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Pillars of theoretical biology: 'Mathematical models for cellular interaction in development, I and II'★

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ABSTRACT

This paper reviews the main idea and impact of the groundbreaking paper by Aristid Lindenmayer, 'Mathematical models for cellular interaction in development, Parts I and II', published in the *Journal of Theoretical Biology* **18**, 1968, pp. 280–299 and 300–315. The paper introduced the idea of L-systems, now the leading formalism for modeling plant development.

1. Introduction

One of the most highly cited and impactful papers published in the *Journal of Theoretical Biology* is the two-part work by Aristid Lindenmayer (1968), 'Mathematical Models for Cellular Interaction in Development', (*JTB* **18**, pp. 280–299 and 300–315). The concept it introduced, subsequently known as Lindenmayer systems or L-systems—a term coined by van Dalen (1971), cf. Lindenmayer and Rozenberg (1972)—has become the prime theoretical framework for constructing plant modeling software and developing individual plant models. It constitutes one of the most successful mathematical concepts with roots in biology.

2. Seminal ideas

To appreciate the problem that Lindenmayer addressed and the impact of his paper, it is useful to put the genesis, evolution, and applications of L-systems in their historical context. In the 1960s, ideas related to computing were rapidly penetrating various areas of science. In biology, cybernetics (Wiener, 1948; Ashby, 1956) unveiled the potential of using information flow and processing to study living organisms, including their development (Apter, 1966). Consistent with this outlook, reaction-diffusion systems (Turing, 1952) and cellular automata (Ulam, 1952, 1962; von Neumann, 1966) provided the first computational frameworks for modeling morphogenetic processes in spatially extended structures. In particular, cellular automata—arrays of interconnected simple computing units—suggested the possibility of modeling morphogenetic processes in multicellular organisms at the level of individual cells. However, the regular structure of cellular automata hinders the modeling of cell division—a key aspect of organism development—because dividing individual cells disrupts the regularity of two- or three-dimensional arrays. Lindenmayer's pivotal insight was that this limitation does not apply to linear or branching filaments. This observation led to the modeling framework he proposed in 1968: linear or branching cellular automata, in which cells in specific states, receiving specific inputs (signals), can divide. He also proposed a data structure—strings of symbols with branches enclosed in brackets—that remains a cornerstone of L-systems to this day.

The 1968 paper triggered multidirectional studies that have resulted in the advancements, modifications, extensions, and applications that constitute the current theory and use of L-systems. A crucial step was the redefinition of the original framework in terms of formal grammars (Lindenmayer, 1971): a mathematical construct for generating sets of strings of symbols (formal languages) using rules called "productions", which iteratively replace symbols in a string with other symbols or substrings (Salomaa, 1973; Rozenberg and Salomaa, 1997). This redefinition—originally restricted to L-systems in which individual cells do not interact with each other, but soon extended to L-systems with interactions (Lindenmayer and Rozenberg, 1972)—is simpler, more concise, and more elegant than the original formulation, and it has remained synonymous with L-systems ever since.

3. Key features of L-systems

The definition of L-systems in terms of grammars has spurred extensive studies of the formalism itself and provided the foundation for

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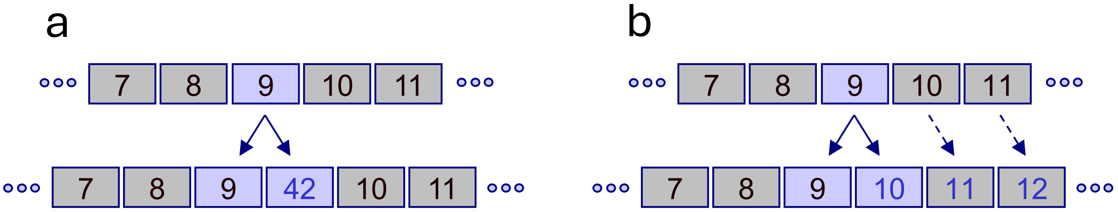

Fig. 1. Inadequacies of cell identification using indices in a growing filament. (a) Assigning an arbitrary number to a newly created cell breaks index arithmetic. (b) Renumbering dissociates indices from the identity of cells. Adapted from Prusinkiewicz and Lane (2013).

its subsequent extensions (Section 4), which in turn have broadened the range of L-system applications (Section 5). Looking back, it is possible to discern the key features of L-systems that have enabled these advancements.

