Lectio Praecursoria 13.02.2009

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Dr. Custos, Dr. Opponent, Ladies and Gentlemen,

Throughout the history, trees have played significant role in our lives. Man has shown great respect and developed virtually Martin Buber's "I-You" relationship with them. A relationship that emphasises mutual holistic existence of two beings. The European Druids worshipped oaks. The gingko tree was sacred to the Chinese and Japanese. Sequoias, those giant redwood trees living for up to 2200 years were holy to North American Indians and Siddhartha Gautama later known as Gautama Buddha, the founder and spiritual leader of Buddhism, achieved his enlightenment under the Bodhi Tree. And let us not forget the traditional pantheistic relationship of the Finns with trees. Finns have worshipped many tree species, the rowan perhaps being the best known example. In Kalevala, the national epic of Finland, it says: "Tend thou well the sacred sorb-tree, Guard the mountain-ashes planted". The trees were believed to have personal powers. People told their worries to trees and asked for help. Trees were respected and even feared.

In fact, many of our expressions and proverbs have close association with trees. In the middle of the ongoing global financial crisis the expression "Money does not grow on trees" comes to my mind.

We use trees in many ways. Wood is still one of the most important raw material to us. The consumption of timber is used from building to paper-making and in the chemical industry. But trees are not only timber for us. Many of the things we eat and drink come from trees. Tea is probably one of the most widely-consumed beverage in the word, and the name of the tea plant Camellia sinensis refer to Chinese who have enjoyed tea drinking for many thousand years. And what would we do without our daily cups of coffee prepared from the roasted seeds of the coffee tree? Fruits of trees are often tasty, perhaps as a result of evolution, so that a tree can disperse its seeds effectively. Many of such species are commercially exploited and cultivated in orchards: citrus fruits, apples, pears, plum, olives to name a few.

In towns and urban areas trees have many benefits for us. They capture and absorb pollution particles with their leaves and moderate the climate. Perhaps the most important advantage of the urban trees is their contribution to our psychological health. People feel better when they see trees around them. They not only beautiful and pleasing but can for example tell us about seasonal changes linking us to the nature.

I hope these opening sentences help you to respect trees not only as objects but as living beings that are important in many ways in our daily lives.

Trees also offer an interesting subject for scientific study. To me such questions include: how do they function, how do they acquire their form and what is the interplay between the structure of the tree and its function? The purpose of this Thesis was to construct a generic modelling tool for woody arborescent plants, i.e. trees addressing these questions. But before we go further into details let us take an overview how a tree functions.

Like in other plants, powered by the sun the foliage of the tree (leaves or needles) produce in photosynthesis carbohydrates or sugars, which are the power source to run the tree. Sugars are the basic building blocks of cellulose and lignin the latter one making trees woody. Just inside the outer bark of the tree, a waterproofed layer, is a so called inner bark (phloem), that is made up of living cells that transport the sugars to different parts of the tree where they are needed. Sugars that are not needed immediately are stored in the trunk, branches and roots. To be able to photosynthesise the foliage need water and minerals that are absorbed by the roots from the ground and pulled up via complex hydraulic network in the trunk of the tree.

Trees grow in two ways. The buds at the tip of the branches dispersed all over the tree are the potential construction sites to make branches longer. Major advantage for the trees is their capability to get fatter by a layer of tissue (cambium) just beneath the bark adding new bark and new wood.

An important difference between animals and trees is the fact that (most) animals act as a single unit but the trees are modular. I have one heart, one pair of hands, one pair of legs, one liver etc. acting for the whole of me. Trees instead are made of similar units added together each functioning independently and each part is replacable. I cannot loose one arm and watch another one develop but a tree can loose a branch and replace it with a new one.

This is the way a tree is arranged into a structured whole. But there is more. Over the years a tree and trees around it grow and this affects how the tree experiences its environment. The modular structure of the tree and the interactions and feedback with its environment affecting the future structure and functioning of the tree are important factors that need to be considered in the tree growth modelling.

