Physical Principles in Biology
Biology 3550
Spring 2024

Lecture 21:

Diffusion in Plants and Bacterial Locomotion

Wednesday, 28 February 2024

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Growth of a Hypothetical Plant

- 1 kg carbon per year, for net growth and replacement of leaves.
- Rate of CO_2 assimilation: 5×10^{-6} mol/s
- Assume 1,000 leaves of 1 cm^2 each:

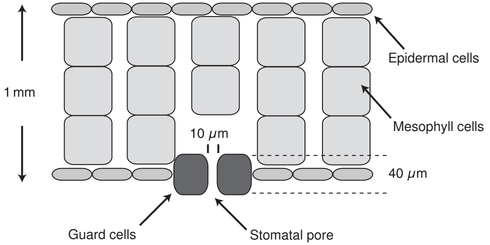
$$1,000\,\text{cm}^2 \times \left(\frac{1\,\text{m}}{100\,\text{cm}}\right)^2 = 0.1\,\text{m}^2$$

- Flux, per second, per unit of leaf area:

$$J = 5 \times 10^{-6}\,\text{mol/s} \div 0.1\,\text{m}^2$$
$$= 5 \times 10^{-5}\,\text{mol} \cdot \text{s}^{-1}\text{m}^{-2}$$

- But, diffusion does not take place across all of the leaf area.

Cross-section of a Plant Leaf



- CO_2 diffuses through stomata into leaf airspace.
- CO_2 diffuses into mesophyll cells and then into chloroplasts.
- CO_2 is reduced, or "fixed", into sugars by ribulose-1,5-bisphosphate carboxylase (Rubisco).
- Steady-state concentration of CO_2 in airspace is about 1/2 atmospheric concentration.

Diffusion of CO_2

- Diffusion coefficient of CO_2 at atmospheric pressure and 298 K:

  $$D = 1.5 \times 10^{-5}\,\mathrm{m}^2/\mathrm{s}$$

- Concentration gradient:

  $$\frac{dC}{dx} \approx 175\,\mathrm{mol} \cdot \mathrm{m}^{-4}$$

- Flux:

  $$J = -D\frac{dC}{dx} = -1.5 \times 10^{-5}\,\mathrm{m}^2/\mathrm{s} \times 175\,\mathrm{mol} \cdot \mathrm{m}^{-4}$$

  $$= -2.6 \times 10^{-3}\,\mathrm{mol} \cdot \mathrm{m}^{-2}\mathrm{s}^{-1}$$

How Many Stomata Does Our Plant Need?

- From before: $1\,\text{kg carbon/yr} = 5 \times 10^{-6}\,\text{mol/s}$
- Surface area required:

$$5 \times 10^{-6}\,\text{mol/s} = J\ (\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}) \times \text{area}\ (\text{m}^2)$$

$$\text{area} = 5 \times 10^{-6}\,\text{mol/s} \div 2.6 \times 10^{-3}\,\text{mol} \cdot \text{m}^{-2}\text{s}^{-1} \approx 0.002\,\text{m}^2$$

- Cross section area of a stoma: $\approx \pi(5 \times 10^{-6}\,\text{m})^2 \approx 10^{-10}\,\text{m}^2$
- Number of stomata:

$$0.002\,\text{m}^2 \div 10^{-10}\,\text{m}^2/\text{stoma} = 2 \times 10^7\,\text{stomata}$$

$$2 \times 10^4\,\text{stomata/cm}^2$$

The Big Problem

Water can diffuse out of leaves, through the open stomata!

- Diffusion coefficient for H_2O (in the atmosphere): $2.4 \times 10^{-5}\,\mathrm{m^2/s}$
- The leaf airspace is nearly saturated with water vapor, $\approx 1.3\,\mathrm{mol/m^3}$
- Immediately outside the leaf, [water] is $\approx 0.65\,\mathrm{mol/m^3}$
- Water vapor concentration gradient:

$$\frac{dC}{dx} \approx \frac{0.6\,\mathrm{mol/m^3}}{4 \times 10^{-5}\,\mathrm{m}} = 1.5 \times 10^4\,\mathrm{mol \cdot m^{-4}}$$

- Flux:

$$J = -D\frac{dC}{dx} = -2.4 \times 10^{-5}\,\mathrm{m^2/s} \times 1.5 \times 10^4\,\mathrm{mol \cdot m^{-4}}$$

$$= -0.4\,\mathrm{mol \cdot m^{-2}s^{-1}}$$

Compare to $-2.6 \times 10^{-3}\,\mathrm{mol \cdot m^{-2}s^{-1}}$ for CO_2.