3.1. Abstract, precise definition of L-systems

Although L-system symbols were originally conceived to represent individual cells in a multicellular organism, the abstract definition of L-systems allows for other interpretations as well. For instance, Frijters and Lindenmayer (1974) used the symbols to denote larger plant modules (components): the interconnected stem segments (internodes) that collectively form a branching plant structure, and plant organs such as apical meristems, leaves, flowers, and fruits. That interpretation opened the door to modeling macroscopic plant architecture, which has become the prime area of L-system applications in biology. Consequently, in the remainder of this text the term “cell” is used synonymously with “module”.

The precise definition of the formalism and its operation serves as a solid foundation for the construction of L-system-based simulators and models. The first such simulator—CELIA, or CEllular Linear Iterative Array simulator—was developed shortly after the publication of Lindenmayer’s 1968 paper (Baker and Herman, 1970). Many subsequent implementations followed. An important feature of these simulators, already highlighted by Baker and Herman (1970), is the separation of individual models from the general-purpose simulator that executes these models. This separation frees modelers from the tedium of reimplementing the generative infrastructure for each individual model, thereby facilitating model construction, communication, and discussion. The models can be expressed in an L-system-based mathematical notation (Prusinkiewicz and Hanan, 1989; Prusinkiewicz and Lindenmayer, 1990; Hanan, 1992; Kurth, 1994), as scripts that incorporate L-systems constructs into higher-level programming languages, e.g., C++ (Karwowski and Prusinkiewicz, 2003), Java (Kniemeyer et al., 2007) or Python (Boudon et al., 2012), or even using a visual programming interface (Veldhuizen, 2023).

The precise definition has also enabled mathematical analyses of the formalism itself. The parallel application of productions (i.e., conceptually simultaneous replacement of all symbols in the predecessor string with new symbols in the successor string), makes the classes of formal languages (sets of strings) generated by L-systems very different from those generated by the previously introduced Chomsky (1956) grammars, in which productions are applied sequentially (Lindenmayer, 1971; Salomaa, 1973). The results, elaborated in hundreds of papers and several monographs (e.g., Herman and Rozenberg, 1975; Rozenberg and Salomaa, 1980), are frequently quite detached from biological applications (Kelemenová and Kelemen, 1984), but they have contributed to, and become an integral part of, the theory of formal languages (Rozenberg and Salomaa, 1997).

3.2. Topology-centered, index-free, declarative character of productions

Components of complex structures are commonly identified by indices. For example, in a one-dimensional cellular automaton, cells are numbered sequentially, such that neighbors of cell i have indices $i-1$ and $i+1$. Simple index arithmetic then suffices to identify cell neighbors, which is a prerequisite for modeling local interaction (signaling) between cells. Unfortunately, in developing structures—even as simple as filaments—indexing cells is problematic (Prusinkiewicz and Lane, 2013). Specifically, if one or both daughter cells resulting from cell division are assigned new index values while previously formed cells retain their indices, consecutive cells no longer remain sequentially numbered, and simple index arithmetic does not suffice to identify cell neighbors (Fig. 1(a)). Conversely, if cell indices are updated to remain consecutive after each cell division, the same cell may be assigned different indices at different points in time (Fig. 1(b)), and keeping track of cells becomes difficult. These problems are further compounded in branching structures. L-systems bypass them by avoiding indices altogether, and identifying elements simply by their state and neighborhood. The neighborhood relations—the discrete topology of the filament—are automatically updated when cells divide. This update is similar to, and as straightforward as, replacing a letter with two letters when editing text. Although indices may be used internally in the L-system-based simulators (e.g., Prusinkiewicz and Hanan, 1989), the formalism conveniently hides them from the end-user, the modeler.

Besides eliminating the tedium of tracking indices, the topology-centered approach has other far-reaching consequences. First, it is key to modeling an indefinitely growing structure using a finite set of productions, because—by definition of state—all cells in the same state and receiving the same input behave the same way. Second, using cell state and the signals it receives as the only factors controlling cell fate facilitates conceptualizing and modeling developmental processes in terms of physically and biologically plausible local interactions. As a result, modeling with L-systems fosters mechanistic explanations of the analyzed phenomena.

4. Key further developments

4.1. Parametric L-systems

The simple, abstract definition of L-systems has paved the way for many subsequent extensions. Perhaps the most momentous of them was the association of continuous, quantitative attributes with L-system symbols (Herman and Liu, 1973; Lindenmayer, 1974; Prusinkiewicz and Hanan, 1990; Prusinkiewicz and Lindenmayer, 1990; Hanan, 1992), conceptually similar to the extension of Chomsky grammars with (inherited) attributes (Knuth, 1968). The resulting parametric L-systems have made it possible to incorporate genetic, physiological, and biomechanical processes into comprehensive models that are commonly termed virtual plants (Room et al., 1996) or functional-structural plant models (Sievänen et al., 1997).

