) for each order and for the total above-ground fresh biomass of Mongolian Scots pines. PA1, trunk; PA2, first-order branch; PA3, second-order branch; PA4, third-order branch: from measured data (symbols) and from the model output (lines).

the biomass of shoot (above-ground part), needles, internodes and growth rings are presented in Fig. 5. For the 6-year-old trees, the above-ground biomass ranged from 677.5 to 1051.8 g with a mean of 846.1 g and variance of 10.8 % (Fig. 5A). Mean values of needle biomasses were close to those of internode biomasses but the dispersion of the biomasses of the needles was much higher than that of internodes (Fig. 5B). Needle biomass ranged from 260.9 to 595.8 g while internode biomass ranged from 393.7 to 490.6 g (Fig. 5C). In the model, rings begin to appear at the end of the year of internode formation. At the sixth year, ring biomass ranged from 268.0 to 364.0 g, with a mean of 328.2 g and a variance of 7.6 %. Ring growth represented an average of 56.9 % of the total increase of above-ground biomass (Fig. 5D). We can see from Fig. 5 that means of all measured values are very close to the simulated lines. However, the long error bars corresponding to standard deviations indicate that the measured values have sparse distributions. The descriptive statistics for biomass partitioning, simulated for trees from 1 to 6 years old, are presented in Table 2.

#### Visualization of canopy architecture

The different architecture of each individual tree is caused mainly by the number of branches in the model. Tree height

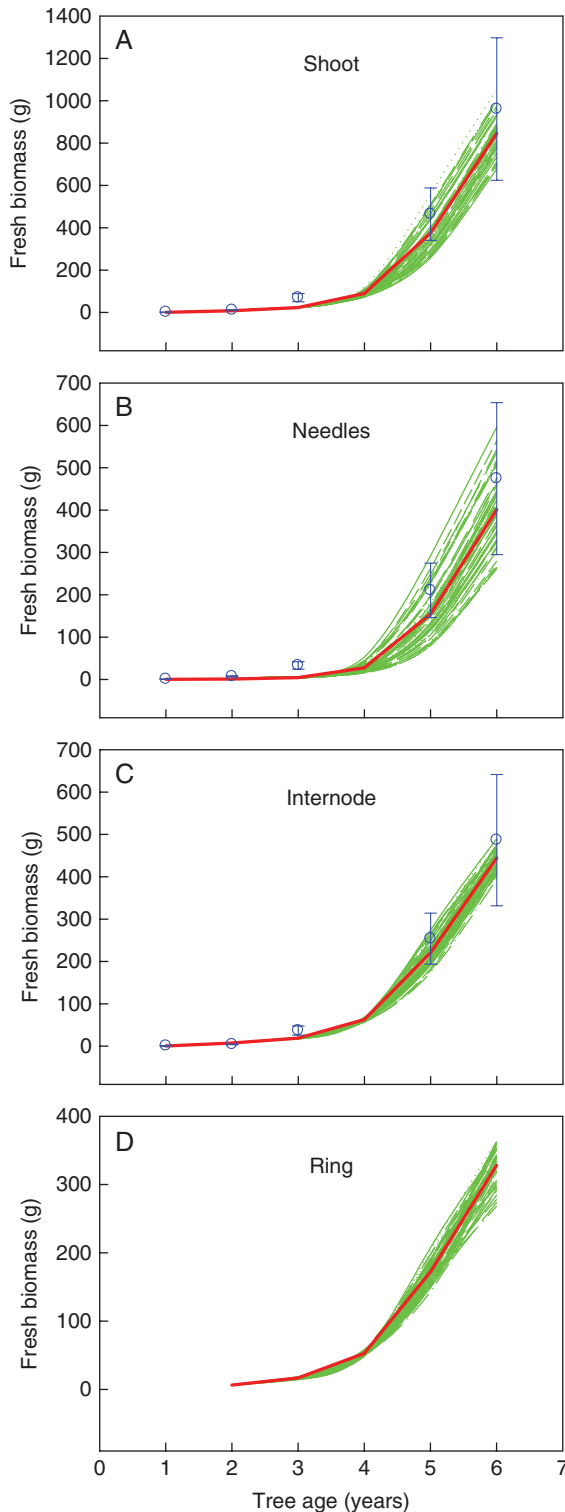


FIG. 5. Simulations and measurements of fresh biomasses of different organ types derived from a Monte Carlo simulation. The green lines represent simulations and the red line represents means of the simulated values obtained. The circles are the measured values and the bars correspond to one standard deviation.