Water Loss Through Stomata

- From requirement for CO_2 diffusion, total average surface area of open stomata: $0.002\,\mathrm{m}^2$
- Total water diffusion (transpiration) in a year:

$$\text{flux } (\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}) \times \text{surface area } (\text{m}^2) \times \text{time (s)}$$

$$= 0.4\,\text{mol} \cdot \text{m}^{-2}\text{s}^{-1} \times 0.002\,\text{m}^2 \times 1.5 \times 10^7\,\text{s}$$

$$= 1.2 \times 10^4\,\text{mol} \times 18\,\text{g/mol}$$

$$= 2 \times 10^5\,\text{g} = 200\,\text{kg}$$

$$\approx 50\,\text{gal}$$

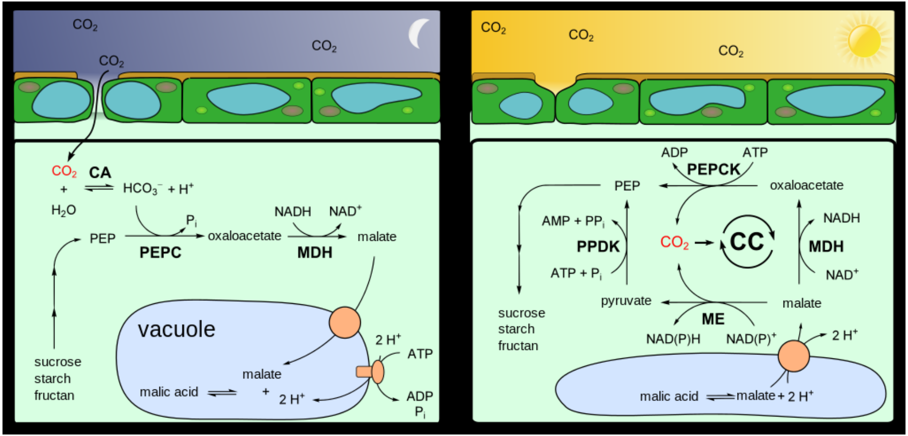
- Water directly used in fixation of 1 kg of carbon: 1.5 kg.

Consequences of Water Losses Through Stomata

- Stomata close when photosynthesis rate is low (*e.g.,* at night, but this is also when water loss is slowest).
- Stomata probably evolved for just this reason.
- All of the water has to pass through roots and stems of the plant. Structures of plants reflect the need to transport large amounts of water.
- For tall trees, there is a huge pressure difference between leaves and roots, which requires unbroken water flow. Bubbles are a big problem!
- Plants represent a very large flow of water from ground to atmosphere, with large potential impact on climate.
- All because diffusion can go both ways!

An Evolutionary Adaptation to the Water-loss Problem

The Crassulacean acid metabolism (CAM) cycle:

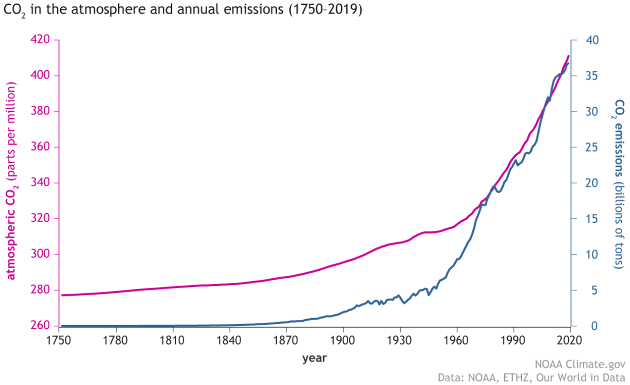


https://en.wikipedia.org/wiki/Crassulacean_acid_metabolism

The CAM cycle

- Stomata only open at night, CO_2 is fixed as malate and stored in vacuoles.
- During daylight, CO_2 is released from malate and used for photosynthesis (Calvin cycle).
- Reduces water loss, but requires more metabolic energy.
- Found in plants adapted to arid regions, including *Crassulacae*, such as jade plant.

What Happens When Atmospheric CO_2 Concentrations Change?

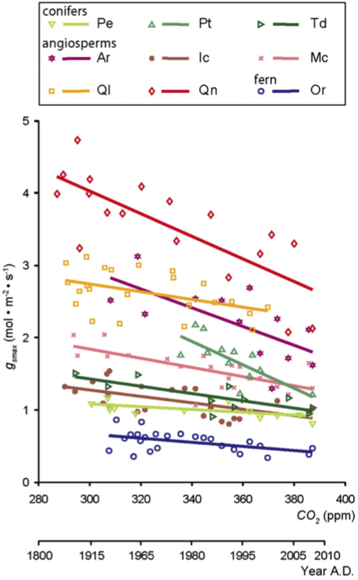


- 400 ppm = 16 μM
- How might plants adapt to this change?