4.2. Geometric interpretations of L-systems

Assigning geometric interpretations to a predefined set of symbols was a stepping stone toward realistic visualizations of modeled plants using computer graphics (Prusinkiewicz et al., 1988; Prusinkiewicz and Lindenmayer, 1990). The most common interpretation is based

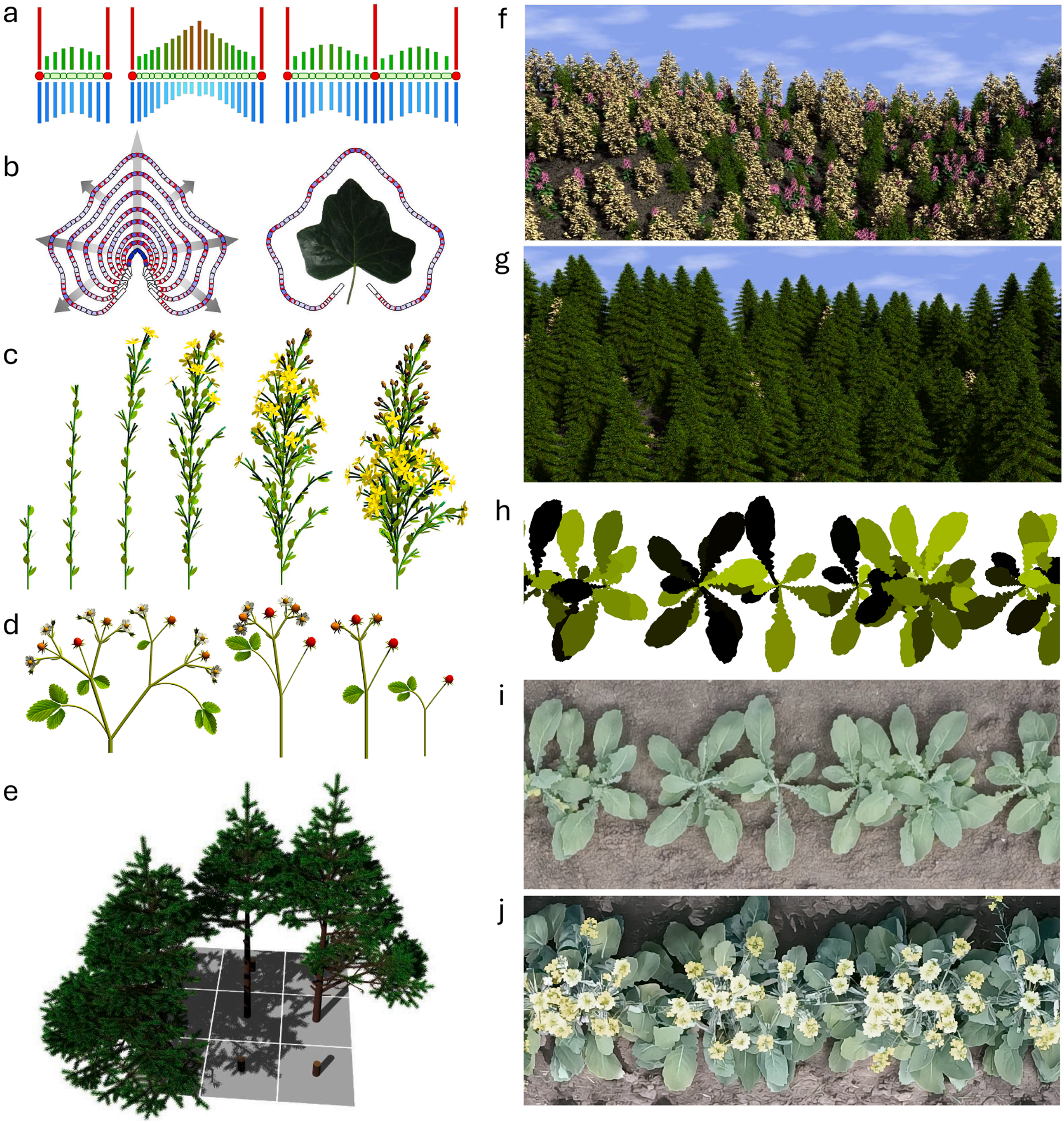

Fig. 2. Applications of L-systems to plant modeling across different scales. (a) Development of a filamentous blue-green bacterium (Coen et al., 2004; Prusinkiewicz et al., 2018). Bars above and below cells indicate concentrations of proteins HetR and PatS, which form a reaction-diffusion system controlling the differentiation of heterocysts (large red cells). (b) Development of a common ivy leaf (Prusinkiewicz and Lane, 2013). Lobes emerge at the sites of high concentration of plant hormone auxin (blue), transported by auxin efflux carriers (PIN proteins, red) located in the membranes of cells on the leaf margin. (c) Development of a compound inflorescence (Prusinkiewicz et al., 1988; Prusinkiewicz and Lindenmayer, 1990). The downward progression of the flowering zone is controlled by a hypothetical interaction between an upward-propagating flower-inducing signal and a downward-propagating flower-suppressing signal (not visualized). (d) Diversity of inflorescences in a wild type (left) and three genetically modified woodland strawberry plants (Lembinen et al., 2023). (e) Tree stand with several trees removed, simulating crown shape plasticity in response to the local light environment (Měch and Prusinkiewicz, 1996). (f,g) Two stages of forest succession, from herbaceous plants and broad-leaved trees to conifers (Lane and Prusinkiewicz, 2002). (h,i) An L-system-generated mask and the corresponding realistic rendering of a row of young canola plants produced using a neural network. (j) The same row at a later stage of development. Panels (a–g) adapted from the author's earlier work as referenced; (h–j) courtesy of Mikolaj Cieslak.

on “turtle geometry”: a computational method for constructing geometric shapes by following a virtual “turtle” that moves and turns in space (Abelson and diSessa, 1982). These motions are controlled by reserved L-system symbols denoting—in the simplest case—line segments and the angles between them (Szilard and Quinton, 1979; Prusinkiewicz, 1986). Other interpretations, for example those based on affine geometry, also exist (Prusinkiewicz et al., 2003). Importantly, the abstract definition of L-systems make it possible to introduce these extensions without affecting the syntax of the modeling languages (although simulation programs executing the models needed to be appropriately extended).

