

# Simulating Tree Plasticity with a Functional-Structural Plant Model: Being Realistic in Behavior

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**Abstract**—Plant plasticity refers the ability of a plant to change its observable characteristics, in response to the environmental changes in its lifespan. We present a method of simulating structural plasticity in trees reacting to different light intensities, pruning policies, competition, and obstacles. The method is based on a functional-structural plant model (FSPM) that simulates two basic underlying processes of plants: development/organogenesis (the formation of plant structure) and growth (expansion of organs biomass production and partitioning). Bi-directional feedback is constructed between these two processes by linking both bud break and biomass partitioning with the internal source-sink ratio of biomass. A secondary mechanism controlling bud break is its local light intensity, by imposing a light distribution in tree canopy, the computational efficiency for which is assured by implementation on GPU. Based on these mechanisms, the virtual trees produce naturally less branches at lower light intensities. In reaction to pruning, the same tree give different shapes as pruning changes the source-sink balance and triggers new branches. Neighboring trees compete for light and lead to different crowns, and the same mechanism can be used to simulate trees grown near buildings. The results show that by constructing the dynamic model describing the underlying development and growth process of trees in cyberspace, the simulated trees can adapt to their virtual environment without need of modifying their geometrical traits. Such property is interesting for simulating landscape, education and interactive training.

**Keywords**—Tree competition; Plasticity; GreenLab; Light environment; Bud break; FSPM; Emergent property.

## I. INTRODUCTION

As plant is a ubiquitous component in nature, the realistic presentation of a plant in cyber-space is an ever-existing aim in computer science. Differing from other physical objects such as fluids, plant is a living organism that exhibits phenotypic plasticity, which is the ability of changing its phenotypes (observable characteristics) in response to changes in the environment [1]. Such a feature has brought tremendous challenges to plant modelers, especially for those who desire not just visually plausible virtual plants.

Since 1970's, there has been endeavor toward generating virtual plants according to the underlying algorithms [2] [3] [4]. Combined with techniques of computer graphics, visually realistic 3D plants can be generated with reaction to environment or obstacle [5] [6]. However, the very important aspect of plant growth, biomass production and partitioning,

is missing in such pure geometrical or structural plant models. This means, the size of each part of plants, such as stem diameter, leaf length, need to be set delicately in order to obtain proper ratio. The wish of having 'live' virtual plant has brought the concept of Functional-Structural Plant Model (FSPM) [7], which simulates two basic underlying processes of plants: development/organogenesis (the formation of plant structure) and growth (expansion of organs biomass production and partitioning).

In this paper, we aim at simulating tree plasticity with a member of FSPM family, GreenLab. Bi-directional feedback is constructed between these two processes by linking both bud break and biomass partitioning with the internal source-sink ratio of biomass. A secondary mechanism controlling bud break is its local light intensity, by imposing a light distribution in tree canopy. The computational efficiency of computing light inception is assured by implementation on GPU. We show in this paper that the virtual trees from this model can respond automatically to different environmental settings, including different light intensities, pruning policies and competition, without the need of manipulating geometrical parameters.

The paper is organized as follows. Related biological concepts are presented in Section 2. Previous works linked to this paper are reviewed in Section 3. We present an overview of our algorithm and the related models in Section 4, while Section 5 presents several simulation results. Conclusion and discussion of the approach are given in the last section.

## II. RELATED BIOLOGICAL CONCEPTS

There are two basic common processes in all plants: *development* and *growth*. Plant development, or organogenesis, deals with the creation of branches and plant organs (leaves, flowers, etc.), while growth refers to the complex process of biomass production by photosynthesis and biomass allocation among individual organs. One of the main hypothesis on biomass allocation is source-sink balance.

For tree development, botanists classified 23 types of *architectural models* [8], according to the organization patterns of botanical units in trees. Each architectural model describes common features of many trees, e.g, the simplest structure is Corner model with a single stem structure. The formation of tree architectures is described as a dynamic process which is “the expression of equilibrium between endogenous growth processes and exogenous constraints exerted by the environment” [9]. In this paper, we present trees of Leeuwenberg model, Rauh model and Roux model.

