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Incorporating Lindenmayer systems for architectural development in a functional-structural tree model

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Abstract

LIGNUM is a functional-structural tree model that represents coniferous and broad-leaved trees with modelling units corresponding to the real structure of trees. The units are tree segments, axes, branching points and buds. Metabolic processes are explicitly related to the structural units in which they take place.

This paper enhances the modelling capabilities of LIGNUM with the possibility to formally describe the architectural development of trees with Lindenmayer systems. This is achieved by presenting an algorithm to convert tree structures generated by Lindenmayer systems to the LIGNUM representation of trees with feedback of results of events or processes from LIGNUM to Lindenmayer system. We then give two example applications that model the development of Scots pine (*Pinus sylvestris* L.) and the dwarf shrub bearberry (*Arctostaphylos uva-ursi* L.). Finally we discuss our approach and its consequences for the future development of LIGNUM.

Keywords: Lindenmayer systems; Functional-structural tree models; Tree architecture

1. Introduction

An increasing number of models (see e.g. Annals of Forest Science. vol. 57, no. 5/6) try to depict the dynamics and growth of woody perennial plants by assessing the physiological processes in their three-dimensional arborescent form. Physiological processes involve, for example, photosynthesis of the foliage, respiration, flow of water or hormones and the allocation of nutrients. The structure of the tree and its changes over time are described with state variables representing different aggregated tree compartments or with detailed modelling components faithful to the botanical or morphological units of plants. Such models have been called functional-structural tree models (FSTM).

Kurth (1994b) has classified tree and forest models on the basis of whether the emphasis is on the structural traits or on the functioning of trees. Accordingly, there are principally two ways to construct a FSTM.

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One can start from an architectural model (Jaeger et al., 1992; Kurth, 1994a) and add functional, i.e. physiological detail to it. The second approach is to begin with a process-based physiological model (Mäkelä and Hari, 1986; Landsberg, 1986; Mäkelä, 1997) and extend it with structural details. Physiological models are usually realized with the aid of differential or difference equations (Landsberg, 1986), whereas architectural models apply Lindenmayer systems (Kurth, 1999; Prusinkiewicz and Lindenmayer, 1990) or other formalisms.

Since the pioneering work by Honda (1971) methods have become available for treating plant architecture in models in an efficient way. Lindenmayer systems or L systems (Prusinkiewicz and Hanan, 1989), are the most widely used method to treat plant architecture although other formalisms also exist (e.g. de Reffye et al., 1997; Godin et al., 1999). L systems were invented by Aristid Lindenmayer (1968, 1971) and were initially meant to describe the development of multicellular organisms. L systems are string-rewriting systems and research on these systems is concerned with the question of what phenomena can be described with formal languages. The theory, tools and applications that utilize a L system framework for modelling plants and their environment have been developed by Prusinkiewicz (Prusinkiewicz and Hanan, 1989, 1992), Kurth (Kurth, 1994a) and other scientists. The theory and the progress made in L systems in modelling plants and trees up until the end of the 1990s is well documented in Prusinkiewicz and Lindenmayer (1990), Prusinkiewicz (1999) and Kurth (1999).

All process-based models (Landsberg, 1986) for tree and stand growth must subsume a notion for crown or canopy structure that matches the objectives of the modelling. A facile solution is to assume horizontally homogeneous layers of foliage used in mainly theoretical studies of tree and forest growth (Hari et al., 1982; Mäkelä, 1997). Models that captured the individual stem structure or partitioned the above ground part of the tree into even finer compartments of branches, shoots, etc. (Kellomäki and Strandman, 1995) expanded the scope of the process-based models for example to wood quality applications (Kellomäki et al., 1999; Mäkelä and Mäkinen, 2003). Though the traits of physiology has been taken into consideration in detail, the tree architecture has been treated in the same model varying in detail and the way it has been embedded in the program implementing the model. Hence, each architectural model is unique and there exist no straightforward way of comparing these models as regards of architecture.

The methods for plant architecture (Prusinkiewicz and Lindenmayer, 1990; de Reffye et al., 1997; Godin et al., 1999) offer means for treating tree architecture in a formal, and therefore comparable way. However, these formalisms have so far not matched the capabilities of general programming languages to deal with diverse programming tasks (e.g. modelling diffusion of substrates). In a number of model or modelling tools, the suitable combination of methods to deal effectively with both architecture and physiology has been addressed (Kurth, 1999; Eschenbach, 2000; Karwowski and Prusinkiewicz, 2003; Yan et al., 2004). The development of models, where the architecture and functioning interact, is of key importance for better understanding the structural dynamics of trees.

The LIGNUM model approaches FSTM from the physiological side; it is a single tree model (Perttunen et al., 1996) with fidelity to process-based modelling (see e.g. Nikinmaa, 1992; Sievänen, 1993; Mäkelä, 1997) but, instead of aggregated tree parts, it has a three-dimensional description of the above ground part of the tree. LIGNUM includes a detailed model of self-shading within a tree crown (Perttunen et al., 1998, 2001), from which the radiation regime for photosynthesis in different parts of the tree can be computed. If the photosynthates produced exceed the respiration costs then the net production is allocated to the growth of new parts. LIGNUM has been applied to both coniferous (Perttunen et al., 1996; Lo et al., 2001) and broad-leaved trees (Perttunen et al., 2001). The main focus in LIGNUM has been on the functional part of the model and less emphasis has been paid to structural development. The model does not include any formal method to define the architectural development of the tree structure.

We describe in the following how the LIGNUM model has been interfaced with L systems for specifying formally the architectural development of trees, thereby improving the applicability and ease of use of this FSTM. The goal is achieved by using the L language, which is an extension of L systems (Prusinkiewicz et al., 1999). Based on the definition of L, R. Karwowski created the original parser of L and has implemented the L + C language (Karwowski,