

Calibration of topological development in the procedure of parametric identification: application of the stochastic GreenLab model for *Pinus sylvestris* var. *mongolica*

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Abstract

Climate, biophysical conditions and human activities all contribute to the occurrences of ecosystem and environment problems, i.e. water scarcity, desertification, salinization, in arid and semiarid zone of North China. Mongolian Scots pine tree (*Pinus sylvestris* var. *mongolica*) is one of the principal species of the windbreak and sand-fixing forest in this area. In this paper, we presented the calibration process of stochastic GreenLab model based on experiment data. Specific plant topology and sink-source parameters were estimated for Mongolian Scots pine trees through optimizing procedure. The fitting results showed that the calibration process were reasonable and acceptable. The model produced a variety of three-dimensional visual representations of Mongolian Scots pine trees with different topological structures simulated by Monte Carlo methods. This model can be used to describe the plant development and growth in a stand level, taking into accounts the variations in plant topology and biomass.

1. Introduction

The ecosystem in the arid and semiarid region of North China is very fragile because of hostile climate and sterile soil. Moreover, human-induced vegetation destruction and soil degradation further intensify the problem. Vegetation protection and optimal water

and soil management are an important pathway to improve the function of local ecosystem services. The selection of appropriate species for restoring vegetation is a key point to prevent desertification.

Mongolian Scots pine tree (*Pinus sylvestris* var. *mongolica*) is one of the principal species of the windbreak and sand-fixing forest in the arid and semiarid area. It possesses many desirable properties, such as trunk straightness, valuable wood material and especially high tolerance to environmental stresses (e.g. coldness, drought, infertility, salinity) [1], which make it fit to grow in sandy land. Therefore, it is widely planted in North China to combat desertification. However, some degenerating phenomena such as top withering, slow growth and stems death have occurred in the early Mongolian pine plantations since the later 1980s [2]. Model-assisted analysis on the canopy architecture development and function of Mongolian Scots pine tree are valuable for better understanding its role and behavior.

Functional-structural plant models (FSPMs) were effective tools to simulate the growth and development of plants by integrating three-dimensional (3D) plant architecture with eco-physiological processes. Plant architecture in this type of models was usually represented as a collection of interconnected elementary units [3]. FSPM simulates physiological and geometrical variation of every elementary unit during plant growth and development [4]. Early FSPMs focused more on the dynamic changes of plant function in

fixed tree architecture than on architectural development, e.g., ECOPHYS [5], EMILION [6] and SIMWAL [7]. One of representative FSPMs was the LIGNUM model [8], which integrated the pipe model theory [9] with a simplified representation of tree architecture. LIGNUM had applied to Scot pines [8], Jack Pine [10], Sugar Maple [11], etc. Another FSPM appeared recently was L-PEACH [12], which described plant architecture using L-systems [13], and the assimilate movements was driven by concentration gradients across resistive pathways based on the “transport-resistance” concept.

Derived from the powerful plant architecture model AMAP, GreenLab was a generic plant growth model that integrates various morphological features with biomass production and allocation at organ scale [14], called GL1. The plant architecture was built based on an automaton which is analogous to L-systems rules, and the biomass acquisition and allocation were based on source-sink relationship. GreenLab model was able to simulate plant's phenotypic plasticity that resulted from feedbacks among growth (biomass acquisition), differentiation (phenology, morphogenesis) and the physiological condition of the organism (e.g. stresses) [15]. At present, GreenLab has been applied to crops, e.g., maize [16], wheat [17], tomato [18], and trees, e.g., Chinese pine saplings [19] and beech trees [20]. However, these calibration processes were performed with deterministic architecture that represented an average topological structure from several samples. No appropriate method was developed to include topological information in the set of target data used for the procedure of parametric identification. Moreover a deterministic topological development is not realistic with regard to the high variability of branching patterns observed in tree stands. To get realistic simulations of tree growth, it is important to consider the randomness of topological development. This motivated the development of a stochastic version of GreenLab, called GL2 [21]. Beside simulation of stochastic plant sample, the theoretical mean and variance of numbers of organs at any growth stage can be calculated.

The aim of this study was to describe the plant development and growth of Mongolian Scots pine tree, taking into account the variations in plant topology and biomass. The benefits of these mathematical properties were taken to fit the parameters driving the topological development, as well as functional processes. We presented the calibration process of GL2 based on experiment data of Mongolian Scots pine trees. The stochastic 3D plant architectures were simulated and visualized.

