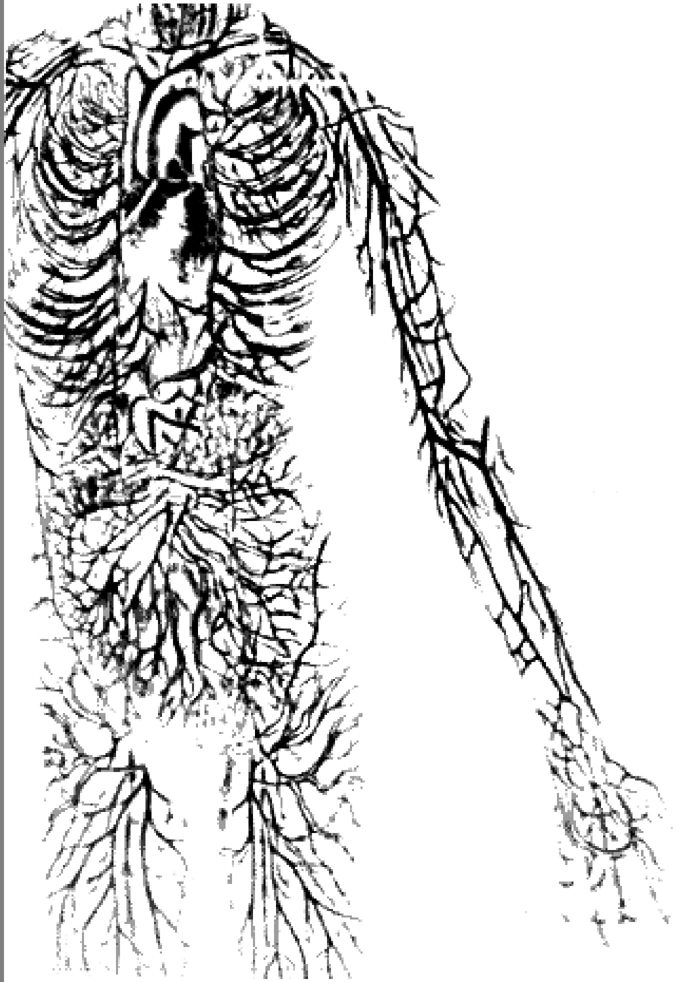

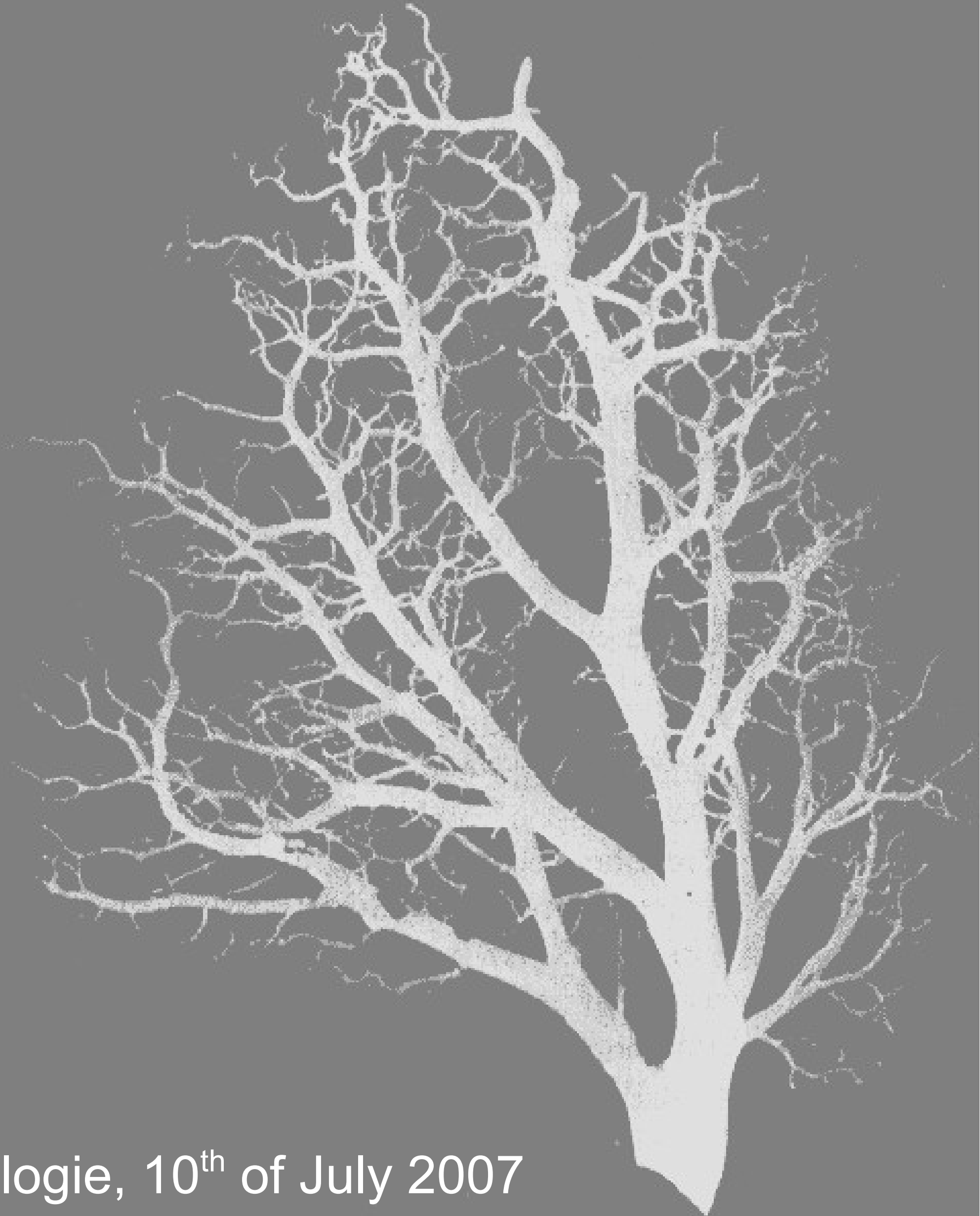

Allometric Scaling Laws In Nature pt. 1

Alexander Bujotzek

Gute Ideen in der theoretischen Systembiologie, 10th of July 2007

Introduction

> *„In jeder reinen Naturlehre ist nur soviel an eigentlicher Wissenschaft enthalten, als Mathematik in ihr angewandt werden kann.“*
>
> Immanuel Kant (1724 – 1804)

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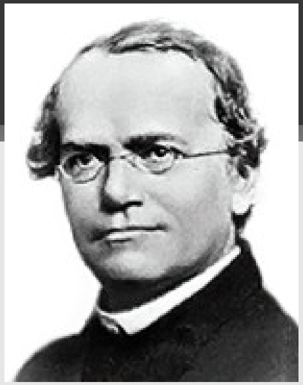
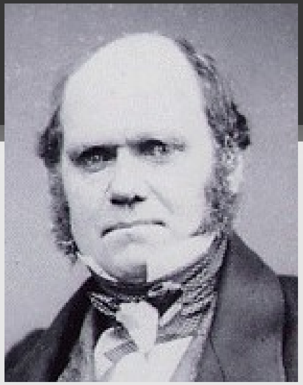
Physics and chemistry (e.g. Newton's laws) have been elevated to true science...

qualitative → quantitative, predictive

But what about biology?

Introduction

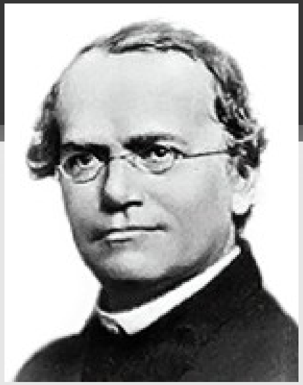

[1]


[2]

We know about general principles:

- Mendelian laws of inheritance
- Natural selection (Darwin's theory of evolution)

Introduction



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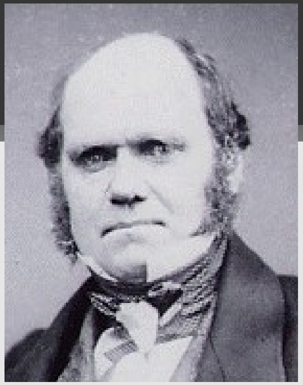


[2]

We know about general principles:

- Mendelian laws of inheritance
- Natural selection (Darwin's theory of evolution)

Does life have more, universal and quantifiable laws?

qualitative → quantitative, predictive

Scaling of biological systems might give us a hint...

Allometric Scaling *Scaling?*

toy ship [3]

real ship [4]

Scaling laws deal with:

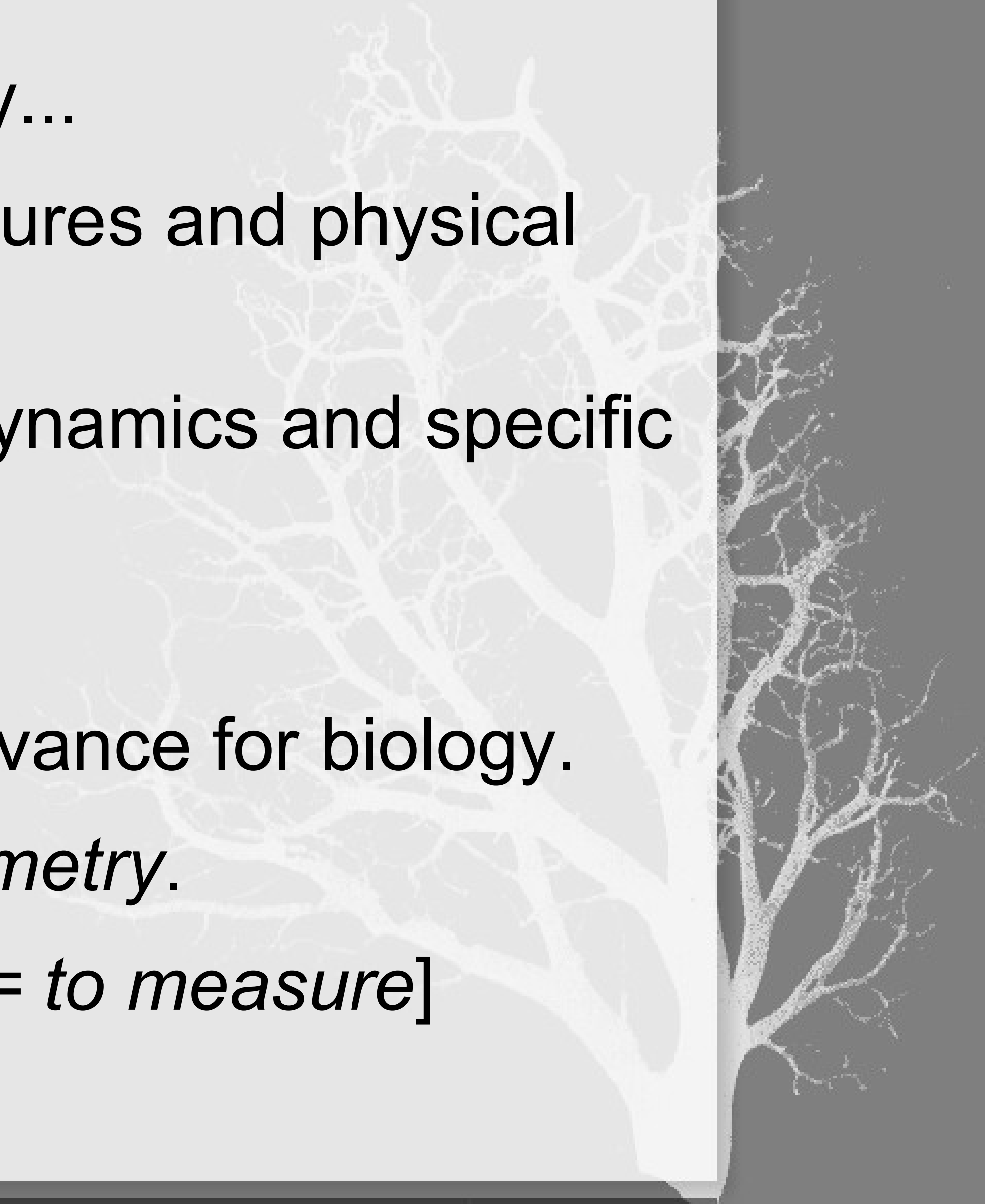
- measuring and comparing *the relation of scale to the parameters of a system*
- revealing *scale invariant quantities*

Allometric Scaling

In physics, scaling laws typically...

- reflect underlying generic features and physical principles
- are independent of detailed dynamics and specific characteristics

Allometric Scaling



In physics, scaling laws typically...

- reflect underlying generic features and physical principles
- are independent of detailed dynamics and specific characteristics

Therefore, scaling also has relevance for biology.

This brought up the idea of *allometry*.

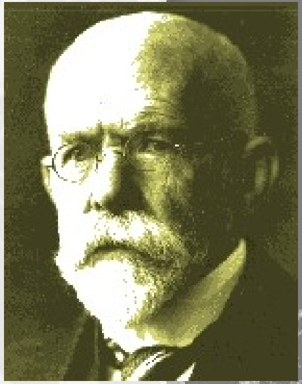
[*greek: allos = different; metrie = to measure*]

Allometric Scaling *Definition*

Allometry deals with

- measuring and comparing *the relation of body size / mass to different biological parameters*

Classical allometric equation (Otto Snell, 1892):



$$Y = Y_0 \cdot M^b ,$$

[5]

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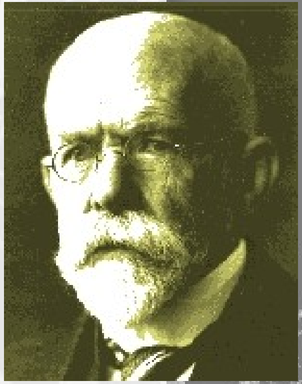

[5]

$$Y = Y_0 \cdot M^b ,$$

dependent parameter Y
integration constant Y_0
body mass M
scaling exponent b
$b > 0$ pos. allometry, $b < 0$ neg. allometry, $b = 1$ isometry

Allometric Scaling *Definition*

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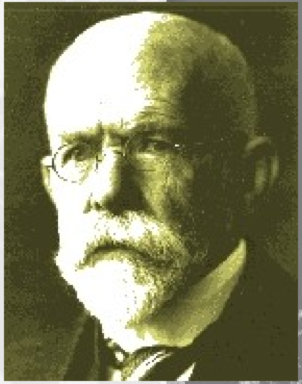


[5]

$$Y = Y_0 \cdot M^b$$

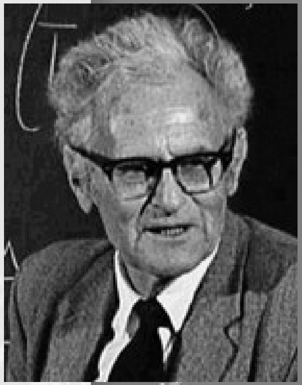
$$\Downarrow$$

$$\log Y = b \log M + \log Y_0$$

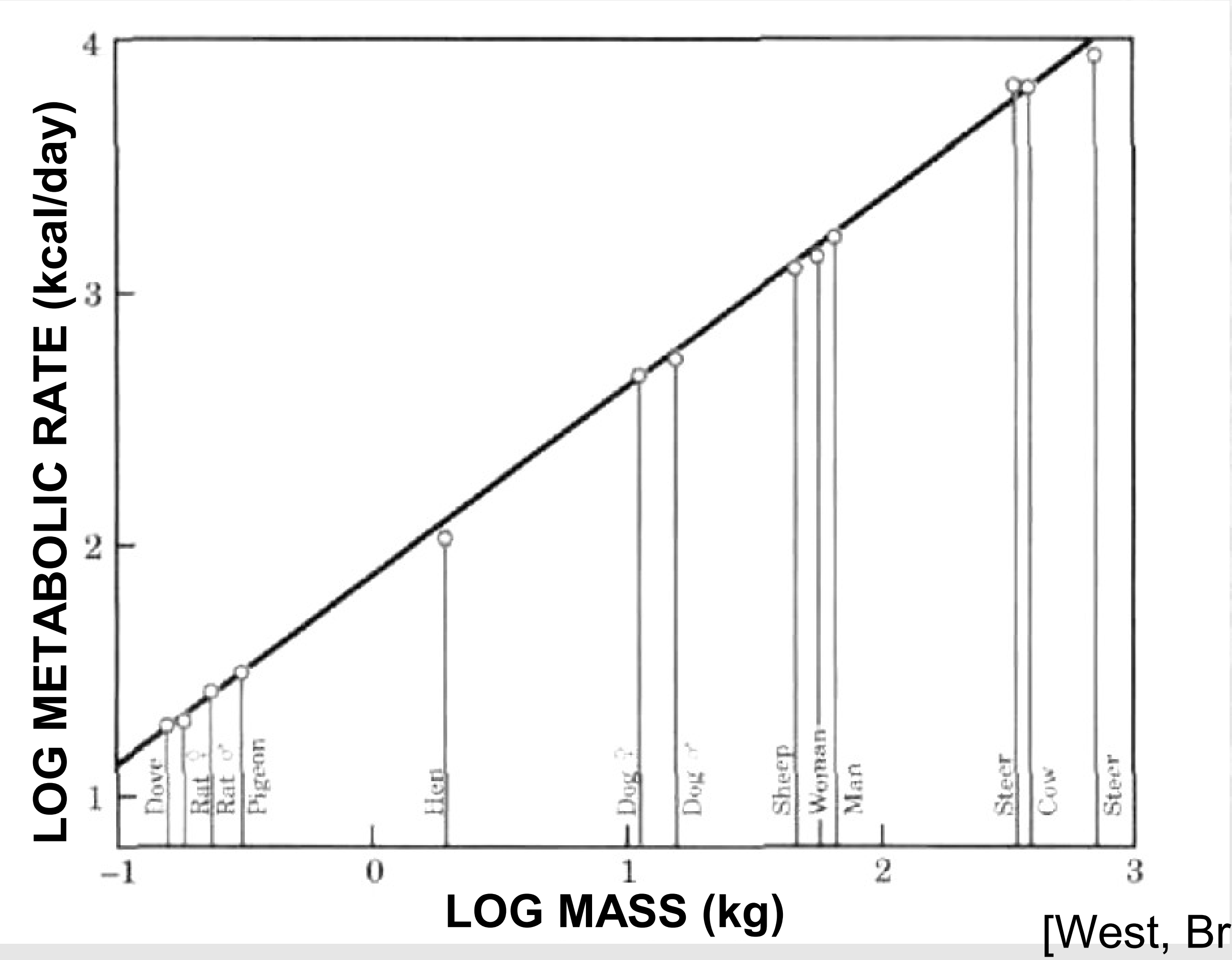
Allometric Scaling *Kleiber's Law*

The work of Max Kleiber (1932):

metabolic rates (kcal/day) of mammals and birds



[6]



[West, Brown (2004)]

