

Constructal pattern formation in stony corals, bacterial colonies and plant roots under different hydrodynamics conditions

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Abstract

This paper explores a new application of the constructal theory, namely in describing and predicting the formation of dissimilar patterns inside elements of the same species under different hydrodynamics conditions. Our study proposes an explanation for the differences found in morphology of stony corals, bacterial colonies and plant roots. It specially provides an answer to the following question: have their shapes (architecture) been developed by chance, or do they represent the optimum structure serving their ultimate purpose? We show that in order to persist in time, these systems must evolve in such a way that an easy access to nutrients is ensured: their shapes develop in such a way as to minimize the time to reach the nutrient source. Moreover, it is also shown that it is the combination of a dispersive (diffusive) and a convective mechanism that allows for the maximization of nutrient transfer through use of the best of these mechanisms at a specific time.

In the light of this outcome, it is straightforward to conclude why the existence of an optimal architecture makes sense: it is because there is an overriding natural tendency and because the system has the freedom to morph its shape in the search for an optimal attainment of this goal within a set of constraints imposed by the situation.

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1. Introduction

The multitude of patterns and shapes present in nature remains a troublesome question for scientists conducting research in the areas of life sciences. Among all the phenomena of formation and development of complex structures involving living organisms, the emergence of different patterns inside elements of the same specie has attracted the attention of scientists in recent years. In bacterial colonies growing within agar plates a variety of shapes which may be circular or branched, can be often observed depending on their environment (Shapiro, 1986; Fujikawa and Matsushita, 1991; Ben-Jacob et al., 1995; Shapiro and Dworkin, 1997). Colonies that have to cope with hostile environmental conditions have more branched growth forms than colonies of the same species from environments more rich in nutrient (Ben-Jacob et al.,

1995). Additionally, it seems that the hydrodynamic motion of the environment can also affect colony growth and colony morphology (Lega and Passot, 2003).

The coral growth process also generates a wide range of morphologies. These morphologies are species specific, but can also present a high intraspecific variability (Merks et al, 2003), apparently due to variability of environmental parameters (Darke and Barnes, 1993; Anthony, 1999; Merks et al, 2003). In stony corals and other organisms with a relatively weakly developed transport system, the amount of nutrients arriving at a certain site in the tissue, and the local deposition speed of the skeleton material, is limited both by the locally available suspended material and the local amount of contact with the environment (Sebens et al., 1997; Anthony, 1999). It is known that stony corals collected from exposed growth sites, where higher water currents are found, present more spherical and compact shape, while corals of same species from sheltered sites have thin-branched morphologies (Kaandorp and Sloot, 2001; Merks et al, 2003).

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Nomenclature			
D	nutrient diffusion coefficient	t^*	transition time from dispersive to convective driven transport
L^*	transition length from dispersive to convective driven transport	t_{conv}	characteristic time that correspond to nutrient convective driven transport
l_{br}	characteristic length of bacteria population or root tips	t_{disp}	characteristic time that correspond to nutrient dispersive driven transport
l_c	characteristic coral length	t_{IL}	critical time
L_{conv}	characteristic length corresponding to nutrient convective driven transport	u	average fluid velocity
L_{disp}	characteristic length corresponding to nutrient dispersive driven transport	v_c	average growth speed
n	concentration of nutrients	w	width of the branch/needle
r	nutrient particles radius	θ	consumption of nutrient
T	absolute temperature	κ	Boltzmann's constant
t	time	γ	Cunningham slip correction factor
		μ	fluid viscosity
		λ	growth coefficient

Root systems constantly provide plants with water and dissolved minerals for their survival. Consequently, plants produce new roots to maximize nutrient absorption and continue to grow. The growth of root system may show intraspecific variability caused by the soil environment, mainly by the availability and distribution of nutrients (Thaler and Pages, 1998). The root systems seem to be able to respond to localized regions of high nutrient supply by proliferating or elongating root branches into these nutrient-rich patches (Robinson, 1994; Hodge et al., 1999). Plants in soil have more open and more thinly branched roots than specimens of the same species which are growing under hydroponics regime (Howard, 1994). In hydroponics, nutrients are always made readily available to the plant, and roots do not need to seek for nutrients as plants in soil do. It seems that there is a strong influence of availability of nutrient on the overall degree of compactness of the root system.

