Physical Principles in Biology
Biology 3550
Fall 2017

Lecture 21

A Plant Faces Diffusion

and

Introduction to Bacterial Chemotaxis

Wednesday, 18 October

©David P. Goldenberg
University of Utah
goldenberg@biology.utah.edu

Clicker Question #1

How Far Apart are Molecules in Air?
(on average)

1. $\approx 1\,\mathrm{nm}$
2. $\approx 3\,\mathrm{nm}$
3. $\approx 10\,\mathrm{nm}$
4. $\approx 30\,\mathrm{nm}$
5. $\approx 100\,\mathrm{nm}$
6. $\approx 300\,\mathrm{nm}$

Correct answer counts for 3 points!

How Far Appart are Molecules in Air?

- The ideal gas law:

  $$PV = nRT$$

  $P =$ pressure, $V =$ volume, $n =$ no. of moles, $T =$ temperature.

  R = gas constant = $8.2\times10^{-5}\,\mathrm{m^3\cdot atm K^{-1} mol^{-1}}$

- Consider 1 mole of air molecules at atmospheric pressure and 298 K (25°C). What is the volume?

  $$V = \frac{nRT}{P} = \frac{1\,\mathrm{mol} \times 8.2\times10^{-5}\,\mathrm{m^3\cdot atm K^{-1} mol^{-1}} \times 298\,\mathrm{K}}{1\,\mathrm{atm}}$$

  $$= 2.44\times10^{-2}\,\mathrm{m^3}$$

How Far Apart are Molecules in Air?

- Volume of 1 mole of air at atmospheric pressure and room temperature:

$$V = 2.44\times10^{-2}\,\mathrm{m}^3$$

- Suppose that the molecules are evenly distributed in the volume, and we divide up the volume into little cubes around each molecule. What is the volume of each cube?

$$\begin{aligned} V &= 2.44\times10^{-2}\,\mathrm{m}^3/\mathrm{mol} \div 6.02\times10^{23}\,\mathrm{molecules}/\mathrm{mol} \\ &= 4\times10^{-26}\,\mathrm{m}^3/\mathrm{molecule} \end{aligned}$$

- How long are the edges of the cubes?

$$l = \sqrt[3]{4\times10^{-26}\,\mathrm{m}^3} = 3.4\times10^{-9}\,\mathrm{m} = 3.4\,\mathrm{nm}$$

Diffusion in Gasses

- Diffusion coefficients of gasses: $\approx 2\times10^{-5}\,\mathrm{m^2/s}$
- From a previous lecture: RMS velocity of $N_2 \approx 300\,\mathrm{m/s}$.
- $D = \delta_x^2/(2\tau)$, and $v = \delta_x/\tau$

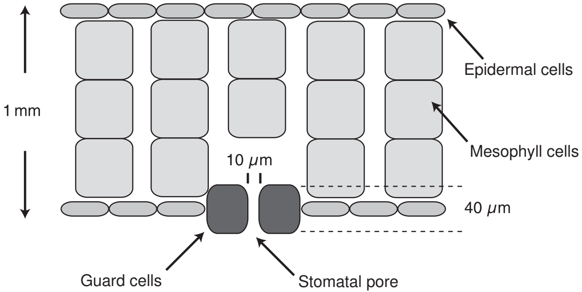
  $$\delta_x = 2D/v = 1.3\times10^{-7}\,\mathrm{m} = 130\,\mathrm{nm}$$

  The “mean-free-path” distance.
- Average distance between molecules $\approx 3\,\mathrm{nm}$.
- Approximate dimension of an air molecule (N_2 or O_2): 0.3 nm.

Growth of a Hypothetical Plant

- 1 kg carbon per year, for net growth and replacement of leaves.
- Total leaf area: $\approx 0.1\,\text{m}^2$
- Requires about 5×10^{-6} mol/s of CO_2 (during daylight)
- Flux, per second per unit leaf area: $5\times10^{-5}\,\text{mol}\cdot\text{s}^{-1}\text{m}^{-2}$
- 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 at atmospheric pressure and 298 K:

  $D = 1.5\times10^{-5}\,\text{m}^2/\text{s}$.

