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Theory of dendritic morphology

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The principle of least effective volume, which is postulated in this study, leads to analytical derivation of dendritic branch angles of pyramidal neurons. Global parameters such as combined length and shaft area measured in anatomical experiments are analytically formulated as functions of some parameters (called *fundamental parameters* in this study). The plots of the formulas are closely consistent with experimental data [Larkman, J. Comp. Neurol. **306**, 307 (1991); **306**, 320 (1991)]. Our result suggests the existence of a few factors, which are probably chemical, responsible for determining the parameters that work in the morphological rules of dendrites. The values of diameters and lengths are given by this theory recursively. It is expected that these values can be used for the morphological data which are the boundary conditions of the cable model and the electrodiffusion model.

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I. INTRODUCTION

Morphology (of any object) is difficult to describe in mathematical terms. In particular, morphology of tree structures has been studied using several methodologies. Existing tree structures must have some stationary character. Tree structures are categorized into two groups by their lying stationary character: (a) Physically stationary structures (such as diffusion-limited aggregation [1], viscous fingering [2]), and (b) evolutionally (or biologically) stationary structures (such as branching patterns in trees, blood vessels [3], and neuronal dendrites).

Although the biological structures are formed in long-term evolutional process, they must be determined by physical mechanisms, while interacting with environments. The evolutionally stationary character itself must have a physical expression.

Our purpose is to understand and mathematically describe the dendritic morphology of pyramidal neurons. We expect that our approach will be applicable to morphology in other biological systems. In the case of morphology of the blood vessel, there are analytical studies based on a local optimality principle [3,4]. To determine the branching angles of daughter branches, they minimize the volume of blood vessels. When we apply the same theory to morphology of neuronal dendrites, the branching angles become zero in an experimentally determined condition (which is shown in the text). Therefore the same method cannot be used in the neuronal morphology. We propose a concept of *effective volume* in this paper as an analogy of the volume of a blood vessel. In the case of axonal morphology, there are excellent studies [5,6]. They use the principle of wiring economy as an evolutionary pressure. We discuss later the difference between dendritic morphology and axonal morphology.

In order to investigate dynamical properties of neural systems, it is fairly important to construct dynamical equations [7,8] of a single neuron. The construction of these equations themselves is a strategically difficult problem. It is, however, often the case that those models are based on phenomenalistic arguments concerning neuronal properties. The formulations of neuronal dynamics have been studied over the past several decades. One approach is based on the cable equations that describe electric flows inside dendritic trees and/or axons [9–11]. Another is based on Hodgkin and Huxley equations [12] which explain nonlinear neuronal properties. Combining cable equations and Hodgkin-Huxley equations enables us to carry out realistic simulations of neural systems. Nevertheless, most of the studies have been done on a small number of interconnected neurons. Recently, simulations of networks with realistic neurons have been enabled by progress in computer technology [13]. There are still some morphological parameters to be determined from biological neurons. Local electric parameters, such as membrane capacitance and resistance used in each cable equation of a dendritic segment, should be experimentally measured beforehand. In addition to those parameters, morphological parameters (such as the diameter of each segment and the segment length) are also necessary as a boundary condition of several electrophysiological models (the cable model [10] and the electrodiffusion model [11]). It would be an advantage to obtain values of those morphological parameters systematically in order to make simulations including as large a number of segments as possible.

Several formulas involving some parameters which rule the global morphology will be derived. The parameters are called *fundamental parameters* in this study, and will be defined in Sec. II. In Sec. III, the concept of *effective volume* will be proposed. Then in Sec. IV *the principle of supremum effective volume* will be postulated. The length of each dendritic segment will be estimated as a function of the segment diameter. Furthermore, *the principle of least effective volume* will be postulated in Sec V. In Sec. VI mathematical formulations for extra global parameters such as the combined length L_{combined} and/or the combined shaft area A_{combined}, which are usually measured in anatomical experiments, will be analytically derived as functions of the above mentioned fundamental parameters. We show that plots of those theoretical formulas are extraordinarily consistent with experimental data. In the final section, we will summarize this paper, draw several conclusions, and finally argue advantages of our postulated principle which describes dendritic morphology.