Much effort has been devoted to the search for the basic principles governing pattern formation in these living organisms. Since the pioneering work of Alan Turing (1952), several attempts have been made to provide patterns in nature with a mathematical and physical description. The development of patterns is very often approached by models of Laplacian growth (Barra et al., 2002), diffusion-limited aggregation (Witten and Sander, 1981) or the closely related Meakin (1986) and Eden models (Dahmen et al., 1998). Very often there are similarities between growth patterns that arise from these model approaches and the patterns developed by corals and bacterial colonies in nature (Lacasta et al., 1999; Kaandorp and Sloot, 2001; Merks et al., 2003; Chavarría-Krauser and Schurr, 2004). A comprehensive review of the literature on this topic can be found in Miguel (2004).

Bejan's constructal theory (Bejan, 1996, 2000; Bejan et al., 2004; Bejan and Lorente, 2005) is a hierarchical way of thinking that accounts for organization, complexity and diversity of man-made systems but also of systems that

occur in nature. The principle that generates geometric structure, called constructal principle, is the search of an objective subject to specified constraints (e.g., availability of nutrient, space, etc.). This principle was enounced by Bejan (1997a) as follows: "For a finite-size system to persist in time (to live), it must evolve in such a way that it provides easier access to the imposed currents that flow through it". This is the principle of configuration generation, or the principle of design. The geometry of the system is free to change while its global performance is being maximized. The morphing of structure is the result of the conflict between the global objective and the global constraints. In other words, the resulting constructal configuration is the means by which the system achieves its global objective under the constraints.

The rapid development of constructal theory has been reviewed in several books (Bejan, 2000, 2004; Bejan et al., 2004; Rosa et al., 2004; Bejan and Lorente, 2005) and articles (Poirier, 2003; Lewins, 2003; Torre, 2004; Bejan, 2005; Reis, 2006). Specifically, biology-inspired studies are also available in the literature. Based on the argument of minimum power expenditure, Bejan (1997b, 2000) addressed some pulsating physiological processes that occur in mammalian, by relating them with body size. Bejan (2001, 2005) gave also theoretical background to the allometric laws such in order to relate body heat loss to body size (Kleiber's law). Respiratory activity has been assessed via the constructal law by Reis et al. (2004). This study describes how the best oxygen access to the alveolar tissues is provided by a flow structure composed of ducts with 23 levels of bifurcation that ends with alveolar sacs from where oxygen diffuses into the tissues. The dimensions of the alveolar sac, the total length of the airways, the total alveolar surface area, and the total resistance to oxygen transport in the respiratory tree were also obtained. Moreover, the study also reports the existence a length defined by the ratio of the square of the first airway diameter to its length that is constant for all individuals of

the same species. More recently, Bejan and Marden (2006) showed that all forms of locomotion (flying, running, swimming) can be described by the constructal theory. Among others, observed allometric laws that relate speed and body mass, frequency (stride, flapping) and body mass were obtained theoretically.

The study described in this paper is motivated by two questions: How the shapes of the biological systems vary as a function of environmental characteristics? Is there an optimal shape for survival in nature? The constructal theory principle invoked in this paper answers this challenge by showing that the architecture of these systems can indeed be deduced from a single principle. The approach used here is completely predictive and simple enough to require little computational time.

2. Growth patterns and environmental conditions

2.1. A growth model for biological systems—theoretical background

In a class of biological systems such as stony corals, the growth process is characterized by a constant rate (Lough and Barnes, 1997; Harriott, 1999)

$$\frac{\partial l_c}{\partial t} = v_c, \quad (1)$$

where l_c is the characteristic coral length, t is the time and v_c is the growth speed (for a specie called *Porites* spp. is about 12 mm/year (Lough and Barnes, 1997)).

