# Subapical bracketed L-systems

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**Abstract.** This paper characterizes the development of modular branching structures that satisfy three assumptions: (a) subapical branching, meaning that new branches can be created only near the apices of the existing branches, (b) finite number of module types and states, and (c) absence of interactions between co-existing components of the growing structure. These assumptions are captured in the notion of subapical bracketed deterministic L-systems without interactions (sBD0L-systems). We present the biological rationale for sBD0L-systems and prove that it is decidable whether a given BD0L-system is subapical or not. In addition, using the assumption that modules, once created, continue to exist, we show that (propagating) sBD0L-systems are too weak to generate acrotonic and mesotonic branching structures, which are often observed in nature. Their development must therefore be controlled by more involved mechanisms, overriding at least one of the assumptions (a-c) above.

## 1 Introduction

Bracketed L-systems, introduced by Lindenmayer [8, 9] to model the development of branching structures, have been investigated to a lesser degree from the theoretical point of view than the L-systems without brackets (*c.f.* [10, page 138]). In contrast, most practical applications of L-systems fall in the areas of modeling, simulation, and visualization of higher plants with branches (for example, see [15]). Consequently, theoretical results pertinent to this class of structures are needed.

We analyze the class of branching structures and developmental sequences generated by *subapical* deterministic bracketed L-systems without interactions (subapical BD0L-systems, or sBD0L-systems in short), formalized and first studied by Kelemenová [7]. For the class of non-branching structures, a related notion of filamentous systems with apical growth was introduced by Nirmal and Krithivasan [13] (see also [1, 14, 20]). Intuitively, a BD0L-system is subapical if new branches are created only near the apices (tips) of the existing branches. This notion captures the fundamental biological observation that new structural components of a growing plant, such as branches, leaves, or flowers, can only be initiated by *apical meristems*, that is the zones of actively dividing cells situated near the apices of branch axes [19, page 1].

A sample developmental sequence generated by a subapical BD0L-system is shown in Figure 1a. For a comparison, Figure 1b shows the development of an "everywhere

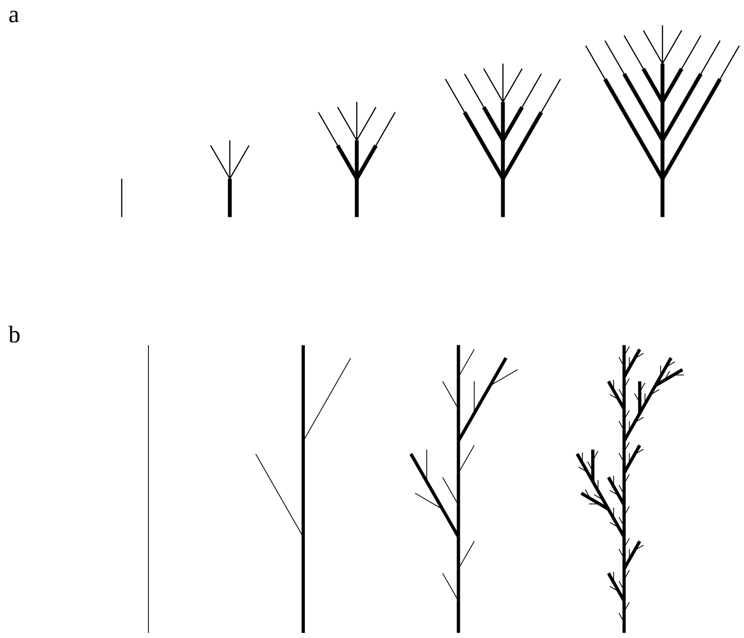

**Fig. 1.** A comparison of the development of two branching structures. Structure (a) develops with subapical branching; structure (b) does not (branches everywhere). The thin lines indicate branches created in the current derivation step.

branching” structure that violates the assumption of subapical branching. In Section 2 we restate Kelemenová’s definition of subapical BDOL-systems, provide a corrected proof of her assertion that it is decidable whether a given BDOL-system is subapical or not, and illustrate the discussed notions using several biologically motivated examples.

Frijters and Lindenmayer [4] observed that in structures generated using subapical BDOL-systems, branches closer to the apex are less developed than those positioned closer to the base. Structures satisfying this property are called *basitonic* [2, page 248] (Figure 2a). In nature one also finds *mesotonic* and *acrotonic* structures, with the most developed branches situated near the middle or the top of the mother branch (Figures 2b and 2c). The problem of generating mesotonic and acrotonic structures using L-systems

