On the Optimal Shape of Tree Roots and Branches

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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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Controlling the growth of living tissues

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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

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

- **Basic object:** \( \mu = \) distribution of leaves
to be optimized among all positive Radon measures supported in \( \mathbb{R}^d_+ \)

- **Payoff functional:** \( S(\mu) \)
measuring the total amount of sunlight collected by the leaves

- **Cost functional:** \( I^\alpha(\mu) \)
describing the cost of building a network of branches which sustain the leaves and transport water and nutrients

- **Constraint:** \( \mu(\mathbb{R}^d_+) = \) total amount of leaves
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A sunlight functional

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

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

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

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

$$Z'(s) = f(y + s\mathbf{n}) \cdot Z(s), \quad Z(+\infty) = 1$$
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Sunlight arrives parallel to the unit vector \( \mathbf{n} \) and is partly absorbed by the leaves

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\[ Z(s) = \text{sunlight reaching the point } y + sn = \exp \left\{ - \int_s^{+\infty} f(y + tn) \, dt \right\} \]

The total amount of light captured by the measure \( \mu \) is

\[
S^n(\mu) = \int_{E_n^\perp} 1 - \exp \left\{ - \int_{-\infty}^{+\infty} f(y + tn) \, dt \right\} \, dy \\
= \int_{E_n^\perp} \left( 1 - \exp \{-\Phi^n(y)\} \right) \, dy
\]

\( \Phi^n = \text{density of the (absolutely continuous part of the) perpendicular projection } \mu^n \text{ of } \mu \text{ onto } E_n^\perp \)

\[ \mu^n(A) = \mu \left( \{ x \in \mathbb{R}^d ; \, \pi_n(x) \in A \} \right) \]
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Generalizations

1 - Light coming from different directions:

- For $n \in S^{d-1}$, the unit sphere in $\mathbb{R}^d$, call $\eta(n) =$ amount of light arriving from the direction $n$

- Assume $\eta \in L^1(S^{d-1})$. Then the total amount of sunlight captured by the distribution of leaves $\mu$ is

$$S^\eta(\mu) \doteq \int_{S^{d-1}} S^n(\mu) \eta(n) \, dn$$
Sunlight captured in the presence of additional vegetation:

- A second measure $\nu$ 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 $S^\eta(\mu; \nu)$ captured by the measure $\mu$ in the presence of additional vegetation with distribution $\nu$. 
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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 \( \eta \in L^1(S^{d-1}) \) and any positive measure \( \nu \), absolutely continuous w.r.t. Lebesgue measure on \( \mathbb{R}^d \), one has

\[ S^n(\mu; \nu) \geq \limsup_{k \to \infty} S^n(\mu_k; \nu) \]
A payoff functional for tree roots

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

- **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:** \( \mathcal{I}^\alpha(\mu) \)
  describing the cost of building a network of roots, transporting water and nutrients to the base of the trunk

- **Constraint:** \( \mu(\mathbb{R}^d_-) = \) total amount of root hair cells
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A harvest functional

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

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
A harvest functional

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+ suitable boundary conditions
\[
\Delta u + f(x, u) - u\mu = 0,
\]
\[
\mu = \mu_0 + \mu_s
\]

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


Given a positive measure $\mu$ and a solution of

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

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

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 the **cost of a pipe** = [length] $\times$ [flux]$^\alpha$.

Minimize the total cost

\[
\alpha = 0 \quad \quad \quad \quad \quad \alpha = 1/2 \quad \quad \quad \quad \quad \alpha = 1
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$$\alpha = 0 \quad \alpha = 1/2 \quad \alpha = 1$$
The general irrigation problem

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

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


Define an “irrigation plan”, describing the trajectory of each water particle.

![Diagram of irrigation plans](image-url)
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Define an “irrigation plan”, describing the trajectory of each water particle
Assume: \( \mu \) 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 \textbf{water particle}
- \( \chi(\xi, t) \) denotes the position of particle \( \xi \) at time \( t \)
- particle speed \( = |\chi_t(\xi, t)| \equiv 1 \) for all \( t \in [0, \tau(\xi)] \)

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

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

The cost of the irrigation plan \( \chi \) is defined as

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

(coincides with the Gilbert cost, in the discrete case)
Assume: $\mu$ is a positive measure on $\mathbb{R}^d$, with total mass $M = \mu(\mathbb{R}^d) < +\infty$

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Optimal irrigation plans

Theorem.