By considering the initial length, l_{c0} , the solution for Eq. (1) is

$$l_c = l_{c0} + v_c t. \quad (2)$$

For systems such as bacteria populations or root tips, growth process obeys a different principle. During its initial stages, the growth process can be characterized by the following equation (Murray, 1989; Dahmen et al., 1998; Chavarría-Krauser and Schurr, 2004)

$$\frac{\partial l_{br}}{\partial t} = \lambda l_{br}, \quad (3)$$

where l_{br} is the characteristic length of bacteria population or root tips and λ is the growth coefficient. By considering the initial length, l_{br0} , the solution for Eq. (3) is

$$l_{br} = l_{br0} \exp(\lambda t). \quad (4)$$

Therefore the speed at which the bacteria population or root tips expands is

$$\frac{\partial l_{br}}{\partial t} = \lambda l_{br0} \exp(\lambda t). \quad (5)$$

This means that during initial stages of growth process bacteria and roots increase exponentially in time.

2.2. Nutrient transport flow—theoretical background

Nutrient transport within a fluid is an example of a transport that can be analysed within the framework of a convective–dispersive phenomenon (see for instance Merks et al., 2003; Lega and Passot, 2003; Bejan et al., 2004). The concentration of nutrients is governed by the macroscopic equation:

$$\frac{\partial n}{\partial t} + u \frac{\partial n}{\partial z} = D \frac{\partial^2 n}{\partial z^2} - \frac{\partial \theta}{\partial t}. \quad (6)$$

Here u is the average fluid velocity, D is the nutrient diffusion coefficient and $\partial \theta / \partial t$ is the consumption rate of nutrient (Murray, 1989), given by

$$\frac{\partial \theta}{\partial t} = \frac{\partial \theta}{\partial n} \frac{\partial n}{\partial t}. \quad (7)$$

For sake of simplicity we assume that $\partial \theta / \partial n = k$ is constant. Therefore, Eq. (6) can be rewritten as

$$\frac{\partial n}{\partial t} + \frac{u}{1+k} \frac{\partial n}{\partial z} = \frac{D}{1+k} \frac{\partial^2 n}{\partial z^2}. \quad (8)$$

The time-scales can be obtained by applying scale analysis (Bejan, 2000; Bégué and Lorente, 2006) to the Eq. (8)

$$\frac{\Delta n}{t} \sim \left(\frac{D}{1+k} \right) \frac{\Delta n}{L^2}, \quad \left(\frac{u}{1+k} \right) \frac{\Delta n}{L}. \quad (9)$$

Therefore, the characteristics times corresponding to the dispersive and convective driven transport are

$$t_{disp} \sim \frac{(1+k)L^2}{D}, \quad (10)$$

$$t_{conv} \sim \frac{(1+k)L}{u}, \quad (11)$$

where t_{disp} and t_{conv} are the characteristics times of nutrient dispersive and convective driven transport, respectively.

The transition time from dispersive to convective driven transport is obtained from the interception of Eqs. (10) and (11)

$$t^* = \frac{(1+k)D}{u^2} \quad (12)$$

and the corresponding transition length is

$$L^* = \frac{D}{u}. \quad (13)$$

Here t^* and L^* are the time and length of transition from dispersive to convective transport, respectively. Notice that the transition time increases with increasing values of k , and the transition length is only dependent on nutrient diffusivity and fluid velocity. If $t < t^*$, then dispersion overcomes convection. Conversely, when $t > t^*$ nutrient transport is mainly driven by convection.

3. The emergence of patterns and nutrient transport flow

Regarding the nutrient transport, according to Eqs. (10) and (11) the characteristics lengths corresponding to

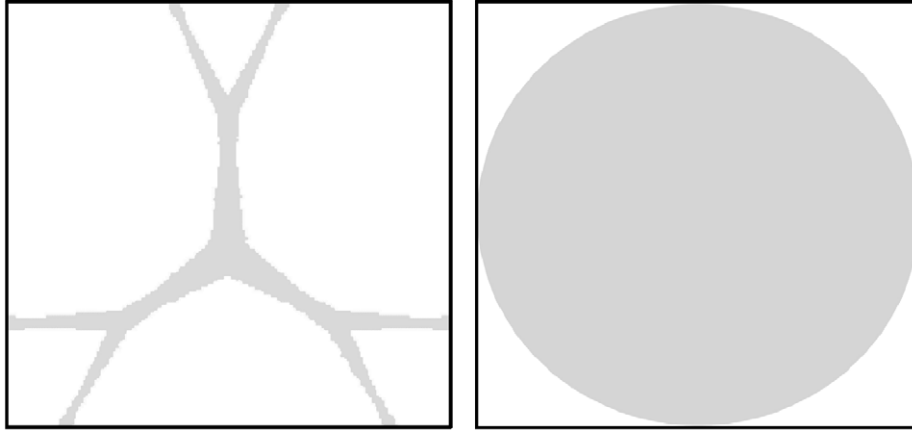


Fig. 1. Branched and circular shape geometries and their ability to fill the space.