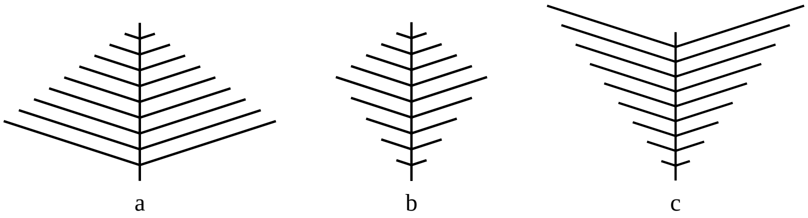

**Fig. 2.** Basitonic (a), mesotonic (b), and acrotonic (c) branching patterns

has been first discussed by Frijters and Lindenmayer in reference to the inflorescences of *Aster novae-angliae* [3], and extended to other inflorescences by Janssen and Lindenmayer [5] (see also [15, Section 3.3.3]). Lück, Lück, and Bakkali [12] (see also [11]) presented a detailed study of acrotonic, mesotonic and basitonic branching patterns using a formalism related to L-systems. In general, the proposed mechanisms for modeling mesotonic and acrotonic structures can be divided into two categories: those postulating control of development using *signals* [3, 5], and those introducing numerical parameters to characterize *growth potential* or *vigor* of individual apices [12]. Both mechanisms require a departure from the class of DOL-systems, either by introducing context-sensitive rules to represent signals, or by assuming an infinite alphabet to represent the set of vigor values. In Section 3 we prove that at least in the case of propagating development (where modules, once created, remain in the structure) these departures are indeed necessary, as neither acrotonic nor mesotonic developmental sequences can be generated by propagating sBDOL-systems. This result is related to Theorem 3.2 of Kelemenová [7], which, however, was formulated without an explicit reference to the notion of acrotony.

## 2 Subapical bracketed DOL-systems

Let $\Sigma$ denote a finite nonempty *alphabet*, the brackets [ and ] be two symbols outside of $\Sigma$ called *branch delimiters*, and $\#$ be another symbol outside of $\Sigma$ called the *branch marker*. We will denote the respective extensions of $\Sigma$ by $\Sigma_E = \Sigma \cup \{[,]\}$ and $\Sigma_\# = \Sigma \cup \{\#\}$.

**Definition 1.** A word over $\Sigma_E$ is *well nested* iff it can be specified by finitely many applications of the following rules:

- every word $u \in \Sigma^*$ is well nested;
- if $u, v \in \Sigma_E^*$ are well nested then $[u]$ and $uv$ are also well nested.

A word $[w] \in \Sigma_E^*$ such that $w$ is well nested is called a *branch*.

**Definition 2.** The *standard decomposition* of a branch $[w] \in \Sigma_E^*$ is a word of the form:

$$[w] = [x_1[\alpha_1]x_2[\alpha_2]\ldots x_n[\alpha_n]x_{n+1}],$$

where the subwords $x_1, x_2, \ldots, x_{n+1} \in \Sigma^*$ do not contain brackets, and the subwords $\alpha_1, \alpha_2, \ldots, \alpha_n \in \Sigma_E^*$ are well nested. The words $x_1x_2\ldots x_nx_{n+1}$ and $x_1\#x_2\#\ldots x_n\#x_{n+1}$ are called the (main) *axis* and the *marked axis* of $[w]$, respectively. Within these axes, the subwords $x_1, x_2, \ldots, x_n$ are called the *internodes*, and the subword $x_{n+1}$ is called the *apex*. The words $[\alpha_1], [\alpha_2], \ldots, [\alpha_n]$ are called the (first-order) *lateral branches* of $[w]$.

It is known that the standard decomposition of a branch is unique, thus the above definition is unambiguous [6]. The terminology corresponds to the standard interpretation of well nested bracketed words as string representations of branching structures [8, 9]. As the "empty branch" [] appears to have no biological interpretation, we assume in practice that the word $w$ in any branch $[w]$ is not empty. This assumption, however, is not essential to the mathematical reasoning presented in this paper.

**Example 1.** Figure 3 shows a branching structure represented by the word

$$[w] = [\,\overbrace{ab}^{x_1}\,\underbrace{[cd]}_{[\alpha_1]}\,\overbrace{ef}^{x_2}\,\underbrace{[g[h]i]}_{[\alpha_2]}\,\overbrace{j}^{x_3}\,\underbrace{[k]}_{[\alpha_3]}\,\overbrace{lm}^{x_4}\,].$$

The word $abefjlm$ is the axis of $[w]$, $ab\#ef\#j\#lm$ is the marked axis, $x_1 = ab$, $x_2 = ef$ and $x_3 = j$ are the internodes, and $x_4 = lm$ is the apex. The subwords $[\alpha_1] = [cd]$, $[\alpha_2] = [g[h]i]$ and $[\alpha_3] = [k]$ denote the lateral branches, where $[\alpha_1]$ and $[\alpha_3]$ have only apices, whereas $[\alpha_2]$ has an internode $g$, an apex $i$, and a (second-order) lateral branch $[h]$.

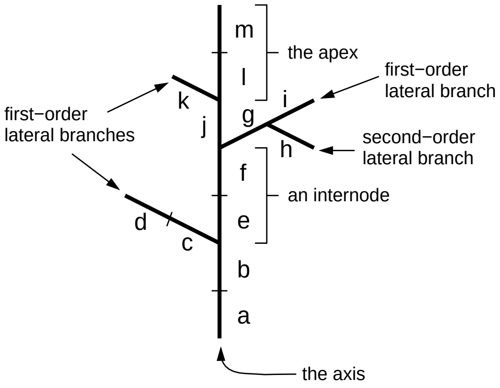

**Fig. 3.** Example of a branching structure

Diagrams such as that shown in Figure 3 can be thought of as graphs representing the branching *topology* of modeled organisms, for example algae, herbaceous plants, or trees. Depending on the complexity of the organism and the abstraction level of the model, symbols may represent individual cells or larger *modules* [16] of the structure. The bracketed words may be also assigned a *geometric* interpretation, needed to automatically visualize the models using computer graphics [15]. Within this paper we focus on the topological interpretation.

