On the Optimal Shape of Tree Roots and Branches

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Controlling the growth of living tissues

- Living organisms (plants, animals) come into an immense variety of shapes
- Through evolution, driven by natural selection, one expects that "optimal shapes" should have emerged

From a mathematical point of view, two main issues arise:

1. **Variational problems**
   - Identify functionals that measure the efficiency of various shapes
   - Study the corresponding variational problems
   - Compare these minimizers with the shapes observed in nature
2. **Control problems**
   - Write suitable equations describing growth
   - Understand what kind of feedback controls can achieve these optimal shapes

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Two variational problems

- Optimal shape of tree branches
- Optimal shape of tree roots

  

Can we identify

- payoff functionals
- cost functionals
- constraints

which generate these shapes as optimal solutions?

An optimization problem for tree branches

$$\mathbb{R}^d_+ \;=\; \{(x_1, x_2, \ldots, x_d)\,;\quad x_d \geq 0\}$$

- **Basic object:** $\mu =$ distribution of leaves
  to be optimized among all positive Radon measures supported in $\mathbb{R}^d_+$
- **Payoff functional:** $\mathcal{S}(\mu)$
  measuring the total amount of sunlight collected by the leaves
- **Cost functional:** $\mathcal{I}^\alpha(\mu)$
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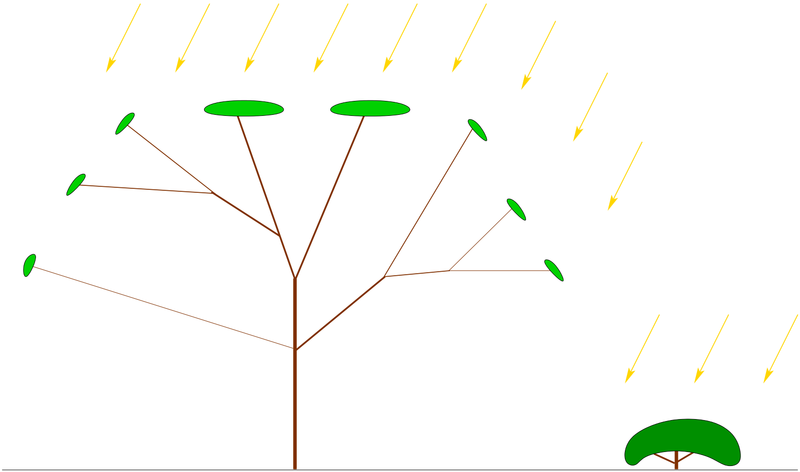
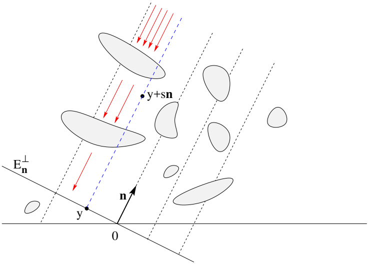


A sunlight functional

Sunlight arrives parallel to the unit vector $\mathbf{n}$ and is partly absorbed by the leaves



$E_{\mathbf{n}}^{\perp}$ = subspace orthogonal to $\mathbf{n}$

Assume: μ has density f w.r.t. Lebesgue measure $\mathcal{L}^d$

For $y \in E_{\mathbf{n}}^{\perp}$, call $Z(s)$ = amount of sunlight that reaches the point $y + s\mathbf{n}$

$$Z'(s) = f(y + s\mathbf{n}) \cdot Z(s), \qquad Z(+\infty) = 1$$

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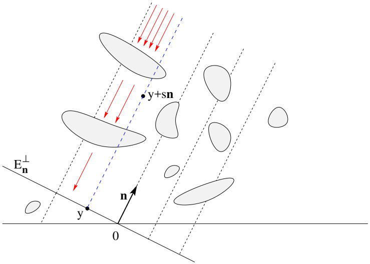