is also influenced by the number of branches. The greater the number branches, the more biomass can be produced, but the larger the consumption of biomass by the internodes of

branches. To obtain an explicit idea of these trees, we reproduced their architecture stochastically using the Monte Carlo method with the branching probabilities given in Table 1. Three sequences of trees with significant differences in topology were selected and visualized at 4, 6 and 8 years of age (Fig. 6). It can be seen that the numbers of branches of each order are random. Taking the 6-year-old trees shown in Fig. 6 as an example, tree heights of the three samples are 175 cm (Fig. 6D), 157 cm (Fig. 6E) and 149 cm (Fig. 6F), and the corresponding numbers of total internodes are 265, 500 and 509.

## DISCUSSION

### Model performance

This paper presents a simulation study of structure and biomass of Mongolian Scots pines using the stochastic FSPM GL2 model. This work is based on the previous study of Wang *et al.* (2007), which presents a stochastic method to reconstruct the 3D architecture of Mongolian Scots pines, and of H. Guo *et al.* (2006), which adapts the deterministic GreenLab model to analyse sink–source relationships in Chinese pine saplings. The specificity of GL2 is used to account for inter-individual variability of plant topology and morphology. By incorporating branching probabilities within the GreenLab model, we ensured that the variability of branching structures observed in the field was preserved in the model output. A major achievement of this study is to have demonstrated the possibility of fitting the branch probabilities using the means and variances of the number of organs from actual Mongolian Scots pine plantation trees. The functional part of the model was calibrated using organ biomass data. The fitting results suggest that the principles of source–sink relationships can be an appropriate modelling choice to simulate the biomass allocation to different organs of a plant during its growth. The fitting results of the mean and variance of organ number represented fairly well the various characteristics of the architecture of tree stands. However, the variance of simulated biomass (Table 2) is smaller than that of measured values (Fig. 5). This may be due to the means of calculation of biomass production based on a Beer–Lambert law formalism, which is not very sensitive to the tree topology because of the phenomenon of saturation of intercepted light (Letort *et al.*, 2009). Therefore, this modelling choice tends to homogenize biomass production, even for trees that do not have the same number of organs. The results suggest that this phenomenon might not be as influential in reality, especially for young trees which can exhibit strong heterogeneity in their canopy geometry. In particular, good estimates of trunk size are useful in predicting tree height and wood volume reasonably precisely. The 3D architecture and biomass of a 6-year-old Mongolian Scots pine was stochastically simulated after model calibration, to represent the stochastic characters observed in a natural tree stand.

An assumption of our model is that the variances observed in tree plantations are merely stochastic, whereas in reality they can be the result of many unknown factors [e.g. the history of carbon allocation, shading influence of neighbours and orientation of the tree with respect to latitude



TABLE 2. The descriptive statistics of fresh biomass (g) simulated for Mongolian Scots pines

Tree age (years)	Shoot		Needles		Internodes		Ring	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
1	0.98	0.00	0.57	0.00	0.41	0.00	–	–
2	8.67	0.00	1.29	0.00	7.38	0.00	6.45	0.00
3	23.59	0.00	4.39	0.75	19.20	0.75	16.88	0.92
4	90.36	10.76	27.45	8.60	62.91	3.11	52.69	2.42
5	375.24	72.83	154.55	51.10	220.69	24.64	172.23	15.35
6	846.05	91.58	401.45	82.06	444.60	23.42	328.17	24.98