In order to describe the development of a structure over time we use the formalism of L-systems. We assume that the reader is familiar with the fundamental notions of L-system theory, such as a DOL-system, developmental sequence, and language generated by an L-system (see [15, 17, 18] for a reference), and only recall the definition of a bracketed DOL-system, which is essential to this paper.

**Definition 3.** A *bracketed DOL-system* (BDOL-system) is a DOL-system $S = \langle \Sigma_E, [w_0], P \rangle$, where the *axiom* $[w_0]$ is a well nested word over the alphabet $\Sigma_E$, and each *production* in the *production set* $P \subset \Sigma_E \times \Sigma_E^*$ has one of the following forms:

- $a \longrightarrow \alpha$, where $a \in \Sigma$, $\alpha \in \Sigma_E^*$, and $\alpha$ is well nested,
- $[ \longrightarrow [$ , or

– $] \longrightarrow ]$ .

**Example 2.** The DOL-system $S = \langle\{1, 2, \ldots, 9, [, ]\}, [1], P\rangle$ with productions:

$$\begin{array}{l} 1 \longrightarrow 23,\ \ 2 \longrightarrow 2,\ \ 3 \longrightarrow 24,\ \ \ 4 \longrightarrow 25,\ \ 5 \longrightarrow 65, \\ 6 \longrightarrow 7,\ \ \ 7 \longrightarrow 8,\ \ 8 \longrightarrow 9[3],\ \ 9 \longrightarrow 9,\ \ \ [ \longrightarrow [,\ \ \ ] \longrightarrow ] \end{array}$$

is a BDOL system. The developmental sequence generated by $S$ begins with the following words:

$$\begin{array}{ll} [w_0] & = [1] \\ [w_1] & = [23] \\ [w_2] & = [224] \\ [w_3] & = [2225] \\ [w_4] & = [22265] \\ [w_5] & = [222765] \\ [w_6] & = [2228765] \\ [w_7] & = [2229[3]8765] \\ [w_8] & = [2229[24]9[3]8765] \\ [w_9] & = [2229[225]9[24]9[3]8765] \\ [w_{10}] & = [2229[2265]9[225]9[24]9[3]8765] \\ [w_{11}] & = [2229[22765]9[2265]9[225]9[24]9[3]8765] \\ [w_{12}] & = [2229[228765]9[22765]9[2265]9[225]9[24]9[3]8765] \\ [w_{13}] & = [2229[229[3]8765]9[228765]9[22765]9[2265]9[225]9[24]9[3]8765] \end{array}$$

This L-system was proposed by Lindenmayer [8] as a mathematical model of the development of a red alga *Callithamnion roseum*. Symbols of the alphabet $\Sigma$ denote individual cells, and the matching pairs of brackets delimit branches. Selected developmental stages obtained by this model with the addition of *turtle geometry* symbols [15] to indicate the direction of branching are shown in Figure 4.

It is easy to notice that BDOL-systems always generate well nested words. The converse, however, is not true, as languages of well nested words can also be generated by DOL-systems that do not satisfy the requirements of Definition 3.

**Example 3.** The DOL-system $S = \langle\{A, B, C, [, ]\}, [AB], P\rangle$ with productions

$$A \longrightarrow A[C,\ \ B \longrightarrow C]B,\ \ C \longrightarrow C,\ \ [ \longrightarrow [,\ \ ] \longrightarrow ]$$

is not a BDOL-system, because the successors of two productions are not well nested words. Nevertheless, it generates well nested words, as suggested by the following initial elements of the developmental sequence:

$$\begin{array}{ll} [w_0] = & [AB] \\ [w_1] = & [A[CC]B] \\ [w_2] = & [A[C[CC]C]B] \\ & \ldots \end{array}$$

In this paper we adhere to the biologically well justified original notion of bracketed L-systems [8, 9], where branches can be initiated only by individual parent modules. In this context, the notion of subapical development is formalized as follows.