dispersive and convective driven transport are

$$L_{disp} \sim \sqrt{\frac{Dt}{1+k}}, \quad (14)$$

$$L_{conv} \sim \frac{ut}{1+k}, \quad (15)$$

where L_{disp} and L_{conv} are the characteristics lengths corresponding to the nutrient dispersive and convective driven transport, respectively.

The propagation in time of the biological system is given by Eqs. (2–4). In general, these systems develop both a branched and a more circular shape. These geometries are quite different regarding their ability to fill the space, and consequently to extract nutrients from the environment in the shortest time. Which configuration will enable the system to fill the space faster? Consider that l is the characteristic length/radius of the biological system and w is the width of the branch/needle (i.e., a very small quantity). The surface area of the biological system is $\sim lw$ for branches/needles and $\sim l^2$ for a circular shape. Undoubtedly, $lw \ll l^2$ which means that the circular shape is the most effective arrangement for filling the space in the shortest time (Fig. 1). This result brings us to the following question: Why should a branched/needle shape geometry occurs, even if it is not the most effective arrangement? This will be broached in the next sections.

3.1. The nutrient transport and the shape of the biological system when $u \ll D$

When $u \ll D$, the time and length of transition for nutrients (Eqs. (12) and (13)) become very large. In this situation, transition from dispersive to convective driven transport is not very likely to occur and the transport of nutrients is linked only to a dispersive phenomenon. This describes systems growing in sheltered places and within delimited environments, such as Petri dishes.

A biological system starts to grow at its birth ($t = 0$). Immediately after $t = 0$, nutrients close to coral, bacterial colonies and plant root surface are quickly depleted. This

consumption of nutrients in the surroundings of the biological system causes a decrease of nutrient concentration ($n < n_{bulk}$) which triggers a wave of nutrients defined by the characteristic length, given by Eq. (14), and the speed of propagation

$$\frac{dL_{disp}}{dt} \sim \frac{1}{2} \sqrt{\frac{D}{(1+k)t}}$$

The initial speed of propagation $dL_{disp}/dt \rightarrow \infty$ is much larger than the growth speed of the biological system ($\partial l_c/\partial t = v_c$; $\partial l_{br}/\partial t = \lambda l_{br0} \exp(\lambda t)$), but decreases as $t^{-1/2}$. Thus, in time the speed of nutrient propagation ends up falling behind the growth speed of the biological system.

The temporal evolution of characteristic lengths l and L is presented in Figs. 2 and 3. These plots show that a critical time, t_{IL} , is reached when the characteristic length of the biological system overtakes the characteristic length corresponding to the dispersive driven transport. The critical time is reached when $l_c = L_{disp}$

$$t_{IL} = \frac{D}{(1+k)v_c^2} \quad (16)$$

and $l_{br} = L_{disp}$

$$\frac{t_{IL}^{1/2}}{\exp(\lambda t_{IL})} = \sqrt{\frac{Dl_{br0}^2}{1+k}} \quad (17)$$

In spite of the circular shape is the most effective arrangement to fill the space (Section 3, Fig. 1), at times slightly larger than t_{IL} , the biological system starts to grow outside of the nutrient diffusion region. To survive, needles/branches are then generated to promote the easiest access possible to the nutrients. This “biological channeling” enables the system to experience again growth inside the nutrient diffusion region from t_{IL} until $2t_{IL}$.