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

- There exists an optimal irrigation plan $\chi$, with finite minimum cost.
- The minimum cost $I_\alpha(\mu)$ is lower semicontinuous w.r.t. weak convergence of measures:

$$\mu_n \rightharpoonup \mu \implies I_\alpha(\mu) \leq \liminf_{n \to \infty} I_\alpha(\mu_n)$$

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: \( \tau_\varepsilon(\xi) \doteq \max \left\{ t \geq 0 ; \ |\chi(t, \xi)|_\chi \geq \varepsilon \right\} \)

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

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

- 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 $\eta \in L^1(S^{d-1})$, measuring the intensity of sunlight coming from various directions
  - an absolutely continuous measure $\nu$ on $\mathbb{R}_+^d$, measuring the density of competing vegetation

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

$$S^\eta(\mu; \nu) - cI^\alpha(\mu) = \text{[total sunlight]} - c \cdot \text{[irrigation cost]}$$
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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 $\mu$ with $\mu(\mathbb{R}^d) = M$
- a solution $u$ to the elliptic equation with Neumann boundary conditions

\[
\begin{aligned}
\Delta u + f(x, u) - u\mu &= 0, \quad x \in \mathbb{R}^d \\
u_{\partial} &= 0, \quad x_d = 0
\end{aligned}
\]

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

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Unconstrained optimization problems (optimal tree sizes)

Unconstrained problem for branches

maximize: \( S^n(\mu) - cI^n(\mu) \)

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

Unconstrained problem for roots

maximize: \( H(u, \mu) - cI^n(\mu) \)

among all positive measures \( \mu \) on \( \mathbb{R}^d_- \)
Unconstrained optimization problems (optimal tree sizes)

Unconstrained problem for branches

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\text{maximize: } \quad S^n(\mu) - cI^\alpha(\mu) \\
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Unconstrained problem for roots

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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 $\mu^*$, 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 $\mu^*$ 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 $(u^*, \mu^*)$.

The optimal measure $\mu^*$ has bounded support.

In dimension $d \geq 4$, $\mu^*$ has finite total mass.

**Conjecture.**

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

In dimension $d = 2$ the optimal measure is unbounded: $\mu^*(\mathbb{R}^2_+) = +\infty$. 
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In dimension \( d = 3 \) the optimal measure is bounded: \( \mu^*(\mathbb{R}_+^3) < +\infty \).

In dimension \( d = 2 \) the optimal measure is unbounded: \( \mu^*(\mathbb{R}_+^2) = +\infty \).
A naive estimate

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

$$\mu = \mu_1 + \mu_2$$

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

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

$$\alpha < 1 \implies \text{ (economy of scale)}$$
Boundedness of the total mass

\[ \mu = \sum_j \mu_j \]

\[ \mu_j = \chi\{2^{-j-1} < |x| \leq 2^{-j}\} \cdot \mu \]

\[ \tilde{\mu} = \sum_{j \in J} \mu_j, \quad J = \left\{ j; \mu_j(\mathbb{R}^d) \leq C_d 2^{-j\left(d-1-\frac{1}{\alpha}\right)} \right\} \]

\[ S^n(\tilde{\mu}) - I^\alpha(\tilde{\mu}) > S^n(\mu) - I^\alpha(\mu) \]

\[ \tilde{\mu}(\mathbb{R}^d) \leq \sum_{j \geq j_0} C_d 2^{-j\left(d-1-\frac{1}{\alpha}\right)} < +\infty \]

because \( 1 - \frac{1}{d-1} < \alpha, \quad d \geq 3 \quad \implies \quad d-1-\frac{1}{\alpha} > 0 \)
**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
Concluding remarks

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

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**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
Concluding remarks

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Answers (provided by the mathematical analysis so far):

1) True 2) False
An explicit solution: sunlight coming from a fixed direction

maximize: $S^n(\mu) - I^\alpha(\mu)$

The optimal positioning of solar panels is very different from the orientation determined by phototropism.
What is the advantage of phototropism?

- The distance from the Earth to the Sun is \( \approx 90,000,000 \) miles.
- Getting a few inches closer cannot make a difference.
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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


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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Can one devise a game-theoretical model, showing the advantage of space-conquering strategies?
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
- If the density is low, the stems bending away from the sun collect the most light
A competition model

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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?
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apple trees
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Happy Birthday, Giovanni and Franco !!!