Graph from National Oceanographic and Atmospheric Administration (NOAA)
https://www.climate.gov/news-features/understanding-climate/climate-change-atmospheric-carbon-dioxide

Changes in Stomatal Conductance Since 1880

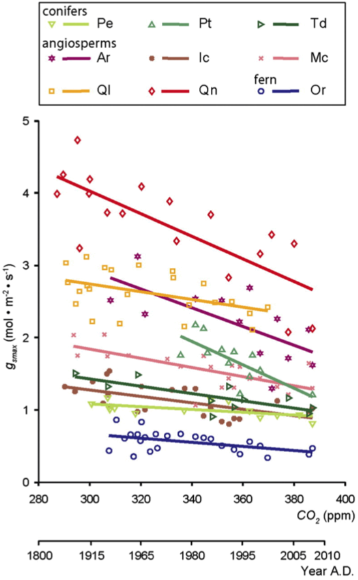
- Data based on examination of preserved leaves.
- g_{smax} = "anatomical maximum stomatal conductance to water vapor"
- Units: $\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$, units of flux, J.
- Reflects diffusion coefficient and stomatal pore area as fraction of leaf area.
- Depends on number of stomata per unit of surface area and dimensions of stomata.



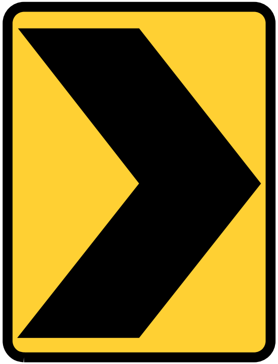
Lammersma, E. I., de Boer, H. J., Dekker, S. C., Ditcher, D. L., Lotter, A. F. & Wagner-Cremer, F. (2011). *Proc. Natl. Acad. Sci., USA*, 108, 4035–4040.
http://dx.doi.org/10.1073/pnas.1100371108

Changes in Stomatal Conductance Since 1880

- Change is primarily due to reduction in number of stomata.
- Change appears to be physiological, not genetic adaptation.
- Is this good or bad for the planet?



Warning!



Direction Change

Diffusion and Bacteria

Diffusion of a Bacterial Cell

- Assume a spherical cell with radius of 1 μm.
  (or an oblong cell with an "effective radius" of 1 μm)
- Use the Stokes–Einstein equation to estimate the diffusion coefficient in water.

$$D = \frac{kT}{6\pi\eta r}$$

$$\begin{aligned} k &= \text{Boltzmann's constant} = 1.38 \times 10^{-23}\,\text{Kg}\cdot\text{m}^2\text{s}^{-2}\text{K}^{-1} \\ T &= 300\,\text{K} \\ \eta &= \text{viscosity} = 1\,\text{centipoise} = 10^{-3}\,\text{Kg}\cdot\text{m}^{-1}\text{s}^{-1} \end{aligned}$$

$$D = 2 \times 10^{-13}\,\text{m}^2\text{s}^{-1}$$

- Compare to $2 \times 10^{-10}\,\text{m}^2/\text{s}$ for a small molecule (1 nm).
- D decreases by 10-fold for each 10-fold increase in radius.

Diffusion via a Random Walk

For diffusion along a single direction:

- Calculate $\langle x^2 \rangle$ (mean-square projection along the x-axis) directly from the diffusion coefficient and total time, t:

$$\langle x^2 \rangle = n\delta_x^2 = 2Dt$$

- The other two dimensions:

$$\langle y^2 \rangle = 2Dt$$

$$\langle z^2 \rangle = 2Dt$$

- Mean-square end-to-end distance in three dimensions:

$$\langle r^2 \rangle = \langle x^2 \rangle + \langle y^2 \rangle + \langle z^2 \rangle = 6Dt$$

Time to Diffuse a Given (RMS) Distance from the Starting Point

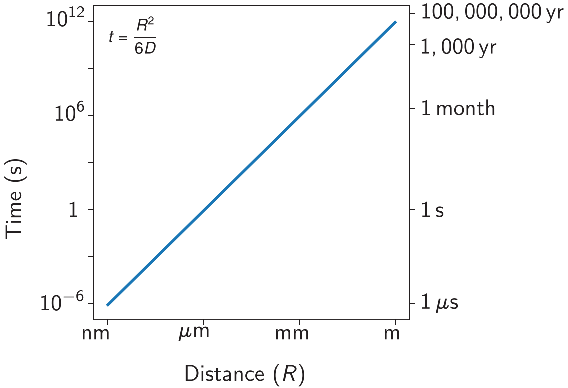
- $\langle r^2 \rangle = 6Dt$
- Solve for t for $\text{RMS}(r) = R$ (a specified value) and,

  $\langle r^2 \rangle = R^2$:

  $R^2 = 6Dt$

  $t = R^2/(6D)$

- For 1-μm bacterium, $D = 2 \times 10^{-13}\,\text{m}^2\text{s}^{-1}$.



