A Detailed Computational Model of Tree Growth

Abstract

Global warming and increased CO_2 emissions are becoming a large problem for the world. Tree plantations sequester carbon at up to 30 times the rate of old growth forests, and are a common way of reducing carbon footprints. We have created a computational model of tree growth that can determine optimal conditions for the planting of trees and significantly increase the effectiveness and viability of these plantations. In our model, leaves on the tree generate biomass for growth using photosynthesis. This biomass is used for, in order, root growth, leaf replacement, growth in width proportional to stress, and growing new branches and leaves. Stresses are computed based on forces due to gravity and wind. Branching is proportional to light availability at the branching site. Where possible, biological parameters are taken from naturally observed values and previous research. Extensive recursive algorithms and a voxel grid (3D index of space) are used to achieve efficient simulation and 3D visualization. We validate the model by confirming that generated trees exhibit allometric rules observed in nature, regarding leaf mass, stem mass, height, trunk diameter, and total mass. When exposed to varying light or wind conditions, statistical analysis confirms that the model successfully predicts characteristics of growth including phototropism and anemotropism. To our knowledge, our model is the first to exhibit these emergent properties without explicitly programming them into the model. We demonstrate one potential application of the model by determining the optimal tree spacing to maximize carbon uptake and timber production in a plantation.

1. Introduction

In nature, trees follow sets of allometric rules, relationships between various quantitative values in trees that typically hold true for all tree growth. However, it has not been determined how these large-scale characteristics of growth arise. An accurate model that exhibits these allometric rules as a result of underlying biological processes would provide a possible explanation for this similarity in growth among all trees. In addition, the model would be useful in predicting if and how trees will grow in a given environment, which has both environmental and commercial applications.

We propose and implement a unique model that simulates deciduous tree growth at the branch level based on underlying biological processes. Leaves on the tree generate biomass from photosynthesis, taking into account light availability at their particular location. This biomass is used to thicken existing branches based on mechanical stresses they experience before growing new branches and leaves. Powerful computing techniques including extensive recursive algorithms with caching, a voxel grid (3D index of space), and multithreading (utilizing different cores of the computer to compute different processes) are used to achieve efficient simulation and 3D visualization. We validate the model by confirming that generated trees exhibit allometric rules observed in nature regarding leaf mass, stem mass, height, trunk diameter, and total mass, as well as other properties of growth including phototropism and anemotropism.

An accurate model of tree growth allows for the ability to test tree growth in many different situations, such as the interaction between a tree and its surroundings (buildings, walls, other trees, etc.). We have made the source code available on an open-source license, so that other groups can use and extend it for additional simulations (which one group has already done).

2. Background and Related Work

Previous work in tree modeling has traditionally been undertaken from two different perspectives: modeling based on real trees and modeling based on biological accuracy (see [TZW+07] for an image-based model and [HN09] for a rule-based model). However, due to factors including but not limited to: geometric complexity, ease of modeling and editing, and realism, scientists have not created a successful model that combines the two perspectives.

Rule-based modeling has traditionally relied on programming specific aspects of tree growth into the model, and using the model to observe other characteristics. For example, Sean Hammond and Karl Niklas explicitly programmed allometric rules into their model, SERA. Trees are represented as a single trunk segment with a hemispherical canopy that grows in response to light availability. The model is used to simulate thousands of trees in a forest, and observe how competition for light affects population dynamics.

Image-based modeling is very useful and popular in the movie and gaming industries, where it is useful to generate visually appealing trees [e.g. TZW+07]. However, these models are not based on any biological rules or principles. The models focus on the use of L-systems and advanced computing techniques to simply reproduce images of real trees, but do not make any attempt to be biologically accurate or model tree growth over time..

To our knowledge, there is no work in tree modeling that achieves accurate simulation based on local environmental factors and inherent biological processes. Using advanced computing techniques, we have created a biological model of tree growth at the level of individual branches.

3. Mathematical Model

Trees grow based on a series of biological and physical processes. At a high level, the tree uses the

process of photosynthesis to fix carbon from carbon dioxide into carbohydrates for cellular respiration and growth, which is apportioned across the tree.

Our model focuses on the scarcity of light as the limiting factor in the process of photosynthesis. Each step of our model, in which all values are calculated and represented, is equal to a time period of one year. Available light in the tree canopy is determined using methods of light propagation. We propose that in the step where carbon must be apportioned across the tree for growth, carbon is first devoted to growth in width based on the stress experienced by a branch, and the leftover carbon is used to branch and grow new leaves. Our model represents trunks and branches of the tree as segments of constant length, with branching occurring only at the ends of segments.