At times slightly greater than $2t_{IL}$, the needle/branch length sticks once again its tip out the nutrient diffusion region. New needles/branches are consequently sent forward in order to experience the growth inside the nutrient diffusion region until a new critical time is

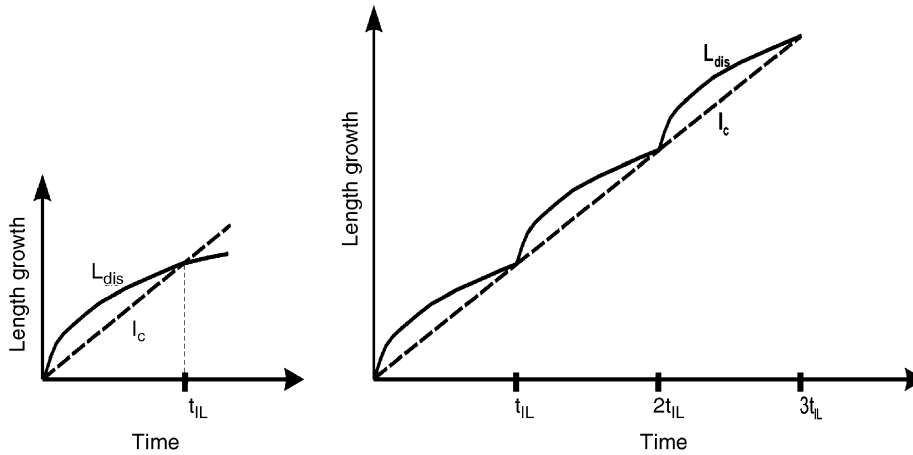


Fig. 2. Simultaneous growth of characteristic lengths l_c and L_{disp} and critical times.

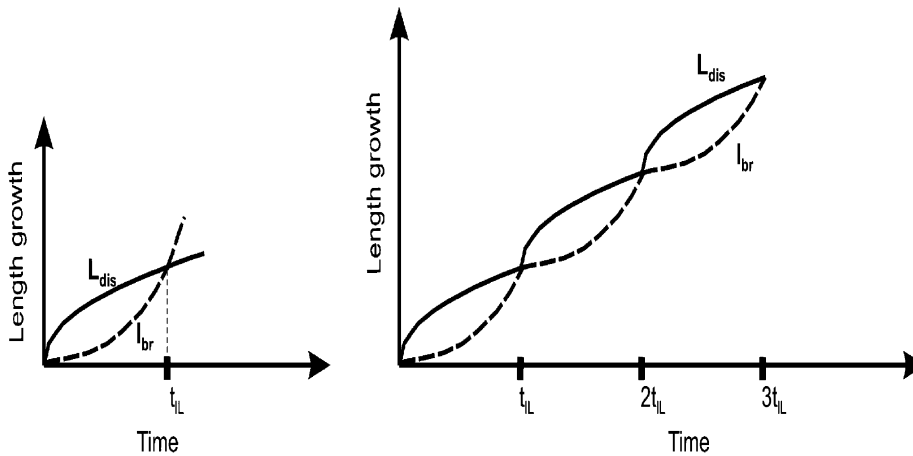


Fig. 3. Simultaneous growth of characteristic lengths l_{br} and L_{disp} and the occurrence of critical times.

reached. That is, each needle/branch generates a new group of needles/branches, and the result of this scenario is a system having a dendritic shape. Thus, in these circumstances this “channeling” becomes clearly the more competitive shape configuration. Notice that this finding is similar to that obtained by Bejan (2000) when describing of the structure of a dendritic crystal formed during rapid solidification.

How does the depletion of nutrient, in an environment with a limited concentration of nutrients, influences the dendritic shape? Figs. 4 and 5 show the characteristic lengths l and L increase in time for different levels of consumption of nutrient k . These plots indicate that an increase of values of k induces the occurrence of an earlier critical time. As soon as the critical time is reached, the system comes out of the nutrient diffusion region and needles/branches are necessarily developed to create paths to reach nutrients. Thus, when k increases the system develops a more branched shape in time.

