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KEYNOTE: Functional-structural modelling with L-systems: Where from and where to

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Highlights: The L-systems formalism with turtle interpretation captures plant structural topology and geometry, signalling within the branching structure, and development over time, forming a basis for plant modelling languages. With the addition of environmental interfaces, they have been successfully used to model a variety of plants. Areas for future development include integration of different aspects of plant function, multi-scale modelling and development as a platform for further simulation.

Keywords: Lindenmayer-systems, plant modelling language

WHERE FROM

Since their inception by Aristid Lindenmayer (1968a&b), L-systems have provided an inspiration and formal foundation for a range of functional-structural plant modelling systems. The original formalism incorporated internal and environmental signalling and branching topology, aiming to capture elements of filamentous growth at a cellular level. Inspired by the ideas of Cohen (1967), Frijters and Lindenmayer (1974) moved from the cellular to the organ level of abstraction, developing an L-system model of aster incorporating signals for control of branching and "vigour" controlling flowering positions. This is the first example of L-systems capturing functional-structural aspects of plant growth and development.

In these early models, plant geometry was added in a post-processing phase. Hogeweg and Hesper (1974) explored patterns generated by a variety of such L-systems and found recurrence relations in line with higher plant growth. Following on from this work, Smith (1984) demonstrated the potential of L-systems for the synthesis of realistic images of plants, while Aono and Kunii (1984) explored modelling of trees. Szilard and Quinton (1979) proposed representation of geometry within the strings defining the plant structure based on a LOGO-style turtle (Abelson and diSessa 1982). This turtle interpretation scheme was further developed by Prusinkiewicz (1986, 1987) and is the standard approach used in L-systems-based systems today.

With a formalism that captures component topology and geometry, signalling within the branching structure, and development over time, the stage was set for development of plant modelling languages that could support functional-structural plant modelling of a broad range of phenotypes (Prusinkiewicz *et al.* 1988, Prusinkiewicz and Hanan 1989, Prusinkiewicz *et al.* 2000). With the addition of continuous parameters (Lindenmayer 1974; Prusinkiewicz and Hanan 1990, Hanan 1992), a greater variety of lineage and endogenous processes could be simulated (Prusinkiewicz and Lindenmayer 1996). Extension of this line of research continued with the inclusion of environmental effects in open L-systems (Mech and Prusinkiewicz 1996) through communication with an external program capturing environmental processes. Kurth (1994) developed a sensitive growth grammar approach representing an alternative line of development of the L-systems idea, initially aimed at eco-forestry applications. This work continued with transformation of the representation of the plant from strings to graphs (Kurth *et al.* 2005, Kniemeyer 2008), extending the possible range of applications. Other lines of L-system-inspired research (Lindenmayer 1987) moved away from the plant level to the tissue and cellular scale (Prusinkiewicz and Runions 2012).

L-system models of a variety of plants, from herbaceous to trees can be found, for example, in journal special issues (Godin and Sinoquet 2005, Hanan and Prusinkiewicz 2008, Fourcaud *et al.* 2008, Vos *et al.* 2010, de Jong *et al.* 2011, Guo *et al.* 2011), and are too many to list individually here. L-systems have also proved a useful reference for other plant modelling approaches, being compared with Greenlab (Loi and Cournede 2008) for example. They have also been incorporated into other plant modelling systems, such as Lignum (Perttunen and Sievänen 2005), and openALEA (Boudon e*t al.* 2012).

WHERE TO

Many advances have been made in simulating individual processes in plants using L-systems-based approaches. Models of light interception (Chelle *et al.* 2004, Cieslak *et al.* 2008) allow local estimation of leaf photosynthesis, while carbon allocation models (Allen *et al.* 2005) disburse photosynthate to drive vegetative and reproductive development. Biomechanics of bending of branches under fruit load (Costes *et al.* 2008) make feedback to the developmental processes possible. Some key future pathways for L-systems modelling will be development of methods to integrate these different aspects easily (Cieslak *et al.* 2011). Development of techniques supporting modelling of self-organisational processes (Palubiki *et al.* 2009) may play an important role, particularly for tree development, where what isn't there plays almost as important a role as what is.

Multi-scale modelling will also feature in L-systems models of the future. For example, current models of genetic and hormonal processes at a plant scale (Buck-Sorlin *et al.* 2005, Han *et al.* 2010) will need to become more localised to drive accurate modelling of genotype-environment-management scenarios. By combining with carbon allocation models, hypothesis-driven modelling of branching and flowering processes can then be explored.

In common with other FSPM systems, another key area of future application will be as a platform for further simulation. Examples include eco-physiological models, spray deposition (Dorr *et al.* 2008), insect-plant interactions (Hanan *et al.* 2002), and plant-pathogen interactions (Pangga *et al.* 2011).

L-systems have proved to be a robust formalism for describing growth and development, forming an integral part of many modern plant modelling languages and systems. As more detailed multi-scaled issues are tackled, both down to genetic scale and up to eco-scale, the challenge will be to extend the underlying formalism, to meet the needs of new scientific issues.

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