Leeuwenberg model consists of a sympodial succession of equivalent sympodial units. Pinus tree follows Rauh model with rhythmic growth, orthotropic axis with monopodial branching. Roux model are plants with vertical orthotropic trunks and plagiotropic branches that are always horizontal without righting at the end [9].

For *biomass production*, *light interception* can be computed as plant level or organ (leaf) level. Beer-Lambert Law assumes that light attenuates in a canopy as if it is a semi-transparent object [10]. It holds for closed tree stand, and the thickness of the canopy can be quantified by leaf area index (LAI, ratio of total leaf area to its projection ground area). With 3D description of tree structure, another approach is to apply photosynthesis model at leaf level, but it needs simulation of light distribution inside tree canopy. In this work, we test both kinds of photosynthetic models.

For *biomass partitioning* inside a plant structure, the mechanism is less known than the overall biomass production [11]. Hypotheses on partitioning include functional equilibria [12], source-sink regulation [13] and allometric relationships [14]. A special feature differing trees from crops is their ring growths. One well-accepted theory is Pipe Model [15], indicating that the diameter at a certain position of a stem is proportional to the number of leaves above it. In this work, ring growth is based on pipe model, and organ size is the result of source-sink regulation.

Mechanism on *bud activity* regulation is multiple: light, auxin, source-sink ratio of assimilates, etc. [16]. Buds are origin of branches, and their activities affect strongly the tree shape. They can stay dormant, die or give birth to branches. Buds are of different *physiological ages*, representing the vigor of branch that it can bear [9]. For example, in Ginkgo tree, some buds bear twigs, while others give birth to long branches. Axillary buds are generally physiologically older than their parent branches. *Reiteration* is an exception, referring to such a phenomenon that a branch inherits the same features of its mother branch [8][9]. This is often considered as 'self-similarity' property in trees and has led to application of fractal method in tree construction. Breakout of bud is highly dependent on plant age and environment. Bud behavior can explain many of tree plasticity in reacting to their environment, i.e., changes of size, amount, orientation or color to fit better during their life time. In this paper, we test two mechanisms controlling bud break: external light condition and internal source-sink regulation.

### III. RELATED WORK

#### A. Simulation of Virtual Plants

Generating 3D tree structures started not long after the birth of personal computers [3]. Recursive generative algorithms have been applied by viewing a tree as an explicitly-defined recursive structure [17]. Started by field investigation and mathematical modeling, AMAP methodology integrates knowledge like physiological age, architectural model and bud activities [4][18]. Botanical tree library has been set up for hundreds of trees. Although tree animation can be achieved by above methods, the size of

compartments is directly defined by rules but not from photosynthesis and biomass partitioning.

Another approach is to use images or point clouds to reconstruct the 3D-tree by registering their input images or using loosely arranged images [19]. To infer the hidden internal branches, iteration rules such as a particle flow system can be imposed to link the main stem with external twigs [20], which link the rule-based and data-based approach. Diameter of trees can be inferred from data but again there is no 'growth'.

#### B. Simulating Environmental Effect

Because of its importance, light is often taken as the principle environmental condition. Greene [21] simulated climbing plants on obstacles using voxel automata and light rays. Derived from a standard L-system, Měch et al. [22] developed open L-systems that have been used for simulating tree competition, based on communication between the plant and its environment. Soler et al. [23] simulated light environment in trees with an efficient method. Van Haevre [24] proposed a ray density estimation of the environmental illumination to guide phototropism morphology. In above works, light casts effects on branch removal or bending, but they have no contribution to photosynthetic production of plants, which plays a principle role in tree growth.

#### C. Functional-Structural Plant Model (FSPM)

LIGNUM [25] is a FSPM dedicated to trees and shrubs that couples L-systems for tree development with an eco-physiological model. L-peach [26] is another FSPM for young peach trees, and it allows the simulation of pruning with empirical description on number of new shoots. AMAPHydro [27] is a branch of AMAP [4], which introduced a hydraulic model for computing biomass production. The computational efficiency of early FSPMs was low, and implementation was usually prone to bugs [7]. GreenLab [28] [29] inherited many concepts from both AMAPHydro and AMAPSim, but the computational efficiency was greatly improved by applying sub-structure method [30], so that it is affordable for complex trees. It is one of few FSPMs that has been calibrated on both crops and trees, by fitting it to multiple biomass data, such as for pine trees [31] and beech trees [29].