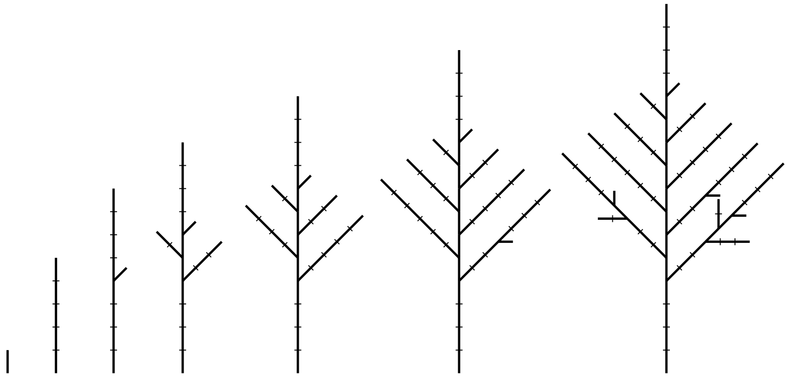

**Fig. 4.** Developmental stages $[w_0]$, $[w_4]$, $[w_7]$, $[w_9]$, $[w_{11}]$, $[w_{13}]$, and $[w_{15}]$ of the model of *Callithamnion roseum*

**Definition 4.** Given a BDOL-systems $S = \langle \Sigma_E, [w_0], P \rangle$, a letter $a \in \Sigma$ is called *branching* iff it produces a word including a lateral branch $[\beta]$:

$$a \longrightarrow \alpha[\beta]\gamma, \quad \text{where} \quad \alpha, \beta, \gamma \in \Sigma_E^*.$$

The subset of $\Sigma$ consisting of all branching letters in $S$ is denoted $\Sigma_B$.

**Definition 5.** A BDOL-system $S = \langle \Sigma_E, [w_0], P \rangle$ is *subapical with respect to the main axis* (of the generated branches) iff for any $[w] \in L(S)$ with the standard decomposition

$$[w] = [x_1[\alpha_1]x_2[\alpha_2] \ldots x_n[\alpha_n]x_{n+1}],$$

the internodes $x_1, x_2, \ldots, x_n$ do not contain branching letters:

$$x_1, x_2, \ldots, x_n \in (\Sigma \backslash \Sigma_B)^*.$$

The class of BDOL-systems subapical with respect to the main axis is obviously included in the class of unrestricted BDOL-systems.

**Example 4.** The BDOL-system $S = \langle \Sigma_E, [F], P \rangle$ with alphabet $\Sigma = \{F\}$ and productions

$$F \longrightarrow F[F]F, \ [ \longrightarrow \ [, \ ] \ \longrightarrow ]$$

generates the sequence of everywhere branching structures shown in Figure 1b. This L-system is not subapical with respect to the main axis, because the branching letter $F$ appears in the internode of the branch $[F[F]F]$ generated by $S$.

**Example 5.** The BDOL-system $S = \langle \{A, B, C\}, [ABC], P\rangle$ with productions

$$A \longrightarrow C,\ B \longrightarrow B,\ C \longrightarrow [B],\ [\ \longrightarrow\ [,\ ]\ \longrightarrow ]$$

is not subapical with respect to the main axis, because in the developmental sequence

$$[ABC] \Longrightarrow [CB[B]] \Longrightarrow [[B]B[B]],$$

the branching letter $C$ appears in the internode. Note that the technique used in [7, page 188] to decide whether a BDOL-systems is subapical or not would misclassify this L-system as subapical.

**Theorem 1.** It is decidable whether a given BDOL-system is subapical with respect to the main axis.

*Proof.* Consider a mapping $f : \Sigma_E^* \to \Sigma_\#^*$ that substitutes branches $[w] \in \Sigma_E^*$ by their marked axes. Thus, assuming the standard decomposition of $[w]$, we have:

$$f([w]) = f([x_1[\alpha_1]x_2[\alpha_2]\ldots x_n[\alpha_n]x_{n+1}]) = x_1\#x_2\#\ldots x_n\#x_{n+1}.$$

Given a BDOL-system $S = \langle \Sigma_E, [w_0], P\rangle$, construct a DOL-system

$$S_\# = \langle \Sigma_\#, f([w_0]), P_\#\rangle,$$

where $P_\# = \{\# \longrightarrow \#\} \cup P'$, and productions in $P'$ are obtained by replacing the successors of productions in $P\backslash\{[\longrightarrow [, ] \longrightarrow]\}$ with their marked axes:

$$\text{if } a \longrightarrow \alpha \text{ belongs to } P \text{ then } a \longrightarrow f(\alpha) \text{ belongs to } P'.$$

It is clear that the L-system $S_\#$ generates the set of marked axes of the words in $L(S)$:

$$L(S_\#) = \{f([w]) : [w] \in L(S)\} = f(L(S)).$$

According to Definition 5, a BDOL-system $S$ is subapical with respect to the main axis iff no branching letters appear in the internodes of words $[w] \in L(S)$. Since the internodes of words $[w]$ and $f([w])$ are the same, the criterion for subapicality can be expressed as

$$L(S_\#) \cap \Sigma_\#^* \Sigma_B \Sigma_\#^* \# \Sigma^* = \emptyset.$$

Thus, a BDOL-system $S$ is subapical with respect to the main axis if and only if the intersection of the language $L(S_\#)$ generated by a related DOL-system $S_\#$ and the regular language $\Sigma_\#^* \Sigma_B \Sigma_\#^* \# \Sigma^*$ is empty. This problem is decidable, because:

- the class of languages generated by DOL-systems is included in the class of languages generated by extended OL-systems (EOL-systems) [17, page 54],
- the class of EOL languages is closed with respect to intersection with regular languages [17, Theorem 1.8],
- the emptiness problem is decidable for EOL languages [17, Theorem 5.6]. ♣

The reference to the general properties of EOL-systems and regular languages makes the proof of Theorem 1 concise, but does not lead to a straightforward algorithm for testing subapicality of given BDOL-systems. Since subapicality is an essential property of biologically motivated models of branching structures, we also present a more direct test.