2. Materials and methods

2.1. Model description

GL2 model was a stochastic functional-structural model, where bud probabilities were introduced in plant organogenesis, including survival probabilities of buds, branching probabilities, growth probabilities of apical buds and appearance probabilities of metamers. Theoretical mean and variance of organ number can be calculated efficiently in an analytical way aside Monte-Carlo simulation [21]. Another component of GL2 model was on biomass production and allocation, following the same principle as in [18]. General description of this sub-model can be found in [14], [16] and [20].

Wang *et al.* [22] defined the topological parameters of the dual-scale automaton, specifically for Mongolian Scots pine tree. The plant architecture description was hierarchically organized using botanical notion of physiological age (PA) [23]. Each bud of Mongolian Scots pine tree developed to a growth unit (GU) (includes one metamer only) each year. In that case, PA was equivalent to branching order: one for trunk, two for first-order branches, three for second-order branches, and four for third-order branches, which was the maximum PA for the Mongolian Scots pine trees in this study. The death or dormant probabilities of apical bud was negligible for young trees according to observation. The variability of Mongolian Scots pine trees architecture was mainly represented by the number of branches at different order. Thus in following study, only the branching probabilities were taken into consideration.

Let p_k be the probabilities that an axillary bud of PA k can develop to a branch, called branching probabilities of PA k . Suppose that there were potentially n_k axillary buds at a node. The model assumed that buds of the same PA have the same branching probabilities, regardless their position inside plant structure. The number of appeared branches on a node then followed a binomial law (n_k, p_k), the mean M_B and standard deviation V_B of number of branches on such a GU was:

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

Total number of GUs in a plant was a function of branching probabilities of each order. Using compound law, their mean and variance can be computed recurrently from highest PA in an analytical way [21]:

$$\begin{cases} M_{S_k} = M_G \cdot M_B' \\ V_{S_k} = V_G \cdot M_B' + M_G \cdot V_B \cdot M_G' \end{cases} \quad (2)$$

In Eqn. (2), M_{S_k} and V_{S_k} were mean and variance of numbers of GUs in a substructure of PA k . When $k = 1$, S_k referred to the plant structure. M_G and V_G were mean vector and covariance matrix of number of branches along the axis of substructure k , their elements computed from Eqn. (1). For V_G , their diagonal elements were zeros supposing that the numbers of branches per node were independent with each other. M_B and V_B were mean vector and covariance matrix of number of GUs in branches along the axis. Started from the simplest branch of maximum PA, Eqn. (2) gave recursively the mean and variance of number of GUs in plant, which followed a binomial distribution as it was a compound law of binomial ones.

Based on the mean of organ number, an average plant can be calculated using sink-source parameters as in GL1 model [14].

2.2. Model calibration

The model parameters were estimated by model inversion with an adequate set of experimental data and simulation outputs. In GL2, the calibration was done in two steps. The first step was on the automaton, aiming at quantifying the branching probabilities for branches of each order so that the organogenesis model produced the closest number of organs to the observations. In observations, the numbers of branches were counted, from which numbers of GUs were calculated. By fitting the observed and calculated number of GUs from Eqn. (2), the branching probabilities were estimated. Notice that the aim of fitting was to find average bud probabilities that gave closest organ number with real data.

The second step was to resolve sink-source parameters by fitting the organ biomass of the average plant. As the number of internodes and needles (consider all needles in one metamer as whole) were equal to that of GUs, the number of sink and source organs of an average plant was known. Following the same fitting process as for GL1 [24], the sink-source parameters were identified. GreenScilab toolbox (<http://www.scilab.org>) for GL2 was used for model calibration and simulation. Based on the calibration, the architecture and biomass of Mongolian Scots pine trees were stochastically simulated with Monte Carlo methods.

2.3. Experiments

The experimental site is located at the plantations station affiliated with Liaoning Sand Fixation and Afforestation Institute (122°22'E, 42°43'N), in Zhanggutai, Liaoning of China. This region is adjacent to Kerqin sandy land, which is one of the four biggest sandy lands in China. The average annual precipitation, potential evaporation, temperature and wind speed are 505.9 mm, 1755.3 mm, 6.0°C and 4.2 m s⁻¹ respectively. Soil type is aeolian sandy soil.

