The Formation of A Tree Leaf

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The beauty of tree leaves

Observation: Tree leaves have diverse and elaborate venation patterns and shapes.

Question: Why tree leaves grow in such an amazing way?

What determines it?

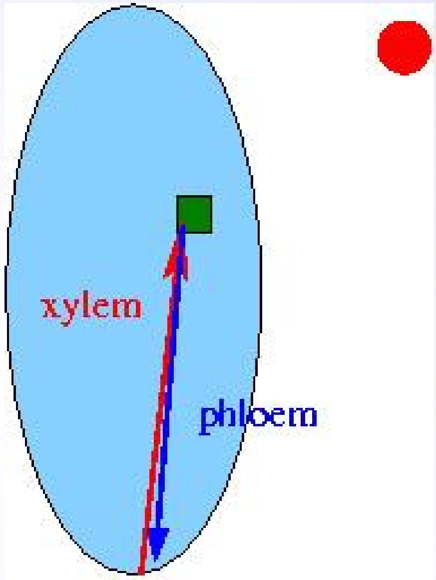
What is the mathematics behind it?

To understand this, we need to understand BASIC functions of leaves.

Basic functions of tree leaves

A leaf will

- transport resources like water and solutes from its root to its tissues via xylem,
- absorb solar energy at its cells through photosynthesis, and then
- transport the chemical products (carbohydrates) synthesized in the leaf back to its root via phloem.



Thus, a leaf tends to

- maximize metabolic capacity by increasing the surface area as large as possible.
  Result: A leaf is a 2 dimensional flat surface.
- Maximize internal efficiency by building an efficient transport system for transporting water and others.

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Claim: From a mathematical viewpoint, the shapes and venation patterns of tree leaves are mainly determined by the second factor.

Tree leaves have different shapes and venation patterns because they have adopted different but similar efficient transport systems.

Questions

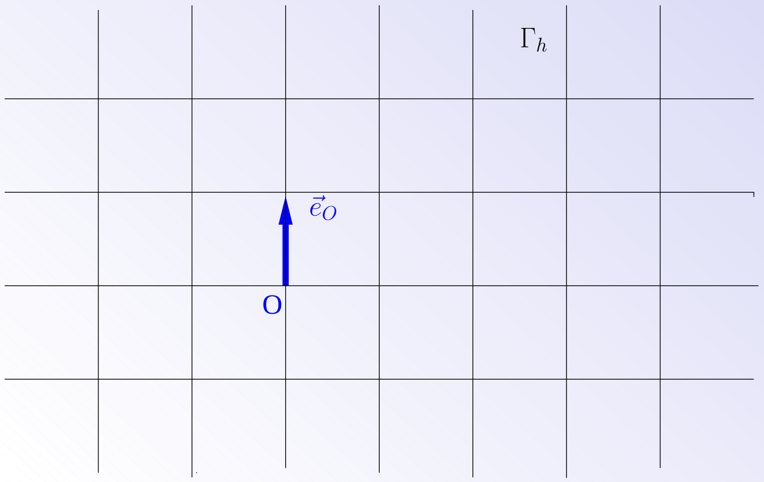
- What is a mathematical leaf?
- What are transport systems on a leaf?
- What is an efficient transport system?– cost functional?
- Given an efficient transport system, how does a leaf grow?
- Is it really the case???

A mathematical model

For simplicity, a leaf may be viewed as a finite union of square cells, centered on a given grid.
Let

$$\Gamma_h = \{(mh, nh) : m, n \in \mathbb{Z}\}$$

be the grid in $\mathbb{R}^2$ of size h.
The origin $O = (0, 0)$ is called the root.
Let $\vec{e}_O = (0, 1)$ be the initial direction of O.
That is, water initially flows out of O in the direction $\vec{e}_O$.

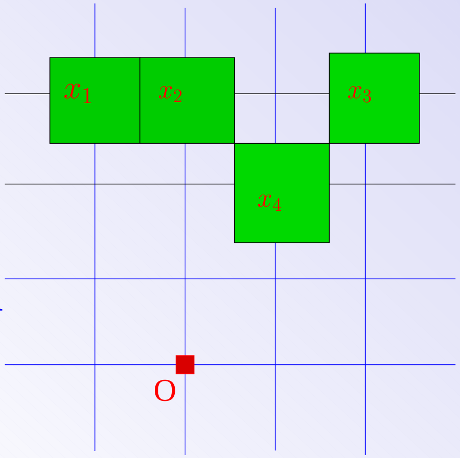


A leaf will be a subset of Γ_h. However, not every subset of Γ_h gives a leaf.
One aim is to understand the speciality of a reasonable tree leaf.

Let

$$\Omega = \{x_1, x_2, \cdots, x_n\} \subset \Gamma_h$$

be any finite subset representing a prospective leaf.



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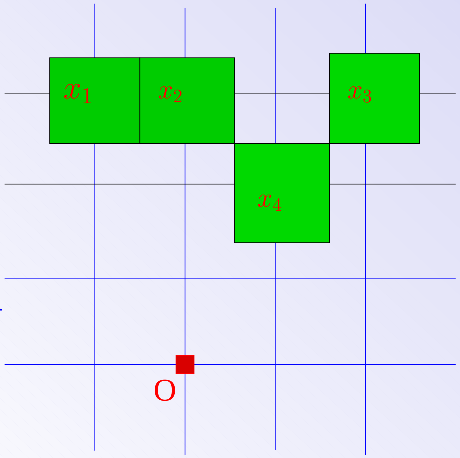

To sustain and reproduce life, water needs to be transported from the root O to cells centered at x_i's.

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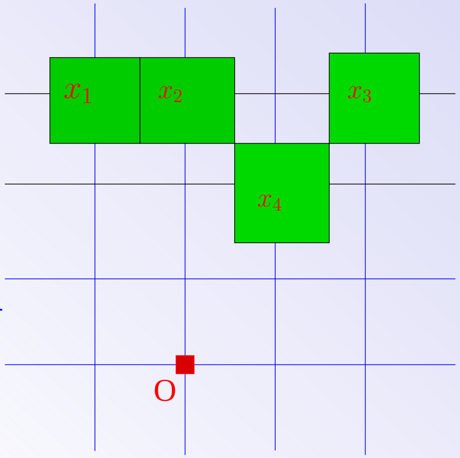
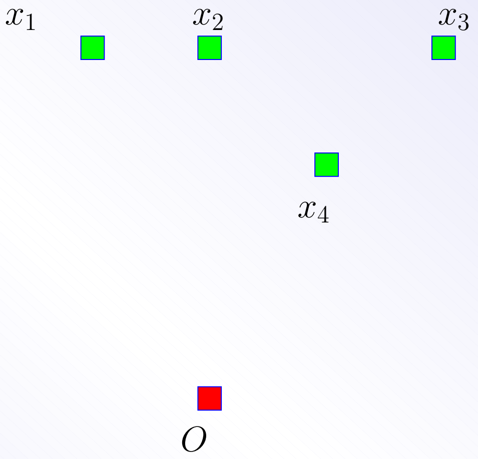


To sustain and reproduce life, water needs to be transported from the root O to cells centered at x_i's.

The amount of water needed at each cell is proportional to its area ($= h^2$). Without losing generality, we may assume it is h^2. So, each $x_i \in \Omega$ corresponds to a particle of mass h^2 located at x_i.