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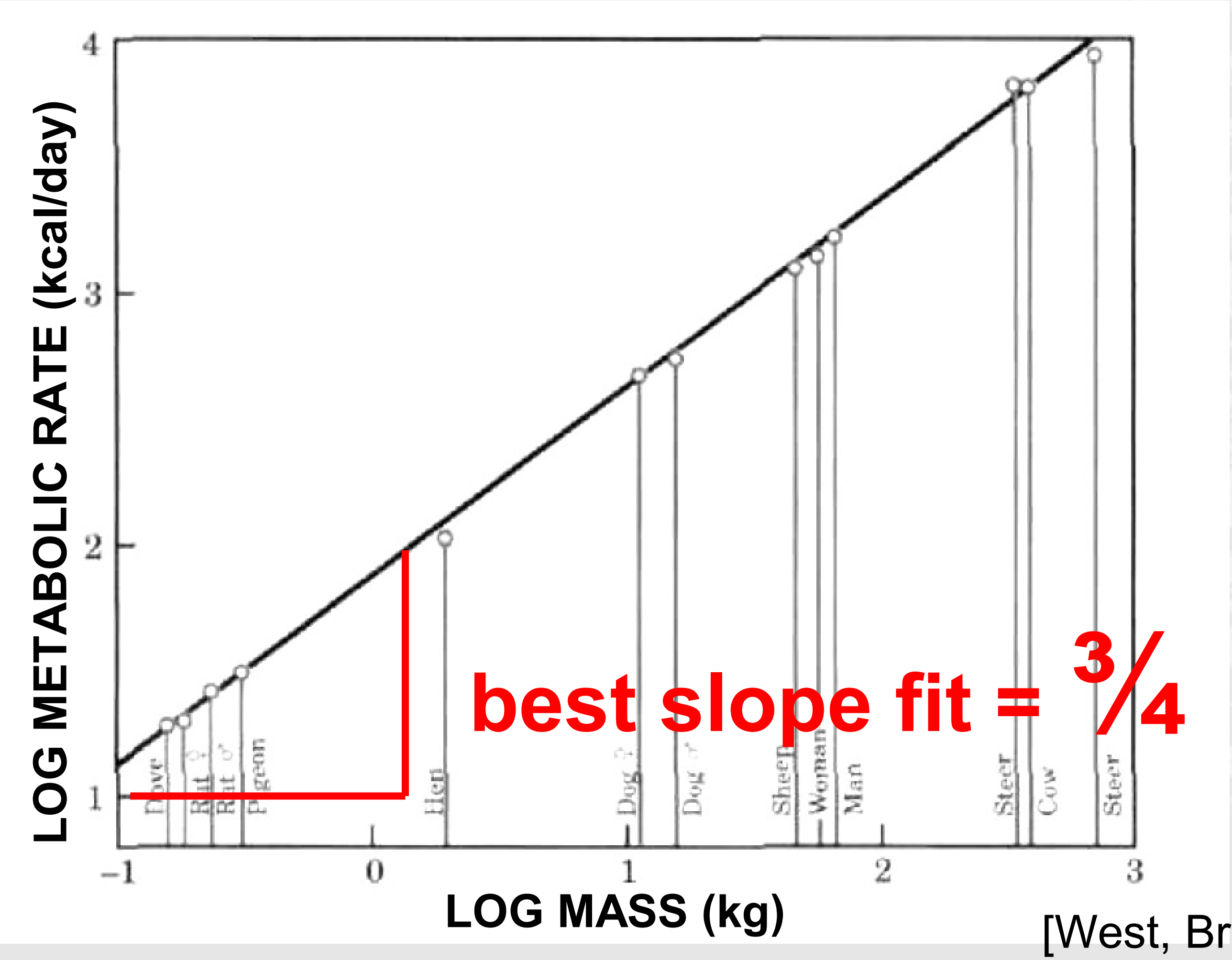
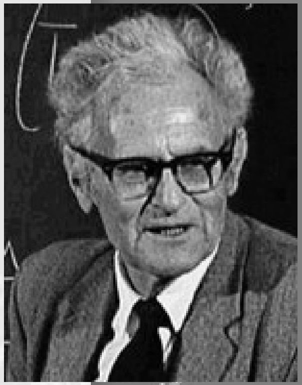


best slope fit = $3/4$

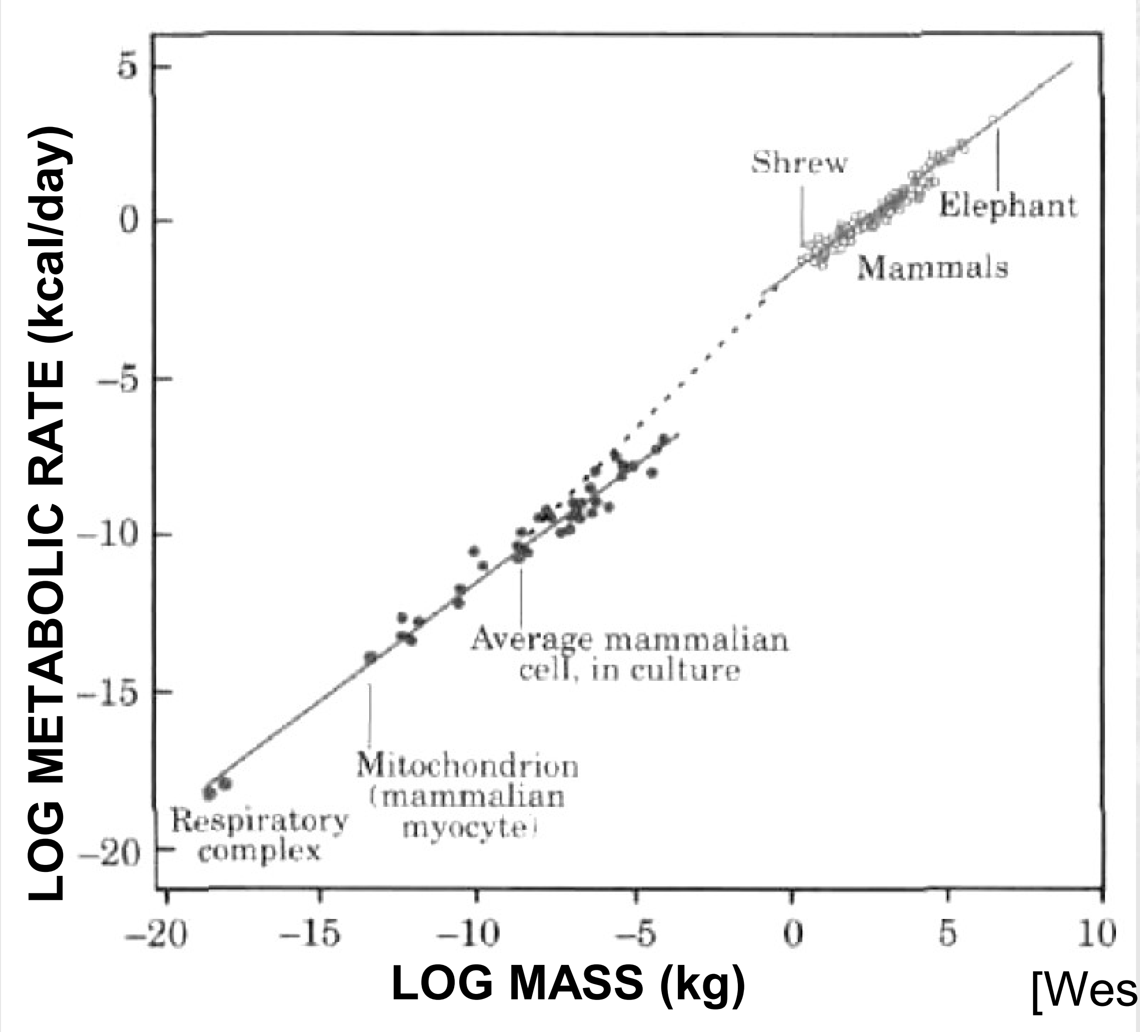


[6]

[West, Brown (2004)]

Allometric Scaling *Kleiber's Law*

Extension of Kleiber's work: metabolic rates of life covering over 27 orders of magnitude in mass



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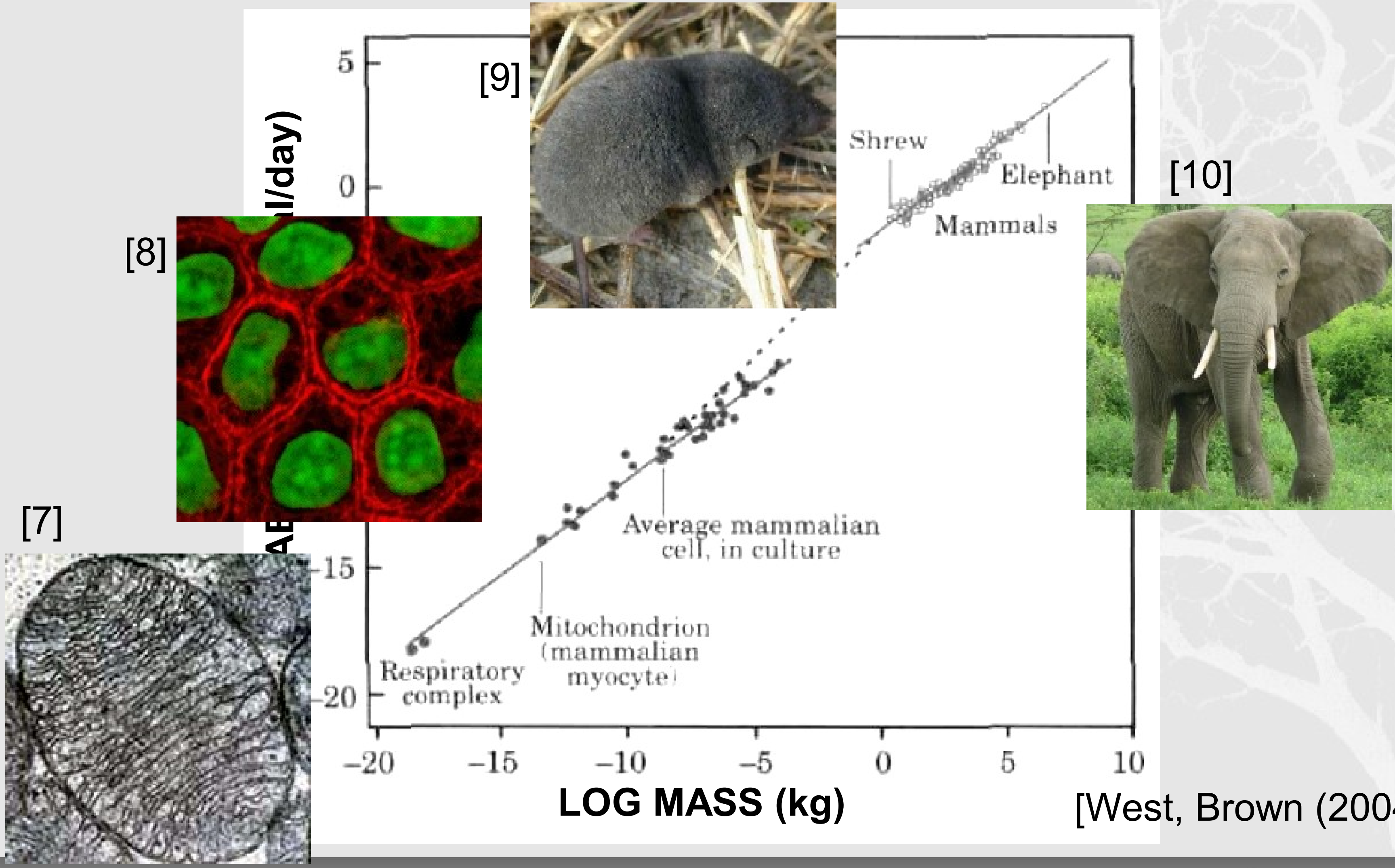

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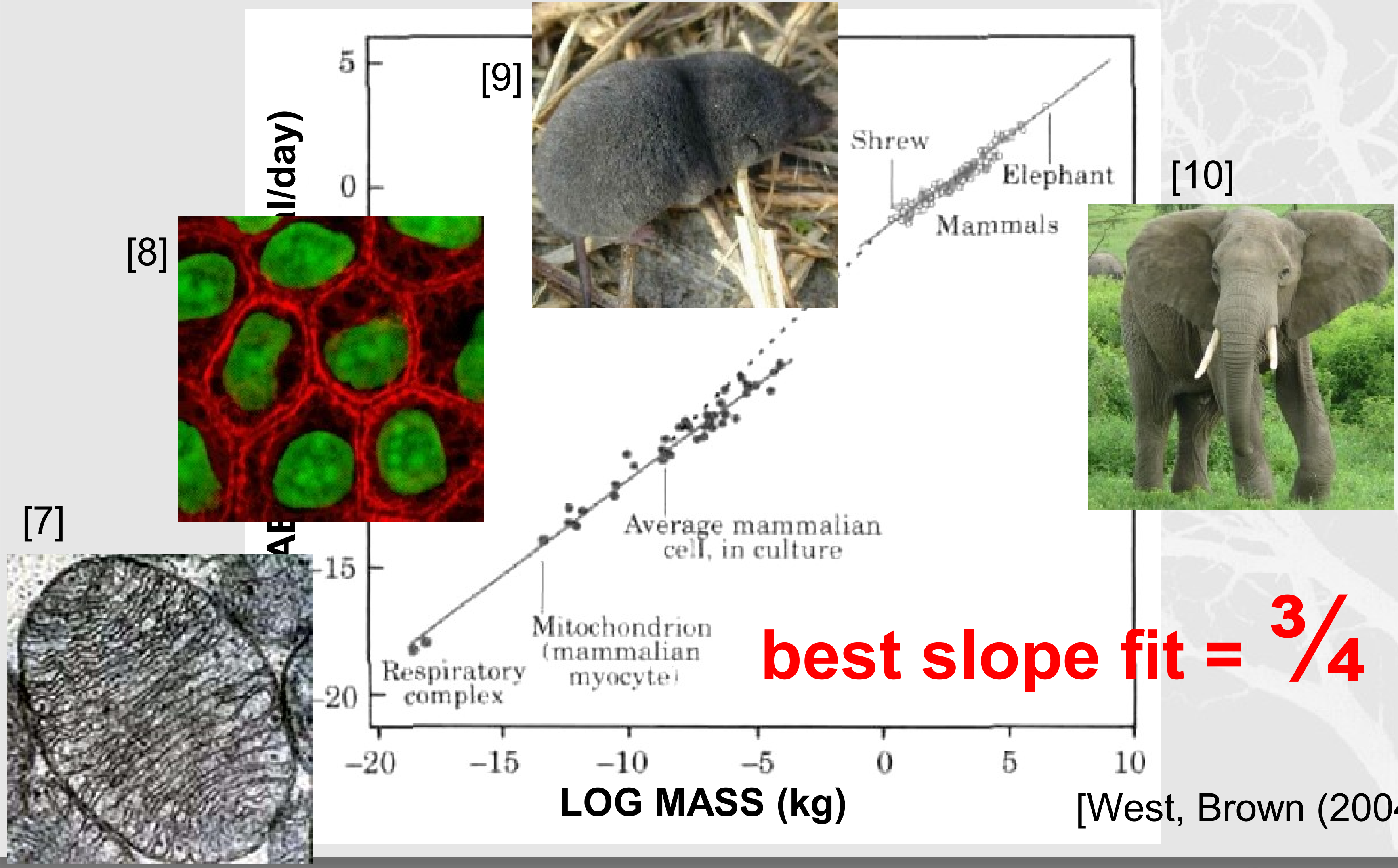

best slope fit = ¾

[West, Brown (2004)]

Allometric Scaling *Kleiber's Law*

This leads to Kleiber's law:

$$B \propto M^{3/4},$$

metabolic rate B
body mass M
metabolic exponent $b \approx 3/4$

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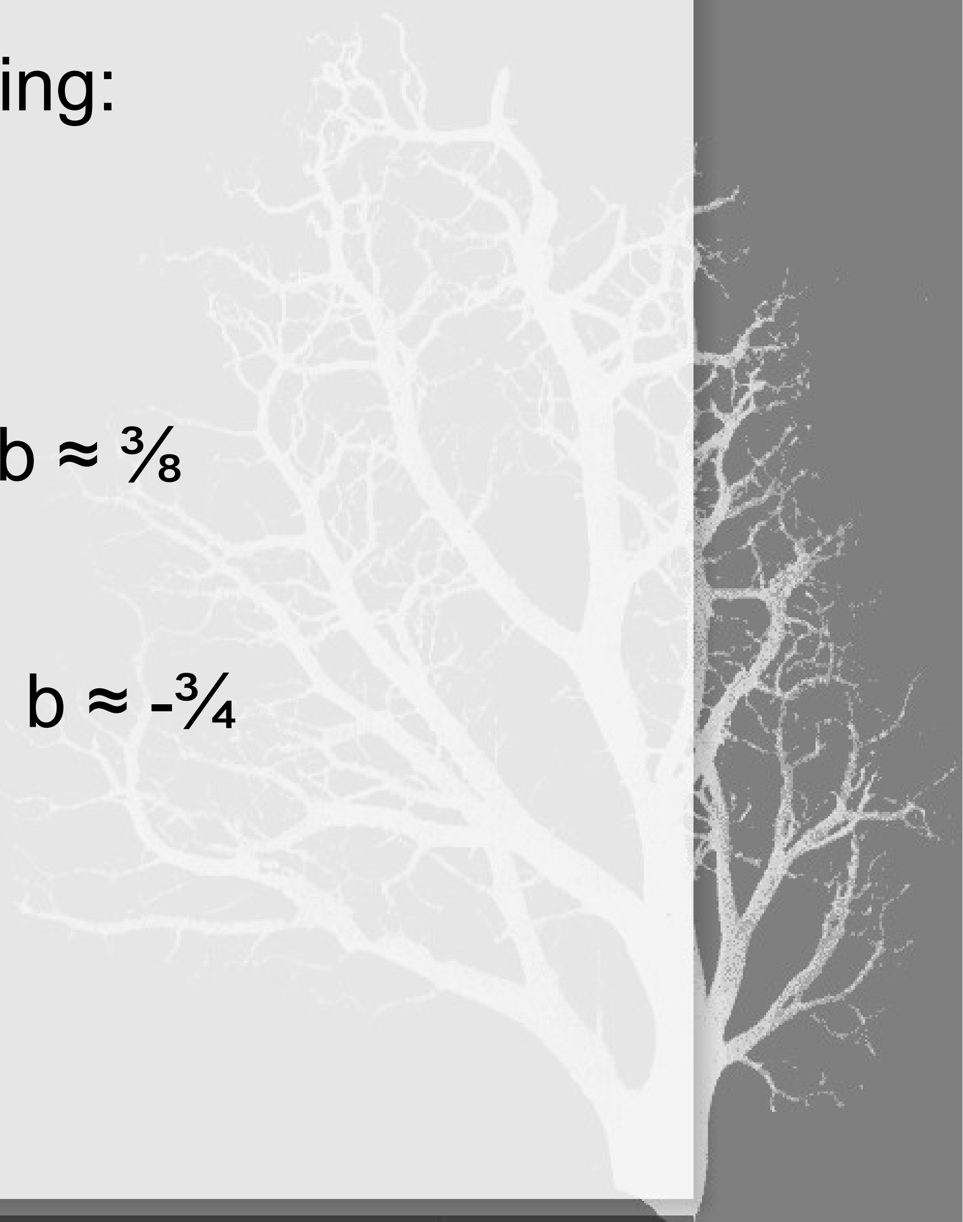
Scaling with *multiples of ¼* seems to be a common principle in nature...

Allometric Scaling *Quarter-Power Scaling*



Examples for quarter-power scaling:

- heart rate → $b \approx -\frac{1}{4}$
- life span → $b \approx \frac{1}{4}$
- aorta / tree trunk diameters → $b \approx \frac{3}{8}$
- genome lengths → $b \approx \frac{1}{4}$
- population density in forests → $b \approx -\frac{3}{4}$
- ...

Allometric Scaling *Quarter-Power Scaling*

As a consequence of quarter-power scaling, some *invariant quantities* emerge.
→ size-independent

Invariant quantities can be regarded as *fundamental, underlying constraints* of a system.