As a tree can be seen as a hierarchical, dynamic and self-regulating system, its functioning is well suited for studies employing systems analysis methods. Process based models are tools to analyse tree and forest growth and performance. A process-based tree model is a dynamic model in which the physiology of the tree is derived from the physical and biochemically based processes that take place in the functioning units of interest. A typical case might be one where the tree is partitioned to stem and branches represented using limited number of variables. Foliage, and root system are taken into account with single variable each. The main processes to consider are photosynthesis, respiration, senescence of living biomass, and the allocation of photosynthates to growth into to the old and new parts of the tree. The model should include how the physiology of the tree is affected by interactions and feedbacks between these units and the environment. Usually this dynamics and functioning of the tree is expressed with the differential or difference equations.

The process based models have been developed about thirty years and they have become well established scientific tools for understanding the processes governing tree and forest growth. They are important tools for theory development because a model should not only produce quantitatively realistic results but also act qualitatively in a logical way. Thus possible applications for process based models, in addition to predict future yield of a forest stand, are the cases when there is a need to provide causal models instead of empirical or statistical fits based on past data, for example the possible effects of climate change on future forest growth. Recently, process-based models have reached a level where they have become of interest for practical forestry and have been embedded in user-friendly educational simulation software.

A great deal of tree functioning has been clarified using process based tree models, but it has become evident that the three-dimensional crown structure affects, for example, shading and light interception in the tree crown and the distribution of photosynthates within the tree. The feedback effects which these processes have on the development of the individual organs of trees have not been considered in the classical process based models.

The fundamental understanding of the three dimensional tree architecture is due to the work of two European botanists Francis Hallé and Roelof Oldeman. They made a broad comparative study of mainly tropical tree species examining the development of trees from seed either in their natural ecosystem or in orchards.

The relatively easily observable features included criteria related to extension growth, branching process, morphological differentiation of the axes and the position of reproductive organs. The features included precise properties of tree shape such as whether the main stem remains unbranched or not, whether the growth of the tree is seasonal (rythmic vs. continuous growth), as well as factors representing a continuum of possibilities such as the orientation of branches.

Hallé and Oldeman provided a well organised and methodical framework to classify the three dimensional tree architecture. The system of Hallé and Oldeman now consists of 23 different architectural models, a surprisingly low number that can capture the estimated more than 80 000 tree species, which suggests that there are not so many ways to become a tree.

The complex modular architecture of trees and plants, their diversity and plasticity, i.e. the ability of plants to adapt to their environment, has attracted plant scientists, mathematicians, computer scientists etc. to find methods to capture this variety in a unified and universally concise way.

From the point of view of this Thesis, an important theoretical framework based on term rewriting systems was introduced in 1968 by the Hungarian botanist, Aristid Lindenmayer, to simulate the development of simple multi-cellular organisms. His approach was later named the Lindenmayer systems or L systems for short. This formalism was closely related to formal languages, and in essence it views the plant development as a parallel rewriting system.

In L systems a plant is viewed as an assembly of discrete modules. A module represents any constructional unit in a plant that is repeated as the plant develops, such as a shoot, a bud (apical meristem), a leaf or a flower. L systems are dynamic, i.e. the shape and state of a plant is the result of development, not its static 'snapshot' configuration in space. The rewriting rules for the plant parts can change the state of a plant part, replace it with new plant parts, or remove it from the plant structure.

Over the years the development of the theory of L systems has gradually extended the formalism to expand the range of phenomena that can be included in plant modelling. For, example, the communication between adjacent plant parts and the propagation of information through the growing plant structure (endogenous interaction) can be performed with context-sensitive L systems.

L systems and their extensions known as growth grammars have been applied in various studies on higher plants, for example, plant-insect interaction the development of boreal shrubs in different environmental conditions, and, of course, in the studies of tree architecture.

A decade a ago many research teams in different parts of the world started to combine process-based tree models and the morphological models. Models that have characteristics of both process-based models and morphological models treating a trees as an assembly of interconnected elementary units have emerged. These kind of models are called functional-structural tree models. If one wants to set the date of birth for this approach the first workshop held in 1996 in Helsinki is the one.