We say that the letter $a$ *occurs to the left of* $b$ in a word $w \in \Sigma^*$, and note $(a, b) \in \Gamma(w)$, iff $w = xaybz$ for some $x, y, x \in \Sigma^*$. We extend this definition to languages using the equation:

$$\Gamma(L) = \bigcup_{w \in L} \Gamma(w).$$

In order to construct the relation $\Gamma(L)$ for the language $L$ generated by an arbitrary non-bracketed DOL-system $T = \langle \Sigma, w_0, P \rangle$, we consider the initial elements of the developmental sequence generated by $T$,

$$w_0 \Longrightarrow w_1 \Longrightarrow \dots w_i \Longrightarrow \dots,$$

and construct the family of relations $\Gamma_i \in \Sigma \times \Sigma$:

$$\begin{aligned} \Gamma_0 &= \emptyset, \\ \Gamma_{i+1} &= \Gamma_i \cup \Gamma(w_i) \quad \text{for} \quad i = 0, 1, 2, \dots. \end{aligned}$$

Since the alphabet $\Sigma$ is finite, there exists a natural number $k \leq (\mathrm{card}(\Sigma))^2$ such that the $k$-th iteration of the above formula will not add new elements to $\Gamma_k$. Due to the context-free character of derivations in DOL-systems, the subsequent iterations also will not add new elements: $\Gamma_k = \Gamma_{k+j}$ for all $j \geq 0$. Thus, the set $\Gamma_k$ contains all pairs of letters $(a, b) \in \Sigma$ such that $a$ occurs to the left of $b$ in some word of $L(T)$, and $\Gamma_k = \Gamma(L(T))$.

In order to apply this result to test the subapicality of a given BDOL-system $S = \langle \Sigma_E, [w_0], P \rangle$, we construct the relation $\Gamma(L(S_\#))$ for the language $L(S_\#)$ generated by the DOL-system $S_\#$ associated with $S$. The L-system $S$ is subapical with respect to the main axis iff there is no branching letter $a \in \Sigma_B$ such that $(a, \#) \in \Gamma(L(S_\#))$.

**Example 6.** We will show that the BDOL-system $S$ from Example 2 is subapical with respect to the main axis. To this end, we first create a DOL-system $S_\# = \langle \{1, 2, \dots 9, \#\}, 1, P_\# \rangle$ associated with $S$. The set $P_\#$ consists of the production $\# \longrightarrow \#$ and productions of $P$ except for $[ \longrightarrow [$ and $] \longrightarrow ]$; production $8 \longrightarrow 9[3]$ is replaced by $8 \longrightarrow 9\#$. The relation *occurs to the left* for the language $L(S_\#)$ is given by Figure 5. An arrow from node $a$ to node $b$ indicates that letter $a$ occurs to the left of $b$ in a word of $L(S_\#)$. The arrows that can be reconstructed as a transitive closure of the graph shown in Figure 5 have been omitted for clarity (the relation $\Gamma(L(S_\#))$ is transitive in this example). We observe that the branching symbol $8$ does not occur to the left of the branch marker $\#$, thus the L-system $S$ is subapical with respect to the main axis.

We will now extend the notion of subapicality from the main axis to the entire branching structure.

**Definition 6.** Given a BDOL-systems $S$, a *branch of order* $N$ is characterized recursively as follows:

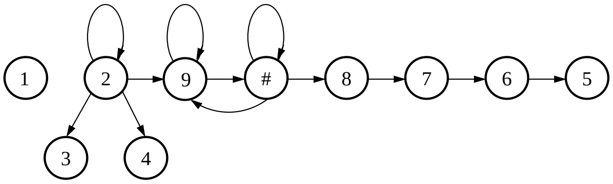

**Fig. 5.** Simplified graph of the relation $\Gamma(L(S_{\#}))$ for the developmental model of *Callithamnion roseum*

- a word $[w] \in L(S)$ is a branch of order $N = 0$,
- if $[w] = [x_1[\alpha_1]x_2[\alpha_2]\ldots x_n[\alpha_n]x_{n+1}]$ is a branch of order $N \geq 0$ then the subwords $[\alpha_1], [\alpha_2], \ldots, [\alpha_n]$ are branches of order $N + 1$.

The set of all branches (of any order $N \geq 0$) generated by $S$ is denoted $L_B(S)$.

**Definition 7.** A BDOL-system $S$ is called *subapical with respect to all branches*, or in short *subapical*, iff in the standard decomposition of any branch

$$[\alpha] = [y_1[\beta_1]y_2[\beta_2]\ldots y_m[\beta_m]y_{m+1}] \in L_B(S)$$

the internodes $y_1, y_2, \ldots, y_m$ do not contain branching letters.