II. THE FUNDAMENTAL SHAPE PARAMETERS

There exist shapes of infinite variety of neurons in the brain. For example, pyramidal neurons have obviously different neuronal shapes from those of neurons in other categories. How can we distinguish pyramidal cells from other cell types? To answer this question, we should elucidate common features of pyramidal cells. The averaged values of some parameters (called fundamental parameters in this paper) describe the common feature.

Some of the parameters are already collected [14]. Although most notations of fundamental parameters are based upon Ref. [14], some parameters (the segment length l, the segment taper ΔA) are excluded from the set of fundamental parameters (because the segment lengths are determined as a function of the fundamental parameters in the following sections, and the segment taper is considered to have small influences on basic neuronal morphology if we use the averaged diameter along a segment). This section concisely describes the mathematical notations.

Branch power (n). If the cross-sectional area is conserved at each branch point, the relation

$$d_0^2 = \sum_{i=1}^{N} d_i^2 \tag{2.1}$$

must be satisfied. N is the number of furcation. d_0 is the diameter of the parent dendrite and d_k the diameter of the kth daughter dendrite. The power 2 is called the "branch power." Impedance matching between dendritic branches requires the power of 1.5 instead of 2. This value is obtained by solving cable equations [10]. The generalized relation is described as

$$d_0^n = \sum_{i=1}^{N} d_i^n, \tag{2.2}$$

with branch power n, which does not necessarily take the value of integer. In the case of cross-sectional conservation, the branch power $n = 2$.

Daughter-branch ratio (R). Most cases of branching are bifurcations. Trifurcations or larger numbers of furcations are rarely observed in actual neurons. Therefore we assumed that only bifurcations occur at every branch point in model neurons. Let the number of furcation N be 2. The daughter-branch ratio R is defined as the ratio between the diameters of daughter branches. Using the two diameters d_1 and d_2 the ratio R is given by

$$R = \frac{d_1}{d_2}. \tag{2.3}$$

From (2.2) and (2.3), the following expressions for the segment diameters:

$$d_1 = R\xi d_0 \tag{2.4a}$$

and

$$d_2 = \xi d_0 \tag{2.4b}$$

can be given, where the parameter ξ is expressed as

$$\xi = \frac{1}{(1+R^n)^{1/n}}. \tag{2.5}$$

Notice that the furcation number N in (2.2) is set to 2 in the definition of the daughter-branch ratio. (2.4a) and (2.4b) are generalized into recursive forms:

$$d_{k+1}^{(1)} = R\xi d_k, \tag{2.6a}$$

$$d_{k+1}^{(2)} = \xi d_k. \tag{2.6b}$$

The level k is the number of branch points on a dendritic path traced from the primary trunk segment to a dendritic position. We can determine all of the diameters of segments by using these equations recursively.

Terminal diameter ($d_{\min}$). Since intracellular microstructures should exist in every segment, we assume that diameters have a minimum size. We define the minimum diameters as the terminal diameter.

Stem diameter (D). Dendritic segment diameters strongly depend on the diameter D of their primary dendrite [15]. We define this diameter as the stem diameter.

Effective dimension (ν). From conventional geometry, the dimension of dendritic volume is 3. When we take the dendritic structure into consideration, the dimension does not always have to have integer value. We define such noninteger dimension as effective dimension ν. This parameter will be discussed in detail in the following section.

Mass constant (C). The constant which combines a dendritic diameter and a segment length is denoted by C. This parameter will be defined in Sec. IV.

III. THE EFFECTIVE VOLUMES OF SEGMENTS

In order to understand the concept of the *effective volume* of a segment, we consider two typical examples. In the case in which segments of dendrites are tubular [Fig. 1(a)], the volume of a segment is proportional to its surface area, and is written by

$$V_{\text{tubular}} = c_2 l d \quad (\propto \pi l d), \tag{3.1}$$

where l is the segment length, d is the diameter of the segment, and $c_2(\propto \pi)$ is called the *mass factor* which depends on the dimensionality of the segment.