3.1 Available Light

In order to calculate the solar radiation incident on a canopy over a period of a year, it is necessary to integrate the incident radiation as the sun moves from morning to evening and through all of its positions in the sky over a year. Since the two-variable integration needed to calculate this is rather complex [N05], we opted to consult an online source to obtain the solar irradiance per year [SEH13]. Our model approximates light to travel in 5 directions: straight down, plus light coming diagonally from North, South, East, and West.

Importantly, the same amount of light is not present at all points in and under the tree canopy. This is a critical factor to model tree growth accurately. To determine the amount of available light at given points on the tree, light must be propagated through the canopy; if leaves are present in the space the light is going through, a certain amount is absorbed by the leaves (see below). This results in fewer branches in the middle of the tree, because branches in the middle are shaded by leaves at the top of the canopy. The shadow is present at all points inside and under the tree canopy; at the bottom of the tree,

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the shadow can be seen on the ground based on the amount of light left.

3.2 Photosynthesis

Plants add dry mass almost exclusively by photosynthesis, which creates chemical energy in the form of carbohydrates from light energy. Chloroplasts within the cells of trees take in light, water, and CO_2, and through a series of chemical reactions, make a monosaccharide. This monosaccharide is used to form more complex carbohydrates which are used for growth. The process of photosynthesis can be summarized by the general reaction:

$$6CO_2 + 6H_2O + \text{light} \rightarrow C_6H_{12}O_6 + 6O_2$$
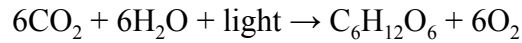
where $C_6H_{12}O_6$ represents a carbohydrate such as sucrose or glucose. These carbohydrates can be assembled into long chain sugar molecules like starch and cellulose, which is the main component of cell walls. The CO_2 comes from the air through the leaves' stomata. H_2O is mostly absorbed from the soil, and light comes from the sun.

All three of the input quantities can be a limiting factor for the process of photosynthesis, although in practice CO_2 is normally abundant. In desert environments, water is usually the limiting factor, but in other locations such as the tropics or other forests, the availability of light is the limiting factor. Other additional factors that affect the rate of photosynthesis include the leaf temperature and the rate of gas exchange through stomata, but those are rarely dominant factors [CN98, ch. 14] (see [CBGB91] for a more complex model, as well as [CN98, Sec. 14.8]). In this project we assume that water and CO_2 are abundant, and we focus on the influence of light availability on plant growth.

Monteith observed that biomass accumulation by plants is proportional to the solar radiation collected by the plants. This suggests a model

$$A_{n,canopy} = ef_S S_t$$

where $A_{n,canopy}$ is the net biomass accumulation of the plant canopy in g/m²/day, S_t is the total solar

radiation incident on the canopy in MJ/day, f_S is the fraction of incident solar radiation intercepted by the

canopy, and e is the conversion efficiency for the canopy [Mon77, CN98]. e must express the fraction

of solar radiation that the plant can use in photosynthesis (photosynthetically active radiation or PAR) as

well as the fraction that is absorbed or reflected. Monteith reported e values around 1.5 g/MJ for a

number of plant species. More recent work limits the solar radiation to the PAR portion, and expresses

e in molar units such as (mol CO_2) / (mol photons). Absorptivity of individual leaves is about 0.5 (0.85

of PAR), but once the leaves are arranged into a canopy, internal reflections among leaves raise

absorptivity of the canopy to 0.85 (0.95-0.98 of PAR) [CN98]. In our model, units will be expressed

in kg/m²/year.

The net biomass accumulation calculated as shown above is the amount of dry mass that can be

apportioned to growth throughout the tree.

3.3 Growth

A tree uses glucose and other products of photosynthesis in order to grow. One of the main questions is

how the tree apportions growth among its various parts. While a tree does have systems in place to

carry out paracrine, or local, signaling, it does not have an endocrine system to perform long distance

signaling. This means that cells in different regions of the tree do not have communication to determine

how much of the available glucose they should use to grow. However, trees still achieve a set of

allometric rules relating sizes/masses of various parts.

We propose one possible method by which trees could apportion their mass growth throughout

the tree. In our model, the growth of each segment is linearly proportional to the mechanical stress that

the segment experiences from environmental forces. When under mechanical stress, trees release the

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hormone auxin which stimulates the growth of cambium. Cambium then specializes into xylem and phloegm, causing the thickening of shoots and roots [ASG+11]. The two main stresses that a tree experiences are from the gravitational force due to its branches and leaves and the forces caused by wind blowing through the leaves of the tree.