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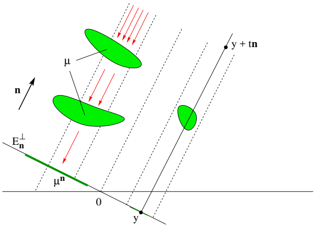
$$Z(s) = \text{sunlight reaching the point } y + s\mathbf{n} \;=\; \exp\left\{ -\int_s^{+\infty} f(y + t\mathbf{n})\, dt \right\}$$

The total amount of light captured by the measure μ is

$$\mathcal{S}^{\mathbf{n}}(\mu) \;=\; \int_{E_{\mathbf{n}}^{\perp}} 1 \;-\; \exp\left\{ -\int_{-\infty}^{+\infty} f(y + t\mathbf{n})\, dt \right\} dy$$

$$= \int_{E_{\mathbf{n}}^{\perp}} \Big(1 - \exp\big\{ -\Phi^{\mathbf{n}}(y) \big\} \Big)\, dy$$

$\Phi^{\mathbf{n}}$ = density of the (absolutely continuous part of the) perpendicular projection $\mu^{\mathbf{n}}$ of μ onto $E_{\mathbf{n}}^{\perp}$



$$\mu^{\mathbf{n}}(A) \;=\; \mu\Big(\big\{ x \in \mathbb{R}^d\,;\;\; \pi_{\mathbf{n}}(x) \in A \big\} \Big)$$

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$$\begin{aligned}\mathcal{S}^{\mathbf{n}}(\mu) &= \int_{E_{\mathbf{n}}^{\perp}} 1 \;-\; \exp\left\{-\int_{-\infty}^{+\infty} f(y+t\mathbf{n})\,dt\right\} dy \\ &= \int_{E_{\mathbf{n}}^{\perp}} \Big(1 - \exp\big\{-\Phi^{\mathbf{n}}(y)\big\}\Big)\, dy\end{aligned}$$

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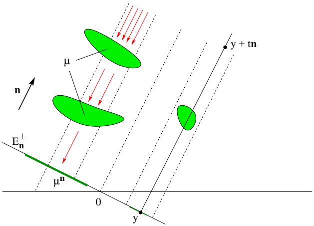
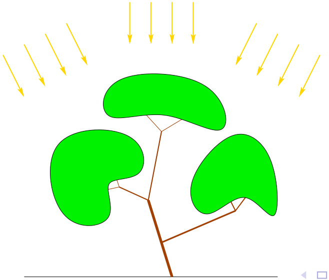


$$\mu^{\mathbf{n}}(A) \;=\; \mu\Big(\big\{x \in \mathbb{R}^d\,;\;\; \pi_{\mathbf{n}}(x) \in A\big\}\Big)$$

1 - Light coming from different directions:

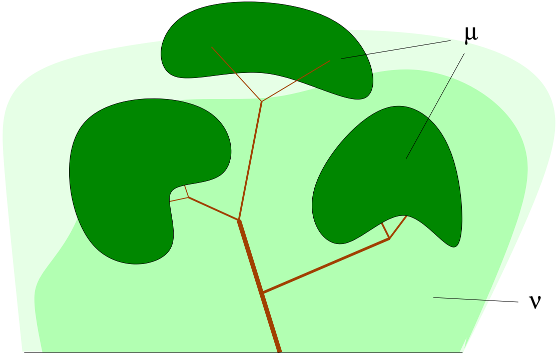
- For $\mathbf{n} \in S^{d-1}$, the unit sphere in $\mathbb{R}^d$, call $\eta(\mathbf{n})$ = amount of light arriving from the direction $\mathbf{n}$
- Assume $\eta \in \mathbf{L}^1(S^{d-1})$. Then the total amount of sunlight captured by the distribution of leaves μ is

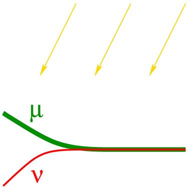
$$\mathcal{S}^{\eta}(\mu) \doteq \int_{S^{d-1}} \mathcal{S}^{\mathbf{n}}(\mu)\, \eta(\mathbf{n})\, d\mathbf{n}$$



Sunlight captured in the presence of additional vegetation:

- A second measure ν on $\mathbb{R}^d_+$ is given, absolutely continuous w.r.t. Lebesgue measure $\mathcal{L}^d$
- A similar formula can be derived, describing the total sunlight $\mathcal{S}^\eta(\mu;\nu)$ captured by the measure μ in the presence of additional vegetation with distribution ν





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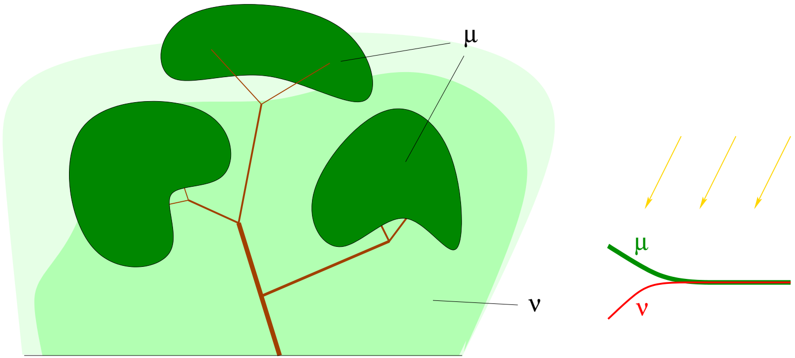

Upper semicontinuity of the sunlight functional

Theorem (A.B., Qing Sun, 2017).

Consider a weakly convergent sequence of positive measures

$$\mu_k \rightharpoonup \mu$$

with uniformly bounded support.

Then, for any positive, integrable function $\eta \in \mathbf{L}^1(S^{d-1})$ and any positive measure ν, absolutely continuous w.r.t. Lebesgue measure on $\mathbb{R}^d$, one has

$$\mathcal{S}^\eta(\mu;\nu) \;\geq\; \limsup_{k\to\infty} \;\mathcal{S}^\eta(\mu_k;\nu)$$

A payoff functional for tree roots

$$\mathbb{R}^d_- = \{(x_1, x_2, \ldots, x_d)\,; \quad x_d \leq 0\}$$

- **Basic object:** $\mu =$ distribution of root hair cells,
  to be optimized among all positive Radon measures supported in $\mathbb{R}^d_-$
- **Payoff functional:** $\mathcal{H}(\mu)$
  measuring the total amount of water + nutrients harvested by the roots
- **Cost functional:** $\mathcal{I}^\alpha(\mu)$
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A harvest functional

- $u(x) =$ density of water + nutrients in the soil
- $\mu =$ distribution of root hair cells

At equilibrium, u satisfies the elliptic equation with measure coefficients

$$\Delta u + f(x, u) - u\mu \ = \ 0$$

[diffusion] + [source] - [absorption] $= 0$

+ suitable boundary conditions

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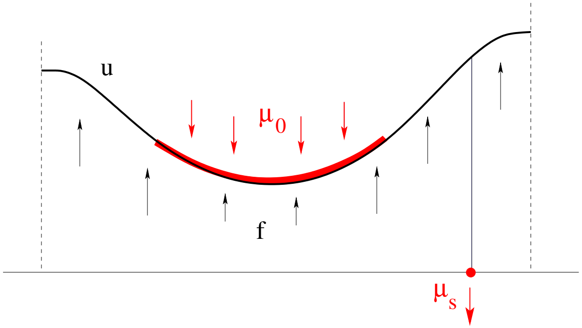
$$\Delta u + f(x,u) - u\mu \;=\; 0, \qquad\qquad \mu = \mu_0 + \mu_s$$



In the measure μ, the part which is singular w.r.t. capacity on $\mathbb{R}^d$ plays no role

L. Boccardo and T. Gallouët, and L. Orsina, Existence and uniqueness of entropy solutions for nonlinear elliptic equations with measure data. *Ann. Institut H. Poincaré Nonlin. Anal.* **13** (1996)

G. Dal Maso, F. Murat, L. Orsina, and A. Prignet, Renormalized solutions of elliptic equations with general measure data *Ann. Scuola Norm. Sup. Pisa Cl. Sci.* **28** (1999)