Two experiments for plant topological structure and organ biomass were carried out in November, 2006 and August, 2007. The observations on number of branches were done in the field on 100 Mongolian Scots pine trees of four, five and six-year-old. The numbers of different order branches at each node of trees were recorded. For organ biomass, samples were taken from one, two, three, five, six-year-old young trees with four replications for each tree age. To prevent water loss during measurements, plants were dug out with roots and soil and transported to the laboratory for measurement (length, diameter and fresh biomass of every internodes and needles fresh biomass).

3. Results

3.1. Model parameters from direct observations

Part of the model parameters can be estimated by direct observations and simply calculations, e.g. maximum branching order, maximum branching number, specific leaf weight (SLW). No second-order branch was observed for four-year-old trees. A maximum branching order of three was observed on the six-year-old trees. The maximum number of branches per node was 15 for first-order branch ($n_2=15$), six for second-order branch ($n_2=6$) and four for third-order branch ($n_3=4$). The maximum number of branches per node reduced with the increasing branching order.

Average SLW and internode allometry scales ratio were estimated directly from experiment data (Table 1). The high correlation coefficients showed the close relationships between internode mass and length for each order branch (Fig.1). These allometric parameters were used to calculate organ size from their biomass.

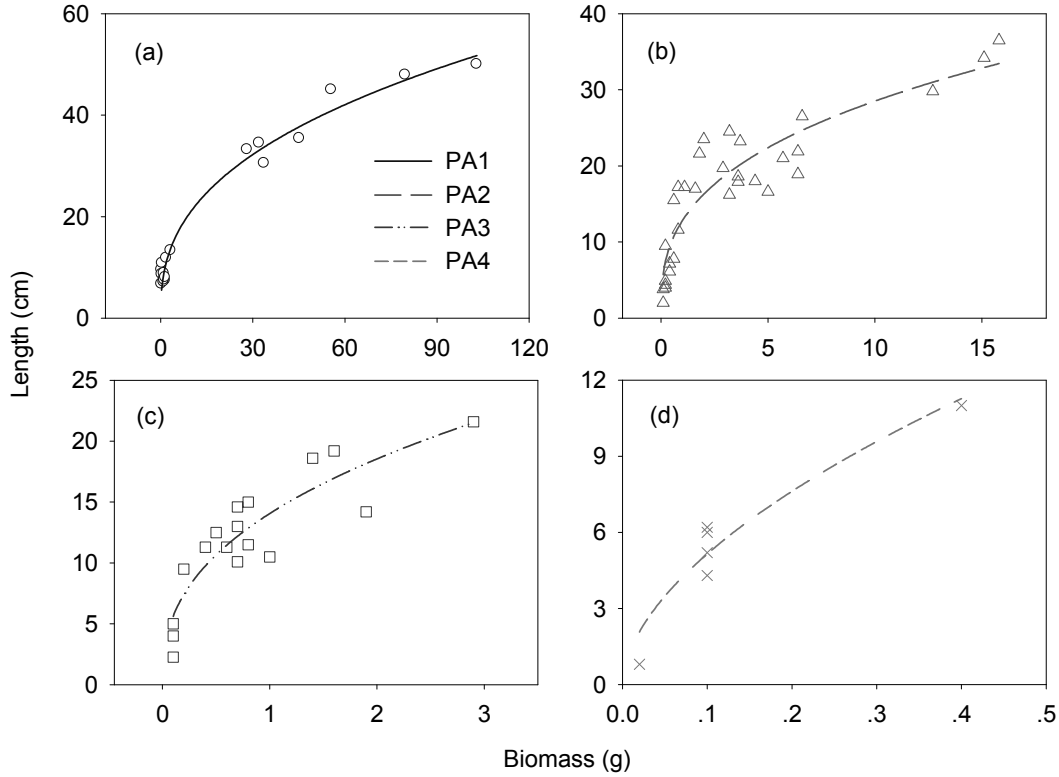


Fig. 1 The allometric relationship of GU of trunk and different order branches for Mongolian Scots pine tree (a) PA1: trunk, $y = 8.74x^{0.38}$ ($R^2 = 0.98$, $n = 19$, $p < 0.0001$); (b) PA2: first-order branch, $y = 12.78x^{0.35}$ ($R^2 = 0.84$, $n = 31$, $p < 0.0001$); (c) PA3: 2nd-order branch, $y = 14.06x^{0.40}$ ($R^2 = 0.81$, $n = 17$, $p < 0.0001$); (d) PA4: 3rd-order branch, $y = 18.92x^{0.57}$ ($R^2 = 0.84$, $n = 6$, $p = 0.0023$). Measured data (symbols) and regression line