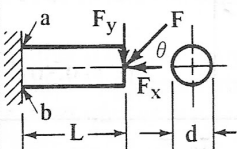The gravitational force on a segment is easy to compute. It follows

$$F = mg$$

where m is the mass of the segment and its descendants (in kg) and g is the acceleration due to gravity (9.8 m/s^2). The gravitational force is applied at the center of mass of the descendants of the segment.

The wind force on a segment is computed by finding the magnitude and center of the wind force felt by its descendants. The force experienced by a single leaf from wind is:

$$F = 0.5 c_d r A s^2$$

where F is in Newtons, c_d is the drag coefficient of the leaves, r is the air density (in kg/m^3), A is the area of the leaf (in m^2), and s is the wind speed in m/s [BW06, N05]. The drag coefficient c_d may vary by leaf shape [BW06, V09] and the maximum horizontal wind speed can vary by location, so both are adjustable parameters in our model to be capable of simulating different tree species. After computing the center of forces on all leaves that are descendants of a given branch, the x and y components of the forces on a given segment are converted into the perpendicular and parallel components, respectively, of the force on the segment.

Our model makes the simplifying assumption that all branches (segments) are cylindrical. The equation for the stress experienced by a cylindrical beam from an attached mass is [MH25]:

Type of Beam and Loading*	Maximum Nominal Tens. or Comp. Stress	Maximum Nominal Shear Stress
(beam diagram with F_y, F, θ, F_x, points a, b, length L, diameter d)	$\sigma_a' = \dfrac{1.273}{d^2}\left(\dfrac{8LF_y}{d} - F_x\right)$	$\tau_a' = 0.5\sigma_a'$
	$\sigma_b' = -\dfrac{1.273}{d^2}\left(\dfrac{8LF_y}{d} + F_x\right)$	$\tau_b' = 0.5\sigma_b'$

where F_x and F_y are the parallel and perpendicular components of the applied force, L is the distance from the base of the segment to the center of mass or center of wind force of the segment and its descendants, and d is the diameter of the segment. The maximum stresses from wind and gravity are summed [MH25].

The first equation, in context, calculates the maximum tensile stress experienced by the branch, which occurs at point a. The second equation calculates the maximum compressive stress experienced by the branch, which occurs at point b. Since wood is much more vulnerable to compressive force than tensile force [MH25, p. 375][N09, p. 336], our model only calculates the compressive force when determining its growth.

After calculating the stress it experiences from the equations above, the tree grows in width proportional to the stress experienced. The constant of proportionality is a parameter of the model and can depend on the tree species. Note that when the diameter increases, the stress decreases according to the above equations, so that growth stabilizes.

Trees are largely composed of dead tissue. The xylem (wood) of the tree does not need to be replaced each year, and so when calculating the carbon used, only the addition in width is calculated; replacement of previous wood is not needed.

3.4 Branching
After the tree has apportioned the required mass to handle the stresses above, the leftover

carbohydrates created from photosynthesis can be used to grow new branches and leaves.

In our model, the chance of branching at any location in the tree is proportional to the light available at that location. Branching in nature is more common where light is present [FKKC10] [EKVS11]. When the tree branches, a new cylindrical segment is created at the end of the parent segment (with a randomly generated angle), creating continuous woody tissues. The biomass of the new segment must be subtracted from the total carbon available for growth.

Our model assumes that leaves are present on the youngest tissues of the tree. Therefore, branching will create new tissues that have leaves on them, and is critical to the survival of the tree. If the tree has no leftover carbon to devote to branching and therefore growing new leaves, then the leaves will fall off over the winter and will no longer generate carbon for growth. Therefore, a tree that is not able to branch and grow new leaves will die.

3.5 Death of Branches

In our model, trees stop apportioning carbon to segments that do not produce a positive return on the carbon invested for them. We calculate the amount required to grow the branch as a whole based on the stress it experiences, and compare it to the amount of carbon generated from its leaves. If the former number is greater, the tree does not invest carbon in the branch and it dies.