Allometric Scaling *Quarter-Power Scaling*

life span increases as $M^{1/4}$, heart rate decreases as $M^{-1/4}$

- heartbeats / lifetime
  $\approx 1.5 \cdot 10^9$
- ATP molecules synthesized / lifetime
  $\approx 10^{16}$

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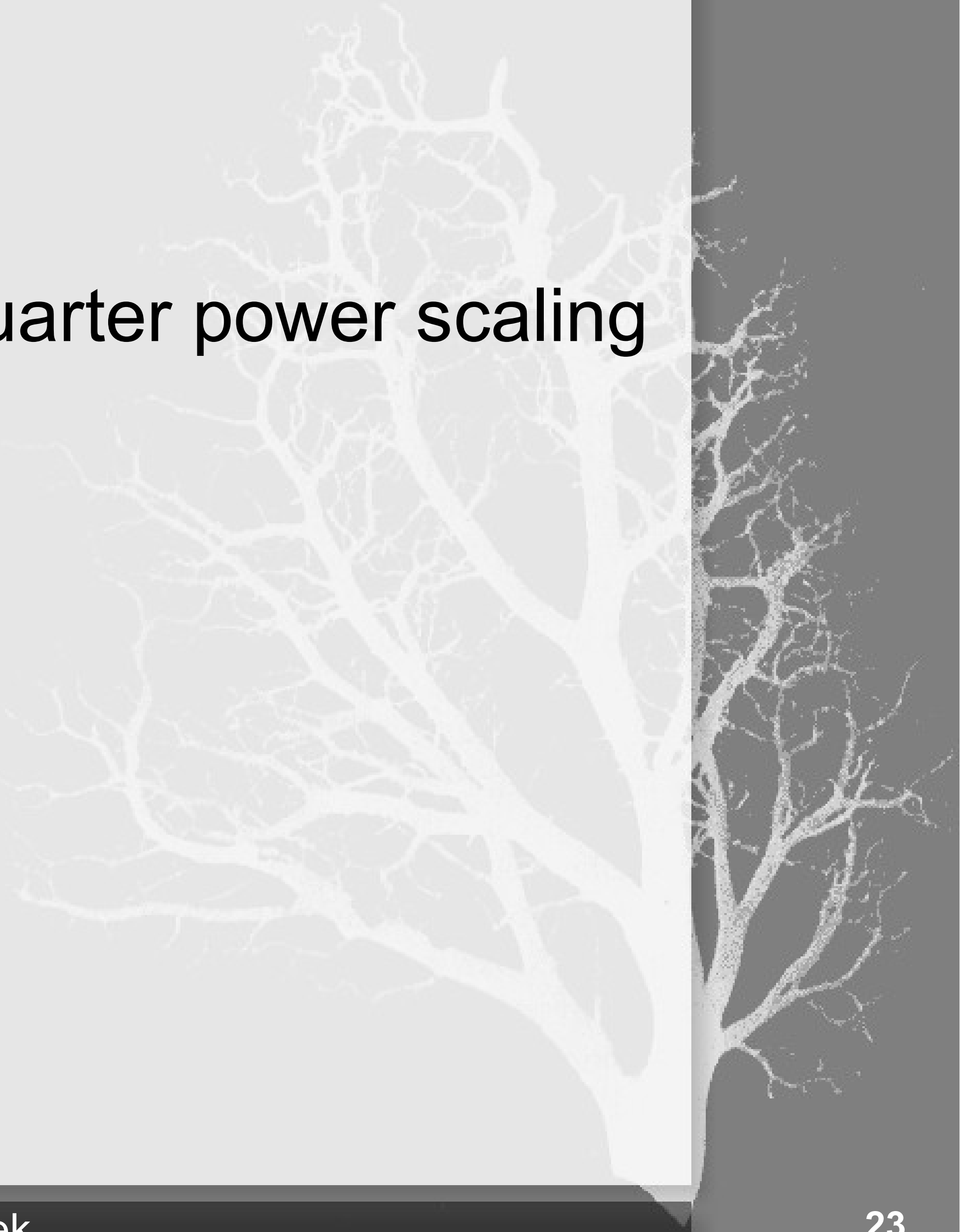
population density in forests decreases as $M^{-3/4}$,

individual power use increases as $M^{3/4}$

- power used by all individuals in any size class
  ≈ invariant

Modelling Approach



How can the predominance of quarter power scaling be explained mathematically?

[West, Brown, Enquist 1997]

Modelling Approach

Life:

complex, self-sustaining, reproducing structures

⇓

need to service *high numbers of microscopic units*

Modelling Approach

Life:

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with

- energy
- metabolites
- information

in a highly efficient way

Modelling Approach

Natural selection evolved *networks* to solve this:

- animal circulatory systems
- plant vascular systems
- ecosystems (e.g. forests)
- intracellular networks
- ...

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Natural selection evolved *networks* to solve this:

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These networks have to fulfill certain properties / *there exist certain constraints*...

Modelling Approach

Constraints on biological *networks*:

(1) the organism's whole volume has to be supplied
→ space filling, *fractal-like* branching pattern

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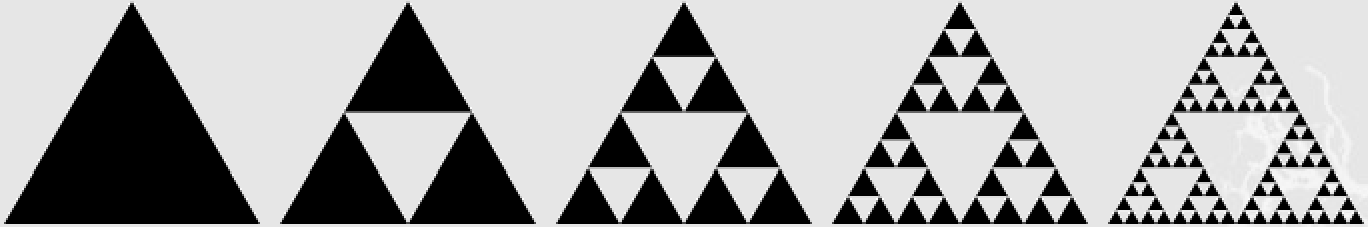
(3) the energy to distribute resources is minimized
→ evolution towards optimal state

Short Excourse: Fractals

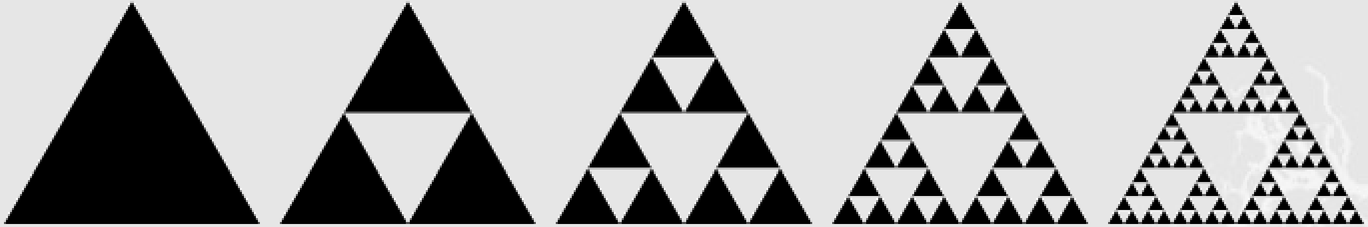


evolution of Sierpinski triangle, recursion depth four [11]

Fractals (lat. fractus: broken):

- fragmented geometric shapes
- each fragment is reduced-size copy of the whole → self-similarity
- simple and recursive definition

Short Excourse: Fractals



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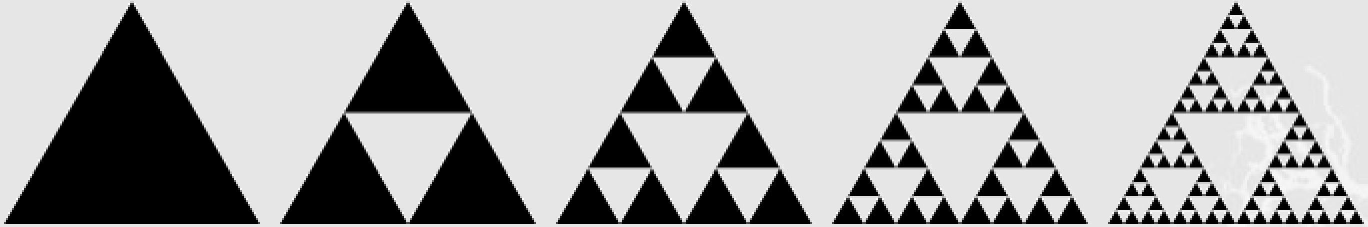
Fractal dimensionality:

- indicates „how completely a fractal will fill space“
- Mandelbrot (1975): fractals, usually, have non-whole numbered dimensionality
- „too big to be thought of as one-dimensional, but too thin to be two-dimensional“

Short Excourse: Fractals



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Example: dimensionality D of Sierpinski triangle

$$D = \lim_{\epsilon \to 0} \frac{\log N(\epsilon)}{\log(\frac{1}{\epsilon})} = \lim_{k \to \infty} \frac{\log 3^k}{\log 2^k} = \frac{\log 3}{\log 2} \approx 1.585$$

$\epsilon =$ linear size of self-similar fragments
$N(\epsilon) =$ # self-similar fragments to cover whole original object
$k =$ recursion depth

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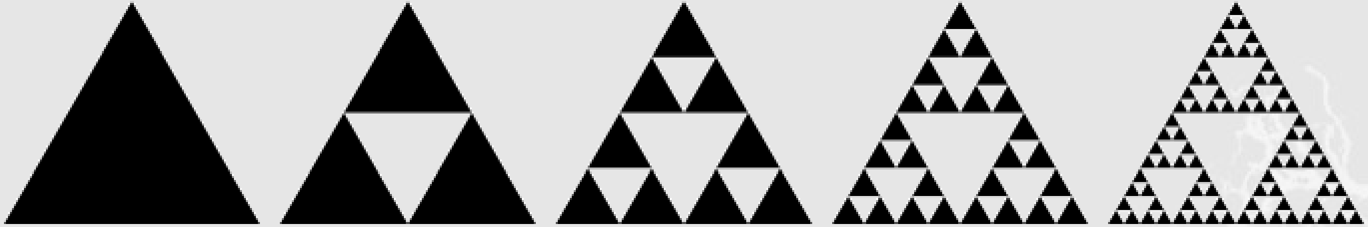

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in each step k 3^k new triangles with side length (½)^k

ϵ = linear size of self-similar fragments

$N(\epsilon)$ = # self-similar fragments to cover whole original object

k = recursion depth

Derivation of Quarter-Power Scaling

Fractal-like structures in nature:

- self-similarity not perfect, but stochastic
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[12]

Derivation of Quarter-Power Scaling

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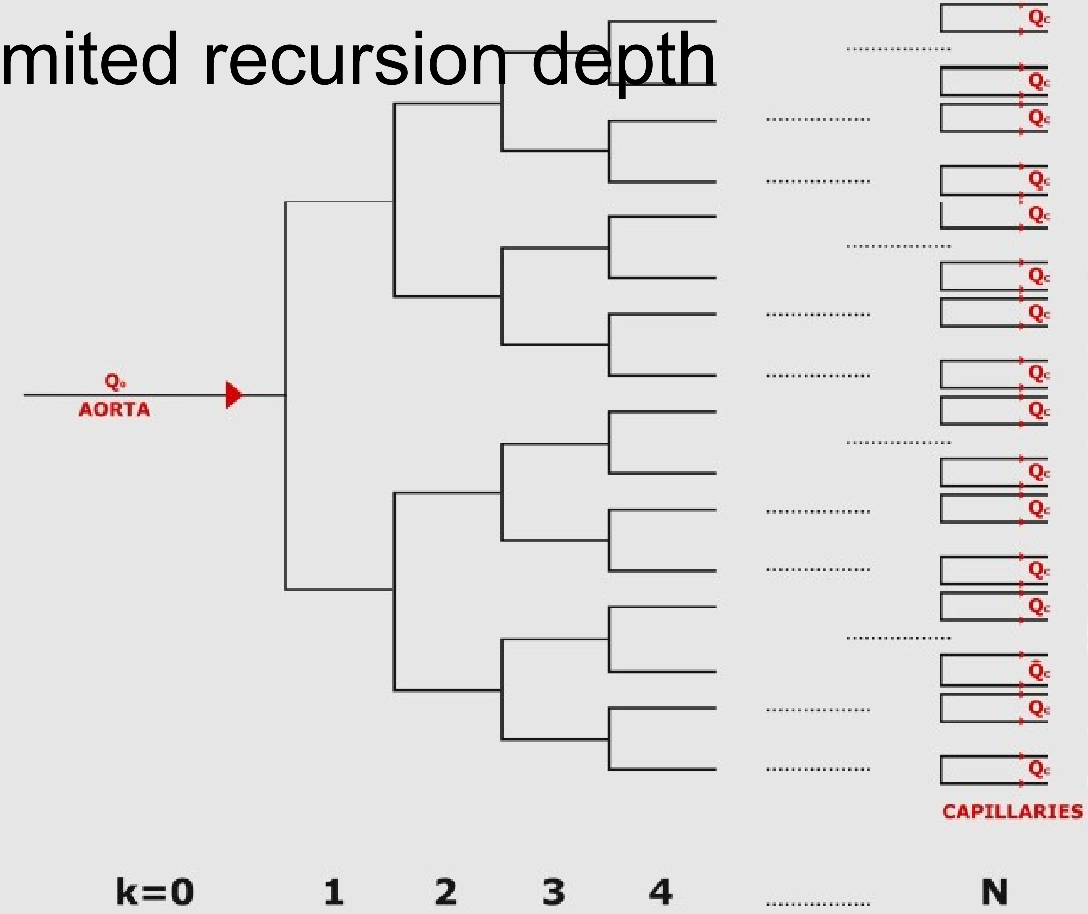

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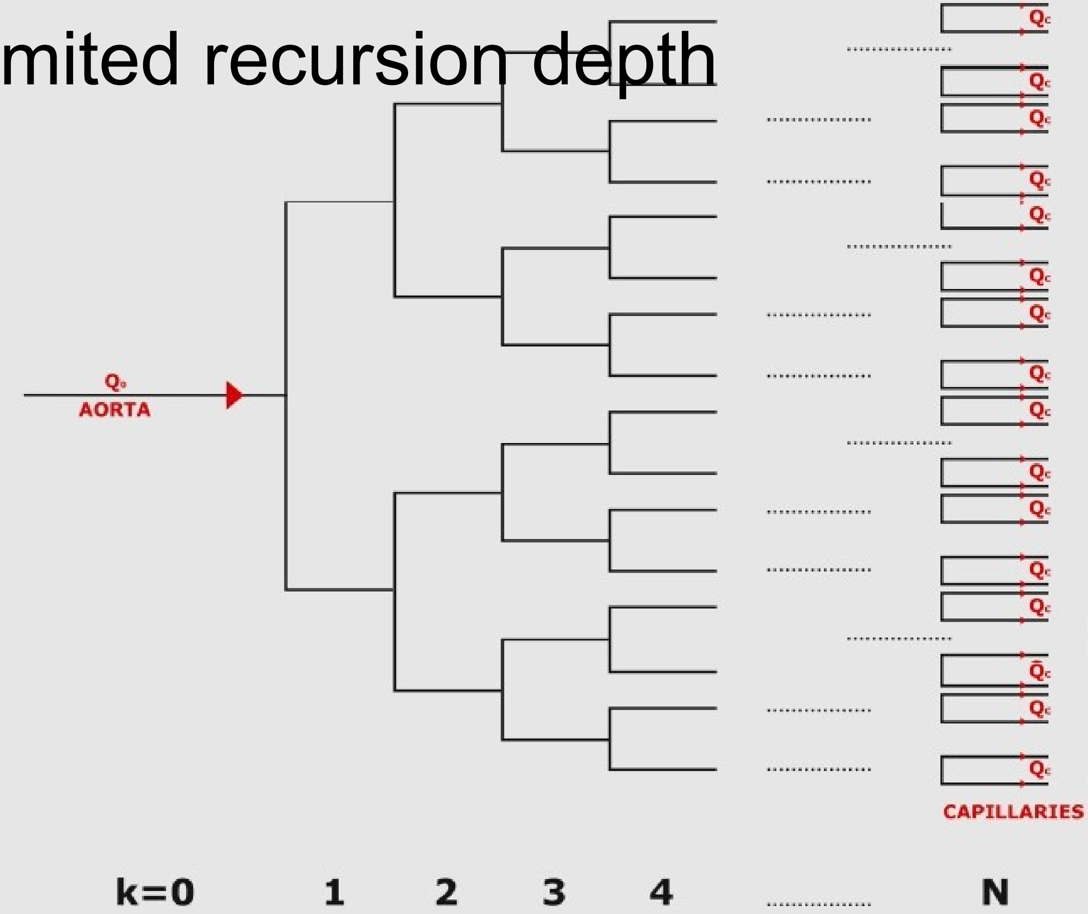

[12]

biological networks (here: circulatory system) are fractal-like

Derivation of Quarter-Power Scaling

(1) space filling, *fractal-like* branching pattern

(2) final branch is a size-invariant unit

(3) energy to distribute resources is minimized
(use of hydrodynamic laws)