In the second case in which segments of dendrites are stuffed [Fig. 1(b)], the volume of a segment is written by

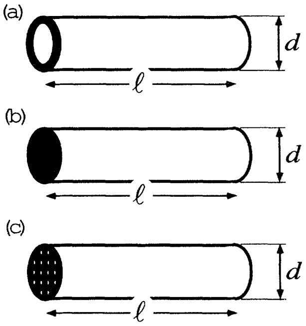

FIG. 1. Dendritic segment. In the case in which segments of dendrites are tubular (a), the volume of a segment is proportional to the surface area of it. In the case in which segments of dendrites are stuffed (b), the volume of a segment is approximated by the cylindrical volume. We generalize such structure dependent volume in segments (c).

$$V_{\text{stuffed}} = \pi l \left(\frac{d}{2}\right)^2 = c_3 l d^2, \tag{3.2}$$

where the mass factor is expressed as $c_3 = \pi/4$.

Generally, a noninteger number (ν) can be defined as the effective dimension of the generalized cross-sectional area. Using the effective dimension ν and the mass factor $c_{\nu+1}$, we are able to write the *effective volume* of a segment as

$$V_{\text{eff}} = c_{\nu+1} l d^{\nu}. \tag{3.3}$$

The effective dimension ν in realistic neurons is considered between 2 (of the stuffed case) and 1 (of the tubular case). See schematic figure [Fig. 1(c)].

IV. THE PRINCIPLE OF SUPREMUM EFFICIENCY OF DENDRITIC ORGANIZATION

Segments of a dendrite do not have interminable lengths or interminable widths. It is fairly reasonable to postulate the principle that the effective volume per segment has a supremum. Let V_{sup} be the supremum effective volume. The principle is expressed as the following inequality:

$$c_{\nu+1} l d^{\nu} < V_{\text{sup}}. \tag{4.1}$$

From this inequality, we get a relation among the segment length l, the segment diameter d, and the effective dimension ν:

$$l < C d^{-\nu}, \tag{4.2}$$

where the constant is written as $C = c_{\nu+1}/V_{\text{sup}}$. This relation is shown in Fig. 2 for a case ($C^{\frac{1}{1+\nu}} = 3.8[\mu\text{m}]$, $\nu = 1.9$). These values of the parameters are determined by least-squares fitting with the experimental data [16] using the expression of averaged segment lengths [see (A3) in the Appendix]. The broken curve shows the left-hand side of (4.2). According to the inequality (4.2), segment lengths should have values under the broken curve. Shorter segments will be allowed than that expressed by the broken curve. Small squares are replots of the experimental data [16]. It shows a qualitative agreement between our theory and the experiment. In both theory and experiment, segments with smaller diameters tend to be longer. Mass constant C is included in fundamental parameters.

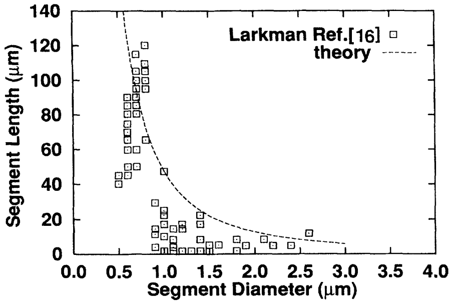

FIG. 2. The relation between segment lengths and segment widths. Our condition in a supremum effective volume gives a qualitative agreement with the experimental data. Small squares (□) show the experimental data which are the replots of Ref. [16].

V. THE PRINCIPLE OF THE LEAST EFFECTIVE VOLUME

We postulate another principle called *the principle of least effective volume* in this section. This principle states that the effective volume of the actual dendritic tree should have the least value. As a first step, we consider the neighborhood of a branch point. The effective volume in the neighborhood of a branch point should have the least value when the dendritic segments elongated from the branch point reach specific points. We determine the branch point such that effective volume is stationary to infinitesimal displacement of the branch point in any direction. The ideal branch point is given by a function of the two fixed points which two bifurcate segments reach. The fixed points are assumed as variable parameters to obtain the branch point. This method is based on the variational principle [17]. The effective volume in the vicinity of the branch point $\mathbf{o}$ is given by

$$V_{\text{eff}} = c_{\nu+1}(|\mathbf{p_0} - \mathbf{o}|d_0^{\nu} + |\mathbf{p_1} - \mathbf{o}|d_1^{\nu} + |\mathbf{p_2} - \mathbf{o}|d_2^{\nu}), \tag{5.1}$$

where $\mathbf{p_0}$, $\mathbf{p_1}$, and $\mathbf{p_2}$ are variable points on dendritic segments (see Fig. 3). The variational problem is to find the branch point $\mathbf{o}$ for which V_{eff} is stationary while $\mathbf{p_0}$, $\mathbf{p_1}$, and $\mathbf{p_2}$ are fixed,