Given a positive measure μ and a solution of

$$\Delta u + f(x,u) - u\mu \;=\; 0 \qquad\qquad (+\text{boundary conditions})$$

the **total harvest** is

$$\mathcal{H}(u,\mu) \;\doteq\; \int_{\mathbb{R}^d_-} u\,d\mu$$

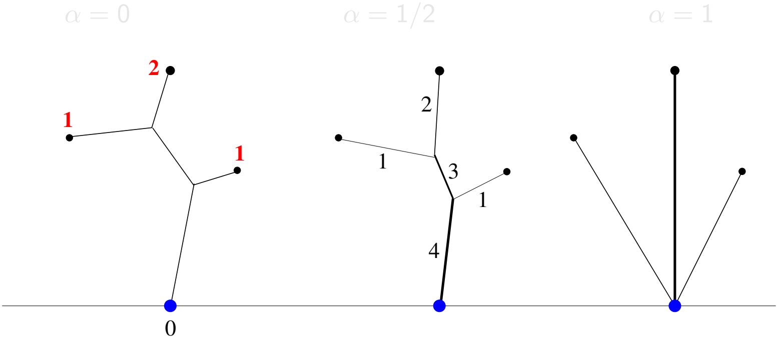
The same equation, for a fish harvesting problem, was studied in

A.B., G.M.Coclite, W.Shen, A multi-dimensional optimal harvesting problem with measure valued solutions, *SIAM J. Control Optim.* **51** (2013), 1186–1202.

Ramified transportation cost

Steiner problem. Given a well located at the origin, and houses locates at $P_1, \ldots, P_N \in \mathbb{R}^d$, construct a pipe of minimum length that connects the well to all houses

Gilbert problem. Assume that the house at P_i requires an amount m_i of water. Given $\alpha \in [0,1]$, assume that **cost of a pipe** $=$ [length] $\times$ [flux]$^\alpha$
Minimize the total cost



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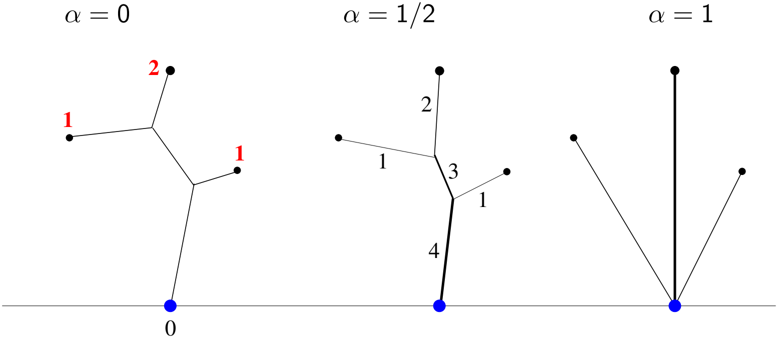


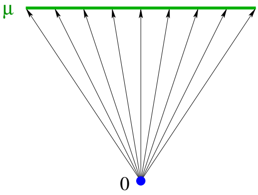
The general irrigation problem

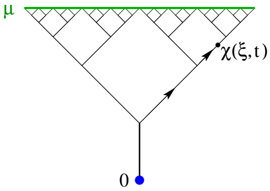
In the Gilbert problem, the **water demand** is an atomic measure, with masses m_i at points P_i, $\quad i = 1, \ldots, N$.

Can this be extended to a general positive, bounded Radon measure μ on $\mathbb{R}^d$?

A Lagrangian approach (F.Maddalena, J.M.Morel, and S.Solimini, 2003)

Define an "irrigation plan", describing the trajectory of each water particle





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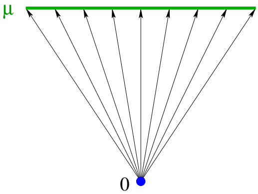

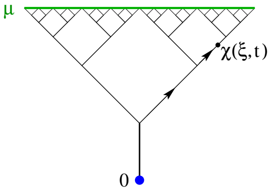

Irrigation plans

Assume: μ is a positive measure on $\mathbb{R}^d$, with total mass $M = \mu(\mathbb{R}^d) < +\infty$