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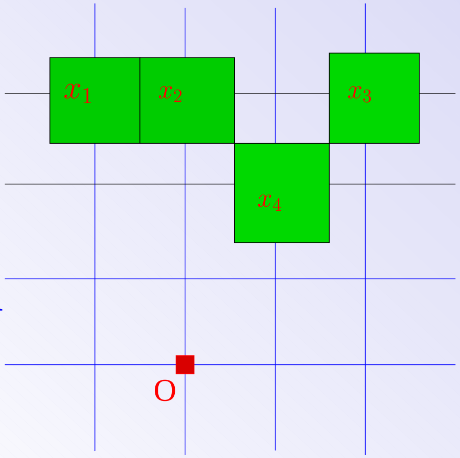

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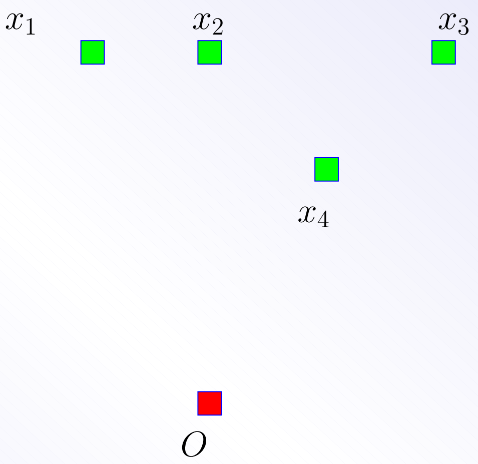
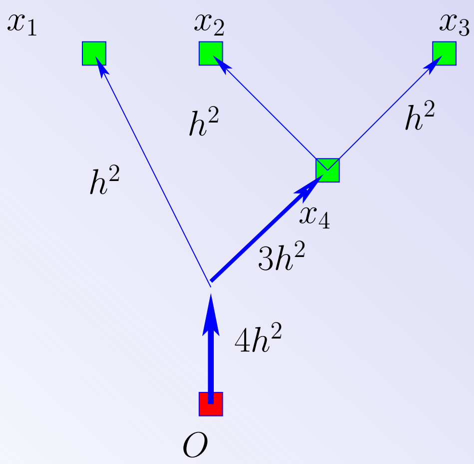


AIM: Transport these particles to O in some cost efficient way.

Given $\Omega \subset \Gamma_h$, a transport system of Ω is a weighted directed graph $G = \{V(G), E(G), w\}$ consists of a finite vertex set $V(G) \subset \Gamma_h$, a set $E(G)$ of directed edges and a weight function



$$w : E(G) \to (0, +\infty)$$

such that

- $\Omega \cup \{O\} \subset V(G)$;
- G is connected and contains no cycles;
- For each vertex $v \in V(G)$, the total mass flows into v equals to the total mass flows out of v. That is,

$$\sum_{\substack{e \in E(G) \\ e^+ = v}} w(e) = \sum_{\substack{e \in E(G) \\ e^- = v}} w(e) + \begin{cases} h^2, & \text{if } v \in \Omega. \\ 0, & \text{otherwise.} \end{cases}$$

Cost functions on transport systems

Note: The collection of all transport systems of Ω may be a pretty large set. So, need some reasonable cost functionals.

First Observation: Ramified transportation

Example: What is the best way to ship two items from nearby cities to the same destination far away.

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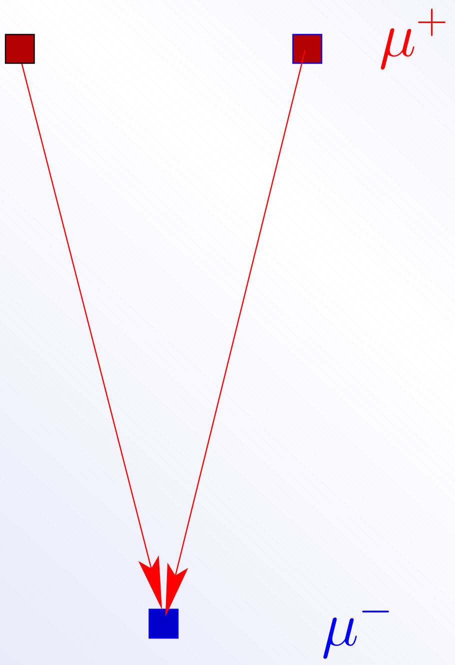

First Attempt: Move them directly to their destination.

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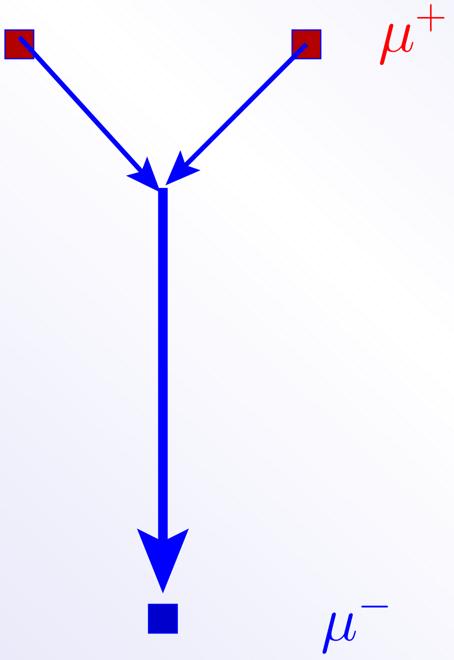
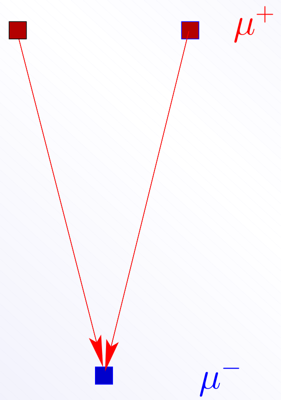
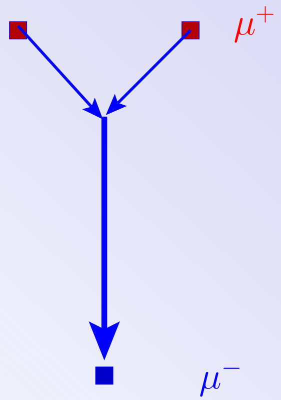


Another way: put them on the same truck and transport together!



A V-shaped path



A Y-shaped path

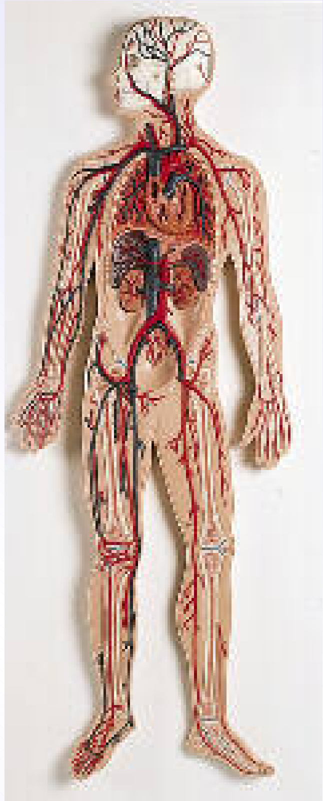
Answer: Transporting two items together might be cheaper than the total cost of transporting them separately. A “Y-shaped” path is preferable to a “V-shaped” path.

In general, a ramified structure might be more efficient than a “linear” structure consisting of straight lines.

Note: Ramified structures are very common in living and non-living systems.

Examples of Ramified Structures

- Trees
- Circulatory systems
- Cardiovascular systems
- Railways, Airlines
- Electric power supply
- River channel networks
- Post office mailing system
- Urban transport network
- Marketing
- Ordinary life
- Communications
- Superconductor



Conclusion: Ramified structures are very common in living and non-living systems. It deserves a more general theoretic treatment.