4. Implementation

We implemented the biological model of tree growth using Java in the Eclipse programming environment. Visualization of output was implemented in OpenGL. As noted above, in our model a *segment* is the basic building block of a tree, representing a piece of trunk or branch. A tree in our model is a collection of segments, where each segment is a cylinder with a constant height but a diameter that grows over time. A tree begins as a single segment, and the segment branches upward to create additional segments. In each time step of one year, the program:

1. Computes the light on the leaves and the mass of carbohydrates created through photosynthesis. This is the "carbon budget" for the year.

2. Uses a percentage of the carbon budget to grow roots.

3. Computes stresses on all segments from gravity and wind.

4. Grows segments in width corresponding to the stresses they experience.

5. Uses leftover carbon to grow new branches and leaves for the next year.

6. Prunes branches that are not harvesting enough carbon.

To accomplish this simulation efficiently, the tree is represented as a recursive data structure, with a Voxel Grid as a spatial index of the area it grows in. These data structures are described in more detail below.

As a stepping stone to our final 3-D model of tree growth, we implemented a basic 2-D model, shown in the figures below:
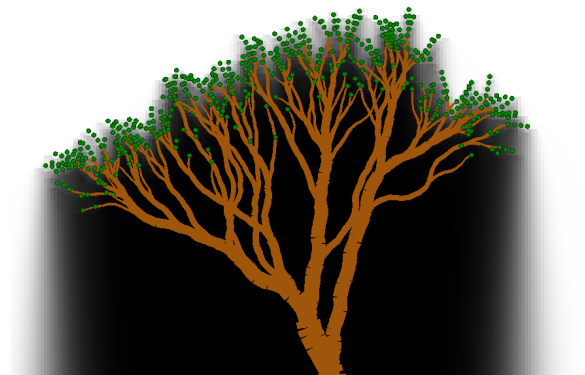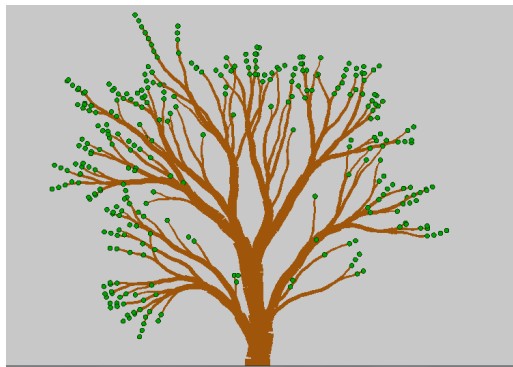
Due to the limitation of 2-D modeling, we dropped the 2-D model in favor of a 3-D one. The 2-D model, however, was critical to building our understanding of core programming concepts.

Constants for the growth of the tree (e.g. branch angle factor, photosynthesis efficiency constant, mass of a single leaf) are stored in a separate class called TreeParams. This organizes the

code and allows species-specific parameters to be easily changed.

4.2 Recursion

Trees are naturally represented as a recursive data structure. Therefore, recursion is critical to a

model of tree growth. Recursion is the repeated application of a procedure or structure until a finite base

case is reached. In our case, recursion consists of carrying out a procedure on a given segment, and the

same procedure is called on all segments that sprout from that current segment. This process will

continue until every segment in the tree has carried out the given procedure. Our program uses recursive

algorithms in many ways. For example, to calculate the total mass of a segment and everything sprouting

from it, the program recursively cycles through each one, adding the masses of the segments as it runs.

Recursive algorithms are also used to calculate the total mass of the tree, calculate the carbon budget

through photosynthesis, calculate the stresses on segments, and grow the segments in width according to

those stresses. All of these are calculated using equations given in the mathematical model above.

4.3 Voxel Grid

A critical component of the 3-D simulation is the implementation of a voxel grid. A voxel grid is

a 3-dimensional index of space with constant spacing of voxels. Each voxel stores certain information

about the cube of 3-dimensional space that it occupies (e.g. whether it is occupied by tree tissues and

amount of light traveling in each direction). Voxel grids are typically used in 3-D computations and

visualization; examples include 3D scene reconstruction from multi-view imagery (e.g. [NZSS13]) as

well as the computer game *Minecraft* [M09].

The voxel grid is critical for our tree simulation's efficiency. It allows us to efficiently propagate

light through the tree canopy. Our model implements directional light propagation. In directional

propagation, the direction of the light going into and out of each cell is stored and will continue to

propagate in the same direction. When a cell is occupied by a branch or leaf, the light leaving the cell

will be significantly smaller than the light that entered the cell. The voxel grid also prevents branch

collision. When segments are added to the tree, the tree can quickly find the location of the segment in

the voxel grid; it sets the location to be full. If another segment tries to grow into this occupied space, it

is unable to.