- Concentration gradient:
  - Atmospheric CO_2 concentration: $15\,\mu\text{M} = 1.5\times10^{-2}\,\text{mol}/\text{m}^3$. ($\approx 400$ ppmv)
  - CO_2 concentration in leaf airspace: $7.5\,\mu\text{M} = 7.5\times10^{-3}\,\text{mol}/\text{m}^3$
  - Length of stomatal pore: $\approx 40\,\mu\text{m} = 4\times10^{-5}\,\text{m}$

$$\frac{dC}{dx} \approx \frac{7.5\times10^{-3}\,\text{mol}/\text{m}^3}{4\times10^{-5}\,\text{m}} = 175\,\text{mol}\cdot\text{m}^{-4}$$

- Flux:

$$J = -D\frac{dC}{dx} = -1.5\times10^{-5}\,\text{m}^2/\text{s} \times 175\,\text{mol}\cdot\text{m}^{-4}$$

$$= -2.6\times10^{-3}\,\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$$

How Many Stomata Does Our Plant Need?

- From before: $1\,\text{kg carbon/yr} = 5\times10^{-6}\,\text{mol/s}$
- Surface area required:

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

$$\text{area} = 5\times10^{-6}\,\text{mol/s} \div 2.6\times10^{-3}\,\text{mol}\cdot\text{m}^{-2}\text{s}^{-1} \approx 0.002\,\text{m}^2$$

- Cross section area of a stoma: $\approx \pi(5\times10^{-6}\,\text{m})^2 \approx 10^{-10}\,\text{m}^2$
- Number of stomata:

$$0.002\,\text{m}^2 \div 10^{-10}\,\text{m}^2/\text{stoma} = 2\times10^7\,\text{stomata}$$

- If total leaf surface area is $0.1\,\text{m}^2$ and each leaf is $\approx 1\,\text{cm}^2 = 1\times10^{-4}\,\text{m}^2$
  - Stomata represent $\approx 2\%$ of leaf area.
  - About 20,000 stomata per leaf, or 200 stomata/mm^2 of leaf area.
  - This is a minimal estimate of open stomata.
    Actual numbers of stomata are typically 100-1,000 per mm^2 of leaf area.
    Exact number varies with plant species and environmental conditions.

The Big Problem

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

Clicker Question #2

Which gas has the largest diffusion coefficient in the atmosphere?

1. N_2
2. O_2
3. H_2O
4. CO_2

But, the differences are not huge!

The Big Problem

Water can diffuse <u>out</u> of leaves, through the open stomata!

- Diffusion coefficient for H_2O: $2.4\times10^{-5}\ \mathrm{m}^2/\mathrm{s}$
- The leaf airspace is nearly saturated with water vapor, $\approx 1.3\ \mathrm{mol}\cdot\mathrm{m}^3$
- Immediately outside the leaf, [water] is $\approx 0.65\ \mathrm{mol}\cdot\mathrm{m}^3$
- Water vapor concentration gradient:

$$\frac{dC}{dx} \approx \frac{0.6\ \mathrm{mol}/\mathrm{m}^3}{4\times10^{-5}\ \mathrm{m}} = 1.5\times10^4\ \mathrm{mol}\cdot\mathrm{m}^{-4}$$

- Flux:

$$J = -D\frac{dC}{dx} = -D = 2.4\times10^{-5}\ \mathrm{m}^2/\mathrm{s} \times 1.5\times10^4\ \mathrm{mol}\cdot\mathrm{m}^{-4}$$

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

Compare to $-2.6\times10^{-3}\ \mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1}$ 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:

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

$$= 0.4\,\mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1} \times 0.002\,\mathrm{m}^2 \times 1.5\times10^7\,\mathrm{s}$$

$$= 1.2\times10^4\,\mathrm{mol} \times 18\,\mathrm{g/mol}$$

$$= 2\times10^5\,\mathrm{g} = 200\,\mathrm{kg}$$

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

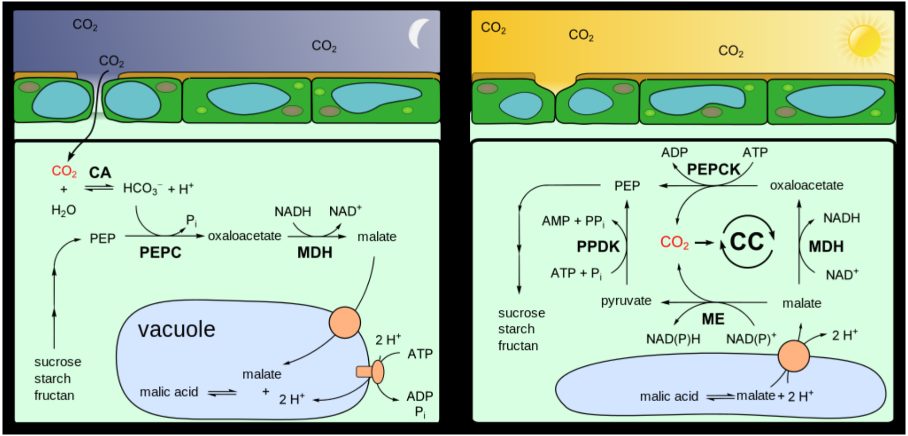
- Water directly used in fixation of 1 kg of CO_2: 1.4 kg.