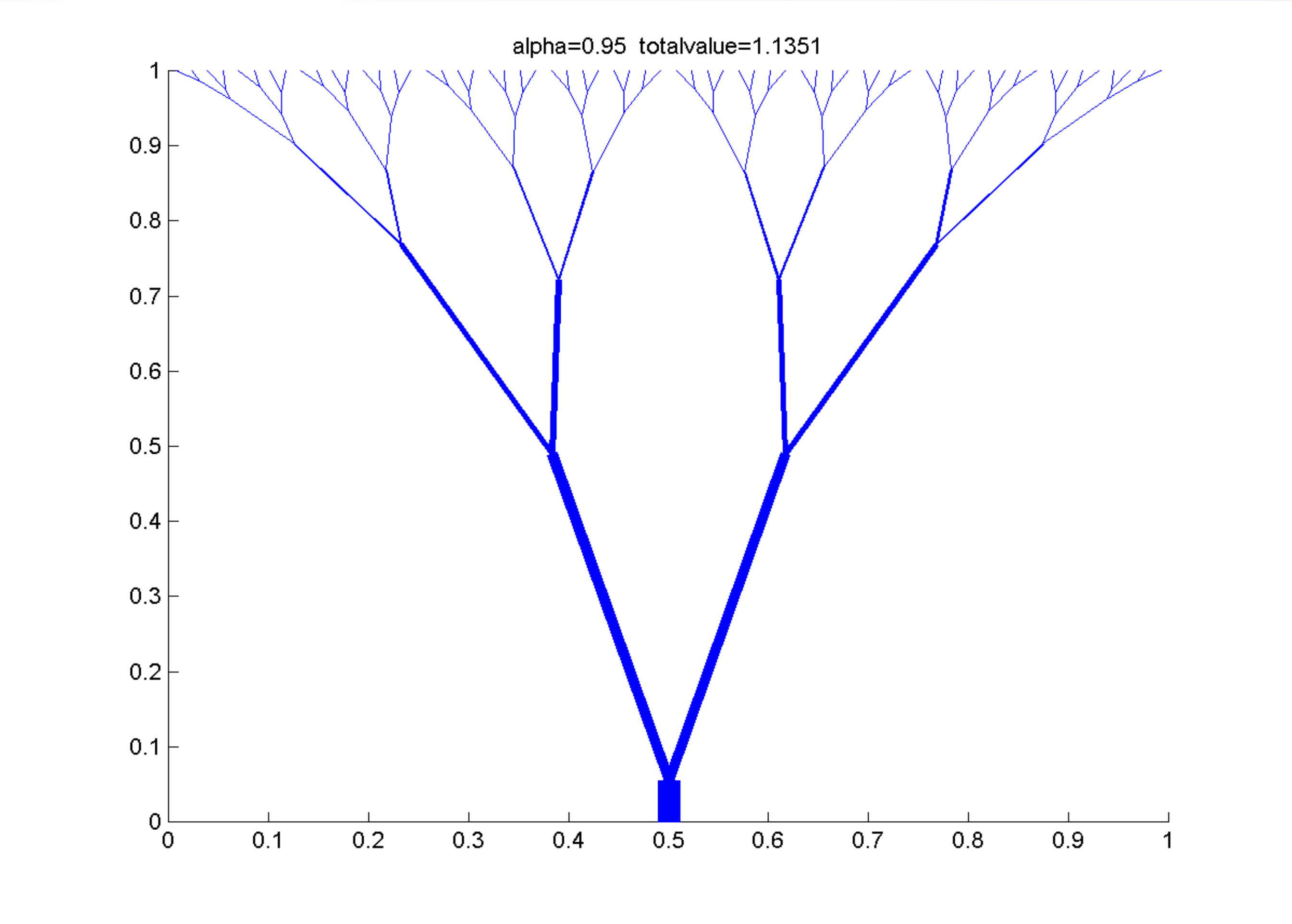
To model such kinds of phenomenon in mass transportation, I introduced the cost functional

$$\mathbf{M}^{\alpha}(G) := \sum_{e \in E(G)} (w(e))^{\alpha} \, length(e)$$

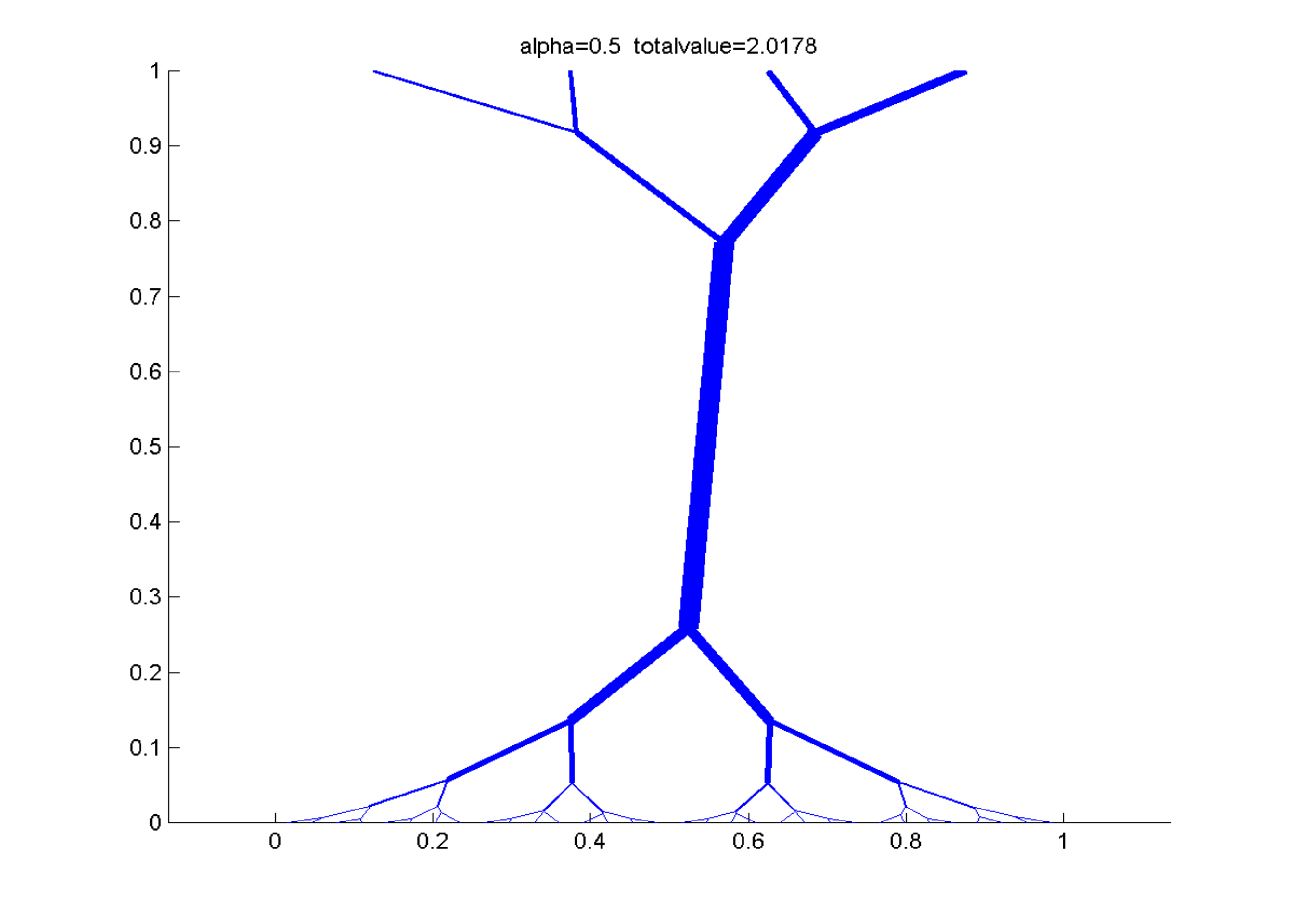
with $0 \leq \alpha < 1$.

In general, one can define "optimal transport paths" between any two probability measures. Optimal transport paths have some nice properties.

From Lebesgue to Dirac



Transporting general measures



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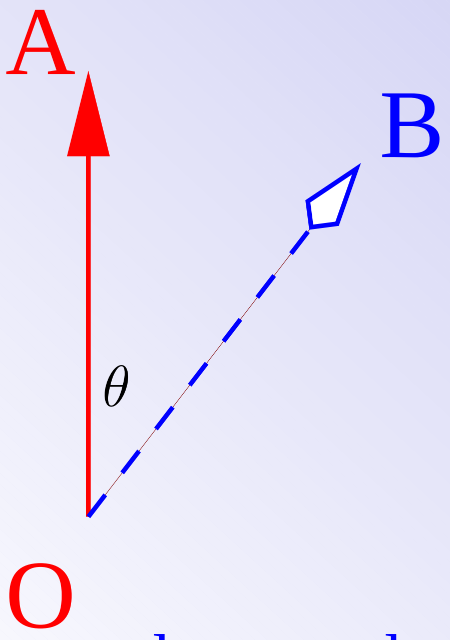
Main Tool: Geometric Measure Theory

The 2nd Observation



When there exists a given transport direction, it is cheaper to transport items in the given direction than transport them in any other direction.