In addition, our model incorporates a wrap-around world so that there are no edge effects. For

example, a branch that goes off the east side of the simulation will enter on the west side. This feature

allows us to essentially model a small plot within an infinite forest, which is useful in applying the model
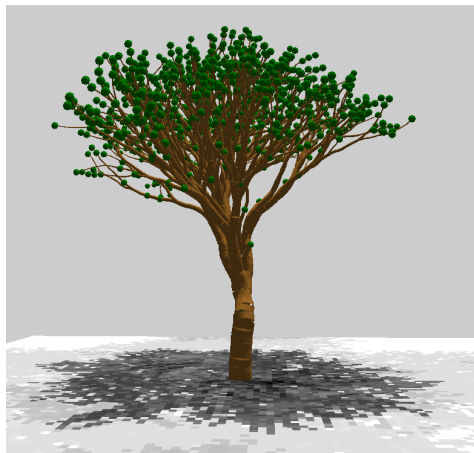
to real situations.

Figure 4.3.2 Tree with directional light propagation

4.4 Code Outline

An overview of the classes that we implemented in our program are as follows:

- **Simulation** is the main class that establishes dimensions for the simulation and creates trees to

  grow. It is the control center of the model.

- **SimulationParams** stores environmental constants for the simulation such as direction of light,

wind speed, and gravity.

- **Tree** is the class object for a single tree, i.e. a collection of segments.

- **TreeParams** stores constants for a given tree species such as the wood density, the branch angle factor, the area of leaves, and the photosynthesis growth exponent.

- **Segment** is the class object for a localized clump of cells in a tree. It is the basic building block of trees.

- **VoxelGrid** is a 3 dimensional grid that stores the amount of light available at any location in the simulation and prevents two segments from taking up the same space.

- **TreeCanvas** opens a window and draws the current tree in it using OpenGL.

- **Vector3** is a 3D vector class that extends Vector3f and adds a few functions that are not available in the Vector3f class.

- **CompareSegmentAge** is a class that implements Comparator to sort segments by their ages.

The full Java code listing can be found online here: http://goo.gl/GUUR2b

5. Model Validation

5.1 Allometric Rules

One of the main validations for our model is the confirmation that it exhibits allometric rules, which are relationships between different quantitative values on a tree. By showing that our model produces allometric rules that are observed in nature, we validate that our mathematical model is one possible explanation for these properties of growth. Although there are many allometric rules, we chose to test four different rules: mass of the leaves vs. mass of the stem, diameter at breast height vs. mass of the leaves, diameter at breast height vs. mass of the stem, and diameter at breast height vs. height. Using data over 60 years for 10 different trees, we compared our data to a dataset of 851 angiosperms and gymnosperms [_insert citation here_]. The graphs are shown below. In each case, our tree simulation