⇩

strict mathematical derivation of exponent ¾ possible

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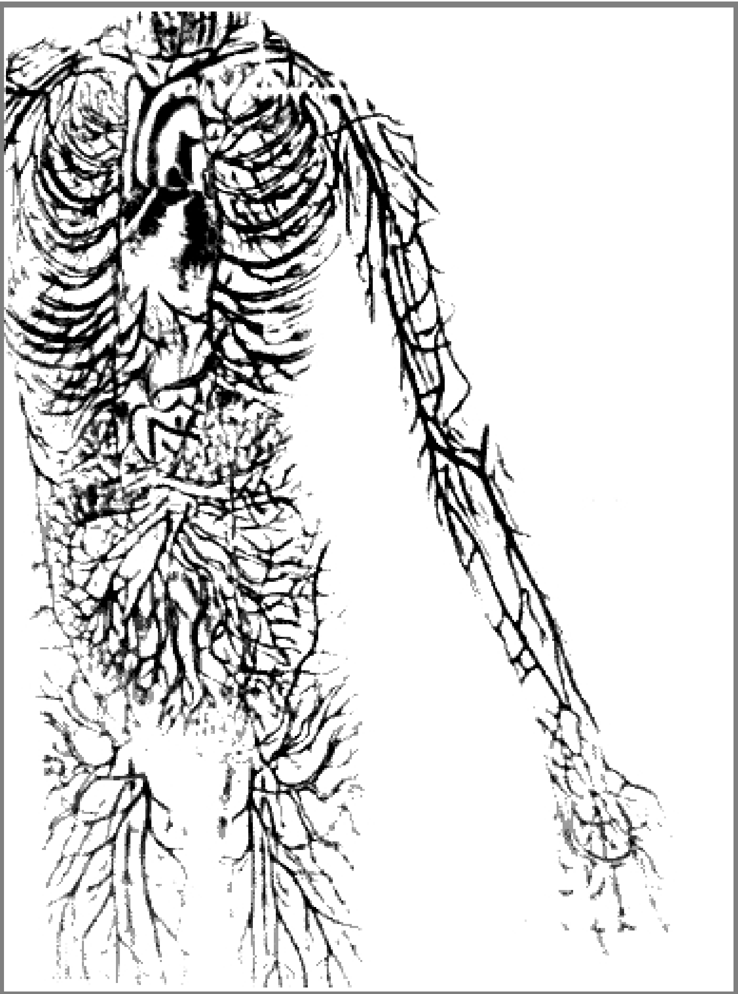
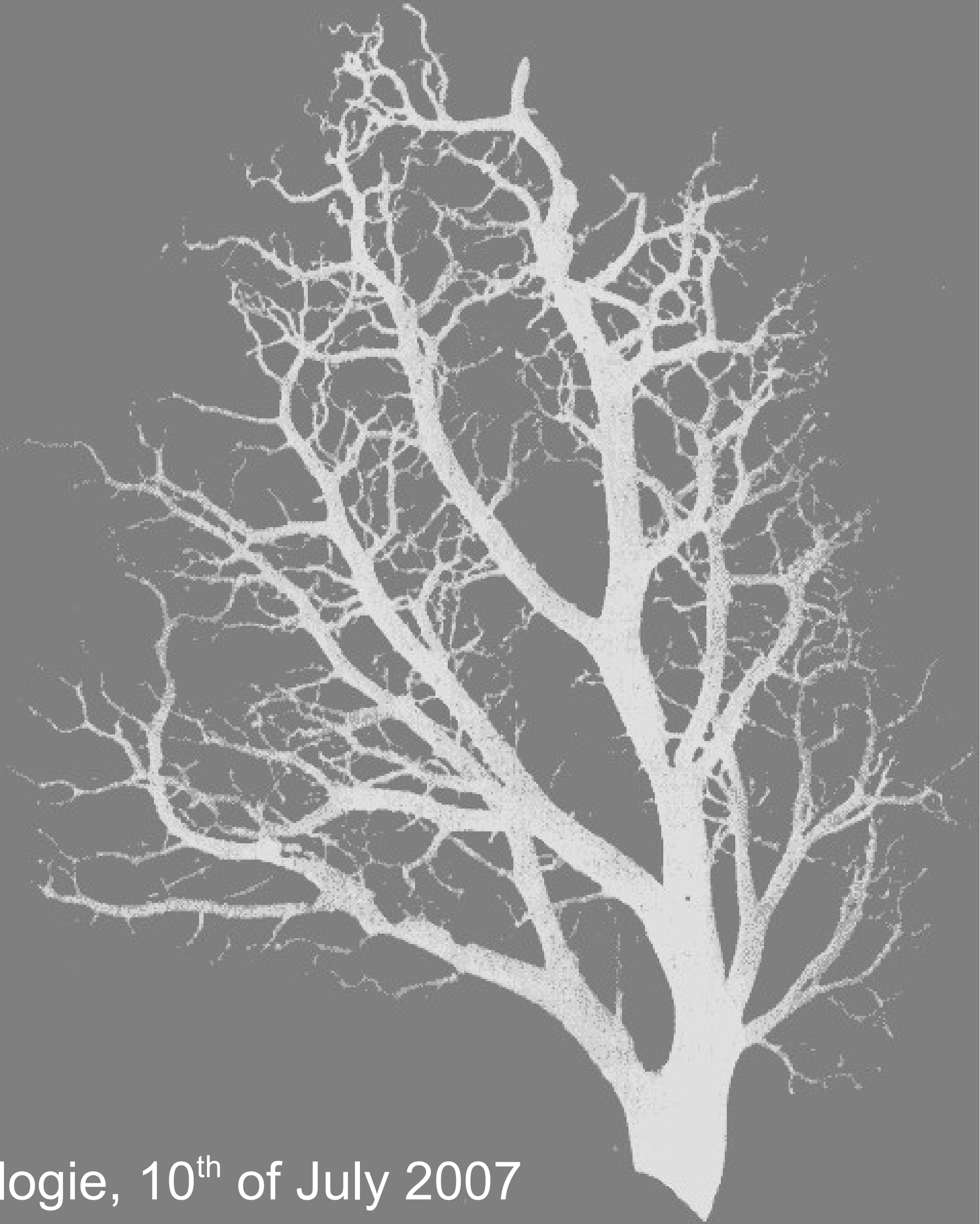
4 = 3 + 1 = increase in dimensionality due to fractal-like space filling





Allometric Scaling Laws In Nature pt. 2

Marcel Grunert

Gute Ideen in der theoretischen Systembiologie, 10th of July 2007

Blood Circulation

Cardiovascular system

→ aorta, arteries, arterioles and capillaries

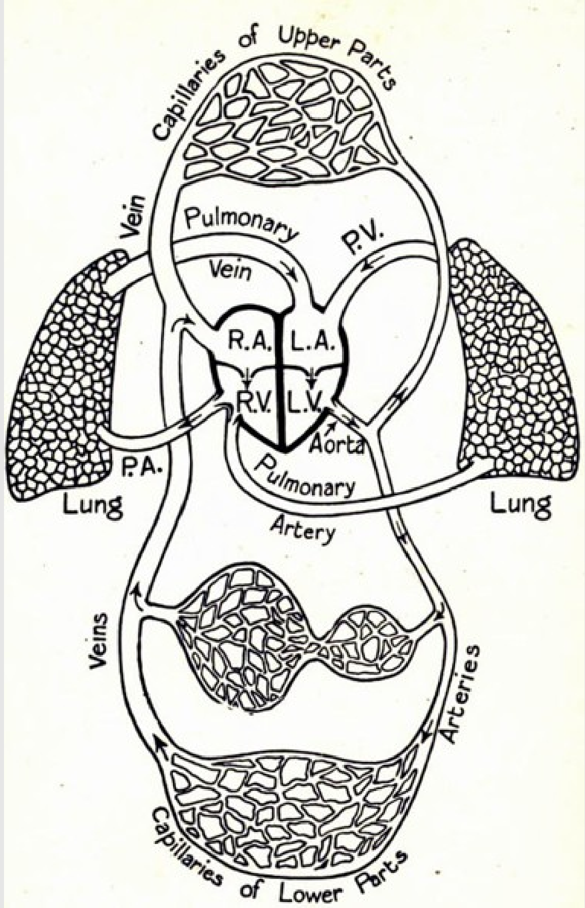
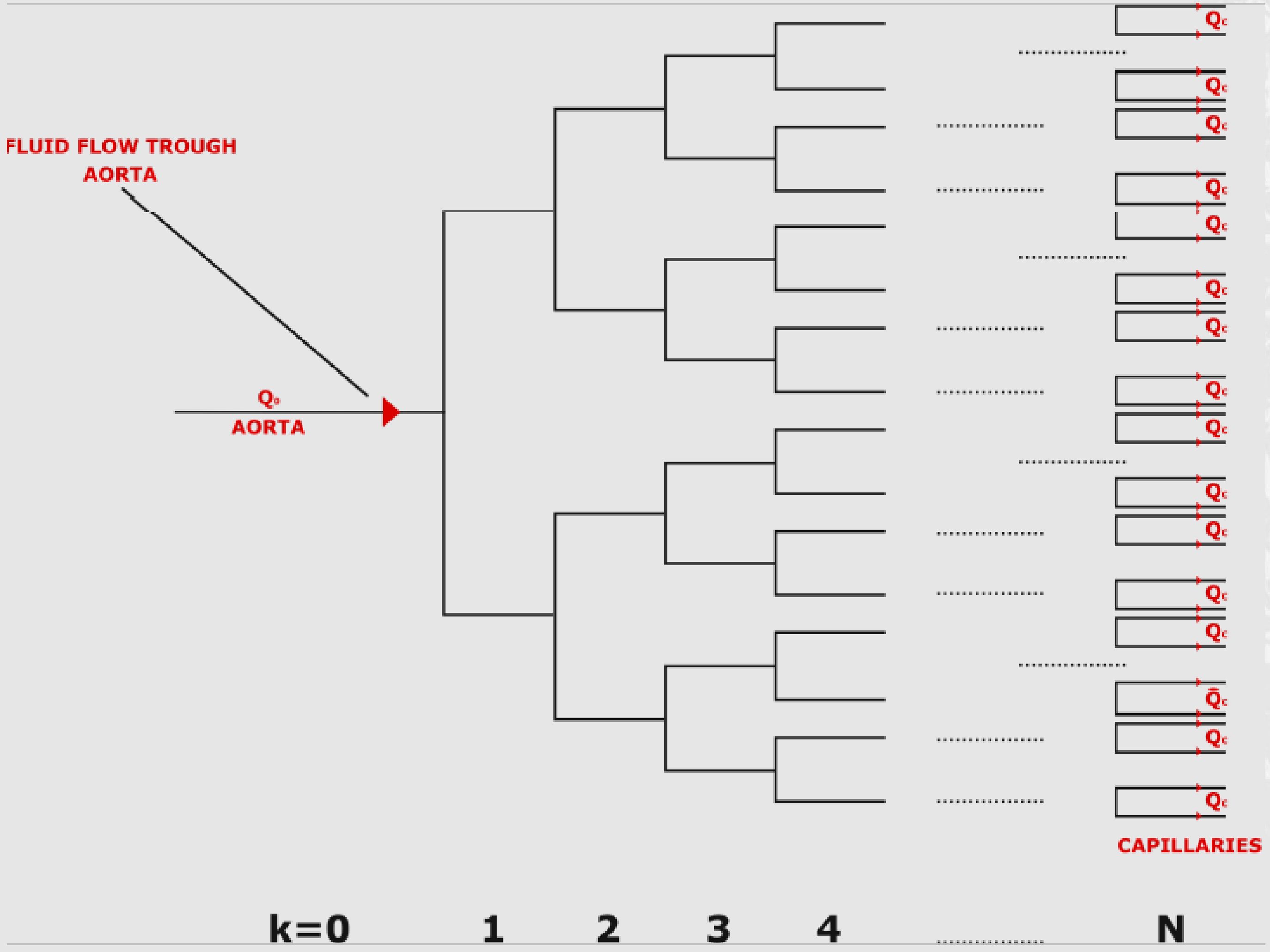


Figure: A representation of the circulatory system of the blood. (http://www.uh.edu/engines/)

Blood Circulation

- N branchings from aorta (level 0) to capillaries (level N)



Conservation of Fluid

Recall: $B \propto M^{3/4}$ (Kleiber's Law)

Since the fluid transports oxygen, nutrients, etc. for metabolism:

$$\mathbf{B \propto Q_0}$$

(metabolic rate ∝ volume flow rate)

⇒ if $\mathbf{B \propto M^a}$ *(a will be determined later)*

then $\mathbf{Q_0 \propto M^a}$

Conservation of fluid:

$$\mathbf{Q_0 = N_c Q_c = N_c \pi r_c^2 u_c}$$

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Volume
flow rate

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Volume flow rate

Total number of capillaries

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Volume flow rate

Total number of capillaries

Volume flow rate in average capillary

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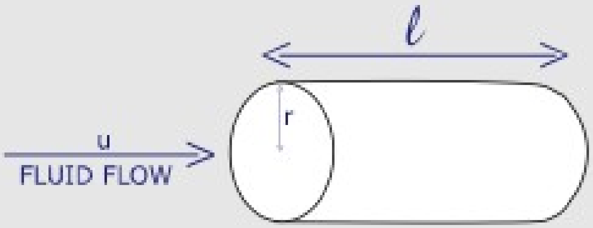
Volume flow rate in average capillary



→ Capillary is an invariant unit
(Recall: scale invariance)

Conservation of Fluid

Capillary is an invariant unit
(Q_c is equal for all mammals)

⇒ number of capillaries (N_c) must scale in same way as the metabolic rate ($B \propto Q_0$):

$\boxed{B \propto M^{3/4} \text{ then } \mathbf{N_c \propto M^{3/4}}}$ *(if a=3/4 → to be shown)*

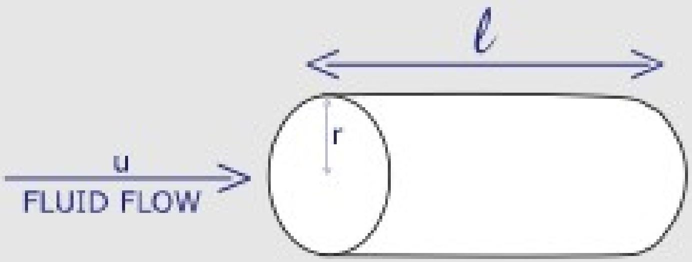
$N_c \propto M^{3/4}$ <u>but:</u> total number of cells: $N_{cell} \propto M$ (linear)

⇒ number of cells fed by a single capillary increases as $M^{1/4}$ *(efficiency increases with size)*

Characterize the Branching

How do radii and length of tubes scale through the network?

- scale factors: $\boldsymbol{\beta_k = r_{k+1}/r_k}$,
  $\boldsymbol{\gamma_k = l_{k+1}/l_k}$



Recall: terminal branches of the network are invariant units

⇒ network must be a conventional self-similar fractal ($\beta_k=\beta$, $\gamma_k= \gamma$ & $n_k= n$)

⇒ number of branches increase in geometric proportion ($N_k=n^k$) as their size geometrically decreases from level 0 to N

Characterize the Branching

$N_c = n^N$ ⇒ number of generations of branches scales only logarithmically with size:

$$\boxed{N = \frac{a \cdot \ln(M/M_0)}{\ln(n)}}$$

⇒ a whale is 10^7 times heavier than a mouse but has only about 70% more branchings from aorta to capillary

Figure: http://www.the-scientist.com

Characterize the Branching

Total volume of fluid in the network ("blood" volume V_b):

$$V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi r_k^2 l_k n^k \propto (\gamma\beta^2)^{-N} V_c$$

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Total number of branches at level k

Volume of tube

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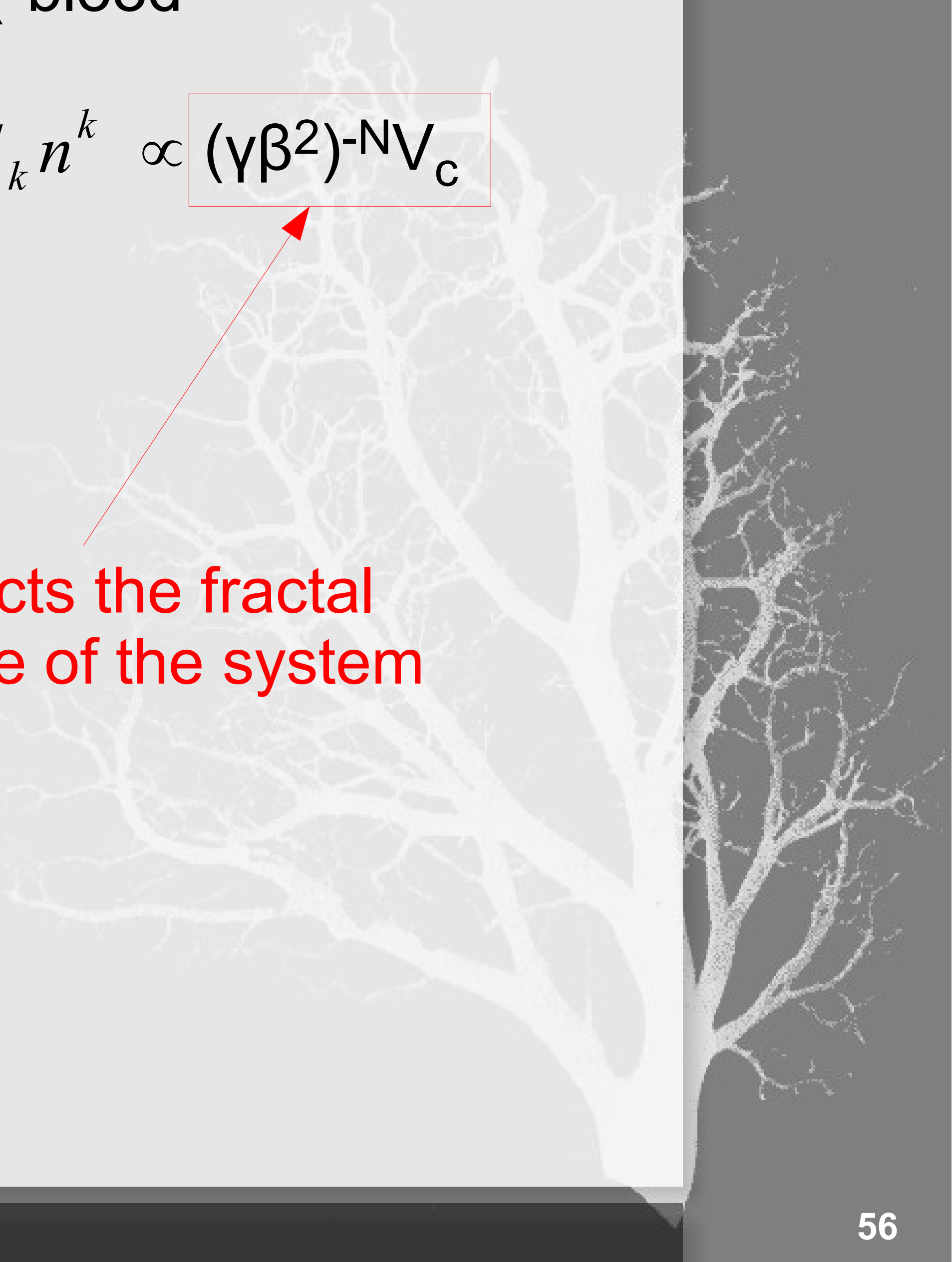
Total number of branches at level k

Volume of tube

Reflects the fractal nature of the system



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Total number of branches at level k

Volume of tube

Reflects the fractal nature of the system

Volume of capillary

Characterize the Branching

Total volume of fluid in the network ("blood" volume V_b):

$$V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi r_k^2 l_k n^k \propto (\gamma\beta^2)^{-N} V_c$$