The cost expenses will be an increasing function of the angle rotated. For any $\beta > 0$, we let

$$H_\beta(u, v) = \begin{cases} |u \cdot v|^{-\beta} = \frac{1}{\cos^\beta(\theta)}, & \text{if } u \cdot v > 0 \\ +\infty, & \text{otherwise} \end{cases}$$

for two unit vectors u, v.

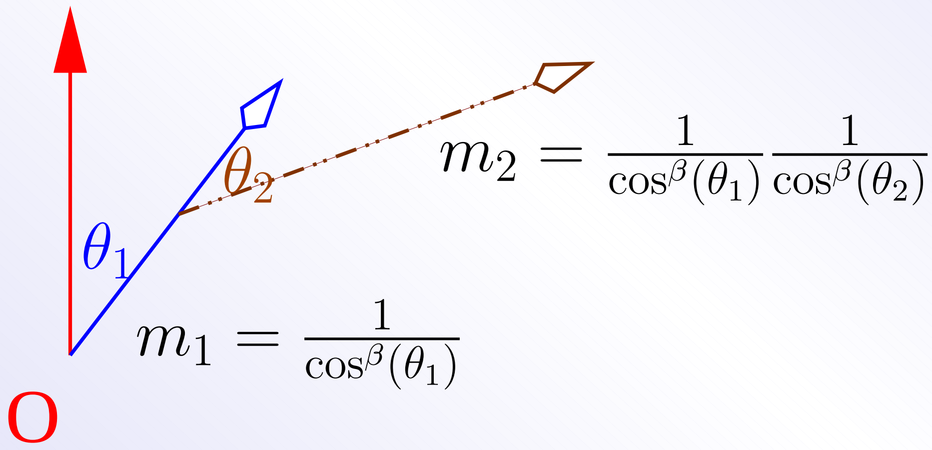
For any given $\beta > 0$, set

$$m_\beta(O) = 1,$$

and each $v \in V(G)$, we set

$$m_\beta(v) = m_\beta(p(v))\, H_\beta\left(\vec{e}_v, \vec{e}_{p(v)}\right),$$

where $p(v)$ is the "parent vertex" of v.



Cost functional on Transport systems

Suppose $\alpha \in [0,1)$ and $\beta > 0$ be two fixed real numbers. For any transport system $G = \{V(G), E(G), w\}$ as above, the cost of G is defined by

$$\mathbf{F}(G) := \sum_{e \in E(G)} m_\beta(e^+)(w(e))^\alpha \, length(e)$$

Optimal transport system

Given $\Omega \subset \Gamma_h$ finite, the set of all possible transport systems of Ω is also finite. Thus, there exists an "optimal $\mathbf{F}$ transport system".

How to get it from a given one?

A local algorithm for optimal transport paths

Given $G = \{V(G), E(G), w\}$, we fix the vertex set $V(G)$, modify the edge set $E(G)$ by finding a ”better parent” for each vertex of G around the vertex as well as its current parent.

Remark: Since the growing of a leave is an evolution process, we want to keep the modified transport system not far away from that of the previous stage. A locally optimized transport system is suitable here.

Growth of tree leaves

A leaf grows by generating new cells nearby its boundary.

Let

$$\mathcal{A}_h := \left\{ \begin{array}{c} (\Omega, G) : \Omega \subset \Gamma_h, G \text{ is an optimal transport} \\ \text{system of } \Omega \text{ under the } \mathbf{F} \text{ cost} \end{array} \right\}.$$

Question: For any $(\Omega, G) \in \mathcal{A}_h$, how to generate new cells around its boundary?

The choice of the positions of those new cells are not random. One would like to distribute them in a way to minimize the total transporting cost.

Since the cost for transporting the same amount of water from the root to every cell outside Ω varies with the position of the cell, the priority of selecting new cells is given to those having smaller transporting costs.

Selection principle: a new cell is generated only if the expense is less than the revenue it produces.

For any $x \in \Gamma_h \backslash \Omega$, and any "boundary point" $b \in B$, we define "the transport cost of x via b" to be

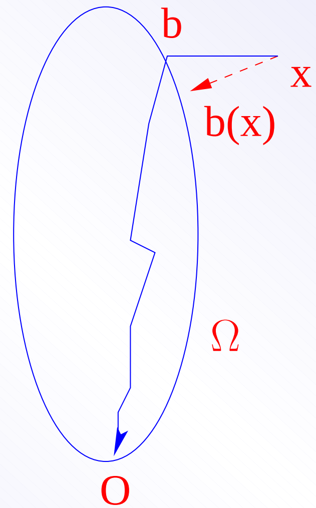
$$C_\Omega(x,b) := h^{2\alpha} |x-b| \, m_\beta(b) \, H_\beta\left(\frac{x-b}{|x-b|}, \vec{e}_b\right) + P_G\left(h^2, b\right),$$

where

$$P_G(y,v) = \sum_{u \in P_v \backslash \{O\}} m_\beta(u) \left[(w(e_u) + y)^\alpha - (w(e_u))^\alpha \right] leng(e_u)$$

measures "the increment of the total cost" if one adds an extra mass of weight y to the point $v \in V(G)$. Then, the expense for generating a new cell at x is mainly given by the transport cost

$$C_\Omega(x) := \min_{b \in B} C_\Omega(x,b) = C_\Omega(x, b(x)).$$



On the other hand, the revenue that a new cell produces is proportional to its area. That is,

$$revenue = \epsilon h^2$$

for some constant ϵ.

Thus, based on the selection principle, for any given $\epsilon > 0$, we set

$$\tilde{\Omega} = \left\{ x \in \Gamma_h \backslash \Omega : C_\Omega(x) \leq \epsilon h^2 \right\} \cup \Omega.$$

Let

$$\tilde{V} = V(G) \cup \tilde{\Omega},$$

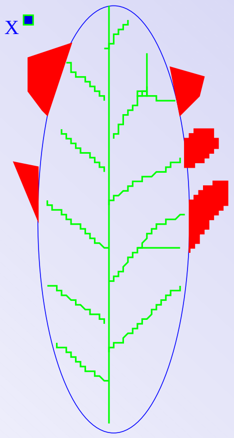
$$\bar{E} = E(G) \cup \left\{ [x, b(x)] : x \in \tilde{\Omega} \backslash \Omega \right\}$$

and $\tilde{G}$ be the optimal transport system of $\tilde{\Omega}$ achieved by modifying $\bar{G} = \{\tilde{V}, \bar{E}, \bar{w}\}$ as before.

Therefore, we get a map $L_{\epsilon,h} : \mathcal{A}_h \to \mathcal{A}_h$ by letting

$$L_{\epsilon,h}(\Omega, G) = \left(\tilde{\Omega}, \tilde{G}\right).$$

Note: $\tilde{G}$ might reduce the transporting costs for cells outside $\tilde{\Omega}$. It is possible that



$$C_{\Omega}(x) > \epsilon h^2$$

but

$$C_{\tilde{\Omega}}(x) \leq \epsilon h^2.$$

By our selection principle, we should also select such cells as new cells. Thus, we need to consider further:

$$L^2_{\epsilon,h}(\Omega, G) = L_{\epsilon,h} \circ L_{\epsilon,h}(\Omega, G),$$

$$L^3_{\epsilon,h}(\Omega, G), \cdots$$

and so on.

Question: will $L^n_{\epsilon,h}(\Omega, G)$ stop growing and stay in a bounded domain when n is large enough?
Answer: Yes, if $\alpha \in (1/2, 1)$.

Proposition 1 *For any $\Omega \subset \Gamma_h$ and any $x \in \Gamma_h \backslash \Omega$, we have*

$$C_\Omega(x) \geq \frac{\alpha(1+\alpha)}{2} \frac{|x|}{||\Omega||^{1-\alpha}} h^{2\alpha}$$

where $||\Omega||$ denotes the number of elements in Ω.
Moreover, if $|x| > \max\{|y| : y \in \Omega\}$, then

$$C_\Omega(x) \geq C_\alpha |x|^{2\alpha-1} h^2$$

where $C_\alpha = \frac{\alpha(1+\alpha)}{2(4\pi)^{1-\alpha}}$.

