Metric-Driven Grammars and Morphogenesis (Extended Abstract)

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Abstract. Expansion of space, rather than the progress of time, drives many developmental processes in plants. Metric-driven grammars provide a formal method for specifying and simulating such processes. We illustrate their operation using cell division patterns, phyllotactic patterns, and several aspects of leaf development.

Keywords: natural computing, computational modeling of plant development, growth and form, L-system, cell complex.

Mathematical studies relating the growth and form of organisms were pioneered at the beginning of the XX century by d'Arcy Wentworth Thompson [24]. Among other concepts, he proposed a "theory of transformations" to describe how the forms of related species can be continuously mapped into each other. He also suggested that similar mappings could be used to describe gradual changes of form due to growth. These ideas have been followed and elaborated over time, leading to the characterization of growth in terms of growth tensor fields [7], which are widely used today [3]. Continuous transformations do not capture, however, the emergence and differentiation of new components of organisms, such as cells and organs. A mathematical description of this aspect of development was pioneered by Aristid Lindenmayer, who in 1968 introduced L-systems as a formalism for modeling the development of structures composed of a changing number of discrete components. L-systems were initially defined in terms of cellular automata [8], but soon afterwards were re-defined more elegantly in terms of formal grammars [9]. In this form they are known and used today. A distinctive feature of L-systems is their parallel operation, which lets us view derivation steps as advancing time by some interval. Correspondingly, consecutive words generated by an L-system can represent a sequence of developmental stages of an organism.

According to their original definition, L-systems describe developing structures at the level of topology, i.e., the adjacency relations between the structure components. L-systems are particularly well suited to model linear (filamentous) and branching structures, although extensions to discretized surfaces (maps) and volumes have also been considered [11, 12]. Geometric representations, when needed, are introduced by the draftsperson illustrating the models, or calculated algorithmically as a graphical interpretation of the generated structures [17]. This focus on topology has two implications. First, time is the only independent variable that can drive simulations. Second, geometric factors, such as size and shape, have no direct impact on the progress of the simulations (this limitation was partially addressed in extensions of L-systems aimed at the animation of plant development in continuous time [14] and the simulation of interaction between plants and their environment [13, 15]). In many developmental processes, however, geometry plays a fundamental morphogenetic role [18]. For example, according to the Errera rule [1, 6], the shortest wall passing through the centroid of the cell determines the most likely orientation of cell division in the absence of specific polarizing factors. Furthermore, the expansion of space may have a more direct impact on the progress of morphogenesis than the progress of time. For instance, according to the conceptual model of phyllotaxis by Snow and Snow [23] and its numerous computational implementations (e.g. [4, 21, 22]), new primordia (precursors of organs such as leaves and flowers) emerge in the growing plant apices when and where there is enough space for them. The plastochron, or the time interval between the appearance of consecutive primordia [5], is not an independent variable, but a result of the changing spatial relations in the plant.

Often it is not known whether an observed morphogenetic process is best described as being driven by the progress of time, the expansion of space, or some combination of both factors. Construction of models exploring alternative hypotheses is then an important part of discovery. To provide a methodology and a formal basis for this exploration, we employ metric-driven grammars as a complement of time-driven L-systems.

A metric-driven grammar operates on a cell complex. A justification for the use of cell complexes as models of biological structures, and examples of L-systems operating on 1-dimensional cell complexes, are presented in [16]. A metric of the cell complex specifies the distances between different elements of the structure. These distances change over time as a result of growth. Functions of distances measured within cells and/or their neighborhood control the application of productions, which locally modify the topology of the complex.

An example of the operation of a metric-driven grammar is shown in Figure 1. The production replaces a line segment that exceeds a predefined threshold length with a simple branching structure (compare the first and the second row in Figure 1). The structures are embedded in surfaces with different growth distributions. In the case of uniform growth (left column), all segments reach the threshold length and produce the successor structure simultaneously. The derivation sequence is then indistinguishable from that generated by an L-system: productions are applied in parallel. In contrast, in the case of non-uniform growth (middle and right columns), faster growing segments reach the threshold length before those in the slower growing parts. Productions are applied asynchronously, yielding patterns that depend on the distribution of growth.