#### D. Control on Bud Break

According to different hypotheses on bud activity control, various methods have been proposed and tested. The first type is based on hormone regulation, which is interpreted as a signaling mechanism [22]. It is often implemented in pure developmental plant model. The second is based on source-sink regulation, with source being provided by photosynthesis and sinks being the demand of organs for resources. By setting that the number of bud break is dependent on the dynamic source-sink ratio, rhythmic branching pattern could be generated [32]; Eschenbach [33] simulated tree structures with gradient according to environmental conditions. Such mechanism can be built only

with functional-structural plant model as there is issue of biomass production (source) and allocation (sink).

The third method is to link directly bud formation to its local light condition. In [34], it was linked to the far red spectrum while [35] supposed that bud fate is decided by light availability. In [22], the branch apices are associated with the radii of interest for collision detection, and a bud will stop growing when there is not enough space available. Such method is commonly used in simulating plant communities where plants compete for resources [35].

In this work, the bud break is controlled by two factors: local light condition and source-sink ratio. Therefore, light can affect bud fate both directly by deciding bud breakout, and indirectly by contributing to the overall source-sink ratio.

### E. Controlling Tree Form by Interaction

A challenge of rule-based model is that one may lose the control over the final tree shape. A pure interactive example is Speedtree, but dynamic growth sequence of trees is not easy to construct. Chiba and Ohkawa [36] simulated interactive pruning of tree for designing Pensai trees. Pirk et al. [6] simulated the removal of branches when a tree meets an obstacle or other trees. In the context of tree pruning, intermediate storage of tree structure can be necessary, using format such as multi-scale tree graph [37].

Although it will be nice to introduce procedural brush as in [5] and [38], we focus on the pruning exercise as done on real trees in final shape control. The tree shape is controlled by interactive pruning on trees, which will break the internal source-sink balance and stimulate the breakout of buds, including the dormant buds.

## IV. SYSTEM OVERVIEW

As described by Měch and Prusinkiewicz [22], the interaction of a plant with the surrounding environment can be conceptualized as two concurrent processes that communicate with each other, forming a feedback loop of information flow. In our case, besides the external one, there is an internal information flow between plant structure and function; therefore, both light (that affects both the structure by controlling bud formation and function by photosynthetic production) and pruning (that affects the structure) have effect on the plant structure. External modification of environment will naturally trigger the response of plant. The double feedback loops are shown in Fig. 1.

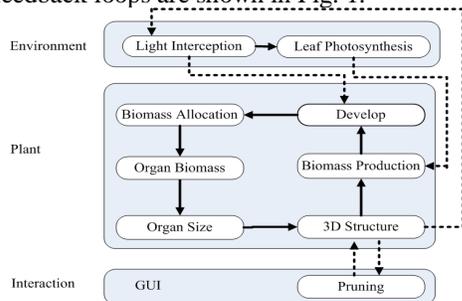


Figure 1. External interaction between plant and environment and internal interaction between plant development and growth.

## V. A FUNCTIONAL-STRUCTURAL MODEL FOR TREES

### A. Development model

The description of organogenesis in GreenLab is based on the definition of the potential bud production. A simple illustration can be seen in Fig. 2, where each circle presents a bud of a certain Physiological Age (PA) [9]. PA of the main stem (blue) is 1. Each rectangle represents a metamer, a minimal botanical unit that is composed by a node, an internode and its axillary leaves and fruits. Branching structure can be formed by the parallel bud development into growth units (from successive appearance of metamers).

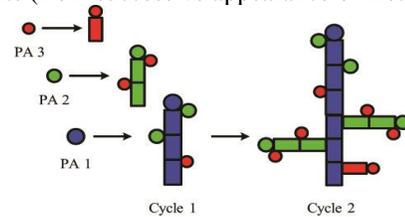


Figure 2. Diagram of plant development model in GreenLab, a deterministic case. Each circle presents a bud.