4.3. Modeling plants in environmental contexts

The geometric interpretation enabled a subsequent extension: open L-systems, in which reserved communication symbols are used to exchange local, position-dependent information between the modeled plant and its environment (Měch and Prusinkiewicz, 1996). Open L-systems make it possible to model plants in their ecological context. In particular, incorporating competition among branches for light and/or space has advanced the modeling of trees (see next section).

5. Impact

Lindenmayer introduced L-systems to model the development of relatively simple filamentous and branching structures composed of individual cells. However, the abstract definition of L-systems has allowed for diverse interpretations of what the model components represent, how they behave, and how they interact. Consequently, the applications and impact of L-systems have far exceeded their original intent.

Since their inception, L-systems have become a common method for modeling plants at a wide range of spatial scales and levels of organization, and for a variety of purposes (Fig. 2). At the lowest level, the activities of individual cells have been simulated down to the genetic regulatory networks, providing insight into the properties of the resulting multicellular structures (Fig. 2(a)). Bridging molecular mechanisms and physiological regulation, L-systems have played a significant role in the exploration of morphogenetic processes involving the interactions between the plant hormone auxin and its transporters (PIN proteins), including activation of branch development (Prusinkiewicz et al., 2009), and the development of leaves (Fig. 2b; Bilsborough et al., 2011). At a slightly higher level, a particularly well-developed application area of L-systems is the modeling of complex inflorescences (flower clusters) (Fig. 2c; Zhang et al., 2021). Some of these models incorporate the effects of genetic manipulations (Fig. 2d; Prusinkiewicz et al., 2007; Azpeitia et al., 2021).

The first computational models of trees (Honda, 1971) were not expressed using L-systems, although they were subsequently re-expressed using the formalism (Aono and Kunii, 1984; Prusinkiewicz and Lindenmayer, 1990). The full power of L-systems to model trees was unleashed by the introduction of open L-systems, which made it possible to incorporate the competition between branches for space and light, a crucial factor in tree development (Měch and Prusinkiewicz, 1996; Palubicki et al., 2009). The resulting models can inherently simulate interactions between plants and their environment, including other trees (Fig. 2(e)). At the highest spatial scale, L-systems can simulate entire plant ecosystems (Fig. 2f,g; Deussen et al., 1998).