A fertile area in which metric-driven grammars provide useful insights is leaf development. There, growing distances appear to trigger the emergence of serrations [2], lobes [16], leaflets, veins [20], and trichomes. Model exploration

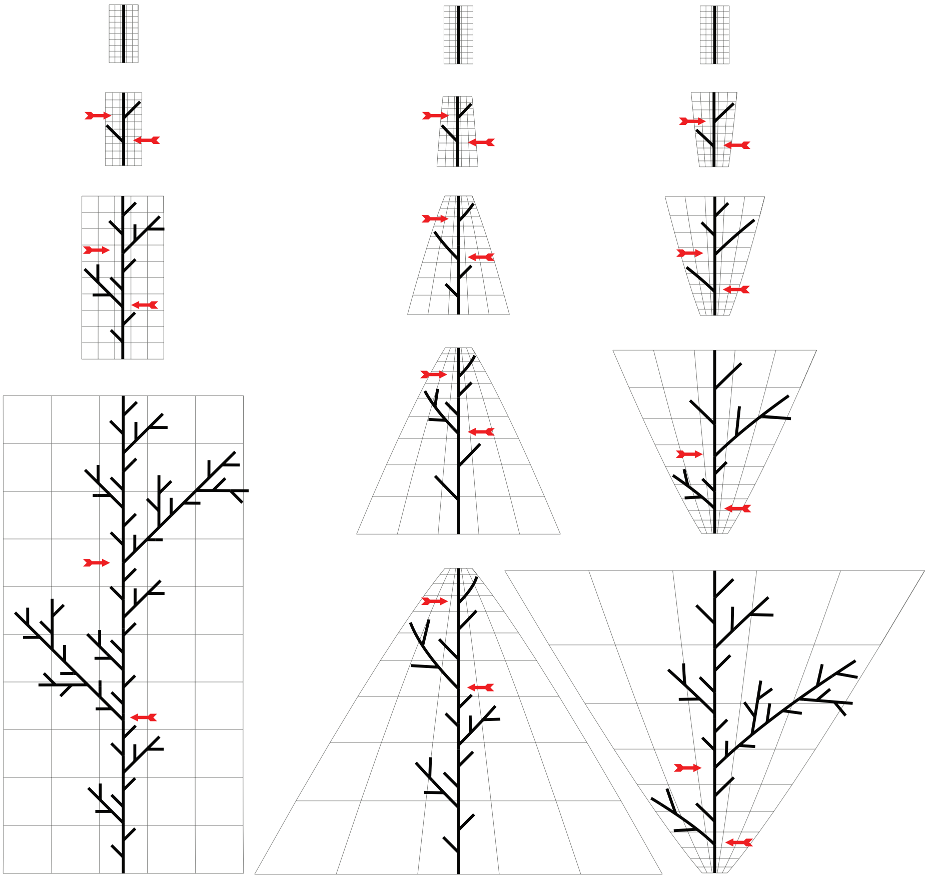

Fig. 1. Selected developmental stages of three branching structures simulated using the same metric-driven grammar. The grammar operates in a space that expands uniformly (left column), grows faster at the bottom than at the top (middle column) and grows faster at the top than at the bottom (right column). Arrows indicate positions of the branching points resulting from the first production application.

suggests that the observed diversity of leaf forms and patterns may result from the variation of a small number of metric-related parameters of development. Further examples of patterning that is likely metric-driven include the initiation of flowers in compound inflorescences and the arrangement of organs within individual flowers.

From a biological perspective, an important question is how distances are measured. The measurement of small distances (on the order of millimeters and less) can be accomplished by diffusion and decay: the concentration of a diffusing substance decreases away from the source, and crosses a threshold value at some distance from it (c.f. [10]). Nevertheless, a different mechanism, based on the active transport of the plant hormone auxin and a feedback between this transport and the distribution of transporters, appears to underlie numerous morphogenetic processes in plants [18], including the measurement of distances in phyllotactic patterning [19, 21] and leaf development [2, 16]. Whether this is a fluke of evolution, the adaptation of a process that evolved in other contexts, or a manifestation of some selective advantage of the transport-based mechanism is currently not known.

In the analyses carried out so far, distances were assumed to be measured instantaneously; in other words, they reflect the actual metric at a given time. It is possible, however, that biochemical mechanisms propagate information about distances at rates commensurate with the rates of growth. Simulations show that such "relativistic" phenomena can qualitatively change the generated patterns. An analysis of the impact of the limited speed of information propagation on morphogenesis is a fascinating topic of current research.