The functional-structural tree models have paved the way for new possibilities to study phenomena that has not been possible with previous generations of plant models. Because they have explicit and detailed description of the three-dimensional structure of the tree, functional-structural tree models are especially well suited to study structural dynamics of trees and their interactions with environment. Such possible applications include the assessment of photosynthetic production that benefits from a three-dimensional canopy model to simulate light interception, effects of tree pruning and development of wood quality and replacing destructive or even impossible experiments.

The construction of a functional-structural tree model varies from case to case but generally speaking there are two ways to finish with a functional-structural tree model. One can start with a structural or geometrical model and add physiological detail into it, or one can have a process-based model and add structral detail and dynamics into it. In principle there is no limit to which processes and activities could be included in a functional-structural tree model. But as photosynthesis produces the energy and consequently the material in the tree its description has been the prime interest and particularly challenging task.

To describe the three-dimensional architecture of the tree in a functional-structural tree model is straightforward to understand. The tree is simply a collection of elementary units. How these elementary units are organised to form larger structures like branches is well studied. These elementary units should permit the description of both metabolic processes and the three dimensional structure of the tree.

From the point of view of modelling an elementary unit should simplify and aggregate the real biological processes to concentrate on the essential phenomena and disregard unnecessary ones. The elementary units are repeated in a tree and its functioning depends on its local micro-climate and neighbouring units. The ageing process causes structural changes in it resulting changing in the whole tree structure. Connected units form a transport medium in a tree. The elementary unit must be small enough to be able to consider its micro-environment but large enough so that the number of units stay low enough when simulating big trees.

The LIGNUM functional-structural tree model has its roots in process-based modelling and can be easily seen as a continuum of the work done by the research group at the Department of Forest Ecology, University of Helsinki. The model LIGNUM represents the three-dimensional tree crown by means of four structural units called tree segment, bud, branching point and axis. An axis or a branch is a sequence of tree segments, branching points and the terminating bud. A branching point is a set of axes, i.e. the position in the tree where one or more tree segments are attached to each other. A tree segment is a section of woody material between two branching points.

The cylindrical tree segment consists of dead heartwood, living sapwood and foliage. It is the main functioning unit of the tree, where the metabolic processes like photosynthesis and respiration take place, and denotes a section of branch or trunk. Initially, the application for Scots pine clearly influenced the choice of units, especially the design of the tree segment that corresponds to the annual shoot in conifers.

For hardwood trees the cylindrical layer of foliage in the tree segment is replaced with explicit leaves. A model for a leaf comprises a leaf blade with orientation in space, and a petiole attached to the tree segment at one end and to the leaf blade at the other.

An important methodological problem in LIGNUM is how to subsume the carbon balance, i.e. allocation of the net photosynthates, in a model consisting of a large number of units. In evaluating the growth increment, photosynthesis and respiration are first summed up for the whole tree. If the photosynthetic production exceeds the respirational costs for foliage, sapwood and roots, then the tree can extend its branches by adding new segments, thicken existing segments, and add new roots. In simple terms primary growth, i. e. elongation of the branches, in the most distal parts in the tree crown is assumed to be proportional to foliage growth and further, it is assumed that the cross sectional area of sapwood in a tree segment connected to segments above is equal to the sum of the sapwood areas of the units above. Once the elongation is known it is possible to calculate the secondary growth, i.e. thickening of the branches and the main stem, all the way down from the tip of the branches to the base of the tree. One of the contributions of the LIGNUM model is how to implement this allocation of net photosynthates in a model consisting possibly of thousands of units.

The LIGNUM model has had many applications during the years of its development. The thesis collects the articles that describe the model development from the first implementation with Scots pine, improvement of the assessment of solar radiation interception, the application with deciduous trees studying the development of understorey sugar maple plant and the enhancement in its modelling capabilities with the possibility to describe the architectural development of a tree with Lindenmayer systems.

I ask you Professor Christophe Godin, as the opponent appointed by the Faculty of Information and Natural Sciences to make any observations on the thesis which you consider appropriate.