- the Lagrangian variable $\xi \in [0, M]$ labels a **water particle**
- $\chi(\xi, t)$ denotes the position of particle ξ at time t
- particle speed $= |\chi_t(\xi, t)| \equiv 1 \quad$ for all $\; t \in [0, \tau(\xi)]$

For $x \in \mathbb{R}^d$, the total amount of water particles that pass through x is

$$|x|_\chi \doteq \text{meas}\Big(\{\xi \in [0, M]\,; \;\; \chi(\xi, t) = x \;\; \text{for some} \;\; t \geq 0\}\Big)$$

The **cost of the irrigation plan** χ is defined as

$$\mathcal{E}^\alpha(\chi) \doteq \int_0^M \int_0^{\tau(\xi)} \Big[|\chi(\xi, t)|_\chi\Big]^{\alpha-1} dt\, d\xi$$

(coincides with the Gilbert cost, in the discrete case)

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Optimal irrigation plans

Theorem.

Fix $\alpha \in [0, 1]$ and let μ is a positive bounded Radon measure with bounded support, concentrated on a set of dimension $< d_\alpha \doteq \frac{1}{1-\alpha}$. Then

- There exists an optimal irrigation plan χ, with finite minimum cost
- The minimum cost $\mathcal{I}^\alpha(\mu)$ is lower semicontinuous w.r.t. weak convergence of measures:

$$\mu_n \rightharpoonup \mu \qquad \Longrightarrow \qquad \mathcal{I}^\alpha(\mu) \leq \liminf_{n\to\infty} \mathcal{I}^\alpha(\mu_n)$$

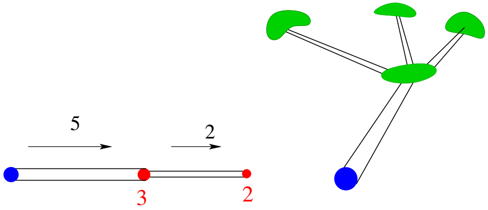
M. Bernot, V. Caselles, and J. M. Morel, *Optimal transportation networks. Models and theory.* Springer Lecture Notes in Mathematics **1955**, Berlin, 2009.

Extension: a cost of ramified transport for branches

- for a pipe laying on the ground (or underground, as a root), one can assume

$$\text{cost} = [\text{length}] \times [\text{flux}]^\alpha$$

- for a branch, even if the flux is constant, the lower portion must be thicker in order to sustain the upper part



- leads to a family of (infinitely many) ODEs with measure-valued right-hand side, one for each branch

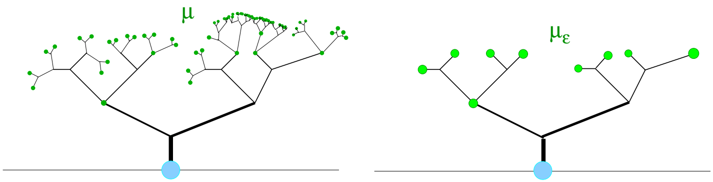
Approximations of the thickness function by stopping times

irrigation plan: $\chi : [0, M] \times \mathbb{R}_+ \mapsto \mathbb{R}^d$

stopping time: $\tau_\varepsilon(\xi) \doteq \max \Big\{ t \geq 0\,; \;\; |\chi(\tau,\xi)|_\chi \geq \varepsilon \Big\}$

Throwing away branches of size $< \varepsilon$, define an approximate irrigation plan

$$\chi_\varepsilon(t,\xi) \doteq \begin{cases} \chi(t,\xi) & \text{if} \quad t < \tau_\varepsilon(\xi) \\ \chi(t, \tau_\varepsilon(\xi)) & \text{if} \quad t \geq \tau_\varepsilon(\xi) \end{cases}$$



- define an ODE on each branch, with data given at the tip
- take the limit as $\varepsilon \to 0$

Optimal shapes of tree branches ?