For $\alpha > 1/2$, let

$$R_\epsilon = \left(\frac{\epsilon}{C_\alpha}\right)^{\frac{1}{2\alpha-1}}$$

and

$$\mathcal{A}_{\epsilon,h} = \left\{(\Omega, G) \in \mathcal{A}_h : \Omega \subset B_{R_\epsilon}(O)\right\}.$$

Proposition 2 *Suppose* $\alpha \in (1/2, 1)$. *Then,* $L_{\epsilon,h}$ *maps* $\mathcal{A}_{\epsilon,h}$ *into itself. That is, for any* $(\Omega, G) \in \mathcal{A}_{\epsilon,h}$, *we have* $\left(\tilde{\Omega}, \tilde{G}\right) := L_{\epsilon,h}(\Omega, G) \in \mathcal{A}_{\epsilon,h}$.

Proof. For any $x \in \Gamma_h$ with $|x| > R_\epsilon$, by the above proposition, we have

$$\begin{aligned} C_\Omega(x) &\geq C_\alpha h^2 |x|^{2\alpha-1} \\ &> C_\alpha h^2 |R_\epsilon|^{2\alpha-1} = \epsilon h^2 \end{aligned}$$

whenever $\alpha > 1/2$. Thus, $x \notin \tilde{\Omega}$ for any $x \notin B_{R_\epsilon}(O)$. Hence

$$\tilde{\Omega} \subset B_{R_\epsilon}(O) \cap \Gamma_h.$$

■

The generation map

Thus, for $\alpha \in (1/2, 1)$ and $(\Omega_0, G_0) \in \mathcal{A}_{\epsilon,h}$, we define

$$(\Omega_n, G_n) = L_{\epsilon,h}(\Omega_{n-1}, G_{n-1}) \in \mathcal{A}_{\epsilon,h}$$

Then,

$$\Omega_0 \subset \Omega_1 \subset \Omega_2 \subset \cdots \subset B_{R_\epsilon}(O) \cap \Gamma_h$$

Therefore,

$$\Omega_N = \Omega_{N+1} = \cdots$$

when N is large enough.

Define $g_{\epsilon,h} : \mathcal{A}_{\epsilon,h} \to \mathcal{A}_{\epsilon,h}$ by sending

$$g_{\epsilon,h}(\Omega_0, G_0) = (\Omega_N, G_N).$$

This map is called the generation map.

Mathematical leaves

The initial stage of any leaf is given by

$$\Omega_0 = \{O\} \text{ and } G_0 = \{\{O\}, \emptyset, -\}. \tag{1}$$

So, Ω_0 consists only the root O, and G_0 contains no edges.
This element (Ω_0, G_0) generates a subset of $\mathcal{A}_h$ by using generation maps. Each element of this subset is called a mathematical leaf . More precisely,

Definition 3 *For any* $\epsilon > 0$ *and* $h > 0$*, a pair* $(\Omega, G) \in \mathcal{A}_{\epsilon,h}$ *is called an* (ϵ, h) *leaf if there exists a list* $\{(\Omega_n, G_n)\}_{n=1}^k$ *of elements in* $\mathcal{A}_h$ *such that for each* $n = 1, 2, \cdots, k$,

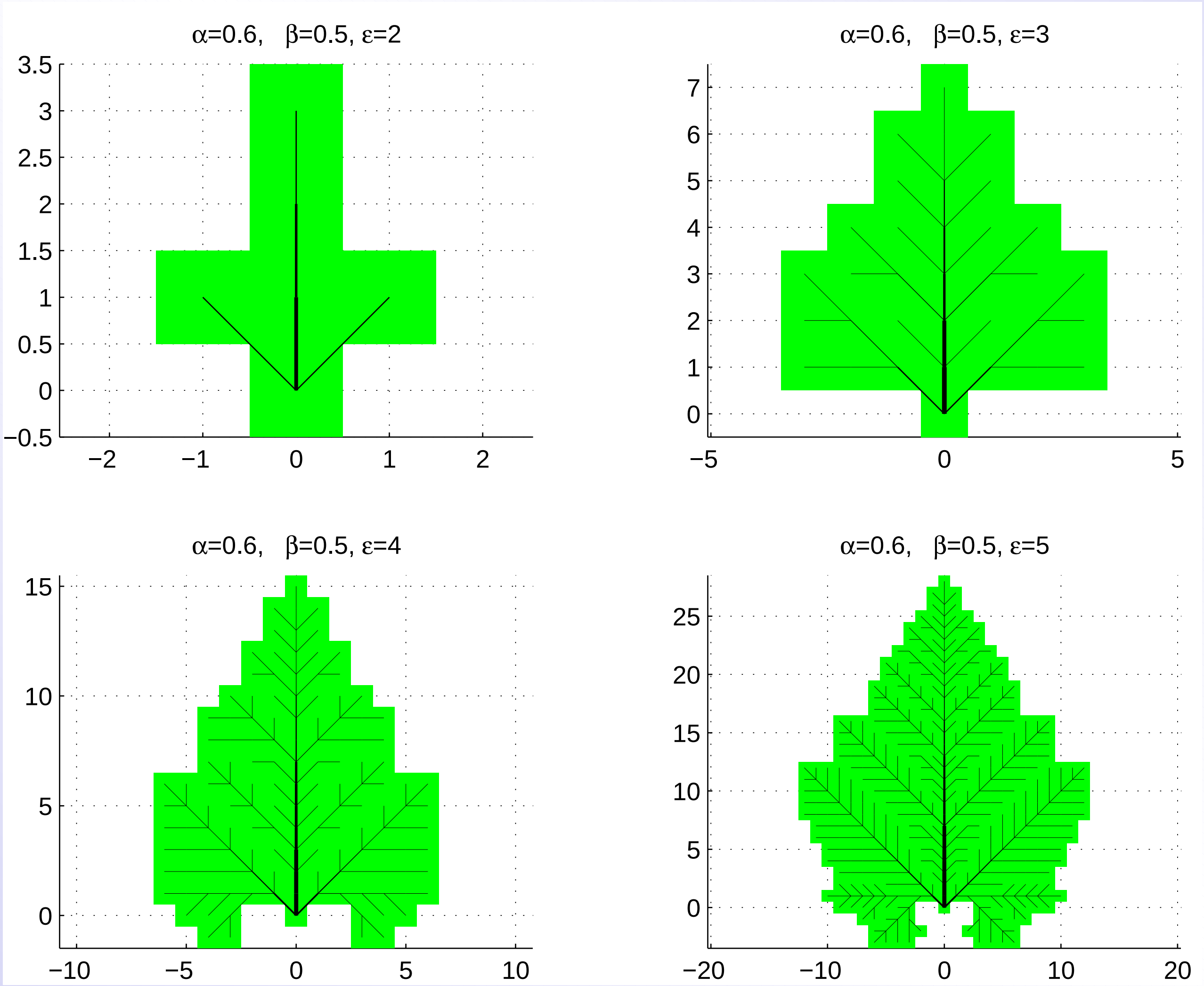
$$(\Omega_n, G_n) = g_{\epsilon_n,h}(\Omega_{n-1}, G_{n-1})$$