Consequences of Water Losses Through Stomata

- Stomata close when photosynthesis rate is low (*e.g.,* at night, but this 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:

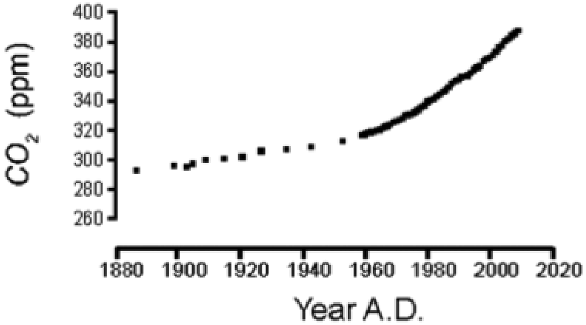


https://en.wikipedia.org/wiki/Crassulacean_acid_metabolism

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?

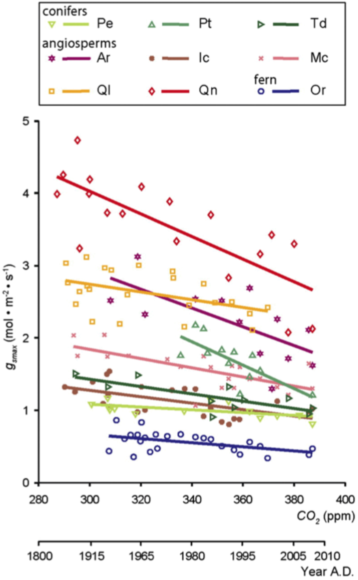


- 400 ppm = 16 μM
- How might plants adapt to this change?

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

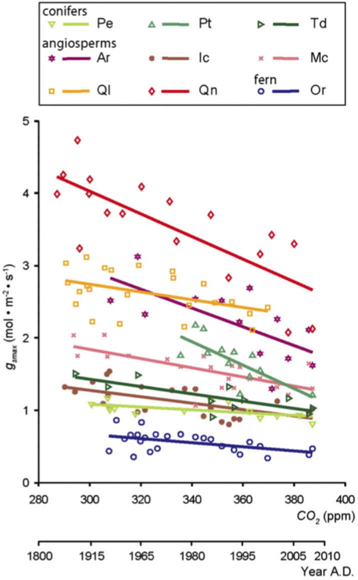
Changes in Stomatal Conductance Since 1880

- 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.
- Data based on examination of preserved leaves.



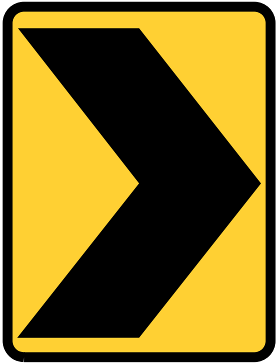
Changes in Stomatal Conductance Since 1880

- 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?



Proc. Natl. Acad. Sci., USA, 108, 4035–4040.
http://dx.doi.org/10.1073/pnas.1100371108

Warning!



Direction Change

How (Some) Bacteria Get Around

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.

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

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

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

- Compare to $2\times 10^{-10}\,\mathrm{m}^2/\mathrm{s}$ 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:

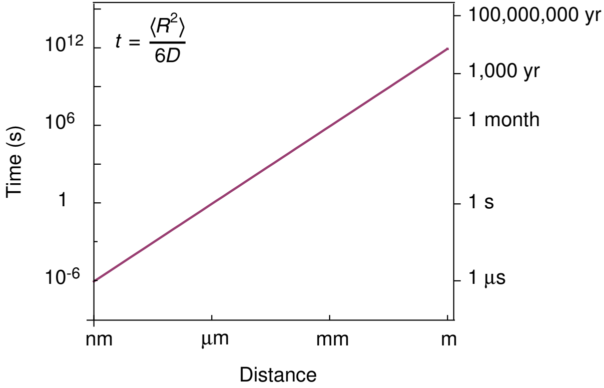
$$\langle r^2 \rangle = \langle x^2 \rangle + \langle y^2 \rangle + \langle z^2 \rangle = 6Dt$$

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

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

$$R^2 = 6Dt$$

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



- For 1-μm bacterium, $D = 2 \times 10^{-13}\ \mathrm{m^2 s^{-1}}$.
- How is a bacterium to find food 1 mm ($\approx$ 1 week) away?

Bacteria Under the Microscope

(Swimming E. coli Movie)

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