The following extension of Theorem 1 provides an effective method for deciding whether a BDOL-system is subapical or not.

**Theorem 2.** Let $S = \langle \Sigma_E, [w_0], P\rangle$ be a BDOL-system, and $[w_1]$, $[w_2], \ldots,$ $[w_p]$ be the branches that occur in successors of productions in $P$ accessible from the axiom $[w_0]$. Denote by $S_i$ the BDOL-system $\langle \Sigma_E, [w_i], P\rangle$, where $i = 1, 2, \ldots, p$. The L-system $S$ is subapical with respect to all branches iff each of the L-systems $S, S_1, S_2, \ldots, S_p$ is subapical with respect to the main axis.

*Proof.* Each branch $[\alpha]$ in the set $L_B(S)$ belongs to a developmental sequence that starts with one of the words $[w_0], [w_1], [w_2], \ldots, [w_p]$. Consequently, the set of the axes of all branches generated by $S$ is the same as the set of the main axes of the branches generated by L-systems $S, S_1, S_2, \ldots, S_p$, and the requirement that no branching letters occur in the internodes of branches $[\alpha] \in L_B(S)$ is equivalent to the requirement that no branching letters occur in the main axes of words $[w]$ generated by L-systems $S, S_1, S_2, \ldots, S_p$. ♣

**Example 7.** We will show that the BDOL-system from Example 2 is subapical with respect to all branches. To this end we consider both the original L-system $S$ and its modification $S_1 = \langle\{1, 2, \ldots, 9, [, ]\}, [3], P\rangle$, in which the original axiom [1] has been replaced by branch [3] created by production $8 \longrightarrow 9[3]$. The graph of the relation $\Gamma(L(S_{\#}))$ for the L-system $S_{\#}$ associated with $S$ was constructed in Example 6 and shown in Figure 5. The graph for the L-system $S_{\#1}$ associated with $S_1$ is similar, except that node 1 is absent and there is no arrow between nodes 2 and 3. The branching letter 8 does not occur to the left of the branch marker # in either graph, thus both L-systems $S$ and $S_1$ are subapical with respect to the main axis, and the L-system $S$ is subapical with respect to all branches.

## 3 Acrotonic languages

According to Section 1, mesotonic or acrotonic structures share the property that the most developed lateral branches are not situated near the bottom of the mother branch. In this section, we introduce a definition of acrotonic languages intended to formalize this intuitive characterization. We then prove that the acrotonic languages cannot be generated by subapical BDOL-systems.

**Definition 8.** A language $L \in \Sigma_E^*$ is called *acrotonic* iff for every natural $k$ there exists a branch $[w] \in L$ with the standard decomposition

$$[x_1[\alpha_1]x_2[\alpha_2]\ldots x_n[\alpha_n]x_{n+1}]$$

and a sequence of indices

$$1 \leq i_1 < i_2 < \ldots < i_k \leq n$$

such that

$$\lg(\alpha_{i_1}) < \lg(\alpha_{i_2}) < \ldots < \lg(\alpha_{i_k}).$$

The notation $\lg(\alpha_{i_j})$ denotes the *size* of the branch $[\alpha_{i_j}]$, measured as the number of letters other than [ and ] in the word $\alpha_{i_j}$.

According to this definition, a language $L$ is acrotonic if it contains branches with arbitrarily long (sub)sequences of lateral branches, the size of which increases while traversing the main axis from the bottom up.

**Theorem 3.** An acrotonic language $L$ cannot be generated by a propagating subapical BDOL-system.

*Proof.* Suppose, by contradiction, that there exists an acrotonic language $L$ generated by a propagating subapical BDOL-system $S = \langle \Sigma_E, [w_0], P \rangle$. Introduce the term *branch initial* to denote any branch appearing in a production successor, and let $N$ stand for the total number of branch initials that appear in the successors of productions in $P$. Consider a word $[w] \in L$ satisfying conditions set forth in Definition 8 for some $k > N$. Since $k > N$, there are at least two branches in the sequence $\{[\alpha_{i_1}], [\alpha_{i_2}], \ldots, [\alpha_{i_k}]\}$, say $[\alpha_p]$ and $[\alpha_q]$, produced from different occurrences of the same branch initial $[v]$:

$$\begin{array}{lcl} a \longrightarrow \mu_1[v]\mu_2 & \text{and} & [v] \Longrightarrow^{m_p} [\alpha_p], \\ b \longrightarrow \nu_1[v]\nu_2 & \text{and} & [v] \Longrightarrow^{m_q} [\alpha_q]. \end{array}$$

Assuming that $p < q$, we have $\lg(\alpha_p) < \lg(\alpha_q)$. According to the principle of subapical branching (Definition 5), branch $[\alpha_p]$ must have been initiated not later than $[\alpha_q]$, thus the derivation length $m_p$ is not less than $m_q$ (Figure 6).