$$\frac{\delta V_{\text{eff}}}{\delta \mathbf{o}} = \mathbf{0}. \tag{5.2}$$

From these equations (5.1) and (5.2), we get a relation

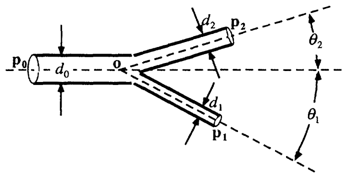

FIG. 3. Branch angles. The figure shows the vicinity of a branch point **o**. The branch angles are defined as the angles between a dendritic segment and its daughter branches.

of the branch angles:

$$\frac{d_0^\nu}{\sin(\theta_1+\theta_2)} = \frac{d_1^\nu}{\sin\theta_1} = \frac{d_2^\nu}{\sin\theta_2}, \tag{5.3}$$

where angles θ_1, θ_2 are between a dendritic segment and its daughter branches (see Fig. 3). The angles do not depend on $\mathbf{p}_0, \mathbf{p}_1$, and $\mathbf{p}_2$ in Eqs. (5.3). Combining (2.2), (2.3), and (5.3), we obtain the following expressions for the branch angles:

$$\theta_1 = \arccos\left\{\frac{(1+R^n)^{\frac{2\nu}{n}} + R^{2\nu} - 1}{2R^\nu(1+R^n)^{\nu/n}}\right\}, \tag{5.4a}$$

$$\theta_2 = \arccos\left\{\frac{(1+R^n)^{\frac{2\nu}{n}} - R^{2\nu} + 1}{2(1+R^n)^{\nu/n}}\right\}. \tag{5.4b}$$

Most experimentally obtained values of the angles satisfy the relation

$$0 < \theta_1,\ \theta_2 < \frac{\pi}{2}. \tag{5.5}$$

Consider the case that daughter diameters are equal, that is, that the daughter-branch ratio R equals 1, to get a *sine qua non* for the branch power n and effective power ν. From the condition (5.5), the arguments of the equations (5.4a) and (5.4b) are confined to the domain (0,1) with the inequality

$$0 < 2^{\frac{\nu}{n}-1} < 1. \tag{5.6}$$

Therefore the relation between the two powers is given by

$$\nu < n. \tag{5.7}$$

Since the branch power n equals 2 in most kinds of neurons [14], the assumption that $\nu = 2$ (the case to which we apply the conventional volume) leads to zero branch angles $\theta_1, \theta_2 = 0$. Therefore in the case of neuronal dendrites, we cannot take the conventional volume whose effective dimension is $\nu = 2$. This result (5.7) is also consistent with the definition of effective power ν, which is conceptually proposed in Sec. III.

VI. MATHEMATICAL EXPRESSIONS OF GLOBAL PARAMETERS

There are pieces of excellent work of neuronal anatomy [14,16], which show several relations between the values of global parameters, such as the segment diameter d vs the combined shaft area A_{combined}, the segment length l vs A_{combined}, the combined segment length L_{combined} vs A_{combined}, d vs L_{combined}, and so on. The mathematical definitions of these parameters and the results of mathematical considerations are described in this section. The derivations of expressions for the values are given in the Appendix. In order to carry out detailed comparisons with experiments, a specific set of the averaged parameter values ($d_{\min} = 0.6[\mu\text{m}]$, $r = 2.0$, $R = 1.2$) of a basal dendrite are chosen from the experimental paper [16]. The values of the parameters C, ν are the same as the ones in Sec. IV. Using the values, the total segment length composed of all the lengths l (which is called combined length L_{combined}) is written as

$$L_{\text{combined}} = CD^\nu \sum_{k=0}^{s_{\max}} \left\{\frac{1}{(1+R^n)^{1/n}}\right\}^{k\nu} \times \sum_{\substack{b=0\\ s(b)\geq k}}^{k} \binom{k}{b} (R^\nu)^b, \tag{6.1}$$

where $s(b)$ is the branch level given by

$$s(b) = \frac{\ln(d_{\min}/D) - b\ln R}{\ln\frac{1}{(1+R^n)^{1/n}}}, \tag{6.2}$$

and the maximum branch level $s_{\max}$ is

$$s_{\max} = \frac{\ln(d_{\min}/D)}{\ln\frac{R}{(1+R^n)^{1/n}}}. \tag{6.3}$$

Similarly, the combined shaft area A_{combined}, which is the sum of segment surface areas of all the branch levels, is given by

$$A_{\text{combined}} = C\pi D^{\nu+1} \sum_{k=0}^{s_{\max}} \left\{\frac{1}{(1+R^n)^{1/n}}\right\}^{k(\nu+1)} \times \sum_{\substack{b=0\\ s(b)\geq k}}^{k} \binom{k}{b} (R^{\nu+1})^b. \tag{6.4}$$