L-system models found applications in agriculture, horticulture, and forestry (Room et al., 1996). For instance, functional-structural tree models simulating carbon allocation have been developed to optimize tree management (e.g., pruning, trellising, and fruit thinning) in orchards (Allen et al., 2005; Cieslak et al., 2011). An intriguing recent application is the use of L-system models in a simulation study evaluating contrasting tree training practices from the viewpoint of optimal fruit harvesting by a robot (Bloch et al., 2018). L-systems have also been adopted to train AI-based computer vision systems designed for precision farming and horticulture (Cieslak et al., 2024). Objectives of such systems include targeted irrigation and fertilization of plants in fields and orchards, disease detection, and robotic fruit harvesting. Synthetic plant images, incorporating stochastic variation, provide a cost-effective complement to the thousands of photographs needed to train vision systems. Incidentally, these training images themselves can be obtained using AI techniques to realistically render L-system-generated models (Fig. 2(h)–(j)).

Occasionally, L-systems have been used to model organisms other than plants, such as algae (Morelli et al., 1991), fungi (Schnepf et al., 2016), and branching structures found in animals or humans, e.g., neurons (Ascoli and Krichmar, 2000), arterial trees (Zamir, 2001), and lungs (Davoodi and Boozarjomehry, 2016). The broad range and visual appeal of L-system models underlie their use in films and computer games (Kelty and Landecker, 2004). In these applications, L-systems are among the earliest examples of procedural modeling: the idea of generating complex graphical structures algorithmically, with compact programs (Smith, 1984). The impact of L-systems on computer graphics extends beyond the modeling of vegetation: they have provided a stepping stone for other procedural models as well, in particular those of cities (Parish and Müller, 2001; Smelik et al., 2014). Further nonbiological applications of L-systems include the generation of decorative patterns, fractals, and even music (Prusinkiewicz and Hanan, 1989). A comprehensive survey of L-system applications would require a separate study.

6. Open problems

Lindenmayer (1968) envisioned two domains of L-system applications: as a basis for computational modeling of plants, and as a mathematical tool for reasoning about them. The mathematical problems have subsequently been divided into three classes: characterization of the modeling power of different types of L-systems; analysis of their computational complexity; and inference, or deduction of L-systems based on experimental data (Lindenmayer, 1987). Many results have been obtained in all three domains and have significantly contributed to the theory of formal languages (Salomaa, 1973; Herman and Rozenberg, 1975; Rozenberg and Salomaa, 1980, 1997). However, from a biological perspective, theoretical advances remain behind the modeling applications of L-systems. The power of inference algorithms has long been limited to very simple L-systems (Ben-Naoum, 2009), although the new heuristic algorithms explored by Bernard (2020) represent progress. Research questions related to complexity appear even more challenging, in part because the complexity of biological structures is generally not well defined. One possible research avenue, suggested by the conciseness of many L-systems, is to develop ideas based on Kolmogorov complexity (Vitányi and Li, 2004). The complexity of biological processes or structures would then be measured by the length of the shortest programs generating them.

Having introduced L-systems as a tool for modeling multicellular linear and branching structures, Lindenmayer concluded his 1968 paper (Part II) by highlighting extensions to fully two- and three-dimensional organs and tissues as an open problem. This problem remains open despite many exploratory proposals and partial solutions. A promising advancement based on the mathematical notion of cell complexes has been presented relatively recently by Lane (2015). It appears, however, that developmental modeling of 2D and 3D structures is inherently more complex than the modeling of linear and branching structures. Perhaps the elegance, simplicity, and modeling power of L-systems simply cannot be matched by their multidimensional extensions. A comparative analysis of the existing proposals may shed light on the fundamental sources of the difficulties and paths to further advancements.

7. Concluding remark

Technically, the cellular automata-based formalism introduced by Lindenmayer in 1968 is no longer used: it was soon replaced by an equivalent, but more elegant definition of L-systems in terms of formal grammars. Nevertheless, it is the 1968 paper that catalyzed extraordinary advances in the computational modeling of plants, and procedural modeling in general. Remarkably, many apparently complex processes and structures can be modeled by strikingly concise and, in this sense, simple L-systems. The importance of this finding is best captured by a quote from Herbert Simon (1969):

> The central task of a natural science is to make the wonderful commonplace, to show that complexity, correctly viewed, is only a mask for simplicity, to find pattern hidden in apparent chaos.

This is what L-systems allow us to do.

CRediT authorship contribution statement

Przemyslaw Prusinkiewicz: Writing – review & editing, Writing – original draft, Visualization, Conceptualization.

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could appear to influence the work reported in this paper.

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