Since the BDOL-system $S$ is deterministic, the following derivation exists:

$$[v] \Longrightarrow^{m_q} [\alpha_q] \Longrightarrow^{m_p - m_q} [\alpha_p].$$

The L-system $S$ is propagating, thus $\lg(\alpha_q) \leq \lg(\alpha_p)$. This contradicts the inequality $\lg(\alpha_p) < \lg(\alpha_q)$ obtained earlier and leads to the conclusion that an acrotonic language $L$ cannot be generated by a propagating subapical BDOL-system. ♣

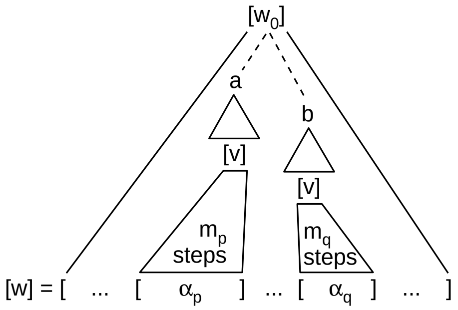

**Fig. 6.** Derivation tree illustrating the proof of Theorem 3

.

## 4 Conclusions

Subapical branching is an essential characteristic of plant development. In Section 2, we recalled the definition of subapical branching formulated by Kelemenová [7] within the conceptual framework of L-systems, and showed that subapicality is a decidable property of BDOL-systems. We also presented a practical method for testing whether a given BDOL-system is subapical or not, and illustrated it using a model of a red alga *Callithamnion roseum* as an example. It is interesting to note that some models of plant-like structures devised for computer graphics purposes, such as the everywhere-branching structure considered in Example 4 and structures shown in [15, Figures 1.24 b,c, 1.25 and 1.26]), do not develop according to the principle of subapical branching and therefore cannot be considered biologically correct.

Branching structures can be generally categorized as basitonic, mesotonic, or acrotonic, depending on whether the most vigorous lateral branches are situated near the base of the plant, in its middle zone, or near the top. In Section 3, we applied notions of L-systems to propose a formal definition of acrotony (including mesotony as a special case) and proved that acrotonic structures cannot be generated by propagating subapical BDOL-systems. Consequently, control mechanisms beyond those expressible using propagating sBDOL-system are necessary to model the development of acrotonic structures. Two types of mechanisms, based on information flow between coexisting plant modules [5, 15] or unlimited number of states that may characterize individual modules [11, 12] have been considered in the literature.

The results reported in this paper leave many questions open for further research. The first group of questions focuses on the formal properties of bracketed L-systems.

- We conjecture that Theorem 3 can be extended to non-propagating subapical BDOL-systems. Is this conjecture true?
- Consider two L-systems with the alphabet $\{A, B, I, L\}$ and axiom $[BA]$. The only non-identity production of L-system $S_1$ is $A \longrightarrow I[L][L]A$, and of L-systems $S_2$ is $B \longrightarrow BI[L][L]$. Both L-systems generate the same developmental sequence $\{B(I[L][L])^n A : n = 0, 1, 2, \ldots\}$, but L-system $S_1$ is subapical while $S_2$ is not. This raises the following questions:

  - Given an arbitrary BDOL-system $S$, is it decidable whether there exists a subapical BDOL-system $S'$ generating the same developmental sequence (or language)? If the answer is positive, is there an effective procedure for finding $S'$, given $S$?
  - Is it decidable whether a given developmental sequence or language can be generated by a subapical BDOL-system?
- The class of L-systems considered in this paper has been limited to BDOL-systems, but similar questions are pertinent to other classes of L-systems as well. For example, is it decidable whether a given bracketed context-sensitive L-system (BIL-system) is subapical or not? Is it decidable whether a given BIL-system generates an acrotonic structure?

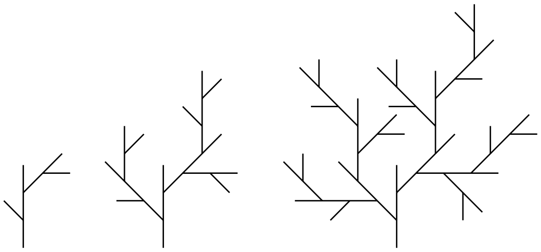

**Fig. 7.** Development of a sympodial branching structure generated by a BDOL-system $S$ with axiom $[A]$ and productions $A \longrightarrow E[C]B$, $B \longrightarrow E[A]E$, $C \longrightarrow D$, $D \longrightarrow A$, $E \longrightarrow E$, $[ \longrightarrow [$, $] \longrightarrow ]$. Biologists would qualify this structure as acrotonic, although it does not satisfy Definition 8. Developmental stages $w_3$, $w_6$, and $w_9$ are shown.

A mathematical definition that aims at capturing the essence of a natural phenomenon is always somewhat arbitrary; we cannot prove that it is "right" or "wrong", although we can argue whether it faithfully reflects our intuition of the phenomenon and is operative as an element of a theory. In the context of this paper, such questions are related to the notions of subapical branching and acrotony.