Optimization problem for tree branches: Given

- constants $\alpha \in [0,1]$ and $M, c > 0$
- a function $\eta \in \mathbf{L}^1(S^{d-1})$, measuring the intensity of sunlight coming from various directions
- an absolutely continuous measure ν on $\mathbb{R}^d_+$, measuring the density of competing vegetation

find a positive measure μ, with $\mu(\mathbb{R}^d_+) = M$, which maximizes the functional

$$\mathcal{S}^\eta(\mu;\nu) - c\mathcal{I}^\alpha(\mu) = [\text{total sunlight}] - c \cdot [\text{irrigation cost}]$$

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An optimization problem for tree roots

Let constants $\alpha \in [0,1]$ and $M, c > 0$ be given, together with a bounded function $f = f(x,u)$.

Optimization problem for tree roots: Find

- a positive measure μ with $\mu(\mathbb{R}^d_-) = M$
- a solution u to the elliptic equation with Neumann boundary conditions

$$\begin{cases} \Delta u + f(x,u) - u\mu = 0, & x \in \mathbb{R}^d_- \\ u_{x_d} = 0, & x_d = 0 \end{cases}$$

which maximize the functional

$$\mathcal{H}(u,\mu) - c\mathcal{I}^\alpha(\mu) = [\text{total harvest}] - c \cdot [\text{irrigation cost}]$$

Existence of optimal solutions, with fixed total mass $\mu(\mathbb{R}^d) = M$

Theorem 1. (A.B., Qing Sun, 2017)

For any $1 - \frac{1}{d-1} < \alpha \leq 1$, the optimization problem for branches has a nontrivial solution μ^*, with bounded support.

Theorem 2. (A.B., Qing Sun, 2017)

For any $1 - \frac{1}{d-2} < \alpha \leq 1$, the optimization problem for roots has a nontrivial solution μ^*, with bounded support.

Main step: prove that there exists a maximizing sequence $(\mu_k)_{k\geq 1}$ where all measures have support contained in a fixed ball $B(0, R)$, then use semicontinuity.

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For any $1 - \frac{1}{d-2} < \alpha \leq 1$, the optimization problem for roots has a nontrivial solution μ^*, with bounded support.

Main step: prove that there exists a maximizing sequence $(\mu_k)_{k\geq 1}$ where all measures have support contained in a fixed ball $B(0, R)$, then use semicontinuity.

Unconstrained problem for branches

$$\text{maximize:} \qquad \mathcal{S}^\eta(\mu) - c\mathcal{I}^\alpha(\mu)$$

among all positive measures on $\mathbb{R}^d_+$ (without the constraint $\mu(\mathbb{R}^d_+) = M$)

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Existence results

Theorem 3. (A.B., M.Palladino, Q.Sun, 2018)

For any $1 - \frac{1}{d-1} < \alpha \leq 1$, the unconstrained optimization problem for branches has a solution μ^*, with bounded support.
Assuming that either (i) $d \geq 3$ or (ii) $d = 2$ and $\frac{\sqrt{5}-1}{2} < \alpha \leq 1$, the optimal measure μ^* has finite total mass.

Theorem 4. (A.B., M.Palladino, Q.Sun, 2018)

For any $1 - \frac{1}{d-2} < \alpha \leq 1$, the unconstrained optimization problem for roots has a solution (u^*, μ^*).
The optimal measure μ^* has bounded support.
In dimension $d \geq 4$, μ^* has finite total mass.

Conjecture.

In dimension $d = 3$ the optimal measure is bounded: $\mu^*(\mathbb{R}^3_+) < +\infty$.
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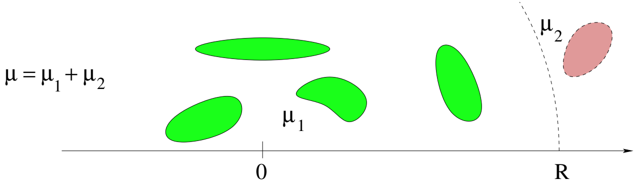
A naive estimate

$$\text{maximize:} \qquad \mathcal{S}^{\mathbf{n}}(\mu) - \mathcal{I}^{\alpha}(\mu)$$



$$\mathcal{S}^{\mathbf{n}}(\mu_1+\mu_2) - \mathcal{S}^{\mathbf{n}}(\mu_1) \;\leq\; \mu_2(\mathbb{R}^d)$$