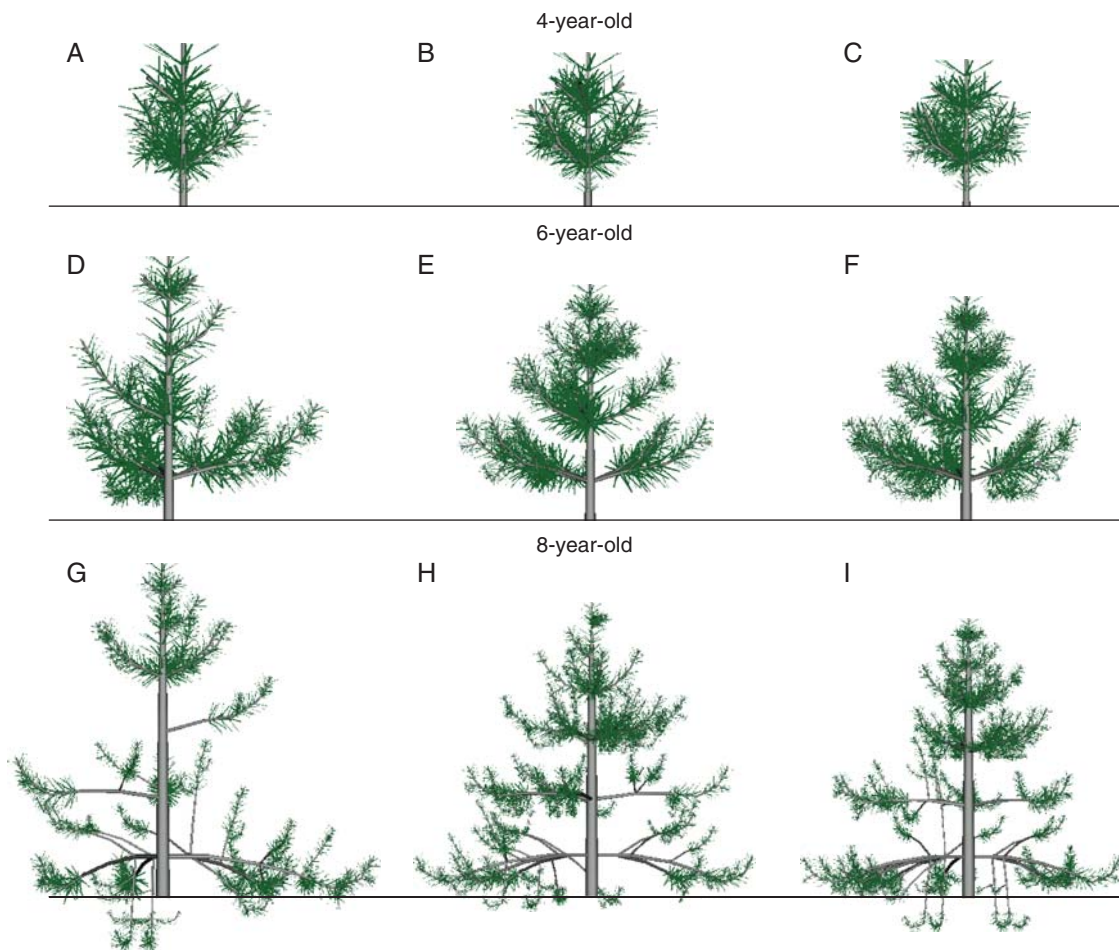


FIG. 6. Three stochastic Mongolian Scots pines at 4, 6 and 8 years old.

(i.e. predominant solar angle]. Therefore, although the true functions that generate the given architectures are certainly not as simple, our results show that these architectures are reproduced well (in mean and variance) by simulations using stochastic functions tied to a binomial distribution.

#### Comparison with other models

Le Roux *et al.* (2001) considered that the description of interactions between tree structure and function was the weakest point of most tree-growth models. In the functional–structural tree models presented by Sterck *et al.*

(2005), the flush probability of each metamer depends on its position, axillary inhibiting factor, local light level and, indirectly, carbon status of the tree. However, these probabilities driving apical and lateral bud breaks in their models were set intuitively, and were obtained merely by simple piecewise functions. In contrast, the branching probabilities in GL2 were estimated based on actual experimental data, and so reflect the observed stochastic characters of a real Mongolian Scots pine stand.

A current research topic is the simulation of stand growth built from an individual-based and functional–structural approach. The complexity of tree growth models raises

problems of computational resource and the time required. The LIGNUM model simulated a forest consisting of individual Scots pines on a small plot (Sievänen *et al.*, 2008). However, their model simplified the stand description by simulating the growth only of one tree in the middle of the plot and by assuming that the other trees were, at all times, identical to it. The differences in structure of individual trees in real stands are obvious and are influenced by light competition during growth (Sievänen *et al.*, 2008). Therefore, the LIGNUM model neglected the inherent differences in tree structure in the initial growth stages. Host *et al.* (2008) implemented a parallel modelling strategy to run simultaneous individual tree models across an  $8 \times 8$  patch of trees. The patch consists of ‘core’ trees, which are individually simulated instances of trees with varied physiological and phenological characteristics, surrounded by rings of ‘neighbour trees’ with canopies created as translations of the core trees. The physiological and phenological characteristics of each tree are individually simulated according to direct and diffuse radiation, hourly temperature, relative humidity, and atmospheric CO<sub>2</sub> and O<sub>3</sub> concentrations. This would require high-performance computers to support multiple simulations in parallel.