3.2. Fitting results

Fig. 2 shows the mean and variance of number of the GUs of trunk and branches of different order. Both the mean and variance were well fit simultaneously by the model, verifying the hypothesis that the number of GU follows a binomial distribution. Trunk grows one GU every year. Thus the mean number of GUs of trunk increased linearly with tree age, and the variance was zero. The mean number of GUs in second-order branch (PA3) increased most rapidly with tree age, so did its variance. This was reasonable as both n_2 and p_2 were higher for PA 2. The identified bud probabilities are shown in Table 1. It can be seen that they decrease with higher branching order. The average numbers of branches per node for first-, second-, third-order branch were 3.98, 1.33 and 0.52 respectively from Eqn. (2). Using the calibrated automaton, the next step was to calibrate the sink-source parameters by fitting biomass and size of organs.

Fig.3 shows the fitting results on fresh biomass of internodes and needles for trunk and branches of all orders in the six-year-old Mongolian Scots pine tree.

Sink-source parameters are shown in Table 1. It can be seen that the fresh biomass of trunk internode was much more than those of branches. Take a six-year-old Mongolian Scots pine tree for example, average internode fresh biomass of PA1, PA2, PA3, PA4 were 50.7, 1.9, 0.3 and 0.04 g respectively. Actually, the sink strength of trunk internode was significantly higher than that of the branches (Table 1). Moreover, the secondary sink strength for branches were very low, which meant the most of biomass for ring growth was allocated to the trunk. The fresh biomass of needles in each GU decreased also with increasing branching order, being 6.5, 2.7, 1.0, and 0.27 g from PA1 to PA 4. Naturally, the relative sink strength of branch needles were lower compared to those in trunk. It can be seen from Fig.3(b), leaf functioning time was three years, and leaves older than three years fell down.

Fig.4 shows the fitting results on length and diameter of each GU in the six-year-old Mongolian Scots pine tree. Tree height and ground diameter were 82.9 cm and 3.1 cm respectively. Good estimation of trunk size is useful to predict precisely tree height and wood volume. Compared with the

fitting on GU fresh biomass of branches as in Fig. 3(a), that of internode length and diameter were worse. This may be due to the ongoing growth of internodes when the measurements were done in August. This result showed that it is important to set the date of measurement for obtaining good allometric rules.

Fig. 5 shows the simulated and measured organ compartment weight and total fresh biomass. They were the sum of the weights of individual organs. The fresh biomass of internodes compartments decreased from trunk to higher order branch.

Table 1 The descriptions and values of main parameters used in GL2 model for Mongolian Scots pine trees

Parameters	Description(unit)	Value
n_k	Max number of branches per node (PA = 2, 3, 4)	15, 6, 4
p_k	Branching probabilities(PA = 2, 3, 4)	0.27, 0.22, 0.13
ε	Specific leaf weight(g cm ⁻²)	0.035
b	Scale coefficient of single internodes (PA=1, 2, 3, 4)	76.4, 163.3, 197.7, 358.0
β	Shape coefficient of single internodes (PA=1, 2, 3, 4)	-0.24, -0.30, -0.20, 0.14
p_e	Relative sink 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) (cm ⁻¹)	0.05, 0.01, 0.001
r_p	Biomass production resistance	0.92

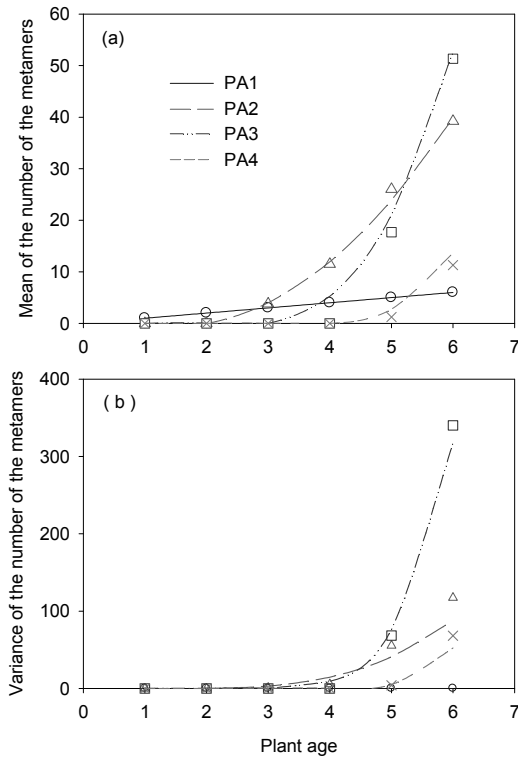


Fig.2 Mean and variance of number of GUs in trunk and branches of different order
PA1: trunk; PA2: first-order branch; PA3: 2nd-order branch; PA4: 3rd-order branch, from measured data (symbols) and model output (lines)