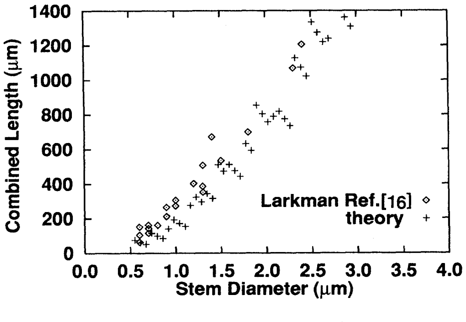

FIG. 4. The relation between stem diameters and combined lengths. The abscissa shows stem diameters D. The ordinate shows the total segment length composed of all the lengths (which is called combined length L_{combined}). Small squares (□) show the experimental data which are the replots of Ref. [16]. The theoretical plots by (6.1) have quantitative agreement with the experimental data.

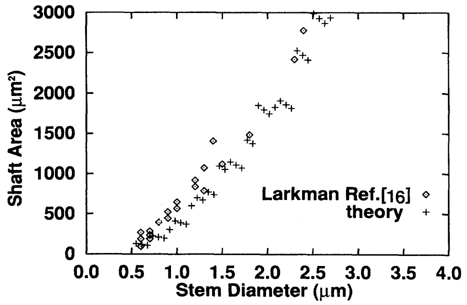

FIG. 5. The relation between stem diameters and shaft areas. The abscissa shows stem diameters D. The ordinate shows the sum of segment surface areas of all the dendritic segments (which is called combined shaft area A_{combined}). Small squares (□) show the experimental data which are the replots of Ref. [16]. The theoretical plots by (6.4) have quantitative agreement with the experimental data.

The formulations are exactly derived from (2.1), (2.3), and (4.2). Substituting the appropriate values for the fundamental parameters, the relations between the global parameters are plotted in Figs. 4–6. The plots have fairly good correspondences with the results on basal dendrites in the experimental paper [16].

VII. SUMMARY AND DISCUSSIONS

In this paper, we derived several formulas, which rule global dendritic morphology.

In the first place, we proposed the concept of effective volume, which can be related to the fundamental parameters.

In the second place, the principle of least effective volume is postulated. This principle led to the analytical derivation of dendritic branch angles.

In the third place, a supremum effective volume per segment is assumed and we derived an inequality between a segment length and a segment diameter. This inequality is consistent with experimental observations.

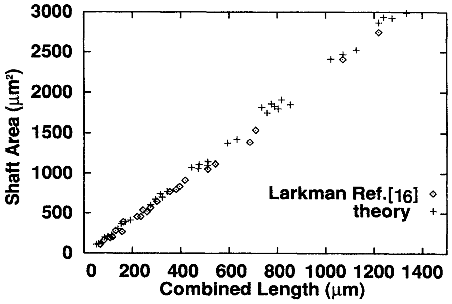

FIG. 6. The relation between combined lengths and shaft areas. The abscissa shows combined length L_{combined}. The ordinate shows combined shaft area A_{combined}. Small squares (□) show the experimental data which are the replots of Ref. [16]. The theoretical plots by (6.1) and (6.4) have quantitative agreement with the experimental data.

In the final stage, mathematical formulations for extra global parameters such as combined length or shaft area, which are usually observed in anatomical experiments, are analytically derived as functions of the above fundamental parameters. The formulas are remarkably consistent with experimental observations [16].