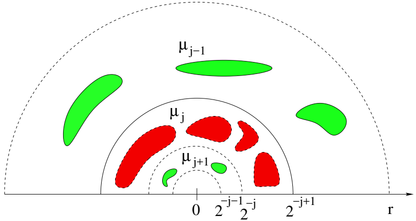
$$\mathcal{I}^{\alpha}(\mu_1+\mu_2) - \mathcal{I}^{\alpha}(\mu_1) \;\geq\; R\cdot\mu_2(\mathbb{R}^d)\cdot\big[\mu(\mathbb{R}^d)\big]^{\alpha-1}$$

$$\alpha < 1 \qquad \Longrightarrow \qquad \text{(economy of scale)}$$

Boundedness of the total mass

$$\mu \;=\; \sum_j \mu_j$$

$$\mu_j \;=\; \chi_{\{2^{-j-1}<|x|\le 2^{-j}\}} \cdot \mu$$



$$\tilde\mu \;\doteq\; \sum_{j\in J} \mu_j\,, \qquad\qquad J \;=\; \left\{ j\,;\;\; \mu_j(\mathbb{R}^d) \;\le\; C_d\, 2^{-j\left(d-1-\frac{1}{\alpha}\right)} \right\}$$

$$\mathcal{S}^{\mathbf{n}}(\tilde\mu) - \mathcal{I}^\alpha(\tilde\mu) \;>\; \mathcal{S}^{\mathbf{n}}(\mu) - \mathcal{I}^\alpha(\mu)$$

$$\tilde\mu(\mathbb{R}^d) \;\le\; \sum_{j\ge j_0} C_d\, 2^{-j\left(d-1-\frac{1}{\alpha}\right)} \;<\; +\infty$$

because $\quad 1-\dfrac{1}{d-1} < \alpha, \quad d\ge 3 \qquad \Longrightarrow \qquad d-1-\dfrac{1}{\alpha} > 0$

Concluding remarks

Underlying question: What has been the primary goal in the evolution of shapes of tree roots and branches?

Conjecture 1: For tree roots: **maximize the amount of water+nutrients** collected from the soil, subject to a transportation cost.

Conjecture 2: For tree branches: **maximize the amount of light** collected by the leaves, subject to the cost of constructing the branch structure.

Answers (provided by the mathematical analysis so far):

1) **True** 2) **False**

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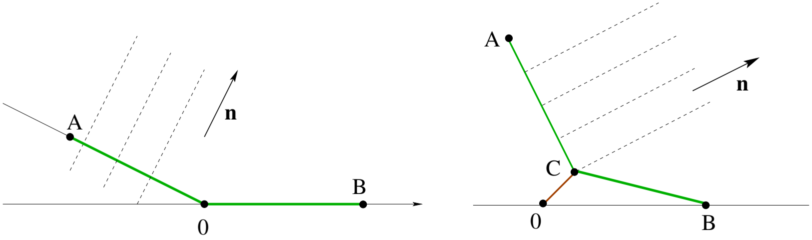
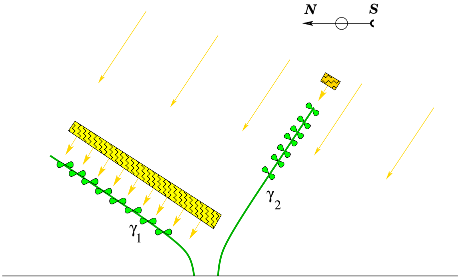
An explicit solution: sunlight coming from a fixed direction

maximize: $\mathcal{S}^{\mathbf{n}}(\mu) - \mathcal{I}^{\alpha}(\mu)$



The optimal positioning of solar panels is very different from the orientation determined by phototropism

What is the advantage of phototropism?