The parameters that describe the development are expressed as a matrix. For the branching structures of Fig. 2, the number of metamers in a growth unit and PA of the axillary buds are written as follows:

$$M_I = \begin{bmatrix} 0 & 2 & 1 \\ 0 & 0 & 2 \\ 0 & 0 & 1 \end{bmatrix}, N_B = \begin{bmatrix} 0 & 1 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{bmatrix} \quad (1)$$

where  $M_I[1,2]=2$  means that in a growth unit of PA 1, there are potentially two metamers that bear buds of PA 2.  $N_B[1,2]=1$  means for such a metamer, the amount of potential buds it carries is 1. Recall that PA of axillary buds is generally higher than its parent stem, except for the case of reiteration. The corresponding structure at iteration cycle 5 is shown in Fig. 3a.

A main feature of the above model is that the botanical axis are organized using the concept of PA. Branches of the same PA share the same parametric settings for development, growth and geometry. Numeric values instead of rewriting rules are needed in designing the topological structure.

### B. Reiteration

In this functional-structural plant model, reiteration is simulated by setting the PA of an axillary bud equal to the age of its mother axis. An example in Fig. 3 illustrates this mechanism. Instead of bearing two buds of PA 2, the growth unit of PA 1 contains one metamer with a reiteration bud ( $M_I[1,1]=1$ ), one metamer with a axillary bud of PA 2 ( $M_I[1,2]=1$ ), and one metamer with a bud of PA 3 ( $M_I[1,3]=1$ ). All metamers carry at most one bud ( $N_B[1,i]=1, 1 \leq i \leq 3$ ).

$$M_I = \begin{bmatrix} 1 & 1 & 1 \\ 0 & 1 & 1 \\ 0 & 0 & 1 \end{bmatrix}, N_B = \begin{bmatrix} 1 & 1 & 1 \\ 0 & 1 & 1 \\ 0 & 0 & 0 \end{bmatrix} \quad (2)$$

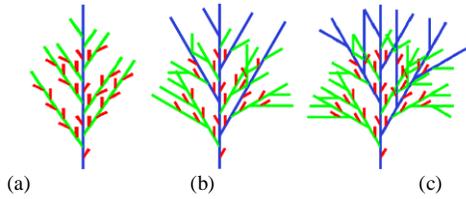


Figure 3. Topological structures at cycle 5. (a) no reiteration, parameters in (1); (b),(c) reiteration of PA 1 and PA 2, parameters in (2), maximal reiteration order being 1 (b) and 2 (c) respectively.

A parameter called maximal reiteration order  $R_m$  limits the level of reiteration, which can be understood as the maximal branching order of reiteration. If there is no control, fractal structure will be born. Fig. 3 shows the resulting structure at cycle 5, with  $R_m=1$  (Fig.3b) and  $R_m=2$  (Fig.3c) for stem of PA 1 (blue) and PA 2 (green). No reiteration in PA 3 (red).

### C. Bud Break

Bud control is based on two kinds of hypotheses: source-sink balance [32] and light condition [35]. We keep the light distribution model as optional in case that fast simulation is needed. The diagram on bud control can be seen in Fig. 4.

To reach the above goal, when the local light condition allows, the number of axillary buds of PA  $q$  in a growth unit of PA  $p$ ,  $N^{p,q}$ , is a function of simulated source-sink ratio; see (3).  $Q(n)$  is computed using plant or leaf level photosynthesis model; see (8) and (9).  $D_V(n)$  is potential plant demand if all candidate buds break.  $\alpha^q$  is a coefficient indicating the dependency of the bud break on source-sink ratio.

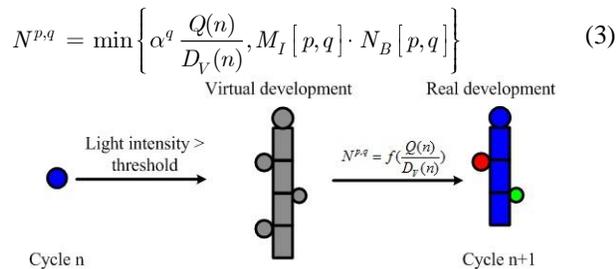


Figure 4. Approach of controlling bud break. Actual bud production is dependent on plant source-sink ratio. The bud production is possible when its local light intensity is above a threshold.