We postulated a few principles which determine the morphology of hundreds of segment lengths and diameters. The constraints for dendritic structures are given by six fundamental parameters. It may be stated that the correspondences between theoretical results from such a few reduced constraints and experimental data are rather surprising. We would thus argue that the fundamental parameters are the most essential elements for dendritic morphology. The correspondences not only guarantee that observed values and computed values from the formulas coincide, but also suggest the existence of a small number of chemical factors responsible for determining the fundamental parameters. It is expected that minimizing effective volume corresponds to maximizing efficiency of molecules organizing fibers and organelles that exclude electrolytes. Since a dendritic core current should flow in electrolytes, we expect that the core resistance of dendritic segments may be expressed by a function of effective dimension ν. This expectation should be confirmed in a future study.

Such chemical mechanisms may explain the mechanisms of dendritic development. A dendritic cross section should have an effective dimension between 1 (tubular segments) and 2 (stuffed segments). Although a cross-sectional area should have a dimension 2 from the conventional point of view, the theoretical condition (5.7) requires a noninteger value. This nontrivial result is consistent with the condition substituting an experimentally determined value.

However, our theory cannot explain axonal morphology satisfactorily. It is considered that the axonal morphology is determined by global (environmental) conditions which result from the principle of wiring economy [5]. Thus we can draw the following picture for neuronal morphology: The axonal morphology is much constrained by environmental conditions of a neuron, whereas the dendritic morphology is much constrained by local (cytochemical) conditions.

The recursive algorithm (2.6a) and (2.6b) derived in this study makes the simulation of actual morphology of neurons possible. The results of computer simulation will be reported elsewhere [18]. In the simulation, whole dendritic trees are graphically created with a few global parameters. We can categorize several kinds of neurons according to the values of our fundamental parameters. Such morphological categorization is also discussed in the paper [18] with computer simulation.

The synaptic distribution based on minimum information transfer principle and self-similar principle [19] may be reproduced by our theory in a different manner. We strongly expect that such a functional principle, evolutionary principle, and our morphological principle must have a close relationship with each other.

Since all of the segment lengths and diameters can be given by this theory from a few parameters, realistic simulations using cable equations will be possible. Finally, we believe that without experimentally observing the detailed dendritic morphology, such a method would have significant advantages for the studies in computational neuroscience. Such a theory based on the variational principle will also be applicable to other biological morphology.

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APPENDIX

Equations (6.1)–(6.4) are derived in the following way. The sum of segment lengths in the same branch level k (the level is the number of branch points on a dendritic path traced from the primary trunk segment to a dendritic position) is given by

$$\sum_{\substack{b=0 \\ s(b)\geq k}}^{k} \binom{k}{b} \langle l \rangle_{d(b)}, \tag{A1}$$

where b is the level of branching into a thinner segment on the path from the primary trunk segment. We express $d(b)$ in the form

$$d(b) = D\xi^k R^b \tag{A2}$$

by using (2.6a) and (2.6b) recursively. $\langle l \rangle_{d(b)}$ shows the mean length of the segments which have the same diameter. The mean segment length is given by

$$\langle l \rangle_{d(b)} = \frac{Cd(b)^{-\nu}}{2}, \tag{A3}$$

averaged by a distribution function of segment lengths,

$$P_{d(b)}(l) = \begin{cases} \frac{1}{Cd(b)^{-\nu}} & \text{if } 0 < l < Cd(b)^{-\nu} \\ 0 & \text{otherwise.} \end{cases} \tag{A4}$$

The distribution function is the simplest interpretation of the inequality (4.2). From (2.5), (A2), and (A3), Eq. (A1) becomes

$$\frac{C}{2} D^{-\nu} (\xi^{-\nu})^k \sum_{\substack{b=0 \\ s(b)\geq k}}^{k} \binom{k}{b} (R^{-\nu})^b \quad (k = 0, ..., s_{\max}). \tag{A5}$$

Summing (A5) over any branch levels ($k = 0, ..., s_{\max}$), we get (6.1).

In a similar way, we can get (6.4) from the sum of the segmental shaft area in the same branch level,

$$\sum_{\substack{b=0 \\ s(b)\geq k}}^{k} \binom{k}{b} \pi d(b) \langle l \rangle_{d(b)}. \tag{A6}$$

(6.2) is obtained from the edge condition of the following inequality:

$$d(b)|_{k=s(b)} = D\xi^{s(b)} R_b \geq d_{\min}. \tag{A7}$$

The maximum branch level $s_{\max}$ satisfies

$$s(s_{\max}) = s_{\max}. \tag{A8}$$

Then we get (6.3) by solving this equation.

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