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- Getting a few inches closer cannot make a difference

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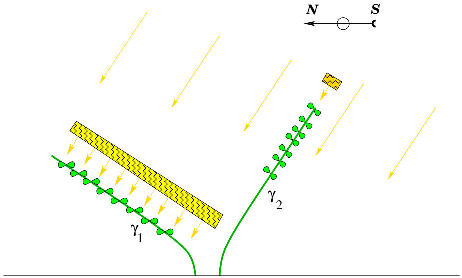

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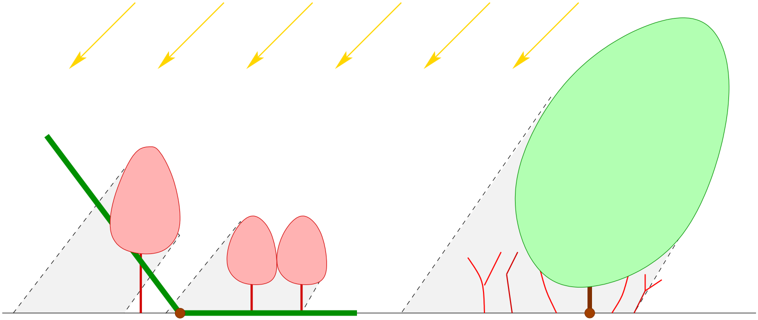
Guess: shapes may result from different selection criteria

- maximizing internal efficiency
- optimizing the response to external competition

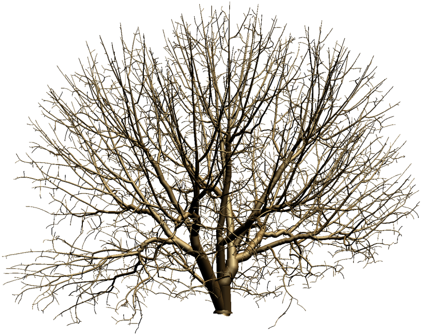


- An extensive literature deals with computer codes which generate tree-like shapes

H.Honda, Description of the form of trees by the parameters of the tree-like body *J.Theoretical Biology* **31** (1971), 331–338.

M.Aono and T.L. Kunii, Botanical tree image generation. *IEEE Computer Graphics and Appl.* **4, 5** (1984), 10–34.

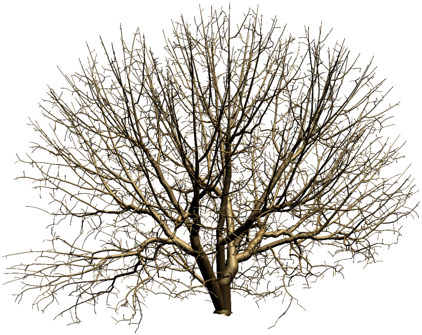
A.Runions, B.Lane, and P.Prusinkiewicz, Modeling Trees with a Space Colonization Algorithm, *Eurographics Workshop on Natural Phenomena*, 2007.



b

- The algorithms producing the most realistic pictures are based on the idea of "conquering space"

- Can one devise a game-theoretical model, showing the advantage of space-conquering strategies?



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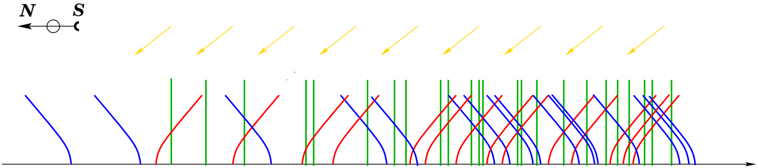
A competition model (unsatisfactory)

Assume: three types of grass grow in a field, all with the same length

- Type 1: bending toward the sun
- Type 2: growing straight upward
- Type 3: bending away from the sun



- If the density is high, the stems growing straight up collect the most light
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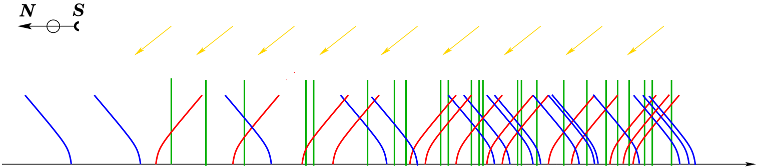

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Concluding remarks

- Apparently, plant shapes have evolved by competing with each other, rather than by optimizing sunlight
- Is there a good mathematical model for such competition?
- In absence of competition, could plants be engineered more efficiently?

apple trees

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Happy Birthday, Giovanni and Franco !!!