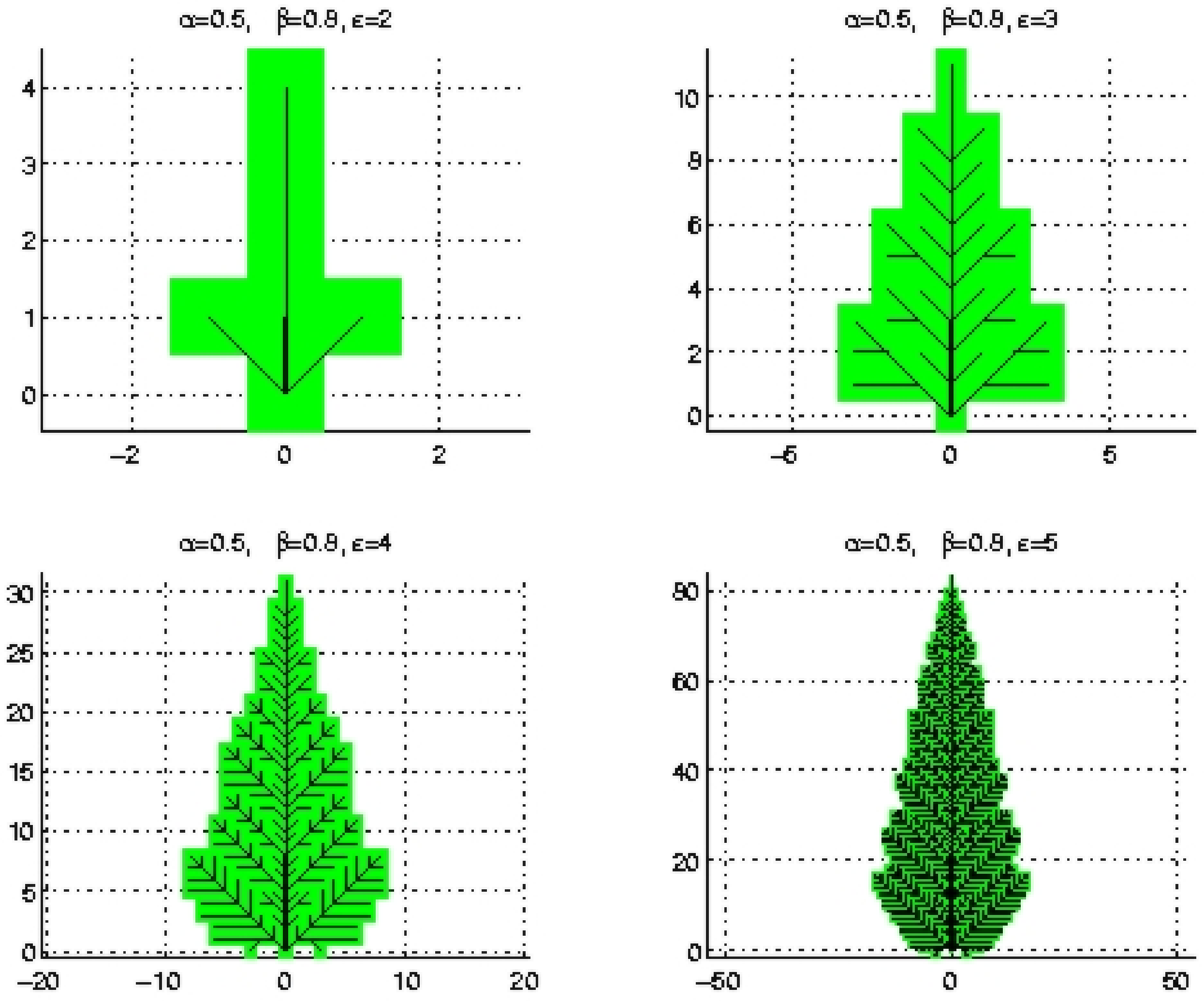
and

$$(\Omega, G) = (\Omega_k, G_k)$$

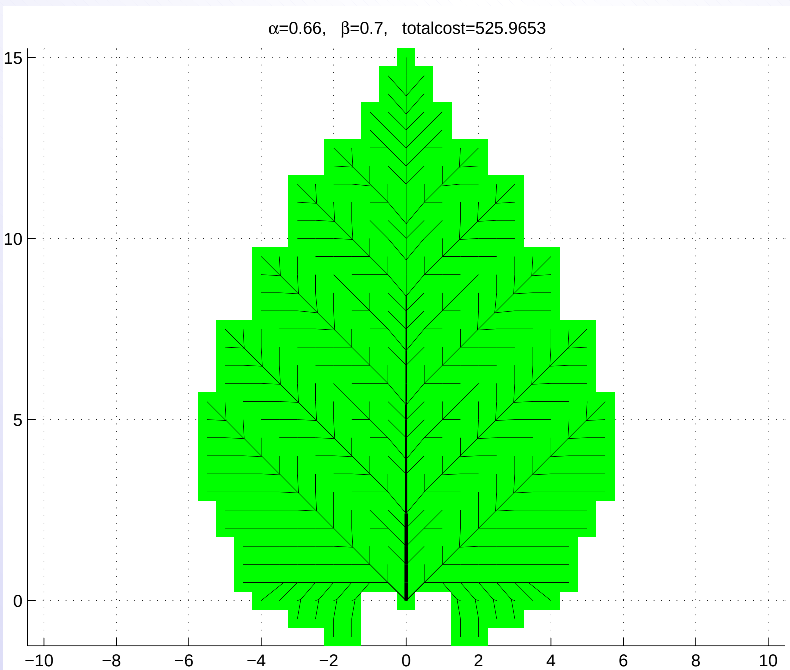
for some positive numbers ϵ_i*'s satisfying*

$$0 < \epsilon_1 < \epsilon_2 < \cdots < \epsilon_k = \epsilon.$$


α=0.6, β=0.5, ε=2
α=0.6, β=0.5, ε=3
α=0.6, β=0.5, ε=4
α=0.6, β=0.5, ε=5



α=0.5, β=0.8, ε=2
α=0.5, β=0.8, ε=3
α=0.5, β=0.8, ε=4
α=0.5, β=0.8, ε=5


α=0.66, β=0.7, totalcost=525.9653
15
10
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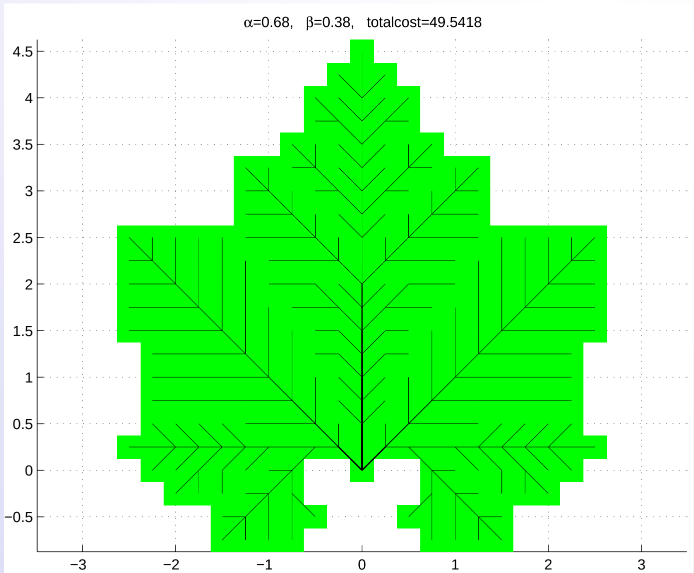
0
−10
−8
−6
−4
−2
0
2
4
6
8
10