### D. Biomass Partitioning

This model is based on the hypothesis of source-sink regulation. All produced assimilates are distributed among the growing organs according to their sink strengths. For trees, it is further hypothesized that the sink for ring growth  $D_L(n)$  is dependent on source-sink ratio [29]; therefore, the thickening rate of stems is dependent on tree age and external conditions. The total demand of plant  $D(n)$  at cycle  $n$  is the sum of all sink strengths, see (4).

$$D(n) = \sum_O \sum_p P_O \cdot N_O^p + D_L(n) \quad (4)$$

where  $N_O^p$  is the number of organ  $O$  at PA  $p$ , whose sink strength is  $P_O$ . The parameters of sink strength can be estimated by inverse method from data [29] [31].

In order to decide the fate of bud, at each cycle, a virtual demand  $D_V(n)$  is firstly computed by summing up all sink strength from potential buds. A sink strength of a bud is defined as the total sink strength of its potential organs.

$$D_V(n) = \sum_p P_O \cdot N_{Bud}^p + D_L(n) \quad (5)$$

The actual plant demand is computed when the bud behavior is fixed according to  $Q(n)/D_V(n)$ . The produced biomass is then shared for creation of new metamers and thickening of old stems. For the latter, distribution of biomass is in relation to the number of functioning leaves above each metamer [29].

### E. Interactive Pruning

At each cycle, through a GUI, users are allowed to select and remove some leaves, flowers or internodes interactively from the virtual plant. This information is fed back to the simulator before moving forward to next cycle (Fig.1). As there is underlying data structure indicating the topological link between all parts, if an internode is removed, all branches above it are removed. Updating of structure changes both source and potential sink, and consequently the source-sink ratio for next cycle. According to the mechanism of bud control, this can trigger different behaviors of buds. As bud extension takes several cycles to be visibly evident, the effect of pruning is not immediate.

### F. Light Interception

In this work, the light intensity around a leaf plays double roles: determining the fate of adjacent bud and the total plant production. To simulate light environment, we emit light rays evenly from a sky hemisphere covering the plant canopy, as in [21]. Each sample ray collides, reflects and decays in the tree canopy. Photon map [39], which is originally used for rendering of a scene, records the information of collision between rays and objects.

The light intensity around a leaf, denoted as  $E_L$ , can be estimated from photons in its neighborhood. As in trees, leaves are generally densely distributed inside the canopy, more photons found in the neighborhood of a leaf means more light interception by surrounding leaves, and hence less intercepted light by the leaf. This is an inverse situation to the original photon mapping algorithm [39]. The absolute light intensity  $E_B$  is computed as in (6):

$$E_B = \left(1 - \frac{E_L}{E_L^{\max}}\right) \cdot (\tau_{\max} - \tau_{\min}) + \tau_{\min} \quad (6)$$

where  $E_L^{\max}$  is the maximal value of  $E_L$  of all blades.  $\tau_{\max}$  and  $\tau_{\min}$  denote the maximal and minimal light intensity above canopy an inside canopy, respectively, both of which can be measurable by canopy analyzers.

### G. Photosynthesis Model

This model concerns on the relationship between Photosynthetic Active Radiation (PAR) intercepted by leaves

and biomass production. We test two kinds of photosynthesis models computed at leaf and plant level, with or without using geometrical information of tree.

1) *Leaf level*: In this case, the photosynthesis model is applied at organ (leaf) level, according to light intensity computed for each leaf. A generalized light-response curve is used to compute instantaneous assimilation rate of an individual leaf ( $I$ ,  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , using a non-rectangular hyperbola [42]:

$$I = \frac{b - \sqrt{b^2 - 4\theta\alpha E_B\beta(I_m + R_d)}}{2\theta} - R_d \quad (7)$$

where  $b = \alpha E_B\beta + I_m + R_d$ . The physical meaning and empirical values of variables  $\alpha$ ,  $\beta$ ,  $I_m$  and  $R_d$  are from [40].