Total number of branches at level k

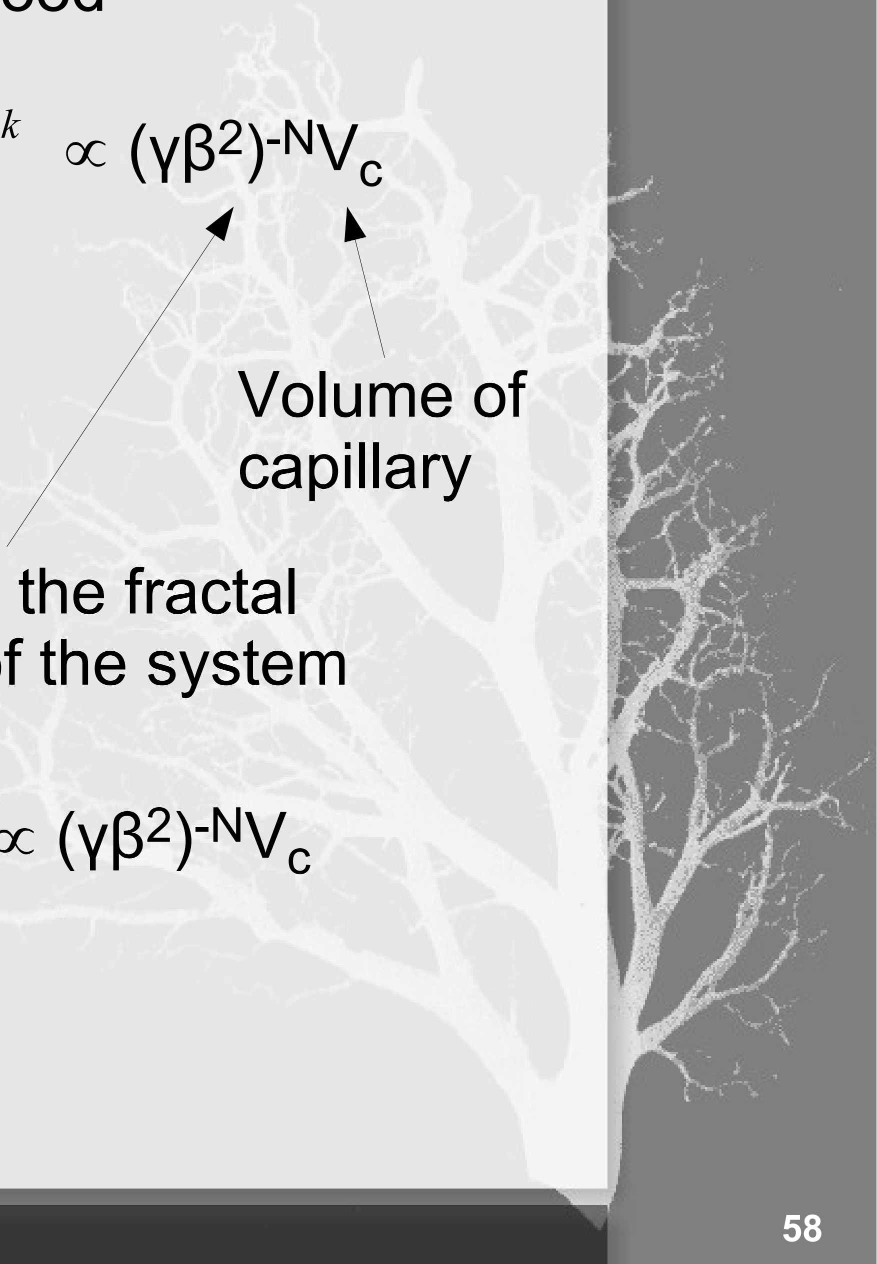
Volume of tube

Volume of capillary

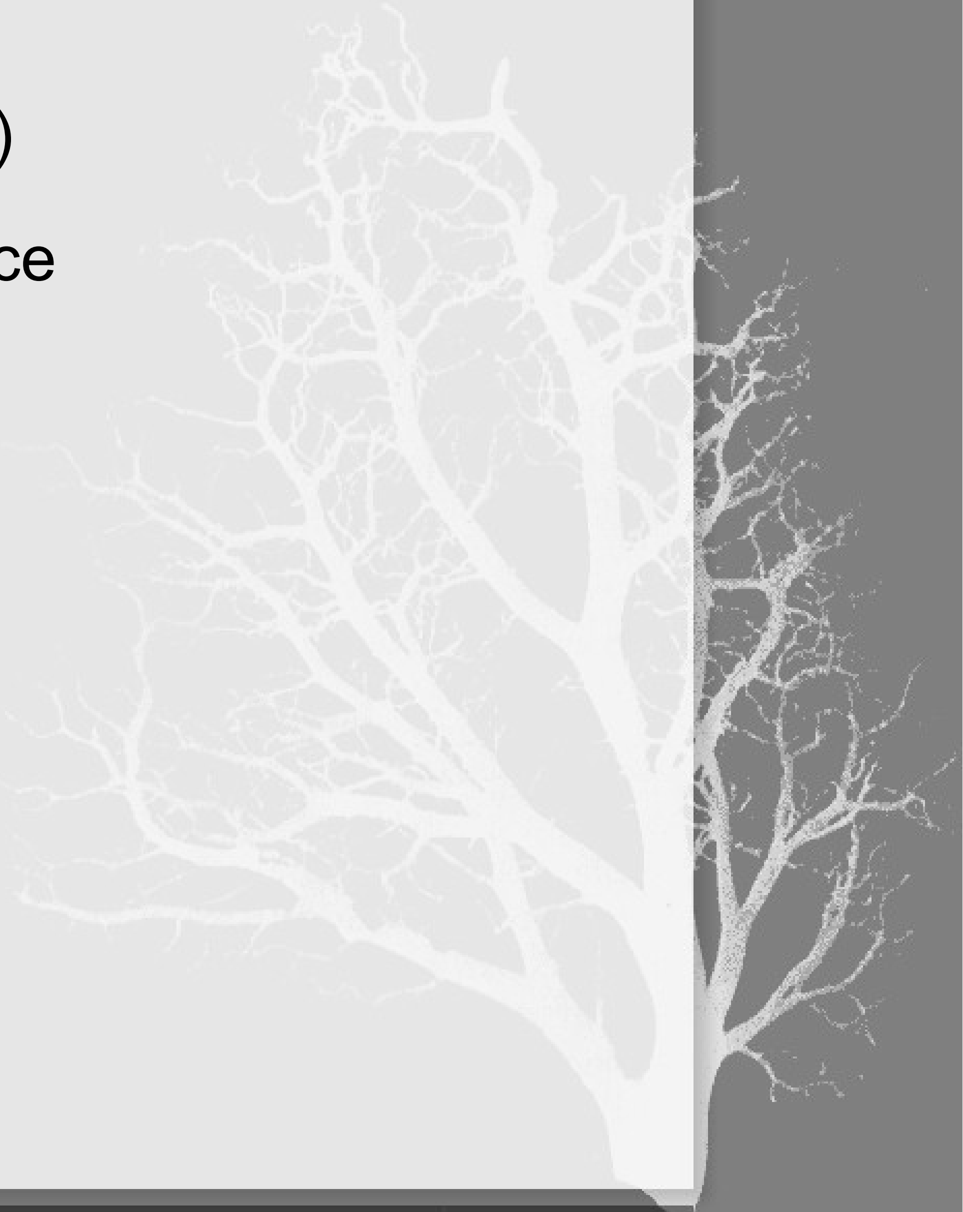
Reflects the fractal nature of the system

Remember: $N = \dfrac{a \cdot \ln(M/M_0)}{\ln(n)}$ & $V_b \propto (\gamma\beta^2)^{-N} V_c$

$$\boxed{\mathbf{a = -\ln(n)/\ln(\gamma\beta^2)}}$$



Derivation of ¾ Exponent



Further knowledge about **β** and γ:

$N_k l^d_k \approx N_{k+1} l^d_{k+1}$ (“volume preserving”)

d-dimensional volume of space filled by branch of size l_k

Number of branches of size l_k

$$\Rightarrow \boxed{\gamma_k = \frac{l_{k+1}}{l_k} = \left(\frac{N_k}{N_{k+1}}\right)^{1/d} = \frac{1}{n^{1/d}}}$$

branches ratio

Derivation of ¾ Exponent

The sum of the cross-sectional areas of the daughter branches equals that of the parent:

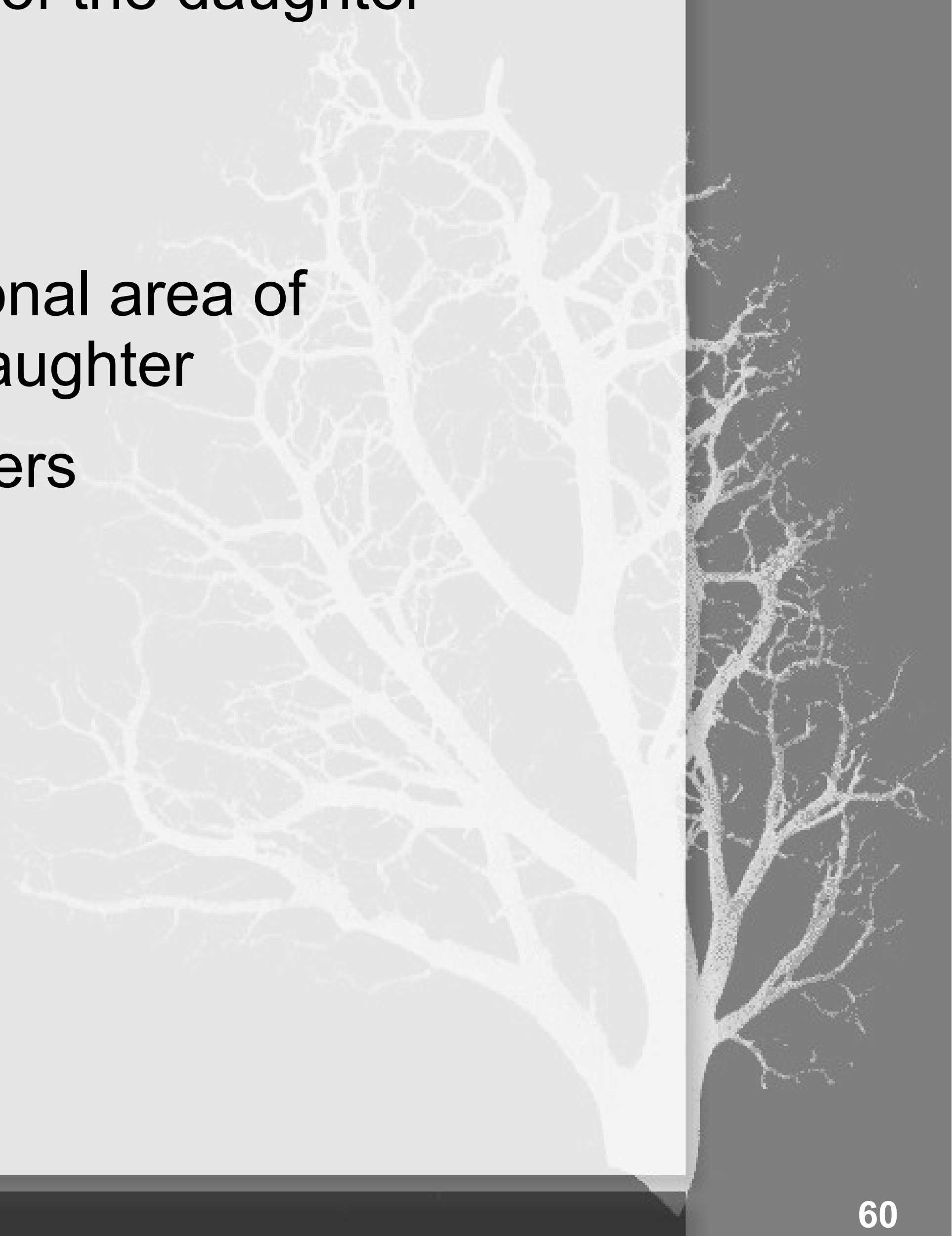
$$\pi r^2_k = n \pi r^2_{k+1}$$

x-sectional area of each daughter

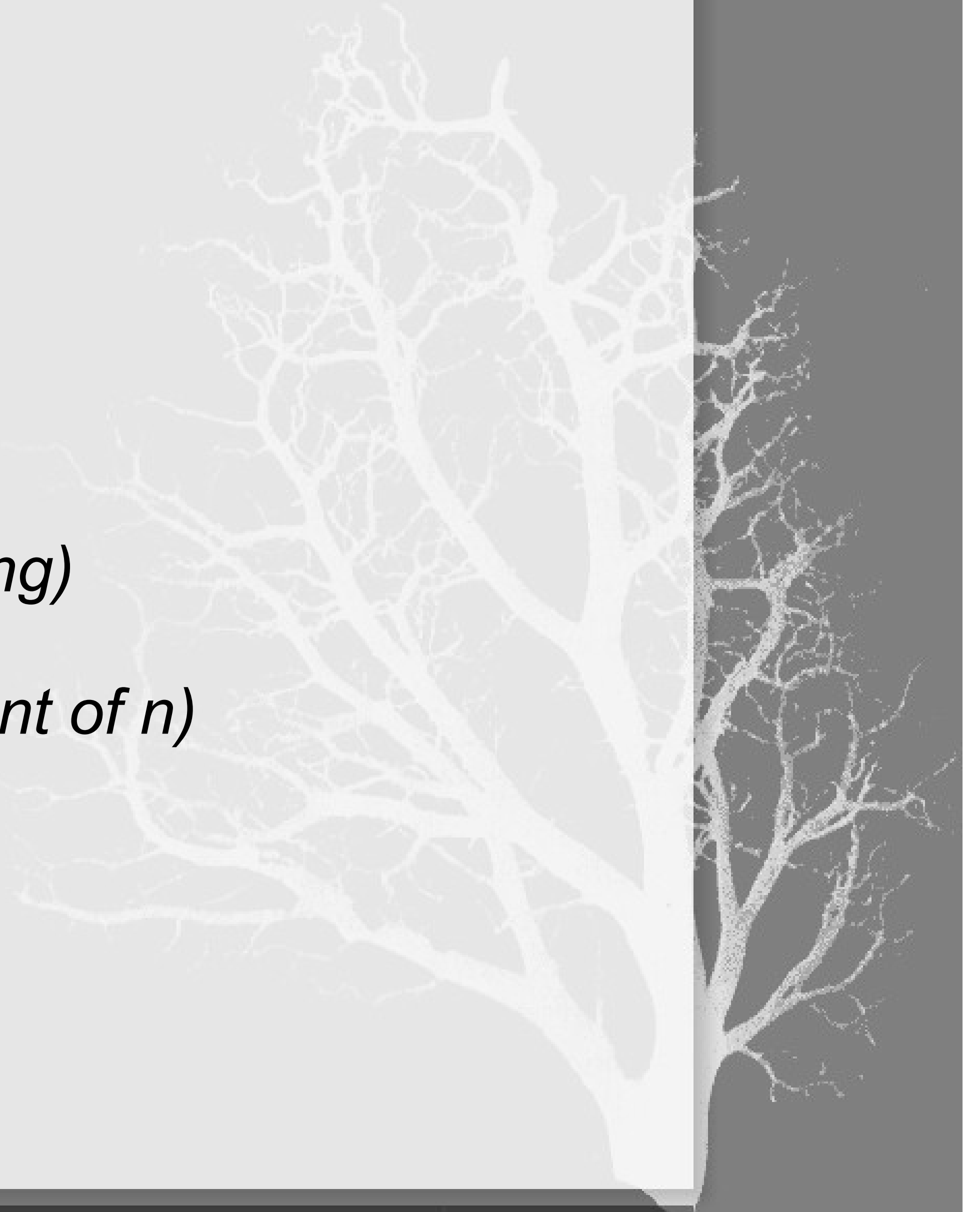
x-sectional area of parent branch

Number of daughters (branching ratio)

$$\Rightarrow \boxed{\beta_k = \frac{r_{k+1}}{r_k} = \frac{1}{n^{1/2}}}$$



Derivation of ¾ Exponent



Recall: if $B \propto M^a \Rightarrow N_c = n^N \propto M^a$

if $V_b \propto M$ and $V_c \propto M_0$

$$\Rightarrow a = -\ln n / \ln(\gamma\beta^2)$$

with $\boldsymbol{\gamma = n^{-1/3}}$ *(space-filling)*

$\boldsymbol{\beta = n^{-1/2}}$ *(area-preserving)*

$$\Rightarrow \boxed{a = 3/4}$$ *(independent of n)*

Derivation of ¾ Exponent

In d-Dimensions: $B \propto M^{d/(d+1)}$

⇒ we live in 3 spatial dimensions, so $B \propto M^{3/4}$

- “3” represents dimensionality of space
- “4” increase in dimensionality due to fractal-like space filling

Further Scaling Laws

Radius and length of aorta:

- Radius: $r_0 = \beta^{-N} r_c = N_c^{1/2} r_c$ $\boxed{\Rightarrow r_0 \propto M^{3/8}}$
- Length: $l_o = \gamma^{-N} r_c = N_c^{1/3} l_c$ $\boxed{\Rightarrow l_0 \propto M^{1/4}}$

Hydrodynamic resistance of the network:

$$\sim 1/M^{3/4}$$

⇒ Total resistance decrease with size
(small may be beautiful but large is more efficient)

Further Scaling Laws

Respiratory system

- Tracheal radius ~ $M^{3/8}$
- Oxygen consumption rate ~ $M^{3/4}$
- Total resistance ~ $1/M^{3/4}$
- Volume flow to lung ~ $M^{3/4}$

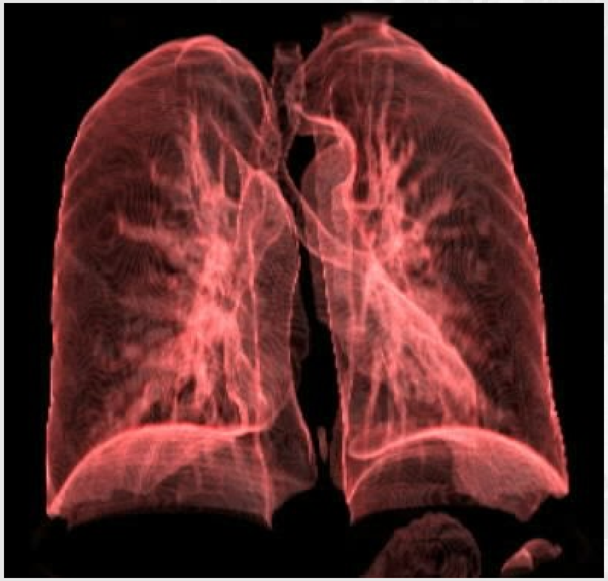
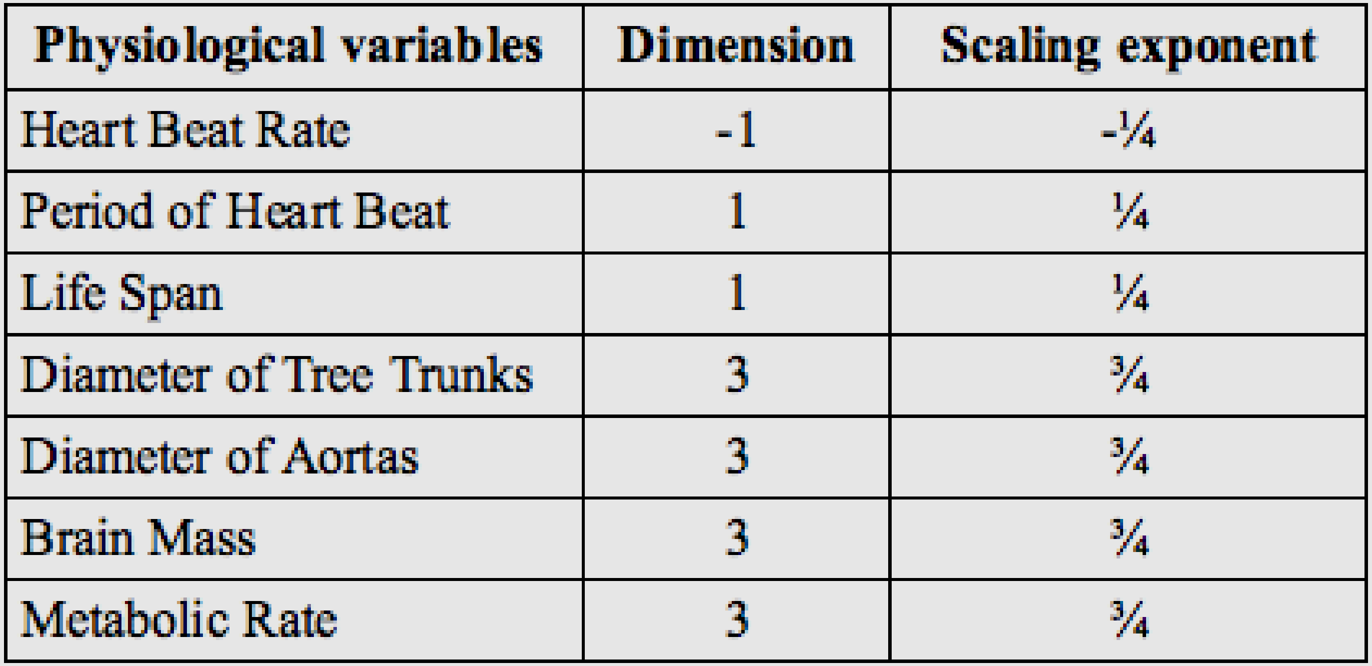


Figure: 3D-Lung (http://www.newportbodyscan.com)