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shows a relatively close match to the data for real tree species.
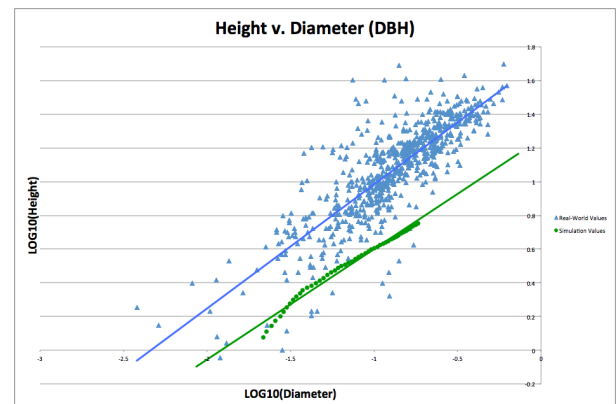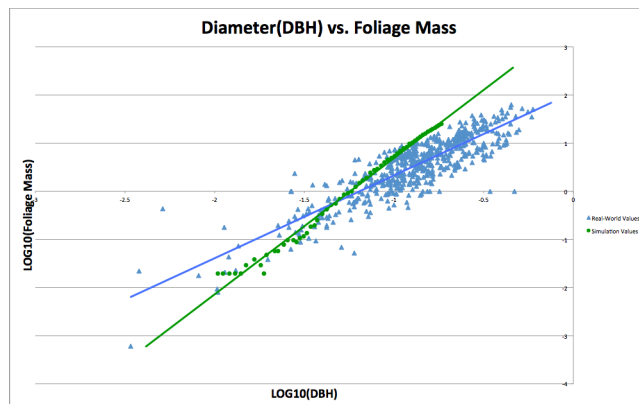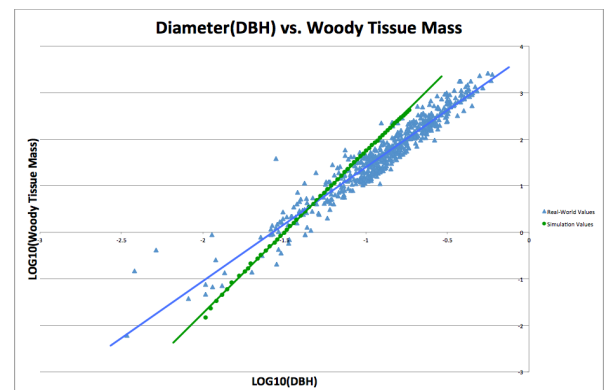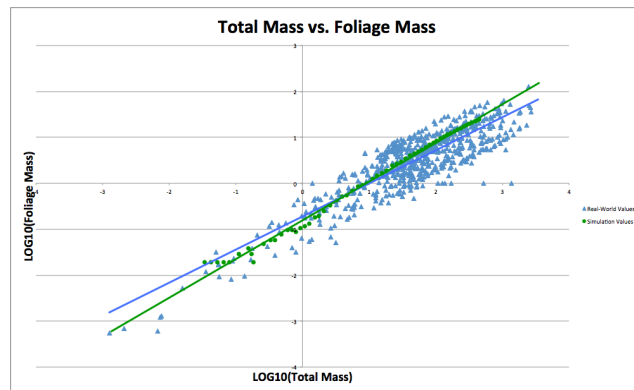
5.2 Phototropism

Phototropism is an important feature of tree growth and is exhibited by all plants. Positive phototropism is the propensity for plants to grow toward a source of light. Some plants have light sensitive tissues that grow toward light, and others simply exhibit phototropism due to the fact that tissues on the lighter side will grow more while those on the darker side will not.

Our model does not account for specialized tissues in plants that are designed to grow toward light, but exhibits phototropism anyway. Using directional light propagation, we can easily change input parameters for light so that the majority of light comes from one direction. If the tree grows towards the light, then its center of mass will be skewed in the direction of the light. Using hypothesis tests, we compared the tree in normal and skewed light conditions.

In testing under normal light conditions, we compared the x and y-coordinates of the center of mass of a simulated tree to the initial center of mass, (5,5). Data was collected on a random sample of 30 trees, and the calculated P-value was 0.37925, showing that the tree does not consistently lean to a side under normal light conditions.

We then changed input light so that the majority of light was coming from the north. If our model exhibited positive phototropism, the y-coordinate of the center of mass would be shifted toward the direction of the light source. Data was collected on a random sample of 30 simulated trees and the calculated P-value was 2.017×10^{-6}. We can conclude with 99.9% confidence that the trees consistently grew into the light.
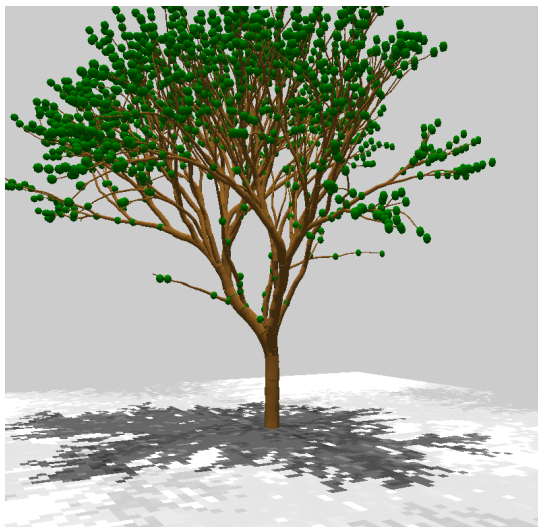
These results can be found in Appendix A.
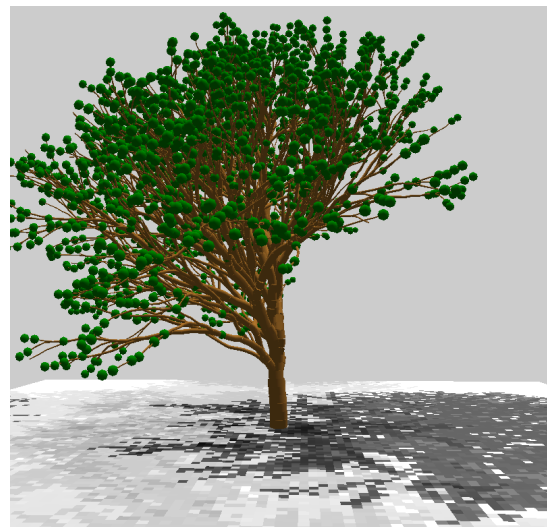
Figure 5.2.1 Tree in normal light conditions   Figure 5.2.2 Tree with majority of light from north