Total biomass production of the whole plant is summed from those of individual leaves, as in (8).

$$Q_L(n) = \delta_t \gamma \sum_{i=1}^{N_B(n)} I_i(n) s_i(n) \quad (8)$$

where  $\gamma$  is a conversion coefficient from assimilate to dry mass,  $\delta_t$  is the duration of a growth cycle (s),  $N_B(n)$  denotes the total number of leaves in the plant.  $I_i(n)$  and  $s_i(n)$  are assimilation rate and the area of  $i^{\text{th}}$  individual leaf, respectively, the latter being computed iteratively by the model. This method has the advantage of taking into account the geometrical shape of trees and obstacles, but it is more time-consuming.

2) *Plant level*: The plant-level photosynthesis model is based on Beer-Lambert law [10]. The thickness of the canopy is quantified by LAI, an important value in evaluating light interception. To estimate LAI for individual trees, in GreenLab, each tree has a characteristic projection area ( $S_p$ ), which can increase with plant age in the beginning and finally stabilize when the tree canopy closes, see (9).

$$\begin{cases} Q_B(n) = E(n) S_p (1 - \exp(-k \frac{S(n)}{S_p})) \\ Q_B(0) = Q_{seed} \end{cases} \quad (9)$$

where  $E(n)$  is a variable representing the plant local environment at growth cycle  $n$ ;  $k$  is a light extinction coefficient to quantify attenuation process of light penetrating into the canopy;  $S(n)$  is the total green leaf surface area at growth cycle  $n$ ;  $Q_{seed}$  is the initial biomass. Under certain parameter values, the results from both methods ( $Q_L$  and  $Q_B$ ) fit each other. This method has high computational efficiency as it is not dependent on tree geometrical structure.

#### H. GPU+CPU implementation

In case of implementing leaf-level photosynthesis model, there are two performance bottlenecks: ray tracing and light intensity estimation. In ray tracing, bounding volume hierarchies (BVH) and k-d tree are widely used to accelerate intersection computation, collision detection and  $k$  nearest neighbor search (KNN). In recent years, these algorithms are implemented successfully on GPU [41][42]. To improve system performance, this part is implemented on GPU. The GPU is Nvidia GeForce GTX560Ti with a 1023MB of dedicated memory.

Simulation of tree development and growth, as well as the interactive pruning, are all implemented in QingYuan software programmed in C++. This kernel of model is still implemented in CPU. Rendering is made in Pov-Ray. All examples in this paper were generated on a desktop computer equipped with Intel(R) Core(TM)2 Quad CPU@2.66GHz with 8GB of memory.

## VI. RESULTS

### A. Tree structure dependent on source-sink ratio

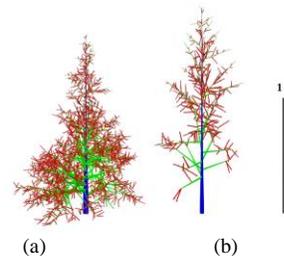


Figure 5. Effect of  $\alpha$  ((3)) on bud break. (a) less dependency on source-sink ratio; (b) more dependency on source-sink ratio.

As the visual output is based on a biophysical model, simply by playing on certain parameters, such as the  $\alpha$  ((3)) that controls bud break, one can obtain trees of different complexities, as in Fig. 5. Fewer branches appear at lower  $\alpha$  value, and the plant automatically becomes taller. This emergent result is in line with a common practise that people remove side shoots to obtain a tall trunk. This parameter can be used to obtain trees of different cultivars. Different colors in Fig. 5 represent different PAs.

### B. Simulating tree plasticity with different light intensities

Using leaf photosynthesis model, tree plasticity under different light intensities above canopy are simulated (Fig. 6). Colors from red to green are used to visually distinguish light intensities inside canopy. Higher light intensity in the right gives positive feedback to bud break out and hence more dense crown, which is visually obvious in Fig. 6b. Notice that excessive light does not mean endlessly branching as this is controlled by potential buds defined in development model. Moreover, the photosynthetic response curve will saturate with the increase of light intensity.