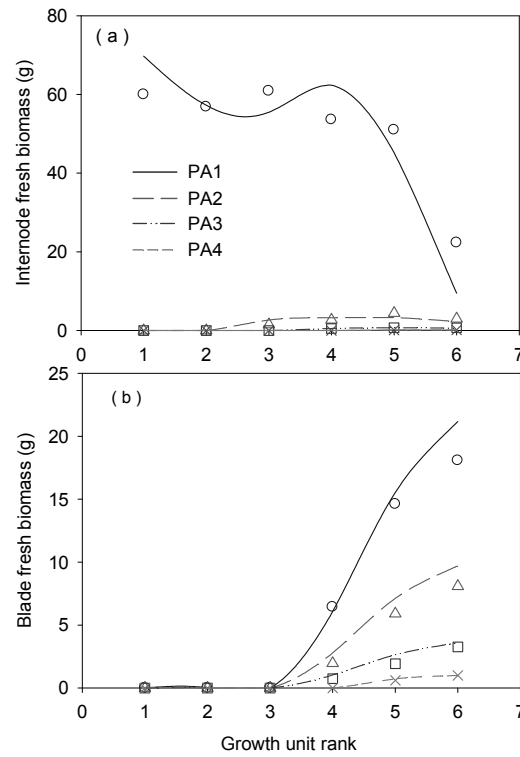


Fig.3 Fitting results of single internodes and needles fresh biomass of trunk and different order branches of a six-year-old Mongolian Scots pine tree
PA1: trunk; PA2: first-order branch; PA3: 2nd-order branch; PA4: 3rd-order branch, from measured data (symbols) and model output (lines)

However, first-order branch bore the highest fresh biomass of needles compartment, because of its high number of organs (Fig. 2a) and relatively more biomass compared with the internodes (Fig. 3). The fresh biomass of internodes and needles compartment of third-order branch was lowest because the number of branches was very small.

Six-year-old Mongolian Scots pine trees were simulated using Monte-Carlo method based on the branching probabilities in Table 1. Five samples with significant difference in topology were selected and visualized in Fig. 6. It can be seen that the numbers of branches of each order are random. For example, the numbers of first-order branches on the bottom node of trunk were 2, 6, 6, 1 and 2, respectively.

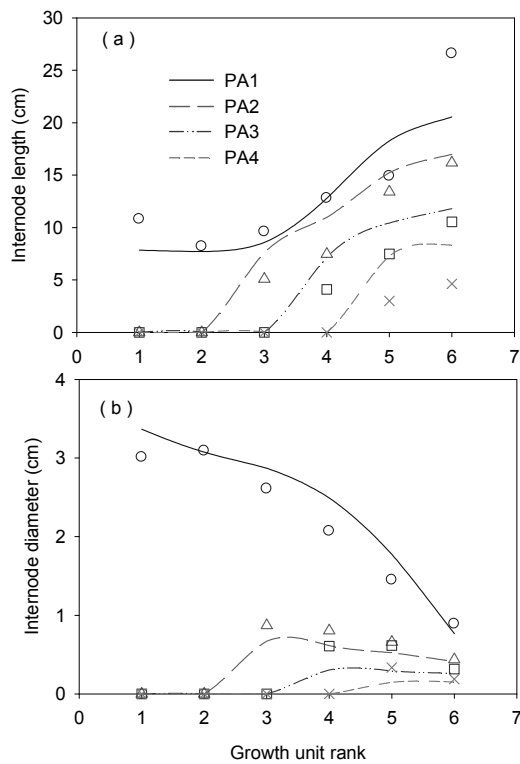


Fig. 4 Fitting results of single internodes length and diameter of trunk and different order branches of a six-year-old Mongolian Scots pine tree

PA1: trunk; PA2: first-order branch; PA3: 2nd-order branch; PA4: 3rd-order branch, from measured data (symbols) and model output (lines)

4. Discussions

This study presented the calibration process of the GL2 model for Mongolian Scots pine trees. It was the first calibration of the GL2 model based on experimental data. The 3D architecture of a six-year-old Mongolian Scots pine tree was simulated after

model calibration, which represented fairly well the stochastic characters of tree stands. The decreasing branching probabilities reflected that higher order branches were more vulnerable to environmental stress, reflecting the adaption of plant architecture to drought condition [25]. On the other hand, losing the second- or third-order branches would not significantly decrease plant growth, as their contributions on leaves areas were small (Fig. 5b). As most of wood biomass was reserved in trunk and primary branches (Fig. 5b), the production was kept.