α=0.68, β=0.38, totalcost=49.5418
4.5
4
3.5
3
2.5
2
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1
0.5
0
−0.5
−3
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−1
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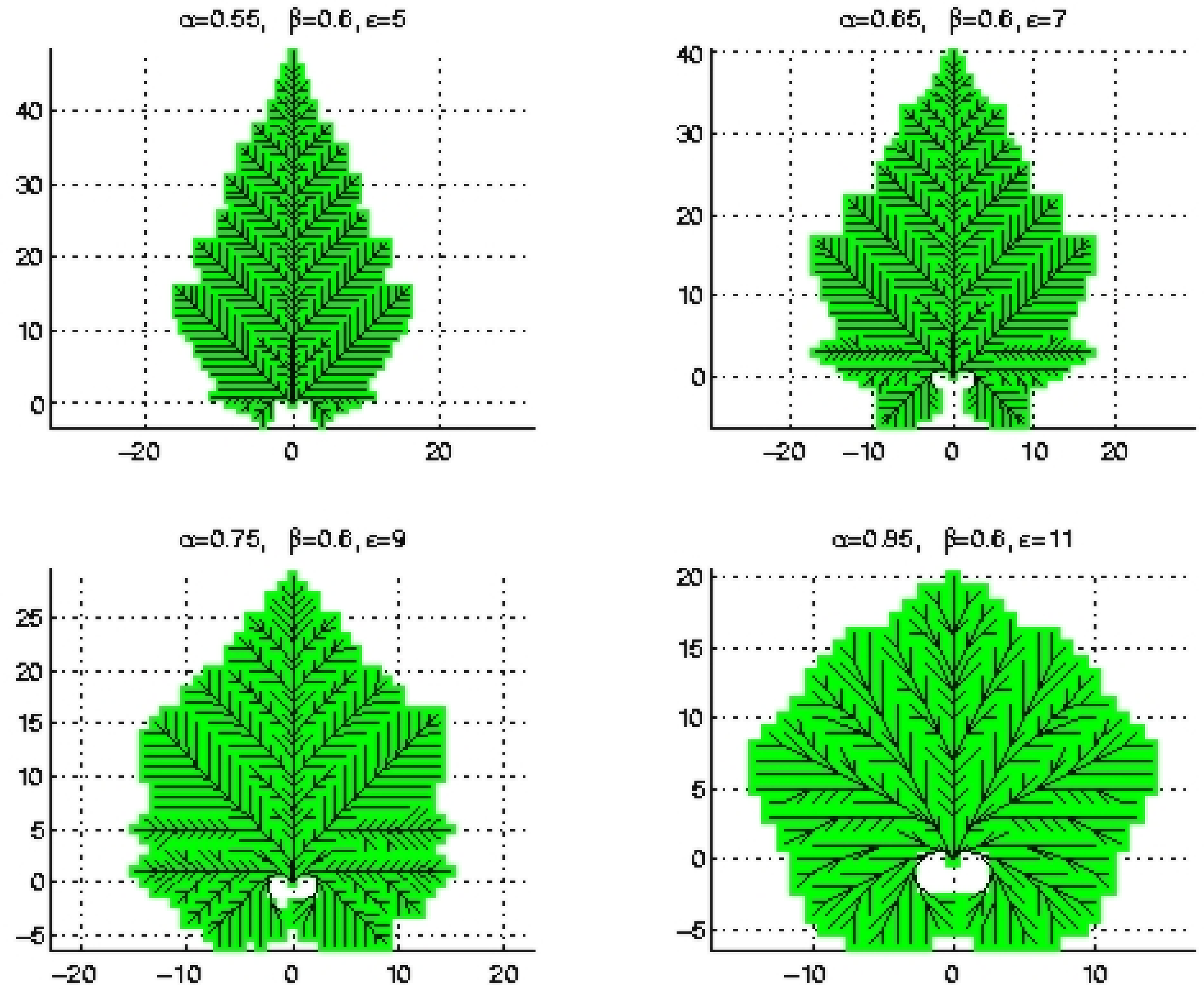
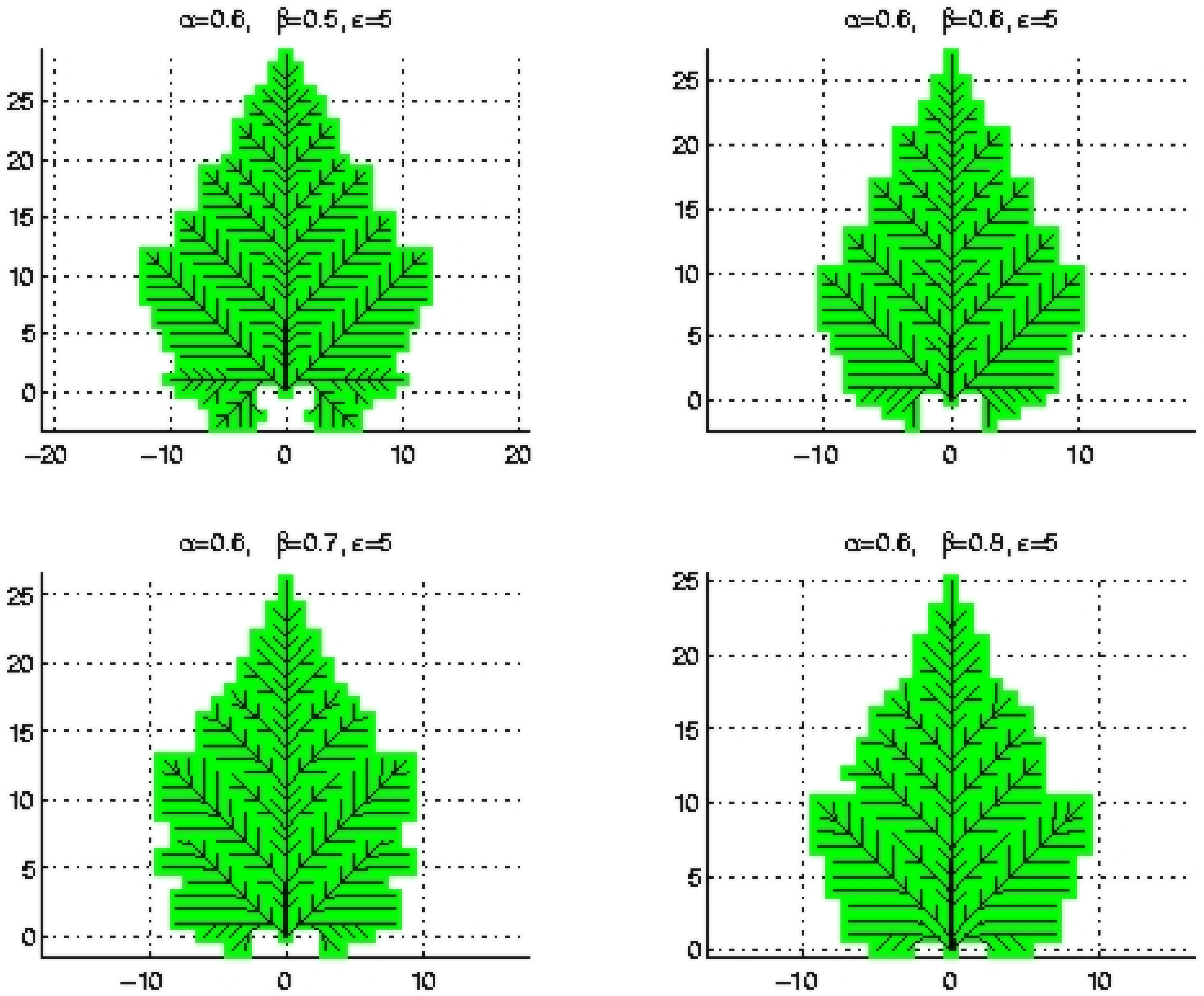
3



α=0.55, β=0.6, ε=5
α=0.65, β=0.6, ε=7
α=0.75, β=0.6, ε=9
α=0.85, β=0.6, ε=11


α=0.6, β=0.5, ε=5
α=0.6, β=0.6, ε=5
α=0.6, β=0.7, ε=5
α=0.6, β=0.8, ε=5
0
5
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15
20
25
−20
−10
0
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20

Let

$$0 < \epsilon_1 \leq \epsilon_2 \leq \cdots \epsilon_k \leq \epsilon_{k+1} \leq \cdots$$

be any nondecreasing sequence $\vec{\epsilon}$. For any k, let

$$(\Omega_k, G_k) = g_{\epsilon_k,h}(\Omega_{k-1}, G_{k-1}).$$

What happens when k approaches ∞?

Case 1. If $\vec{\epsilon}$ has an upper bound ϵ, then since

$$\Omega_k \subset B_{R_\epsilon}(O) \cap \Gamma_h,$$

for any k, we know that (Ω_k, G_k) is fixed when k is large enough. (i.e. stop growing).

Case 2. $\vec{\epsilon}$ is unbounded.

Idea: Each Ω_k corresponds to a Radon measure

$$\mu_\Omega = \Sigma_{x\in\Omega} h^2 \delta_x,$$

and G_k corresponds to a vector measure

$$\Theta_G = \Sigma_{e\in E(G)} w(e) H^1 \lfloor_e \vec{e}.$$

Then, $div\Theta_G = M(\mu)\delta_O - \mu_\Omega$.

Let $(\mu_k, \Theta_k) = (\varphi_{\lambda_k})_\#(\mu_{\Omega_k}, \Theta_{G_k})$ with $\lambda_k = \epsilon_k^{\frac{1}{1-2\alpha}}$. Then

$$sup_k M(\mu_k) + M(\Theta_k) < \infty.$$

Proposition 4

$$\mu_{n_k} \rightarrow \mu$$

and

$$\Theta_{n_k} \rightarrow \Theta$$

weakly on $B_{R_1}(O)$ *such that*

$$div\Theta = M(\mu)\delta_O - \mu.$$

Moreover, $spt(\mu)$ *is connected, compact, and contained in* $B_{R_1}(O)$.