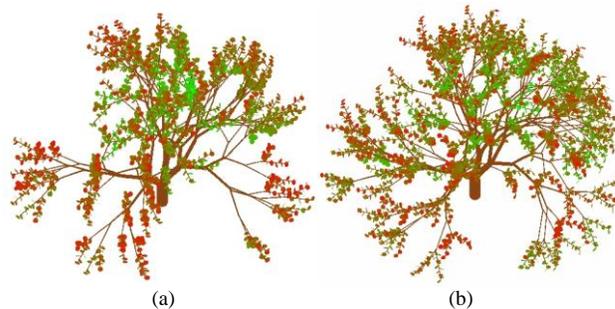


Figure 6. Trees simulated with low (a) and high (b) light intensities. Colors represent relative light intensity inside canopy, with red and green for high and low light intensity respectively.

C. Simulating tree response to pruning

Realistic tree behavior in reaction to pruning is shown in Fig. 7. The age of displayed trees is 15 cycles, and they were pruned at cycle 9. From left to right, policy of pruning is no pruning, removal of terminal bud of main stem, removal of terminal buds of all stems, and cutting top of main stem, respectively. As less buds are presented after pruning, the sequence, more pruning leads to more branches near the bottom. Trees are taller or shorter, dependent on the time and position of pruning. There is no forced rule indicating number of new shoots after pruning.

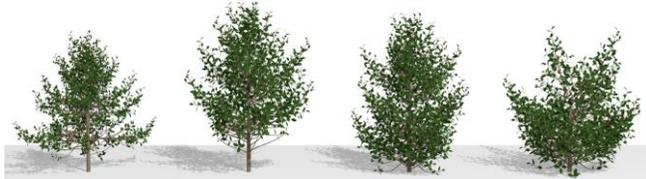


Figure 7. Response of trees to pruning. From left to right, policies of pruning are no pruning, removal of terminal bud of PA 1, removal of terminal buds of all branches, and cutting top of main stem, respectively.

D. Simulating tree competition

As plant-level photosynthesis model has high computational efficiency, we first test tree plasticity with the single control of bud break with source-sink regulation. From a predefined seed (a given set of source and sink parameters), the same tree exhibits plastic behaviors in response to different  $S_p$  values as in (9); see Fig. 8. Higher density gives smaller, thinner and slightly shorter trees.



Figure 8. Trees simulated under different population densities, from left to right:  $S_p = 64 \text{ m}^2$ ,  $S_p = 16 \text{ m}^2$ ,  $S_p = 4 \text{ m}^2$ ,  $S_p = 1 \text{ m}^2$ .

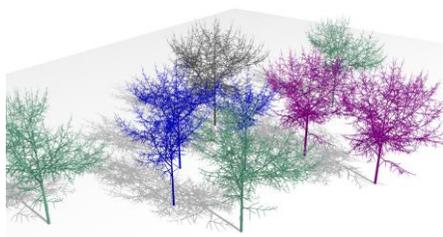


Figure 9. Trees of different crown size in response to their local area ( $S_p$ ). The trees with same color have the same  $S_p$  value.

This way, given the location of each individual tree in a stand, the local occupied area of each tree can be computed and this will automatically limit the size of tree crown from invading other trees. Fig. 9 shows a tree stand where individual trees are distributed randomly. Here no branch collision detection is applied.

Without consideration of local light control on bud break, the simulated tree crown is isotropic. Taking into the secondary mechanism of bud control with light, we simulated two neighboring trees grown up in parallel (Fig. 10). The competition for light started at a certain age of plants. The asymmetrical tree shapes are caused by low light intensity at neighboring area where less buds break out. There are self-pruning in the trees in that old branches fall down automatically.

E. Simulating tree response to obstacle



Figure 11. Effect of pagoda on tree shape.

With simulation of light distribution in canopy, we simulated a tree grown near a pagoda whose buds sense the local light level (Fig. 11). While the standard-alone tree (left) shows full canopy, the tree in the right loses part of branches. This is also visible for the same tree at younger stage (middle).