Therefore, a simplified tree model such as GL2 is a useful tool to realize individual-based stands with varied structures and functions for each tree. It would thus be possible to reconstruct a virtual forest canopy with stand characters of structure and function by using field observations and a relatively small number of destructive measurements. The original version of the stochastic model was coded in Scilab (GreenScilab software) and run on a personal computer with a Microsoft Windows operating system. It took less than 1 s to simulate a single Mongolian Scots pine at 6 years old. Stand simulation cannot be performed using the same software as GreenScilab is dedicated to single tree simulation. However, previous studies based on other software implementing the GreenLab model have underlined that the introduction of structure factorization (Yan *et al.*, 2004) results in a substantial gain in the computational cost of simulation: the runtime is now simply proportional to the chronological age and the number of physiological ages (and not to the number of organs that have to be simulated). For instance, it takes around 4700 s to simulate a 15-year-old pine with the classical method simulating every organ, whereas it takes only 0.7 s for the same simulation with the factorization (Cournede *et al.*, 2006).

#### *Improvements of the model and future applications*

Although the strong influence of the environmental constraints and endogenous growth processes on plant organogenesis has been extensively reported by botanists (Barthélémy and Caraglio, 2007), there are no retro-active effects of plant biomass production on tree development in the stochastic model presented here. In nature, plant architecture is the result of both genotypic and environmental influences. The numbers of branches is strongly influenced by plant physiological activities (Buck-Sorlin and Bell, 2000). For instance, it can be expected that branching probabilities are dependent on soil water content. Therefore, a new functional and structural tree model coupled with soil water balance is currently under development for Mongolian Scots pines.

In GL2, biomass is allocated to the different parts of the plant according to their numbers and types of sinks, which means that we actually ignore the effects of source variations on sink numbers and types (Dingkuhn *et al.*, 2005). From our data, we can see that the number of first-order branches increased with plant age and with node rank (Fig. 1), and the same trend is observed with the second- and third-order branches. This suggests that bud behaviour may be strongly related to plant biomass production, which is neglected in our study. Thus, another perspective is to integrate these observations into a recent version of GreenLab where plant development is mechanistically determined by the current trophic state of the plant, represented by the ratio of biomass supply to demand (Mathieu *et al.*, 2009). This mechanistic model, with retro-actions between plant physiology and development, has been first applied to simulate the growth plasticity of two beech trees (*Fagus sylvatica*) grown in different local environments (Letort *et al.*, 2008). However, the model used was fully deterministic and only partial measurements of the trees were available. Thus, from the perspective of the present work, a significant improvement would be to account for the inter- and intra-individual topological variabilities in that mechanistic version. A possible method would be to modulate the stochastic variables of tree development by this supply-to-demand ratio. It would also require the adaptation of the parameterization method. It would allow simulation of the variations of topological structure depending on dynamic sink–source relationships of trees.

#### *Concluding remarks*

The stochastic FSPM GL2 has been calibrated successfully for young Mongolian Scots pine plantations from 1 to 6 years old in northern China. It is the first calibration of GL2 and the method benefits from the analytical expressions of mean and variance of organs numbers. The model parameters include different order branch probabilities, parameters for the biomass production equation and organ sink strengths. They were obtained through a fitting method from actual experimental data of plant topology and biomass. After calibration, it is possible to assess the range of variations in the numbers of different organ types and their corresponding masses. The results show that simulated numbers of organs and their mass are consistent with actual measurements of stands of living trees. This suggests that the hypothesis that the number of GUs follows a binomial distribution is reasonable. Our simulation has produced several samples of stochastic 3D architectures of Mongolian Scots pines. The results here provide the characteristics of a stand’s structure and biomass for building a 3D virtual Mongolian Scots pine plantation.

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