Further Scaling Laws

Overview of further scaling laws



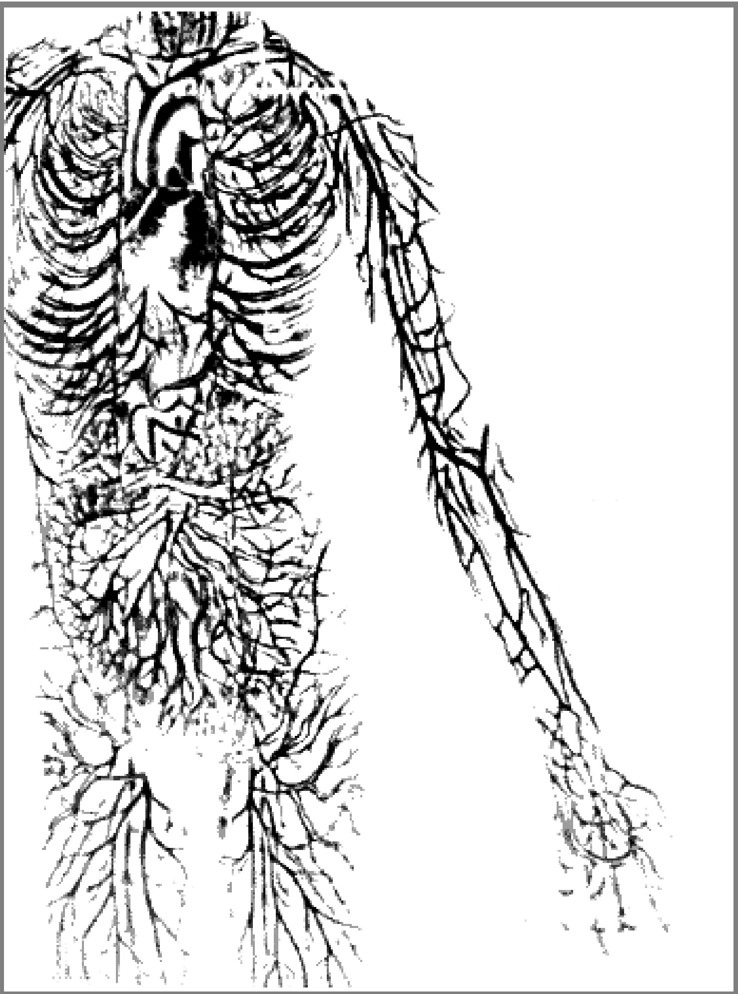
Physiological variables	**Dimension**	**Scaling exponent**
Heart Beat Rate	-1	-¼
Period of Heart Beat	1	¼
Life Span	1	¼
Diameter of Tree Trunks	3	¾
Diameter of Aortas	3	¾
Brain Mass	3	¾
Metabolic Rate	3	¾

Further Scaling Laws

Model ($Y=Y_0M^b$) predicts the known scaling relations of mammalian systems:

Cardiovascular		
Variable	**Exponent**	
	Predicted	**Observed**
Aorta radius	3/8 = 0.375	0.36
Circulation time	1/4 = 0.25	0.25
Total resistance	-3/4 = -0.75	-0.76
Metabolic rate	3/4 = 0.75	0.75

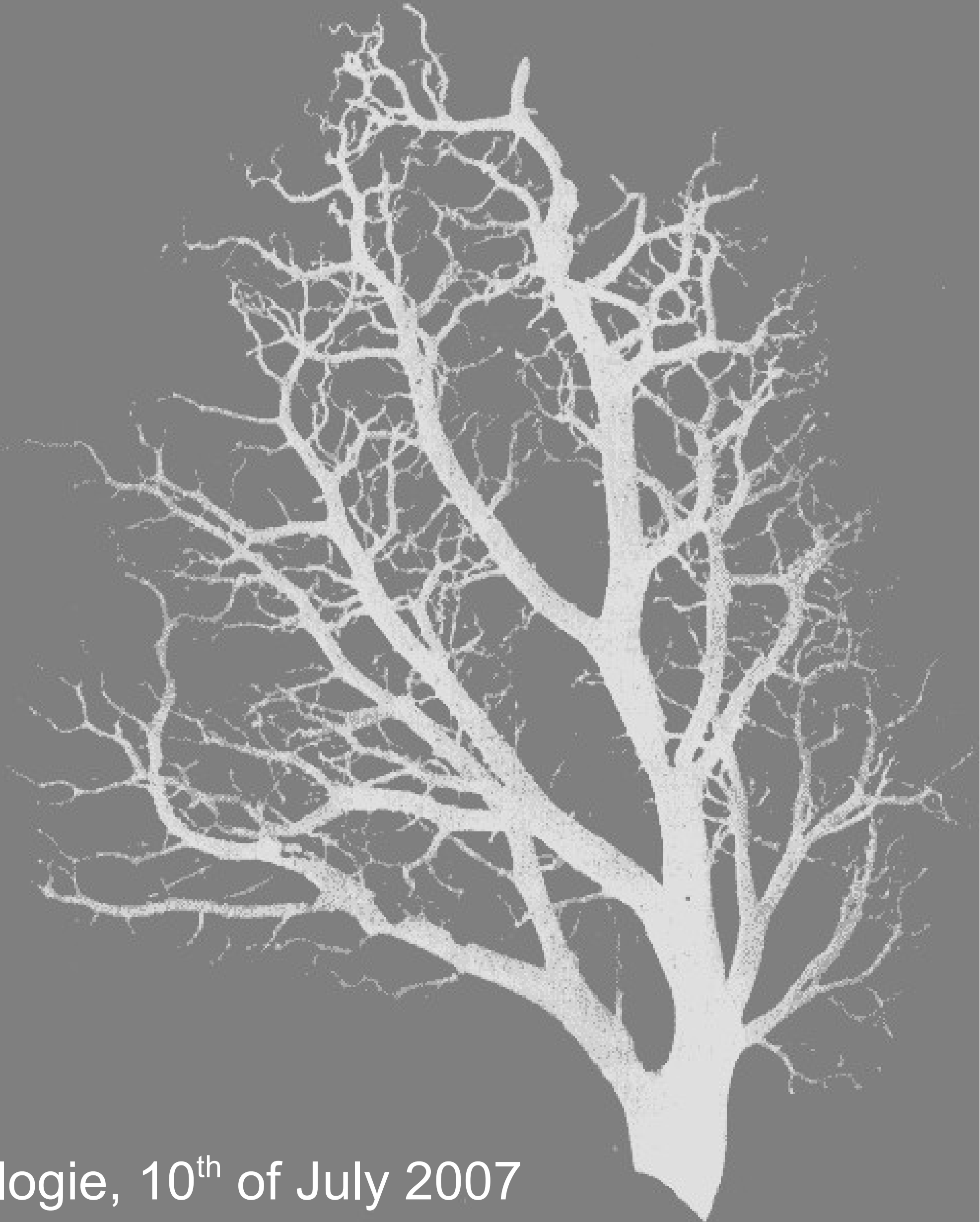
Respiratory		
Variable	**Exponent**	
	Predicted	**Observed**
Tracheal radius	3/8 = 0.375	0.39
Volume flow to lung	3/4 = 0.75	0.80
Respiratory frequency	-1/4 = -0.25	-0.26
Total resistance	-3/4 = -0.75	-0.70
Oxygen consumption rate	3/4 = 0.75	0.76



Allometric Scaling Laws In Nature pt. 3

Katharina Albers

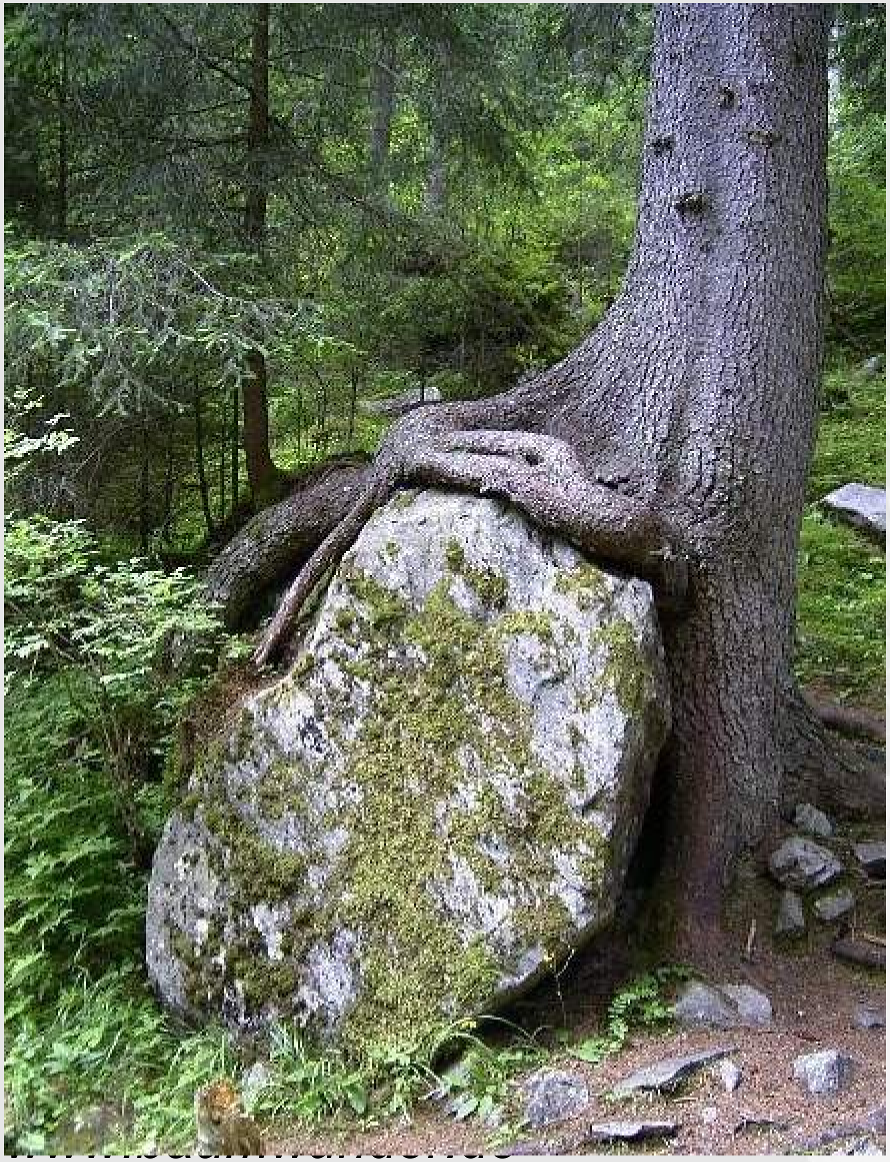
Gute Ideen in der theoretischen Systembiologie, 10th of July 2007



Motivation

Trees are the biggest and most durable organisms!

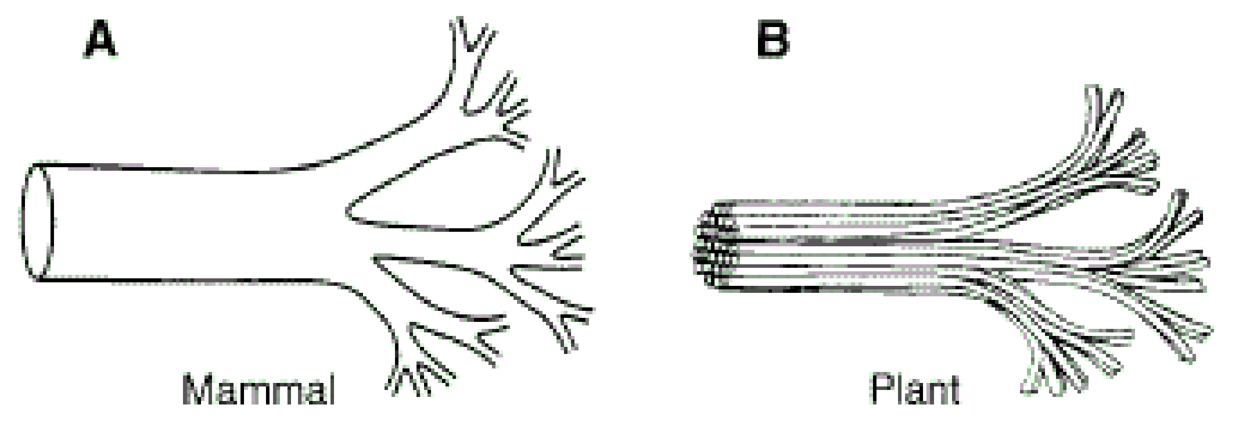
Why do they grow as they do?



Motivation

Scaling laws for trees

Diameter of aortas
Diameter of tree trunks
in both cases: b ≈ ⅜

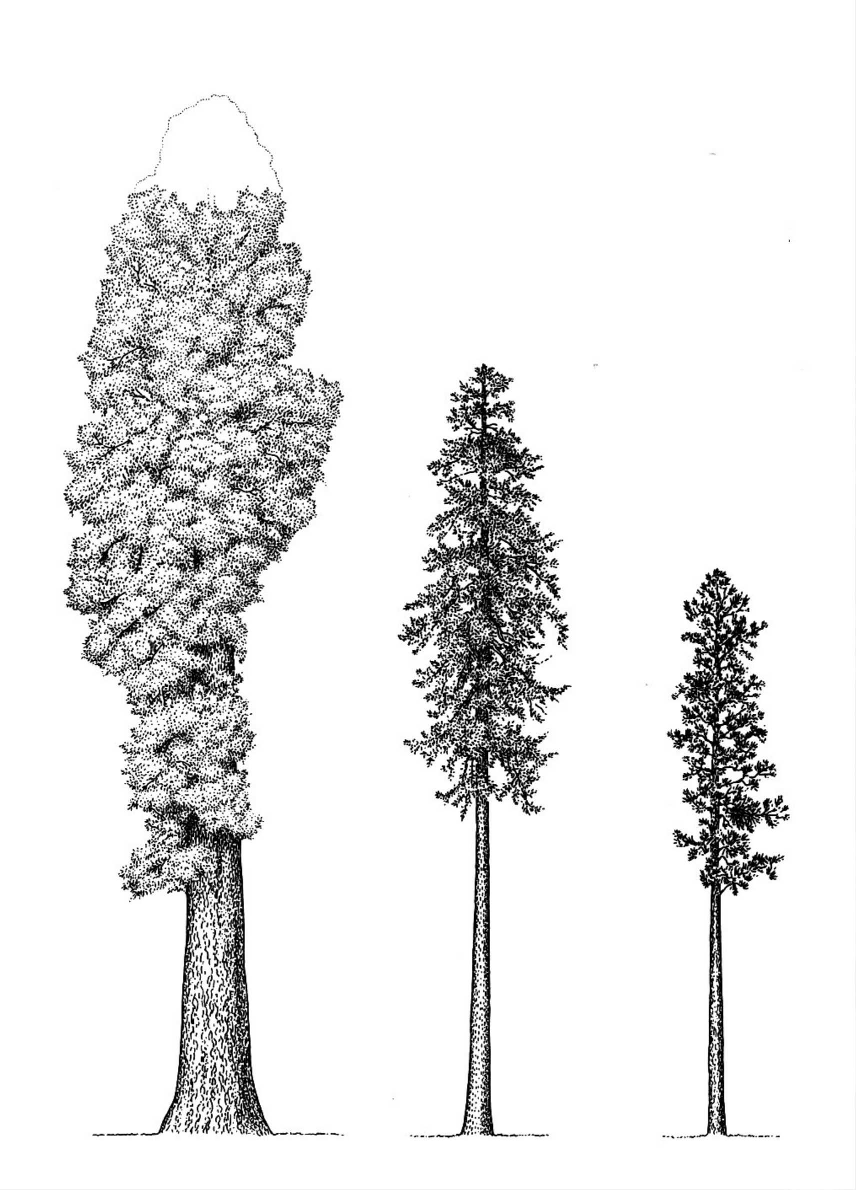


West et al: A General Model for ... (1997)

Scaling laws for trees

- Diameter of trunk in proportion to the height bigger in larger trees

- Can be explained with help of dimensional analysis



McMahon et al: Form und Leben (1985)

Dimensional Analysis

- Conceptual tool applied in physics, chemics and engineering
- To understand physical situations involving a mix of different kinds of physical quantities
- Used to form reasonable hypotheses about complex physical situations

- Example: Mach-number. Air stream around plane changes dramatically when it's faster than Sound. Dimensionless relation flight velocity/acoustic velocity given by Mach-number.

Scaling laws for trees

- Important variables:
  - Diameter
  - Height
  - Elastic modulus
  - Relative density

- Dimensional analysis yields:

$$\frac{Elastic\,modulus \cdot (Diameter)^2}{Gravity \cdot Relative\,density \cdot (Height)^3}$$

Scaling laws for trees

- Relation of elastic modulus and specific gravity alike for living wood

$\Rightarrow \frac{(Diameter)^2}{(Height)^3}$ nearly constant

$$Height \propto Diameter^{2/3}$$

Scaling laws for trees

Same conclusion by Greenhill in 1881, but with different arguments:

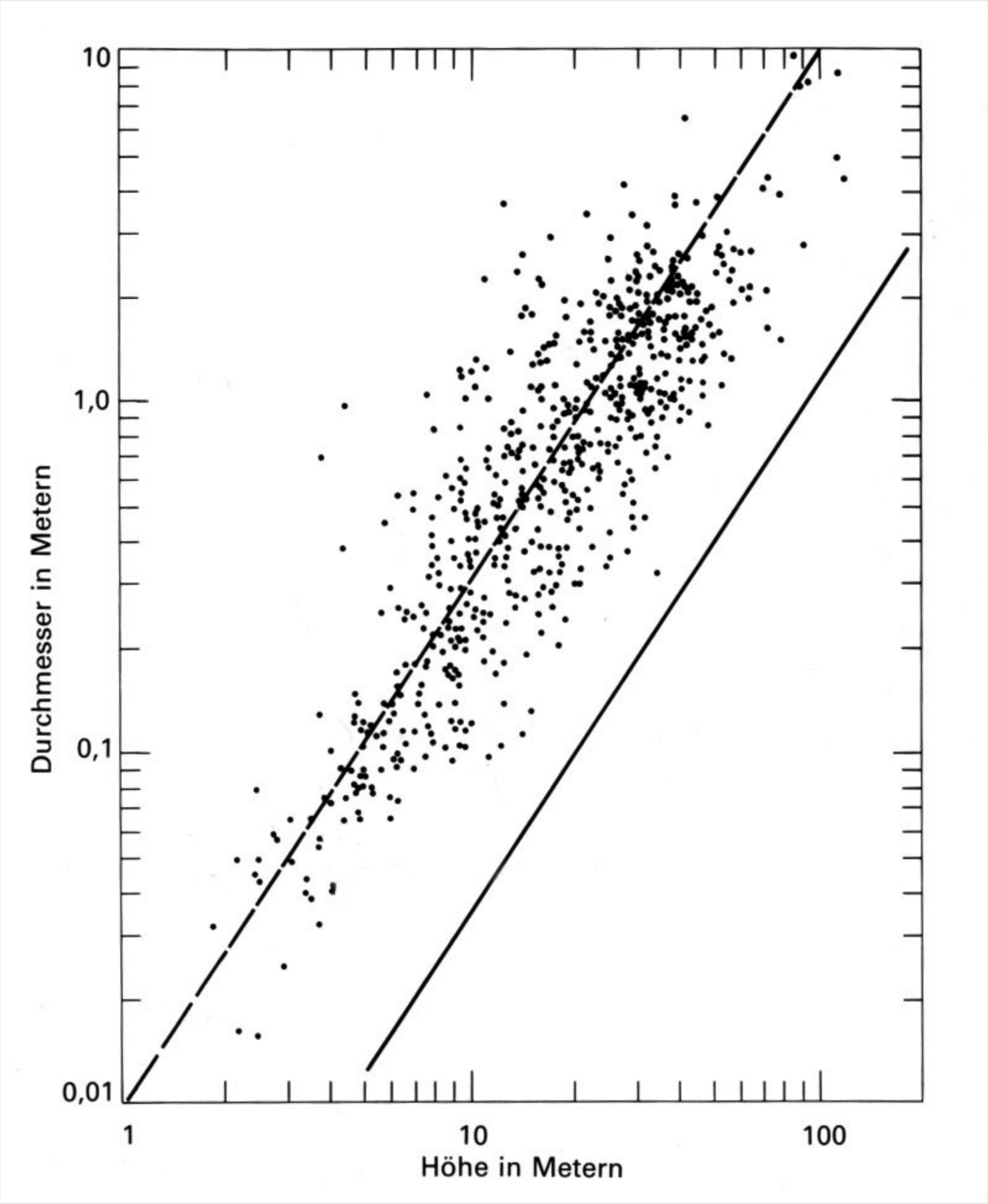
How high can a (cylindric) flag pole become without collapsing?