It is interesting to see whether the size of the nutrient particles and ambient temperature have any effect on the geometrical form of biological systems. According to the Stokes–Einstein relationship, the nutrient diffusion coefficient is (Atkins, 1986)

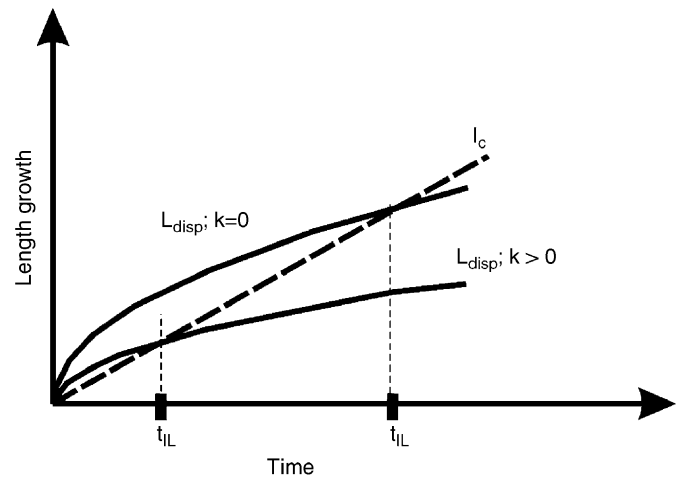


Fig. 4. Effect of consumption of nutrient k on temporal evolution of L_{disp} and on the occurrence of critical time t_{IL} in biological systems described by Eq. (2).

cient is (Atkins, 1986)

$$D = \frac{\gamma \kappa T}{6 \pi \mu r} \tag{18}$$

Here κ is the Boltzmann’s constant, T is the absolute temperature, μ is the fluid viscosity, r is the nutrient particles radius and γ is the Cunningham slip correction factor. Temperature and nutrient size have dissimilar effects on the diffusion coefficient. In the case of nutrient particle size, an increase on its size leads to a decrease in the diffusion coefficient. Consequently, the speed of propagation of the nutrient ($\sim \frac{1}{2}\sqrt{D/(1+k)t}$) becomes smaller (Fig. 6), which, in turn, means that the critical time is reached sooner. As a result, the biological system morphs into a more branched shape with needles/branches being created to provide an easier access to nutrients.

The ambient temperature affects the diffusion coefficient directly, but also through viscosity (liquids become less viscous as temperature increases). Therefore, the diffusion coefficient becomes higher at high ambient temperatures and the critical time is reached later (i.e., the system experiences growth inside the nutrient region during a longer time interval, so that branching takes longer). On

the other hand, a decrease of ambient temperature contributes for an early critical time and a more branched (dendritic) system.

In summary, the biological system, in its struggle for survival, needs to morph towards the configuration that provides an easier access to nutrients. The generation of needles/branches is the response of the system when growth takes out of nutrient rich region. These needles/branches provide then the paths that maximize the access to nutrients (i.e., needles/branches constitute the optimal shape under these circumstances).

3.2. The nutrient transport and the shape of the biological system when $u \gg D$

Let us now consider that $u \gg D$. This describes a multitude of systems growing in open sites where convection currents are important. As the fluid velocity is much larger than the nutrient diffusivity, the transition length (Eq. (13)) and the transition time (Eq. (12)) are very small. The initial dispersive speed

$$\left(\frac{dL_{disp}}{dt} \sim \frac{1}{2} \sqrt{\frac{D}{(1+k)t}} \rightarrow \infty\right)$$

is larger than any constant convective speed

$$\left(\frac{dL_{conv}}{dt} \sim \frac{u}{1+k}\right),$$

but decreases as $t^{-1/2}$. Thus, dispersion is the mainly nutrient driven type of transport at very first growth times ($t < t^*$). For times slightly greater than t^* , convective transport becomes the main mechanism with the L length starting to increase linearly with time (Eq. (15)). This result shows that the system composed of fluid and nutrients also displays the capacity to morph (evolve) in order to work in an optimized way. Once again, optimization can be seen as the trade-off between two competing trends—dispersion and convection. In this way, the transport of nutrients is