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References

1. S. Besson and J. Dumais. A universal rule for the symmetric division of plant cells. *Proceedings of the National Academy of Sciences*, 108:6294–6299, 2011.
2. G. D. Bilsborough, A. Runions, M. Barkoulas, H. W. Jenkins, A. Hasson, C. Galinha, P. Laufs, A. Hay, P. Prusinkiewicz, and M. Tsiantis. Model for the regulation of *Arabidopsis thaliana* leaf margin development. *Proceedings of the National Academy of Sciences*, 108:3424–3429, 2011.
3. E. Coen, A.-G. Rolland-Lagan, M. Matthews, A. Bangham, and P. Prusinkiewicz. The genetics of geometry. *Proceedings of the National Academy of Sciences*, 101:4728–4735, 2004.
4. S. Douady and Y. Couder. Phyllotaxis as a dynamical self organizing process. Parts I–III. *Journal of Theoretical Biology*, 178:255–312, 1996.
5. R. O. Erickson and F. J. Michelini. The plastochron index. *American Journal of Botany*, 44(4):297–305, 1957.
6. L. Errera. Sur une condition fondamentale d'équilibre des cellules vivantes. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, 103:822–824, 1886.
7. Z. Hejnowicz and J. A. Romberger. Growth tensor of plant organs. *Journal of Theoretical Biology*, 110:93–114, 1984.
8. A. Lindenmayer. Mathematical models for cellular interaction in development, Parts I and II. *Journal of Theoretical Biology*, 18:280–315, 1968.
9. A. Lindenmayer. Developmental systems without cellular interaction, their languages and grammars. *Journal of Theoretical Biology*, 30:455–484, 1971.
10. A. Lindenmayer. Adding continuous components to L-systems. In G. Rozenberg and A. Salomaa, editors, *L Systems*, Lecture Notes in Computer Science 15, pages 53–68. Springer-Verlag, Berlin, 1974.
11. A. Lindenmayer. Models for plant tissue development with cell division orientation regulated by preprophase bands of microtubules. *Differentiation*, 26:1–10, 1984.

12. A. Lindenmayer and G. Rozenberg. Parallel generation of maps: Developmental systems for cell layers. In V. Claus, H. Ehrig, and G. Rozenberg, editors, *Graph grammars and their application to computer science; First International Workshop*, Lecture Notes in Computer Science 73, pages 301–316. Springer-Verlag, Berlin, 1979.
13. R. Měch and P. Prusinkiewicz. Visual models of plants interacting with their environment. Proceedings of SIGGRAPH '96 (New Orleans, Louisiana, August 4–9, 1996). ACM SIGGRAPH, New York, 1996, pp. 397–410.
14. P. Prusinkiewicz, M. Hammel, and E. Mjolsness. Animation of plant development. Proceedings of SIGGRAPH 93 (Anaheim, California, August 1–6, 1993). ACM SIGGRAPH, New York, 1993, pp. 351–360.
15. P. Prusinkiewicz, M. James, and R. Měch. Synthetic topiary. Proceedings of SIGGRAPH '94 (Orlando, Florida, July 24–29, 1994). ACM SIGGRAPH, New York, 1994, pp. 351–358.
16. P. Prusinkiewicz and B. Lane. Modeling morphogenesis in multicellular structures with cell complexes and L-systems. In V. Capasso, M. Gromov, A. Harel-Bellan, N. Morozova, and L. Pritchard, editors, *Pattern Formation in Morphogenesis*, pages 137–151. Springer, Berlin, 2012.
17. P. Prusinkiewicz and A. Lindenmayer. *The Algorithmic Beauty of Plants.* Springer, New York, 1990. With J. S. Hanan, F. D. Fracchia, D. R. Fowler, M. J. M. de Boer, and L. Mercer.
18. P. Prusinkiewicz and A. Runions. Computational models of plant development and form. *New Phytologist*, 193(3):549–569, 2012.
19. D. Reinhardt, E. R. Pesce, P. Stieger, T. Mandel, K. Baltensperger, M. Bennett, J. Traas, J. Friml, and C. Kuhlemeier. Regulation of phyllotaxis by polar auxin transport. *Nature*, 426:255–260, 2003.
20. A. Runions, M. Fuhrer, B. Lane, P. Federl, A.-G. Rolland-Lagan, and P. Prusinkiewicz. Modeling and visualization of leaf venation patterns. *ACM Transactions on Graphics*, 24:702–711, 2005.
21. R. S. Smith, S. Guyomarc'h, T. Mandel, D. Reinhardt, C. Kuhlemeier, and P. Prusinkiewicz. A plausible model of phyllotaxis. *Proceedings of the National Academy of Sciences*, 103:1301–1306, 2006.
22. R. S. Smith, C. Kuhlemeier, and P. Prusinkiewicz. Inhibition fields for phyllotactic pattern formation: A simulation study. *Canadian Journal of Botany*, 84:1635–1649, 2006.
23. M. Snow and R. Snow. Experiments on phyllotaxis. I. The effect of isolating a primordium. *Philosophical Transactions of the Royal Society of London B*, 221:1–43, 1932.
24. d'Arcy Thompson. *On Growth and Form, 2nd edition.* University Press, Cambridge, 1942.