Laws of solid mechanics:

A pole with diameter 53 cm can be 91 m high at most.

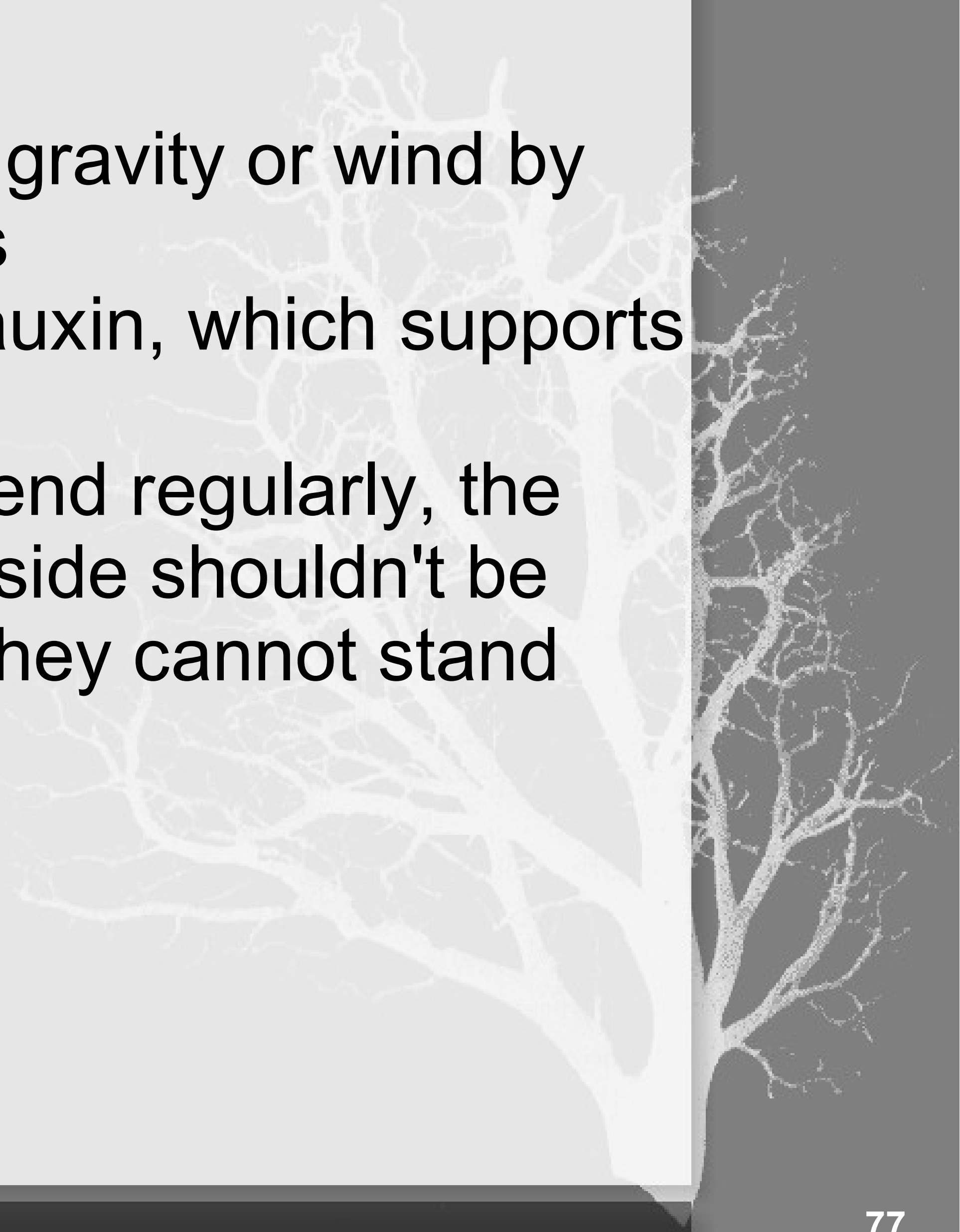
→ Complies with conclusion of dimensional analysis!!

Scaling laws for trees



McMahon et al: Form und Leben (1985)

Self-optimizing Trees



- Trees react on outer stimuli like gravity or wind by thickening according to the stress
- Controlled by growth hormone auxin, which supports growth of cambium
- If trees in the greenhouse are bend regularly, the trunk grows bigger, and trees outside shouldn't be supported for too long, because they cannot stand alone afterwards

Self-optimizing Trees

➡ stems represent a mechanical optimum with respect to tapering, branch and root junctions, and inner architecture

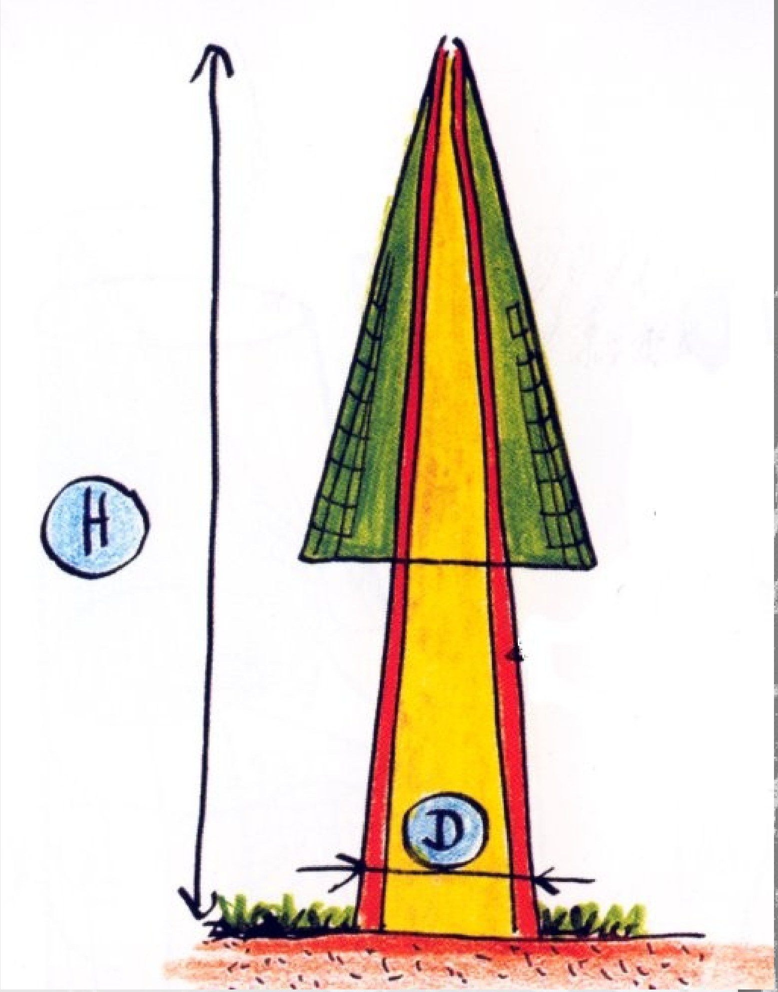
www.umdiewelt.de

Self-optimizing Trees

Trees are perfect self-adjusting optimizers:

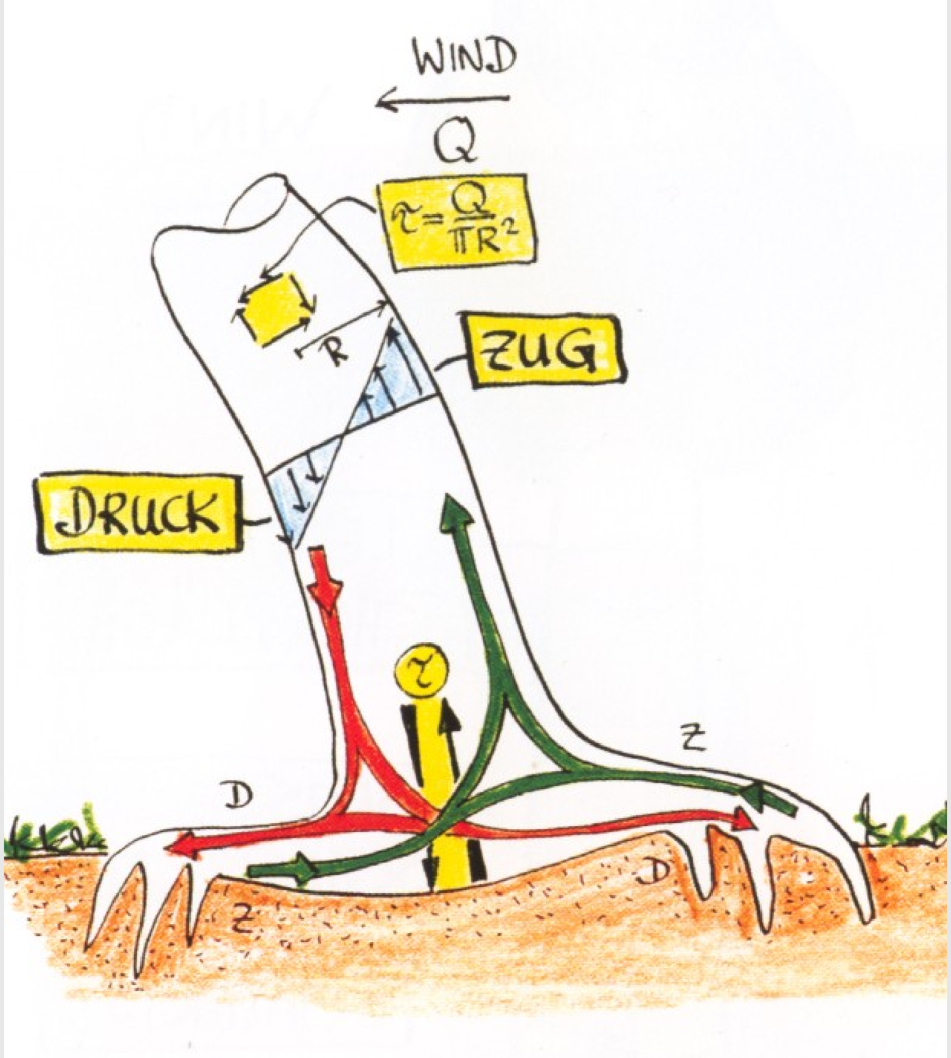
- grow according to forces
- aim at an even distribution of the mechanical stresses

→ Diameter of trunk increases downwards



Mattheck: Warum alles kaputt geht (2003)

Self-optimizing Trees

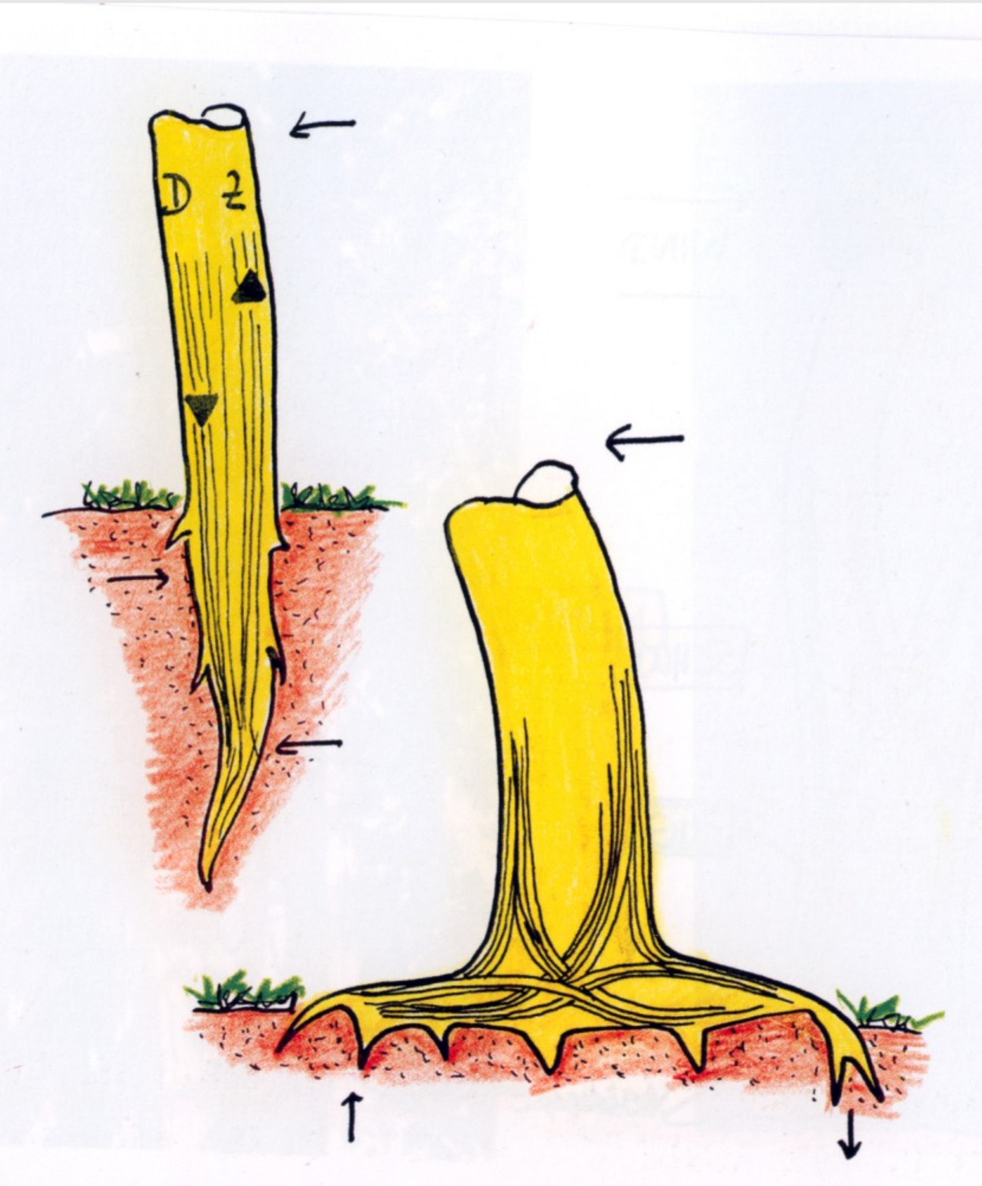


Mattheck: Warum alles kaputt geht (2003)

In transition of trunk and radix tractive efforts and compressive forces cross

Self-optimizing Trees

- Woodfibres run unfavourably



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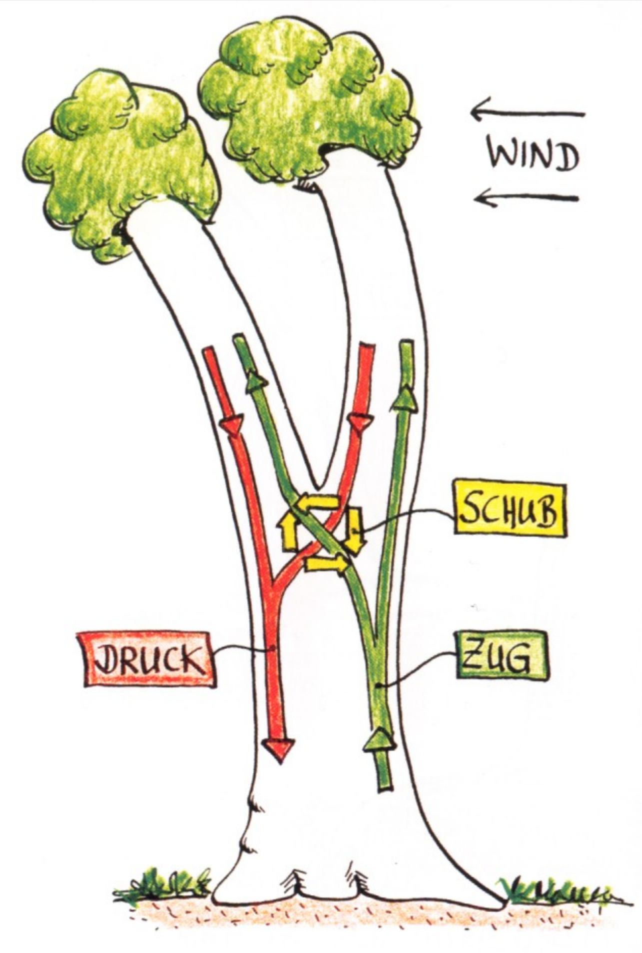
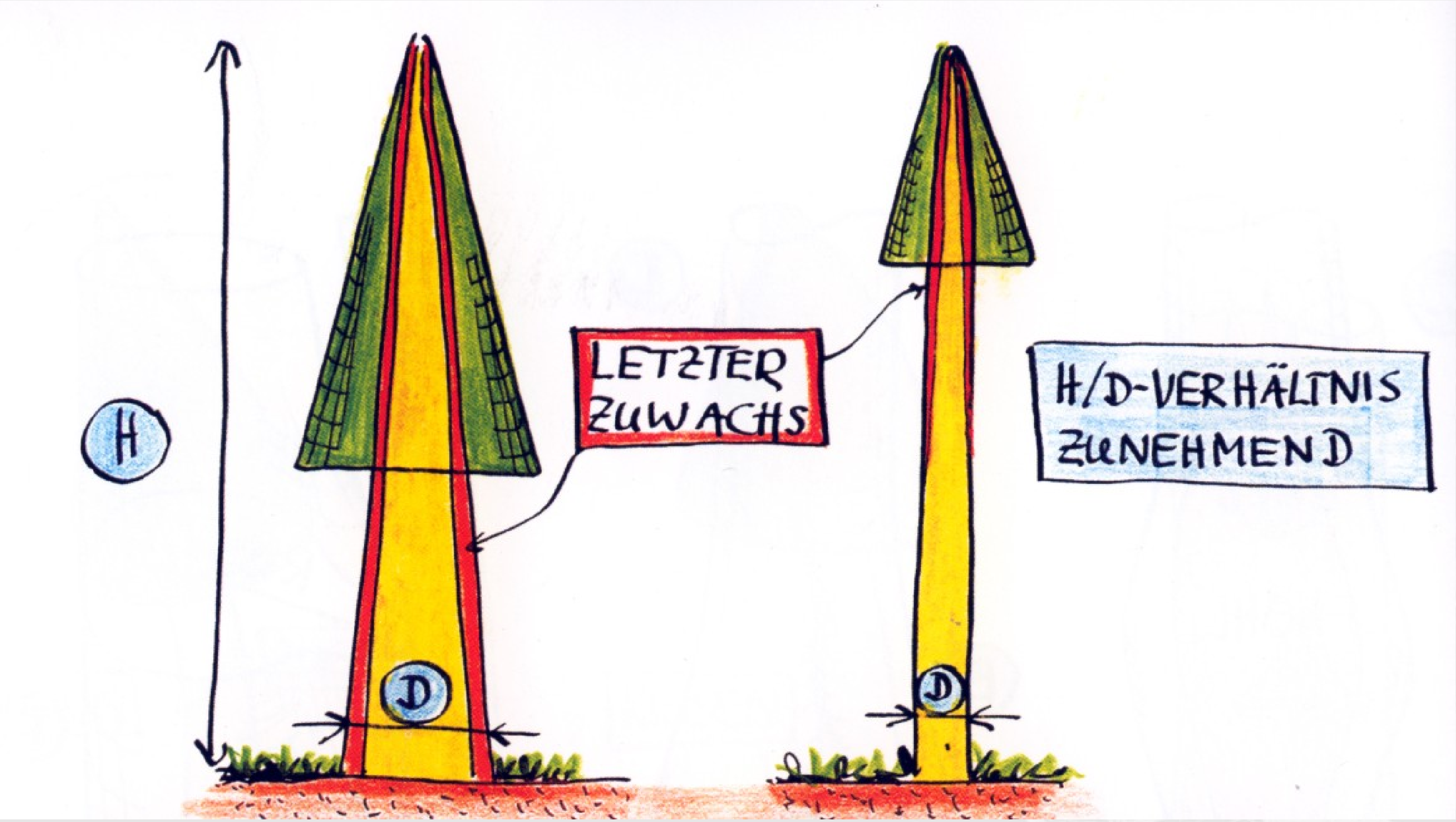
Self-optimizing Trees