Some historical models

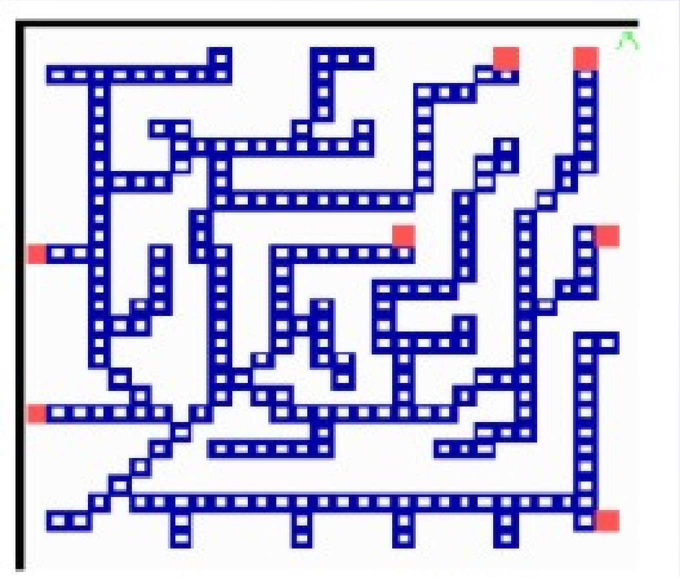
Ramifying structures are common phenomenon in living and non-living systems. There are at least three well known attempts to model the formation of ramified structures.

- Reaction-diffusion model
- L-systems
- Diffusion-limited aggregation

Reaction-diffusion model

Reaction-diffusion model was developed by Turing (1952), and extended by Meinhardt (1976, 1982) and others.

The patterns result from the interaction between two or more morphogens that diffuse in the medium and enter into chemical reactions with each other. These patterns appear as spatially non-uniform stationary solutions of coupled reaction-diffusion equations on a predetermined domain.

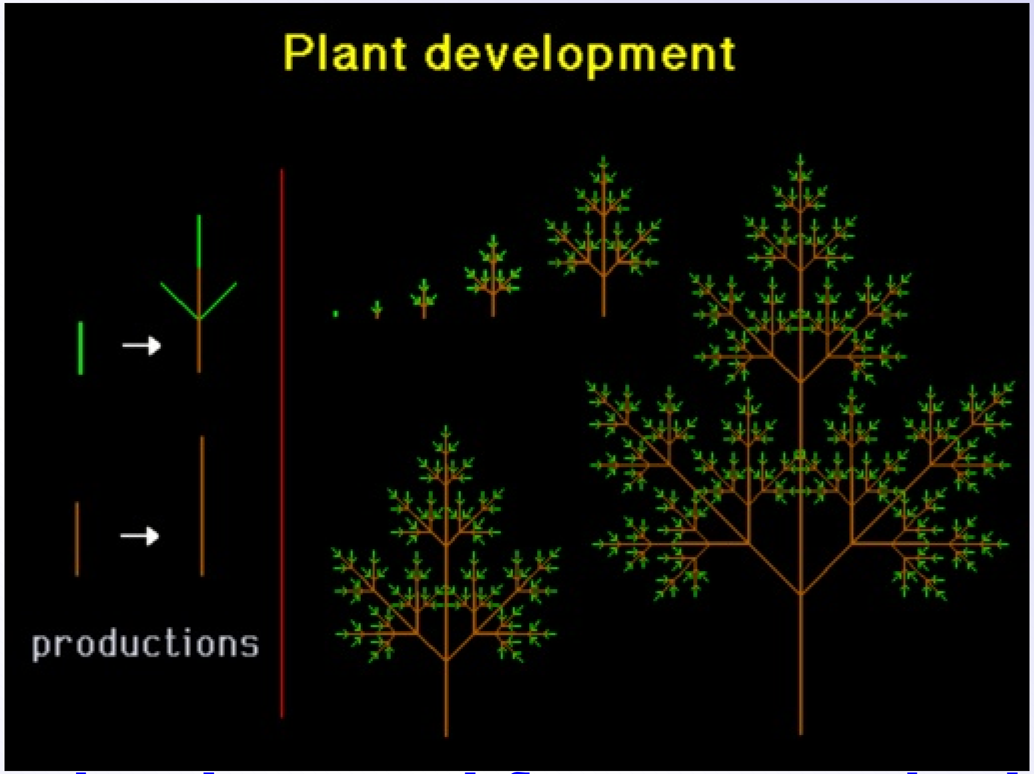


In this model, however, the shape of the leaf (or the domain of the variables) is predetermined.

L-systems

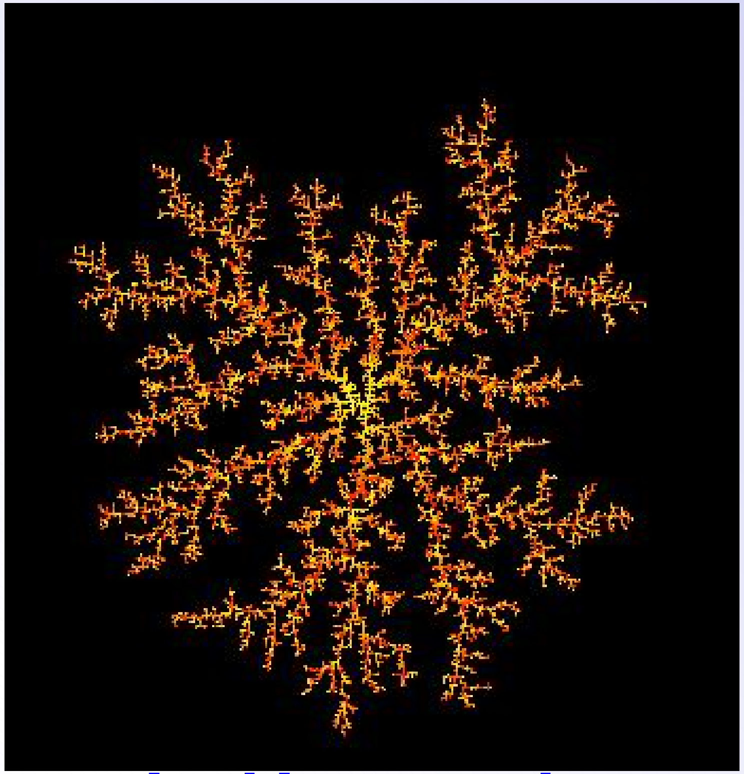
L-systems is introduced by the biologist Aristid Lindenmayer.

With some conditional rule selection, it uses a context-free rewriting expression to model a realistic plant form. The computer graphical output from computer software that uses L-systems resembles some real plants very well.



However, some parts of the plants such as leaves and flowers cannot be derived by a rewriting expression. In some computer softwares, predefined leaf or flower shapes are used to compose a plant. Also, it is not easy to deal with environment change here.

Diffusion-limited aggregation—Random Walk



It captures diffusion of nutrients by simulating random movement of particles in a grid. The growing structure originates with a single cell. Free particles move in the grid, with the displacement direction chosen at random at each simulation step. Once a moving particle touches the structure formed up to the stage, it sticks to it rigidly.

Diffusion-limited aggregation has attracted considerable research interest, due in part to the fractal character of the emerging branching structures. It is a faithful model of many physical phenomena. However, it neglects the active role of the organism using to build its body, and thus its application is also limited.

Our model

There are several advantages of our model over the above well known models.

- The shapes of tree leaves are not predetermined here, which is neither the case in the reaction-diffusion model nor in the L-systems.
- It is also possible to use this model to classify leaves by their corresponding cost functionals.
- Easy to deal with environment change.
- Moreover, unlike the diffusion-limited aggregation model which neglects the active role of the organism, our model is a functional driven aggregation model. The aggregation of cells is driven by the aim of building an efficient transport systems on the leaves to maximize internal efficiency, which is one of the basic functions of the leaves.

Thank You and Enjoy the Nature