Fig. 12 shows a nice example on how bud behavior is controlled jointly by light intensity and source-sink ratio. There is no more control on bud break when the tree grows over the roof, its crown recovered by reiteration structure (the top branches are the same).



Figure 12. A tree grows over a roof, with fate of bud controlled by light intensity and source-sink ratio.

F. Performance

To evaluate the performance, we compare the time used for computing the tree using plant-level photosynthesis model, leaf-level photosynthesis model on CPU, and leaf-level photosynthesis model on CPU + GPU (Table I). The other modules of biomass allocation and organogenesis remain the same. The computation time for light intensity at each cycle (light model) is very costly for CPU implementation, but the CPU + GPU method improved greatly the efficiency of light calculation, being more obvious for complex trees (177 times for age 25). Total simulation time for tree development and growth reduced greatly accordingly. The computational efficiency is much



Figure 10. Response of trees to pruning. From left to right, policies of pruning are no pruning, removal of terminal bud of PA 1, removal of terminal buds of all branches, and cutting top of main stem, respectively.

higher when plant-level model is applied ( $<1s$ ), independent on plant age or tree complexity. This means response to planting density or pruning of trees can be achieved in real-time.

TABLE I. PERFORMANCE FOR COMPUTING TREES AT DIFFERENT AGES. TIME FOR LIGHT INTENSITY AT EACH CYCLE (LIGHT MODEL) IS REDUCED BY CPU+GPU (C+G) IMPLEMENTATION.

Tree age	Organs	Plant-level Simulation Times (s)	Organ-level			
			Simulation Times (s)		Light Model (s)	
			CPU	C+G	CPU	C+G
10 years	3,860	0.11	31.08	10.6	8.42	1.06
20 years	55,466	0.28	631.37	32.3	257.62	2.52
25 years	547,832	0.49	4,181.00	99.71	931.74	5.26

## VII. CONCLUSION

We presented a dynamic biophysical tree model, GreenLab, which simulates tree structure and its plasticity in response to environment (obstacle, density, light) and management (pruning). The adaption of trees is automatic by deciding bud fates from internal and external conditions, without applying deformation or collision detection. The same tree (defined by a set of parameters) can display vastly different structures, because of the power of underlying mathematical model. Our method is affordable to create dynamic tree library for various circumstances. Depending on needs, different combinations of photosynthesis models and treatments can be chosen, with corresponding tree shape and cost. By using GPU programming, computational efficiency is high even when leaf-level light interception and photosynthesis model are conducted.

A limit of our work is that to design a tree based on GreenLab, users should possess some knowledge of botany and eco-physiology. Once the parameters are given for a tree, user can modify environment and interact with the virtual tree, as if it were a living organism, without caring for the internal mechanism of tree growth. It is interesting for scene designer, since putting a virtual tree is similar to putting a seed, and then one can see the interaction and dynamic evolution of the trees. The potential of our work also lies in

the possibility of simulating effects of other environmental conditions, such as temperature and  $CO_2$ . Users can even have optimal solution of treatment if applying optimal control on the virtual plant.

Our work is similar to some previous works as it also simulates the light environment and plant response. The major difference is that we simulate not only tree development, but also tree growth with an internal feedback mechanism between both processes. Light stimulates not only bud break but also photosynthetic production. Furthermore, we can simulate more complex botanical plant architecture and modify the meristem activities (depending of Q/D). Growth Units are very flexible, which makes the interaction between growth and environment very efficient and faithful.

By means of these simulation methods and models, it could be easily used on education of botany, landscape design, games and so on. What a potential and more valuable aspect is the application on agroforestry. By combining light model and pruning management into one organic whole, we could evidently ameliorate light environment in canopy under different pruning strategy, which reduces pests and thus play a role in improving fruit quality. These virtual experiments provide quantitative standards for fruit cultivation and management. This is the future direction of our research.

Based on current hypothesis chosen in the model, tree plasticity from the potential development pattern, regarding to bud breakout, organ sizes and final tree shape become emergent properties of the model. However, the model is still open to other mechanisms, such as hormone regulation by signal propagation.

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