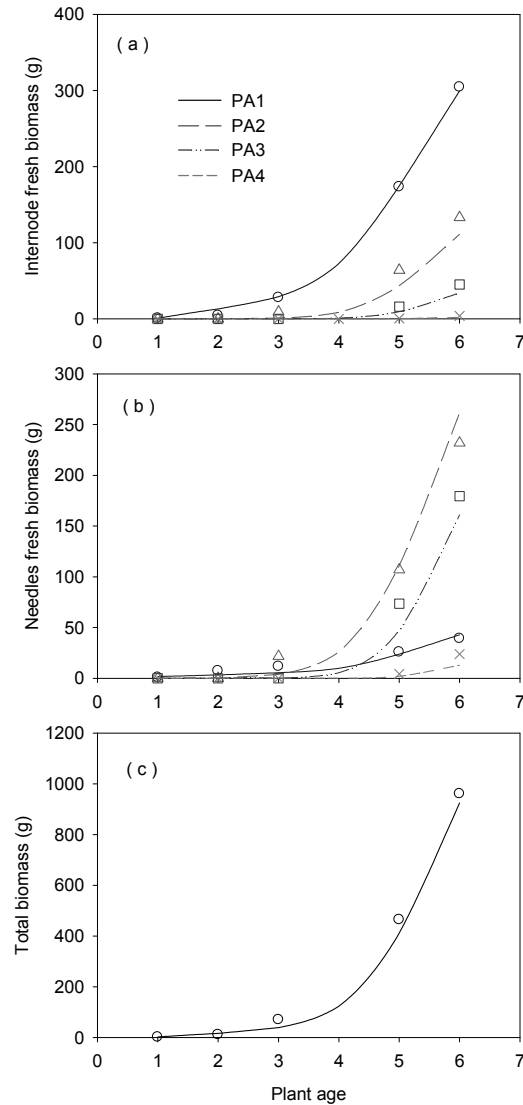


Fig.5 Fitting results of internodes, needles and total fresh biomass of trunk and different order branches

PA1: trunk; PA2: first-order branch; PA3: 2nd-order branch; PA4: 3rd-order branch, from measured data (symbols) and model output (lines)



Fig. 6 Simulated stochastic architecture of six-year-old Mongolian Scots pine trees using fitted branching probabilities

Due to high topological complexity and tremendous number of organs in trees, most functional-structural tree models only used scarce experimental dataset to indicate the functional nature of plant growth and development, and lacked full calibration [12] [26]. The fitting results of this paper showed that considering mean and variance of number of organs to calibrate the GL2 model of topological development was reasonable and acceptable for Mongolian Scots pine trees. The GL2 model can simulate variability of plant morphological plasticity and biomass fairly well based on stochastic dual-scale automaton and source-sink relationships. By introducing branching probabilities into the GreenLab model, the GL2 version allowed to reproduce the variability of branching structures that can be observed within plant communities.

Guo *et al.* [19] applied the GreenLab model to simulate the Chinese pine trees for deterministic case. However, the stochastic characters of the tree development cannot be captured with this version of model. The functional and structure tree models by Sterck *et al.* [27] and Renton *et al.* [28] accounted for stochastic phenomena of bud behavior. However, the parameter values driving apical and axillary buds breaks in their models were set intuitively. The branching probabilities in GL2 were estimated from experimental data of mean and variance of numbers of organs, which reflected the observed stochastic characters of Mongolian Scots pine trees stand in this region.

In the stochastic architecture model presented here, the resulting plant architecture was not influenced by biomass production. In nature, the plant architecture is the result of both genotype and environment influence. The numbers of branches are strongly influenced by plant physiological activities [29]. It can be expected that the branching probabilities is dependent on the water content of the

soil. The biomass was allocated into determined number and type of sinks in GL2, which omits the effects of source variations on sink numbers and types [30]. In the experiments, we found the number of second and third-order branch increased with plant age. Thus plant buds behavior might be highly related to plant biomass production. A perspective was to integrate these observations into the new version of GreenLab model based on the previous work [15]. Thus the variation of topological structure depending on dynamic sink-source relationships of trees can be simulated.

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