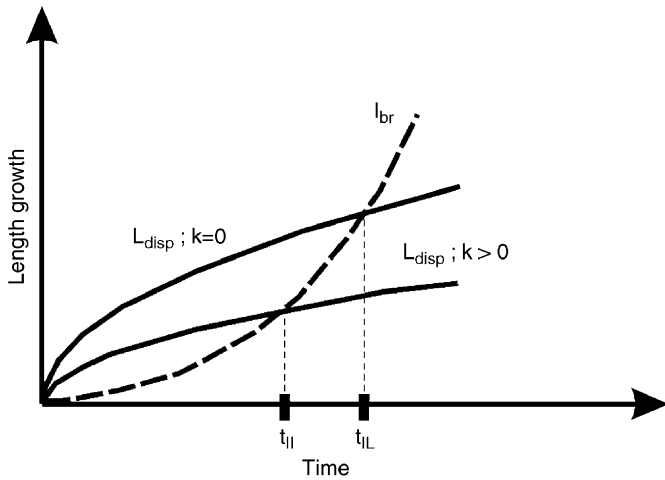


Fig. 5. Effect of consumption of nutrient k on temporal evolution of L_{disp} and on the occurrence of critical time t_{lL} in biological systems described by Eq. (4).

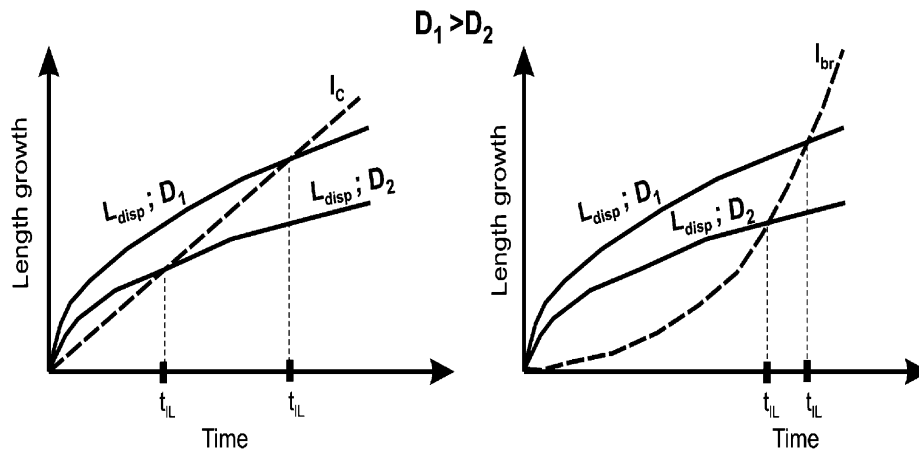


Fig. 6. Nutrient propagation with different sizes (diffusion coefficients), system growth and critical time.

maximized by using the best mechanism of transport at the right time.

What about biological systems growing in such conditions? Generally speaking, the speed of the biological systems growth is very small (e.g., the growing speed of coral specie called *Porites* spp. is around 12mm/year). The fluid velocity is usually much larger than the growth speed of the biological system and its characteristic length never overtakes the characteristic length corresponding to nutrient driven transport (e.g., the critical time is never reached). The biological system therefore grows always inside a region where nutrients are ready available. Consequently, the system is able to develop the most effective arrangement for filling the space in the shortest time—the round and compact shape (Section 3). There is no need to develop needles/branches because it is not necessary to promote an easier access to nutrients. This explains, for instance, why stony corals collected from exposed growth sites to water currents and planter roots from hydroponics develop a more compact shape.

4. Conclusion

In this paper we invoked the constructal law to explain the formation of dissimilar patterns inside of biological systems under different hydrodynamics conditions. The constructal law transposes the common observation that flow systems that survive are those that evolve in time into a shape (architecture) that makes it easier for currents to flow.

We showed that it is the combination of dispersive and convective mechanism that allows the maximization of nutrient transfer through the use of the best of these mechanisms at the right moment. In this way, the currents of nutrients have a maximum access through the volume.

We have also demonstrated that the presence of different hydrodynamics conditions leads to a variety of shapes in biological systems. The shape of the biological system is optimized as to it provide the internal paths such maximizes nutrients access with time (e.g., provide a quick depletion of nutrients).

The key conclusion in this study is that both the architecture of the nutrient transport and the biological systems develop in an optimized way. They do that simply because they have a purpose to fulfill—to provide internal paths such that the nutrient currents and the access to nutrients are maximized (i.e., ensures the best performance). Therefore, we can conclude that performance optimization is not only a target in engineering flow systems (see for example Bejan 2000; Bégué and Lorente 2006), but it is also the ultimate purpose of the emergence of living things.

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