- Definitions of subapical branching (5 and 7) present only one possible formalization of the underlying biological concept. What are the implications of alternative definitions, for example based on the conditions that:

  - branch creation is restricted to a predefined number of distal (topmost) modules in branches of all orders, or
  - no new branch can be created below a predefined number of existing branches (counting from the apex down)?
- The proposed definition of acrotony (8) refers to the number of modules in a branch as a measure of the branch size. Other measures are also possible, for example based on the number of modules along the axes of lateral branches, the maximum branching order within the lateral branches, or the lengths of the axes in case of models operating on the geometric level. What are the implications of these definitions?
- Definition 8 requires that an arbitrarily long sequence of branches of increasing size be found while traversing the axis of a developing plant from the base up (acropetally). In nature, however, we always deal with finite structures, thus assumptions describing what an underlying developmental mechanism would produce if it was allowed to operate indefinitely cannot be experimentally verified. Is there an alternative formal definition of acrotony that would capture the increased complexity of acrotonic structures compared to basitonic structures, yet would apply to finite structures?
- The proposed definition of acrotony is more appropriate for *monopodial* than *sympodial* branching structures. A monopodial structure is characterized by a pronounced main axis that may carry an arbitrarily large number of lateral branches. In contrast, a sympodial structure has a repetitive branching pattern in which the number of lateral branches carried by each axis may be small, even if the whole structure is potentially unlimited (Figure 7). Biologists would qualify a structure that has increasingly long (or better developed) branches along each axis as an acrotonic structure irrespective of the number of branches carried by each axis. How should the definition of acrotony be improved to encompass both monopodial and sympodial structures?

In spite of the spectacular progress of the L-system theory since its inception almost thirty years ago, many fundamental problems pertinent to plant modeling remain open. They point to a fertile area for a continuing research bridging biology, computer graphics, and theoretical computer science.

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## References

1. T. Bălănescu, M. Gheorghe, and Gh. Păun. Three variants of apical growth filamentous systems. *Int. J. of Computer Mathematics*, 22:227–238, 1987.

2. A. Bell. *Plant form: An illustrated guide to flowering plants.* Oxford University Press, Oxford, 1991.
3. D. Frijters and A. Lindenmayer. A model for the growth and flowering of *Aster novae-angliae* on the basis of table (1,0)L-systems. In G. Rozenberg and A. Salomaa, editors, *L Systems*, Lecture Notes in Computer Science 15, pages 24–52. Springer-Verlag, Berlin, 1974.
4. D. Frijters and A. Lindenmayer. Developmental descriptions of branching patterns with paracladial relationships. In A. Lindenmayer and G. Rozenberg, editors, *Automata, languages, development*, pages 57–73. North-Holland, Amsterdam, 1976.
5. J. M. Janssen and A. Lindenmayer. Models for the control of branch positions and flowering sequences of capitula in *Mycelis muralis* (L.) Dumont (Compositae). *New Phytologist*, 105:191–220, 1987.
6. H. Jürgensen, H. Shyr, and G. Thierrin. Monoids with disjunctive identity and their codes. *Acta Mathematica Hungarica*, 47(3–4):299–312, 1986.
7. A. Kelemenová. Complexity of L-systems. In G. Rozenberg and A. Salomaa, editors, *The book of L*, pages 179–191. Springer-Verlag, Berlin, 1986.
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. Models for multicellular development: Characterization, inference and complexity of L-systems. In A. Kelemenová and J. Kelemen, editors, *Trends, techniques and problems in theoretical computer science*, Lecture Notes in Computer Science 281, pages 138–168. Springer-Verlag, Berlin, 1987.
11. H. B. Lück and J. Lück. Approche algorithmique des structures ramifiées acrotone et basitone des végétaux. In H. Vérine, editor, *La biologie théorique à Solignac*, pages 111–148. Polytechnica, Paris, 1994.
12. J. Lück, H. B. Lück, and M. Bakkali. A comprehensive model for acrotonic, mesotonic, and basitonic branching in plants. *Acta Biotheoretica*, 38:257–288, 1990.
13. N. Nirmal and K. Krithivasan. Filamentous systems with apical growth. *Int. J. of Computer Mathematics*, 12:203–215, 1983.
14. Gh. Păun. Some further remarks on regular controlled apical growth filamentous systems. *Bull. Math. de la Soc. Sci. Math. de la R. S. de Roumanie*, 32(4):341–344, 1988.
15. P. Prusinkiewicz and A. Lindenmayer. *The algorithmic beauty of plants*. Springer-Verlag, New York, 1990. With J. S. Hanan, F. D. Fracchia, D. R. Fowler, M. J. M. de Boer, and L. Mercer.
16. P. M. Room, L. Maillette, and J. Hanan. Module and metamer dynamics and virtual plants. *Advances in Ecological Research*, 25:105–157, 1994.
17. G. Rozenberg and A. Salomaa. *The mathematical theory of L systems.* Academic Press, New York, 1980.
18. A. Salomaa. *Formal languages.* Academic Press, New York, 1973.
19. T. A. Steeves and I. M. Sussex. *Patterns in plant development*. Cambridge University Press, Cambridge, 1989.
20. K. G. Subramanian. A note on regular-controlled apical-growth filamentous systems. *Intern. J. Compu. Inf. Sci.*, 14:235–242, 1985.

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