5.3 Anemotropism

Trees in different environments experience different speeds of wind. In climates such as the tropics, trees can focus on growing in height rather than width; in harsher climates such as tundra, trees grow shorter in height but larger in width to stabilize themselves, preventing problems such as windthrow.

To test if our model responds to different wind conditions in the same manner, we compared the z-coordinates of the center of mass of trees experiencing different wind speeds. Data was collected on two different random samples of 30 simulated trees, with one group experiencing 20 m/s wind speeds and the other group experiencing 30 m/s wind speeds. The resulting P-value was 1.331×10^{-10}. With a significance level of 0.001, we can conclude with 99.9% confidence that the trees consistently grew shorter when the wind speed was higher.
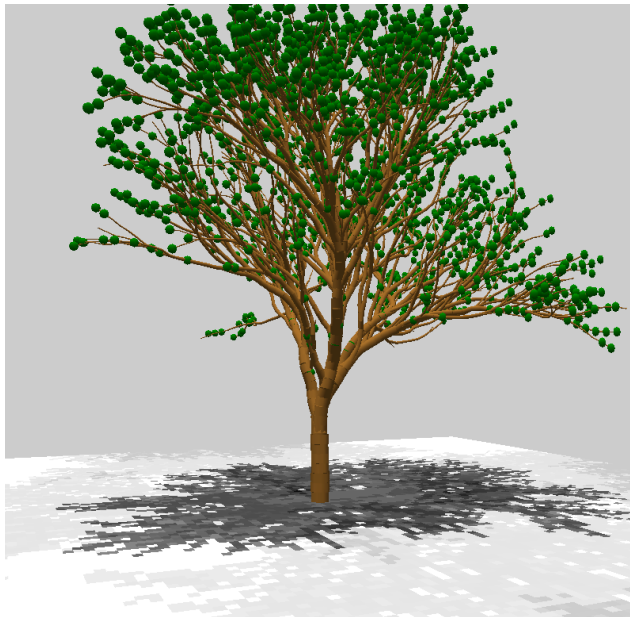
These results can be found in Appendix A.
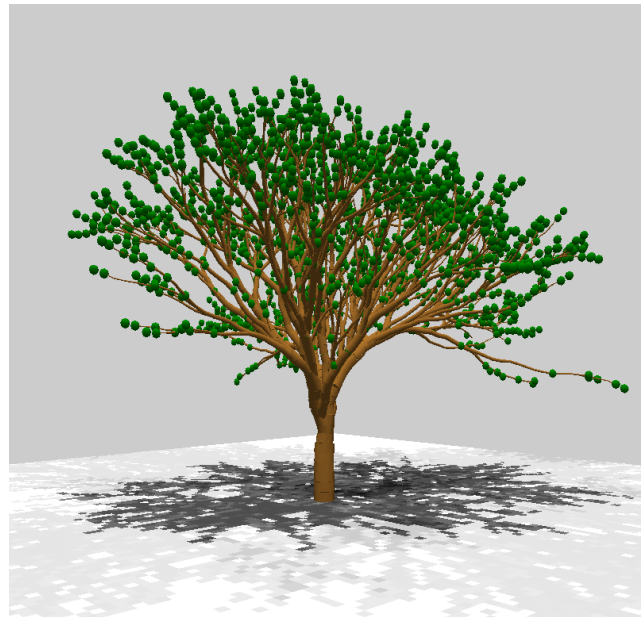

Figure 5.3.1 Tree Experiencing 20 m/s winds   Figure 5.3.2 Tree Experiencing 30 m/s winds
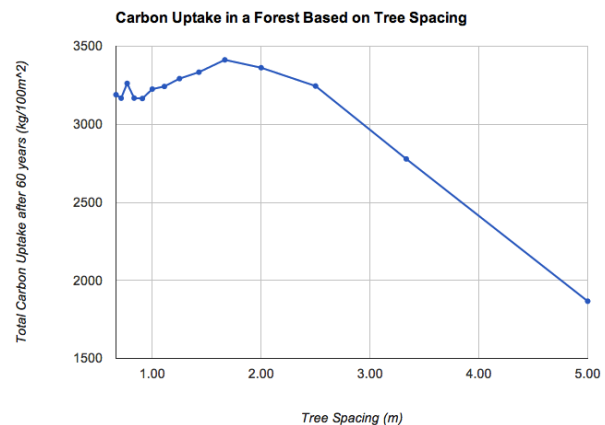
6. Applications

There are many possible applications for an efficient and accurate biological model of tree growth.