Mattheck: Warum alles kaputt geht (2003)

- In bifurcations the same forces take effect

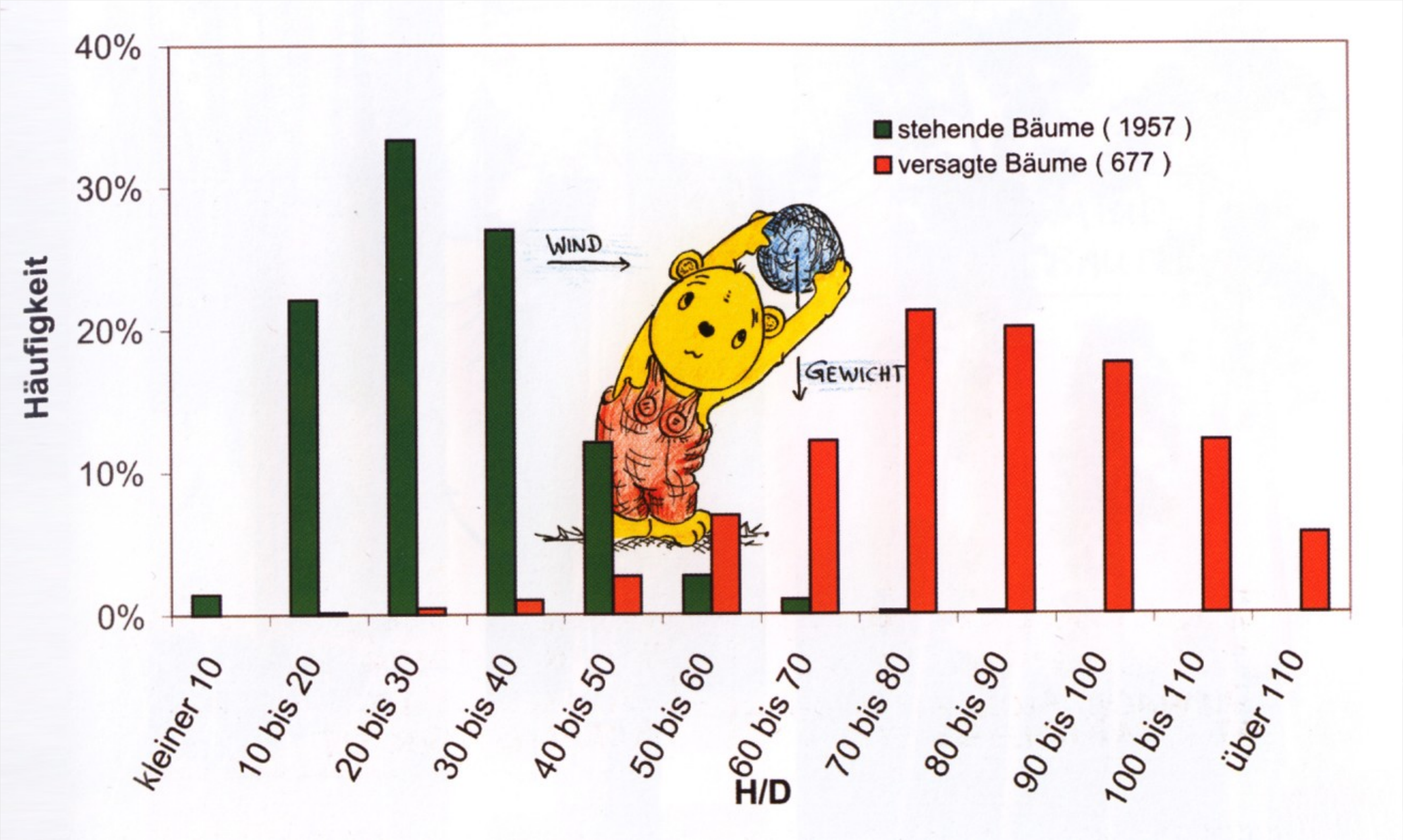
Self-optimizing Trees



Mattheck: Warum alles kaputt geht (2003)

- Increasing trunk-diameter only in vital trees with low top

Self-optimizing Trees

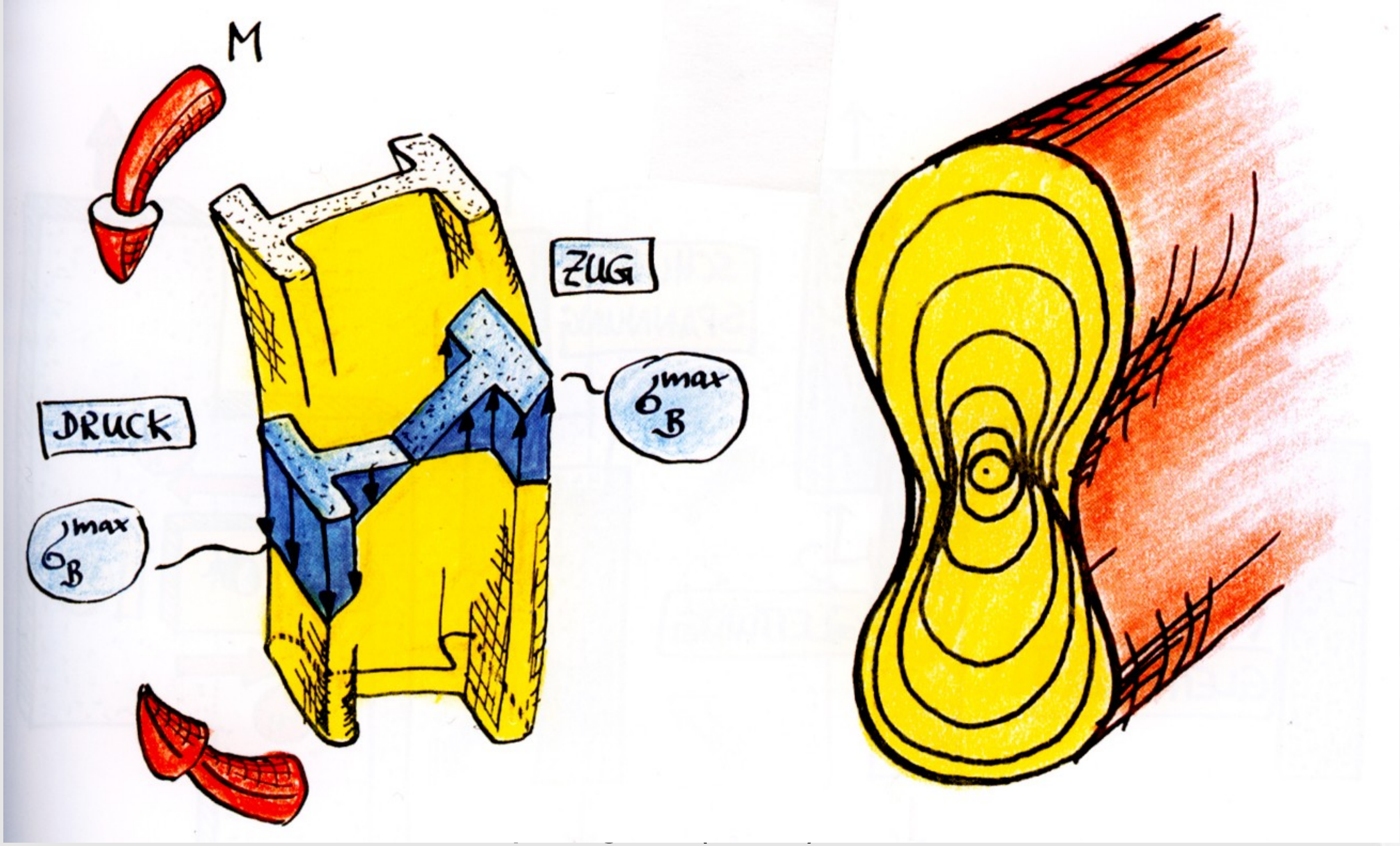


Mattheck: Warum alles kaputt geht (2003)

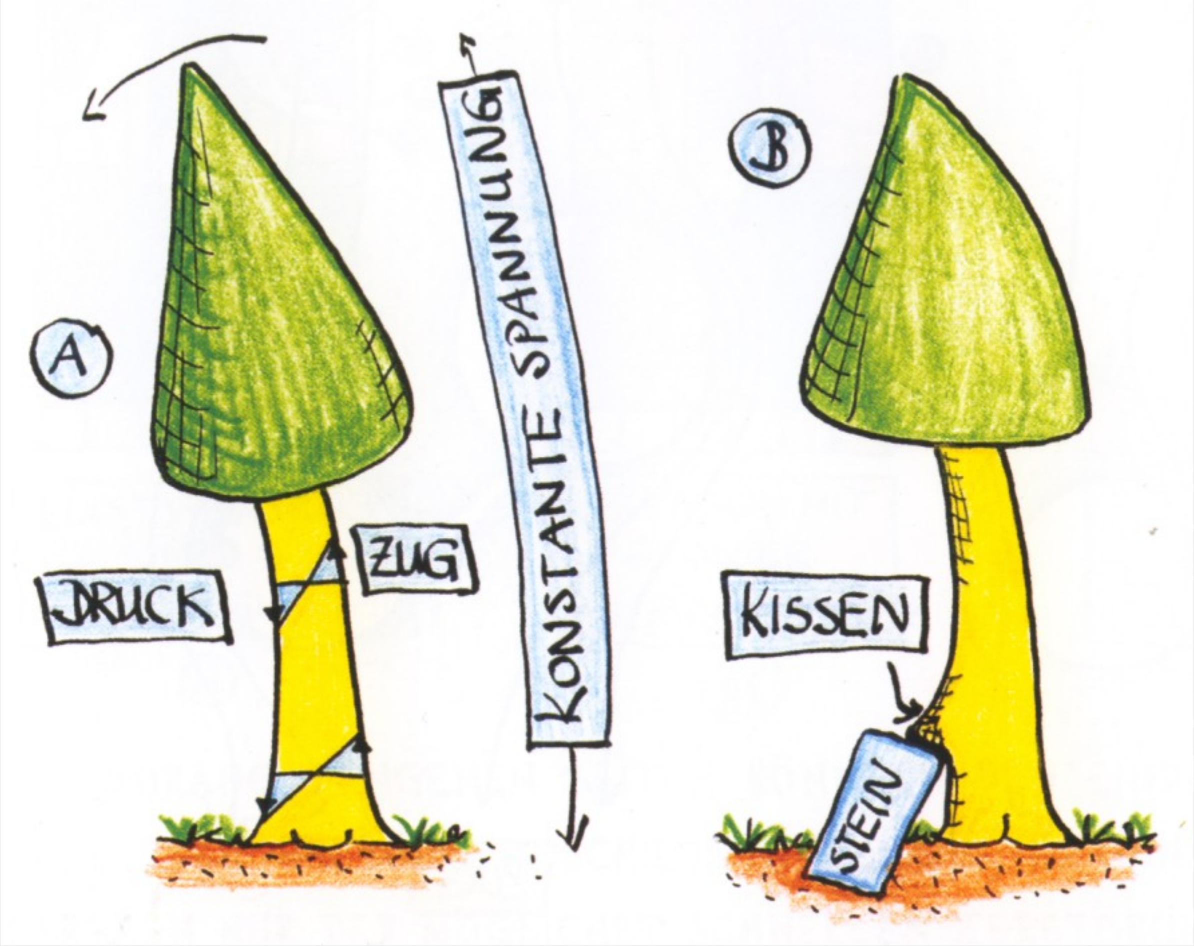
- Rule of thump: with relation H/D > 50, tree likely to collaps

Self-optimizing Trees

- Radix forms an eight, alike the I-beam



Self-optimizing Trees



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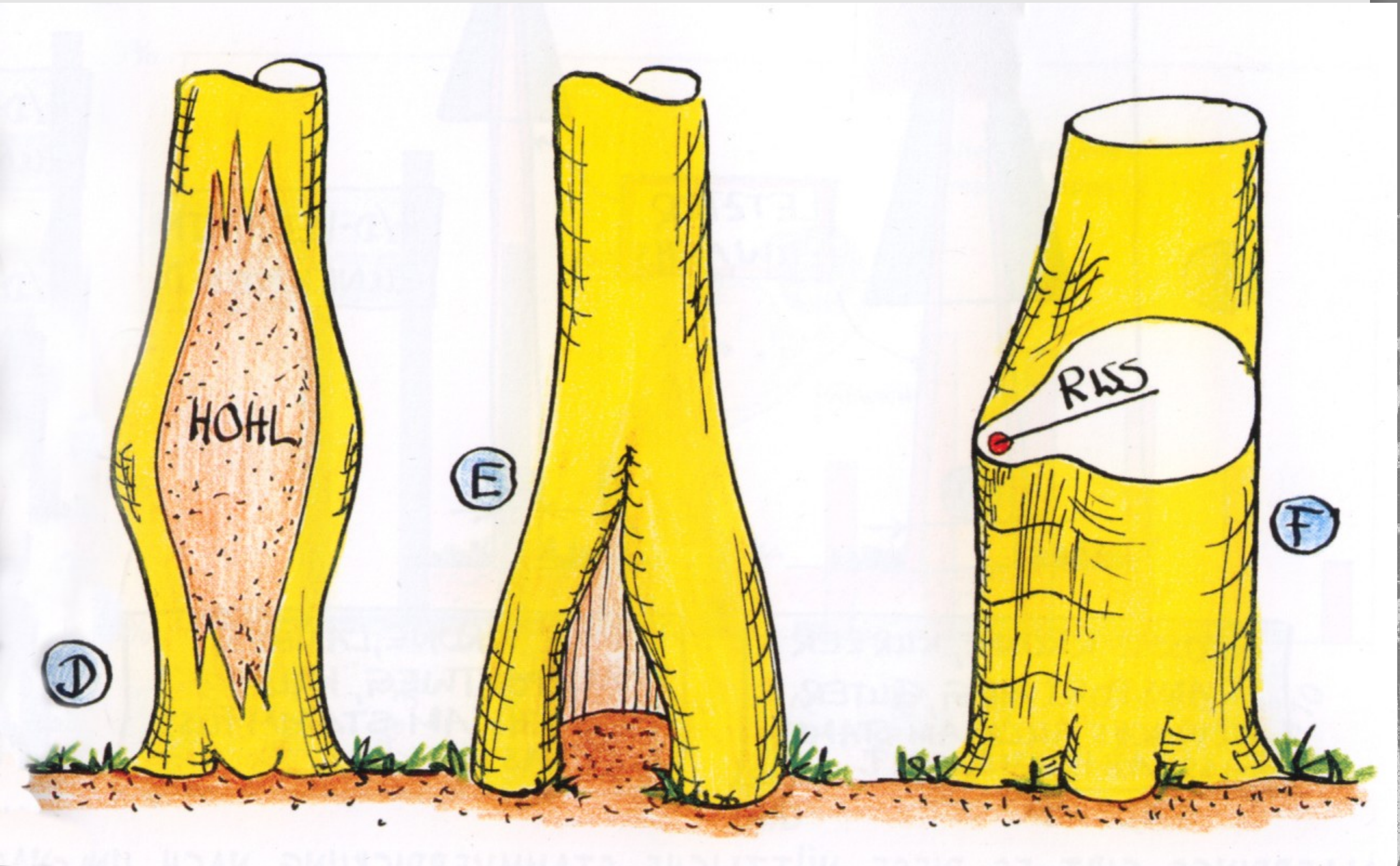
www.baumwunder.de

Self-optimizing Trees



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Self-optimizing Trees

Self-optimizing Trees

In tropical rain forest trees have huge wide-spread roots, because they grow very high

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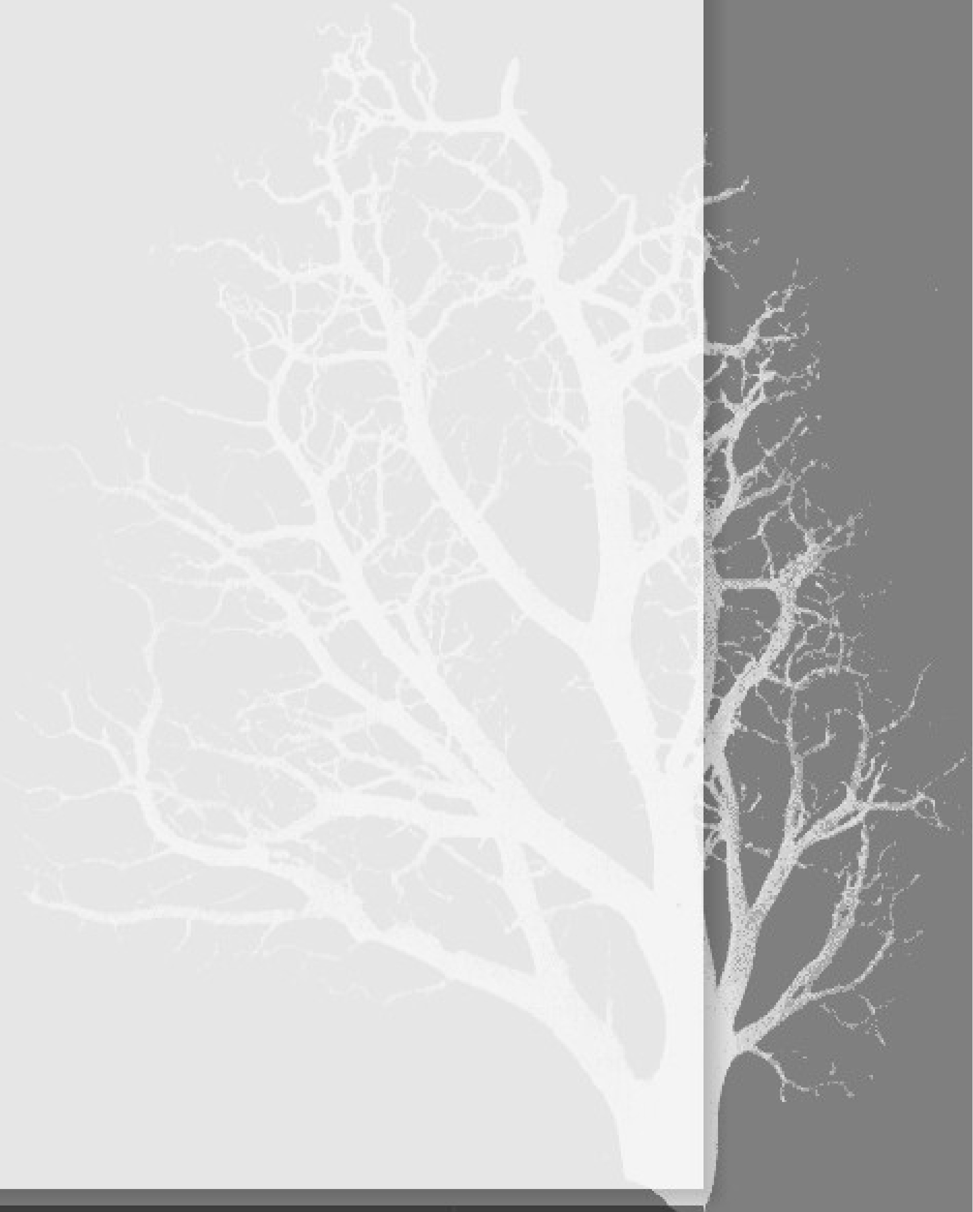

Pictures

(1) http://upload.wikimedia.org/wikipedia/de/3/3e/Charles_Darwin_1854.jpg

(2) http://upload.wikimedia.org/wikipedia/commons/d/d3/Gregor_Mendel.png

(3) http://www.smc-hamburg.de/bilder/veranstaltungen/anschippern2007/image/anschippern_2007_054.jpg

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