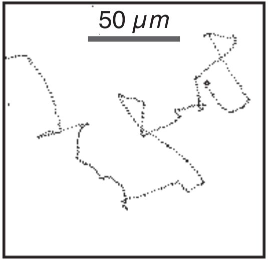
How is a bacterium to find food 1 mm ($\approx$ 1 month) away?

Bacteria Under the Microscope

(Swimming E. coli Movie)

- Movie from: http://www.rowland.harvard.edu/labs/bacteria

Tracking the path of a single *E. coli* Cell



30 seconds

- It looks like a random walk! (with variable step size)
- Step sizes are larger than the bacterium ($\approx 1\ \mu$m) and *much* larger than step sizes expected for diffusion.

Berg, H. & Brown, D. (1972). *Nature*, 239, 500–504.
http://dx.doi.org/10.1038/239500a0

Clicker Question #1

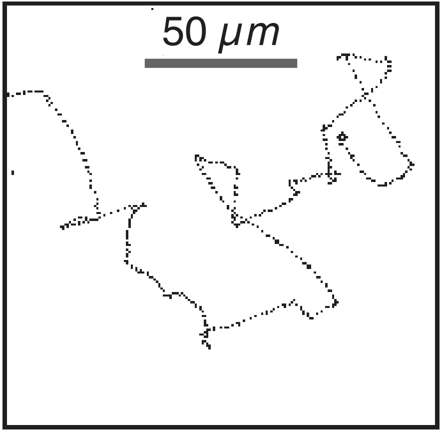
Estimate the average step length in the random walk (projection onto two dimensions).

A) 5 μm

B) 20 μm

C) 40 μm

D) 80 μm



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Clicker Question #2

Estimate the velocity of the bacterium
(projection onto two dimensions).

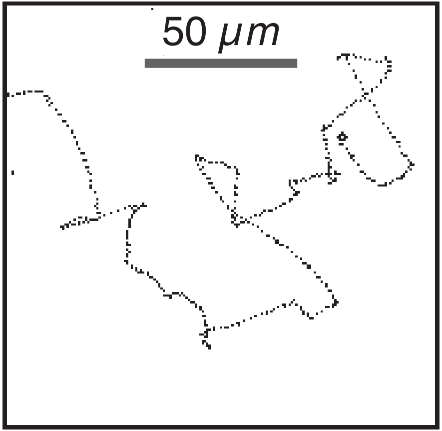
A) 10 μm/s

B) 20 μm/s

C) 40 μm/s

D) 80 μm/s

E) 200 μm/s



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Random Walk Parameters, in 3-dimensions

From careful analysis of 3-dimensional data:

- Average step length: $l = 60\,\mu\text{m}$
- Average velocity: $v = 20\,\mu\text{m}/\text{s}$
- Average duration of each step ("run"):

$$\tau = l/v = 60\,\mu\text{m} \div 20\,\mu\text{m}/\text{s}$$
$$= 3\,\text{s}$$

- Number of steps: $n = t/(3\,\text{s})$

Clicker Question #3

How long, on average, would it take an *E. coli* bacterium to travel 1 mm from it's starting place?

- Avg. step length: $l = 60\,\mu\text{m}$
- Avg. velocity: $v = 20\,\mu\text{m/s}$

A) 1 min

B) 10 min

C) 100 min

D) 1,000 min

E) 10,000 min

Time for a Bacterium to Travel 1 mm (RMS) Distance From the Starting Point

- Avg. step length: $l = 60\,\mu\text{m}$
- Avg. velocity: $v = 20\,\mu\text{m/s}$
- Avg. time per step: $\tau = l/v = 3\,\text{s}$
- Number of steps in time t: $n = t/3\,\text{s}$

$$\text{RMS}(r) = l\sqrt{n} = 1\,\text{mm} = 10^3\,\mu\text{m}$$

$$\langle r^2 \rangle = nl^2 = (10^3\,\mu\text{m})^2 = 10^6\,\mu\text{m}^2$$

$$(t/3\,\text{s}) \times (60\,\mu\text{m})^2 = 10^6\,\mu\text{m}^2$$

$$t = 3\,\text{s} \times \frac{10^6\,\mu\text{m}^2}{3600\,\mu\text{m}^2} = 833\,\text{s} \approx 14\,\text{min}$$

- Compare to $\approx$ 1 month for diffusion!
- A smaller number of longer steps in a given time period always goes further!