A common way of reducing carbon footprints is the sequestration of carbon in tree plantations. Studies have shown that tree plantations sequester carbon at up to 30 times the rate of old growth forests [D13]. Experiments to optimize tree planting conditions are extremely time-consuming, taking upwards of 15 years to complete. In many commercial situations, differences of a few percent in

efficiency can make the difference between commercial success and failure. Being able to simulate and optimize tree growth and carbon uptake on tree plantations could make a significant difference in the commercial viability of carbon sequestration.

To find the optimal spacing between trees, we tested grids of 2x2 trees up to 15x15 trees in a 10x10 meter plot, finding the combined mass of all the trees after 60 years of growth. There are no edge effects in the simulation due to the implementation of a wrap-around world, which allows our simulation to essentially represent a small plot in an infinite forest. Data was collected on a random sample of 10 simulations in each setup. We found that at a spacing of 1.67 m between trees, the total carbon uptake was maximized. Compared to a spacing of 2 m, the amount of carbon sequestered is increased by 1.3 million kg in a square mile plot per year.

Using the same experiment, the dependent variable was changed to be the amount of usable timber produced. We defined usable timber as wood that had a greater diameter than 15 cm.
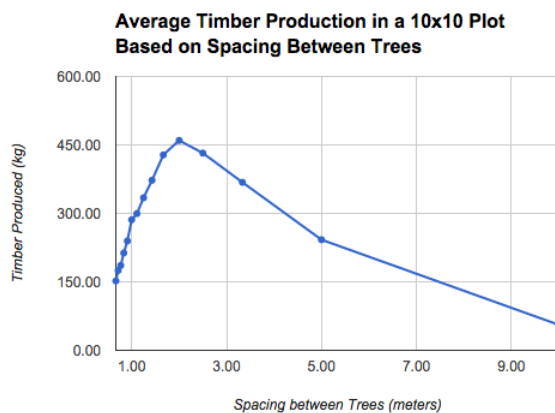
The optimal spacing of trees for timber production is 1.5 m, which is different than the optimal value for carbon sequestration. This demonstrates the capabilities of a model such as ours in applications for multiple fields.

7. Conclusion and Future Work

Based on the results of our model validation, we can conclude that we have successfully created a biologically accurate model of tree growth. The model combines the biological accuracy of a rule-based model with the graphics output of a image-based model. Additionally, the model exhibits critical emergent properties of tree growth without them being explicitly programmed into the code. These results provide one possible explanation for the reason that global allometric rules arise in tree growth without endocrine communication across the tree. In addition, the model can be used in a variety of different ways for practical applications. We demonstrate two potential applications of the model by determining the optimal spacing for trees in a plantation to maximize carbon sequestration and/or timber production.

There is significant future work that could be done to improve the model and increase its accuracy. Examples include expanding the simulation to model varying tree species. Additionally, adding the limitation of water in the growing process would allow for the modeling of more diverse environments. Adding water as a limitation may require more advanced root simulation systems.

Appendix A: Data

Phototropism

	Tree in Normal Light Conditions (30 trials)		
	Center of Mass (X)	Center of Mass (Y)	Center of Mass (Z)
Mean	4.9535	5.2447	2.2668
Standard Deviation	0.2617	0.2367	0.1261
P-value	0.3383	2.01689 E -6	-----------------------------

	Tree with Majority of Light Coming From the North (30 trials)		
	Center of Mass (X)	Center of Mass (Y)	Center of Mass (Z)
Mean	4.9535	5.2447	2.2668
Standard Deviation	0.2617	0.2367	0.1261
P-value	0.3383	2.01689 E -6	-----------------------------

Anemotropism

	Tree in 20 m/s winds	Tree in 30 m/s winds
	Center of Mass (Z)	
Mean	2.2668	2.0535
Standard Deviation	0.1261	0.0927
Two Sample T Test P-Value	1.331 E -10	

9. References

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