Physical Principles in Biology
Biology 3550
Fall 2018

Lecture 22:

A Plant Faces Diffusion (Part II)

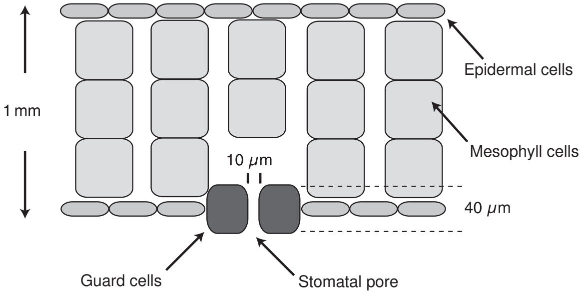
Monday, 22 October 2018

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

Growth of a Hypothetical Plant

- 1 kg carbon per year, for net growth and replacement of leaves.
- Total rate of CO_2 assimilation: 5×10^{-6} mol/s
- Estimated leaf area: $\approx 0.1\,\mathrm{m}^2$

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:

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

- Concentration gradient:
  - Atmospheric CO_2 concentration: $15\,\mu\mathrm{M} = 1.5 \times 10^{-2}\ \mathrm{mol/m^3}$. ($\approx$ 400 ppm)
  - CO_2 concentration in leaf airspace: $7.5\,\mu\mathrm{M} = 7.5 \times 10^{-3}\ \mathrm{mol/m^3}$
  - Length of stomatal pore: $\approx 40\,\mu\mathrm{m} = 4 \times 10^{-5}\ \mathrm{m}$

$$\frac{dC}{dx} \approx \frac{7.5 \times 10^{-3}\ \mathrm{mol/m^3}}{4 \times 10^{-5}\ \mathrm{m}} = 175\ \mathrm{mol \cdot m^{-4}}$$

- Flux:

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

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

Group Problem #1

- Plant's carbon requirement: $1\,\mathrm{kg\ \ carbon/yr} = 5\times10^{-6}\,\mathrm{mol/s}$
- Flux of CO_2 through stomata: $-2.6\times10^{-3}\,\mathrm{mol\cdot m^{-2}s^{-1}}$
- Length of stomatal pores: $\approx 40\,\mu\mathrm{m}$
- Diameter of stomatal pores: $\approx 10\,\mu\mathrm{m}$
- How many stomata does the plant need?

How Many Stomata Does Our Plant Need?

- Plant's carbon requirement: $1\,\mathrm{kg\ \ carbon/yr} = 5\times10^{-6}\,\mathrm{mol/s}$
- Flux of CO_2 through stomata: $-2.6\times10^{-3}\,\mathrm{mol\cdot m^{-2}s^{-1}}$
- Surface area required:

$$5\times10^{-6}\,\mathrm{mol/s} = J\ \ (\mathrm{mol\cdot m^{-2}s^{-1}}) \times \text{area}\ (\mathrm{m^2})$$

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

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

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

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

The Big Problem

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

Group Problem #3

- Diffusion coefficient for H_2O: $2.4\times10^{-5}\ \mathrm{m^2/s}$
- The leaf airspace is nearly saturated with water vapor, $\approx 1.3\ \mathrm{mol/m^3}$
- Immediately outside the leaf, $[\mathrm{water}]$ is $\approx 0.65\ \mathrm{mol/m^3}$
- Length of stomatal pores: $\approx 40\ \mu\mathrm{m}$
- Diameter of stomatal pores: $\approx 10\ \mu\mathrm{m}$
- Calculate the flux, J, of water through the stomata.

Flux of Water Through Stomata

- Diffusion coefficient for H_2O: $2.4\times10^{-5}\,\mathrm{m^2/s}$
- The leaf airspace is nearly saturated with water vapor, $\approx 1.3\,\mathrm{mol/m^3}$
- Immediately outside the leaf, $[\mathrm{water}]$ is $\approx 0.65\,\mathrm{mol/m^3}$
- Length of stomatal pores: $\approx 40\,\mu\mathrm{m}$
- Water vapor concentration gradient:

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

- Flux:

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

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

Compare to $-2.6\times10^{-3}\,\mathrm{mol\cdot m^{-2}s^{-1}}$ for CO_2.

Group Problem #3

- From requirement for CO_2 diffusion, total average surface area of open stomata: $0.002\,\text{m}^2$
- Flux of water through stomata: $chris.clinker@utah.edu 0.4\,\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$
- Calculate the total amount of water (kg) passing through the stomata per year.

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:

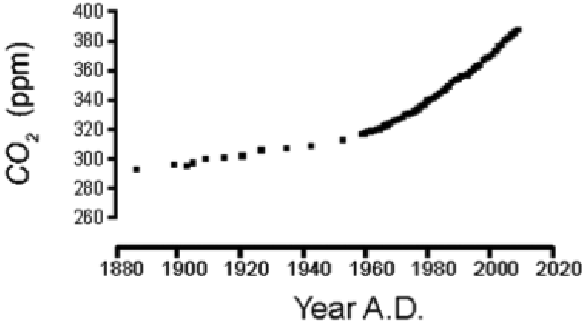
$$
\begin{aligned}
&\text{flux } (\mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1}) \times \text{surface area } (\mathrm{m}^2) \times \text{time } (\mathrm{s}) \\
&= 0.4\,\mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1} \times 0.002\,\mathrm{m}^2 \times 1.5\times10^7\,\mathrm{s} \\
&= 1.2\times10^4\,\mathrm{mol} \times 18\,\mathrm{g/mol} \\
&= 2\times10^5\,\mathrm{g} = 200\,\mathrm{kg} \\
&\approx 50\,\mathrm{gal}
\end{aligned}
$$

- 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!

What Happens When Atmospheric CO_2 Concentrations Change?

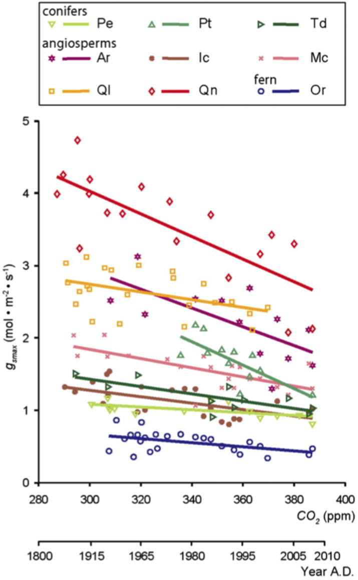


- 400 ppm = 16 μM
- How might plants adapt to this change?

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

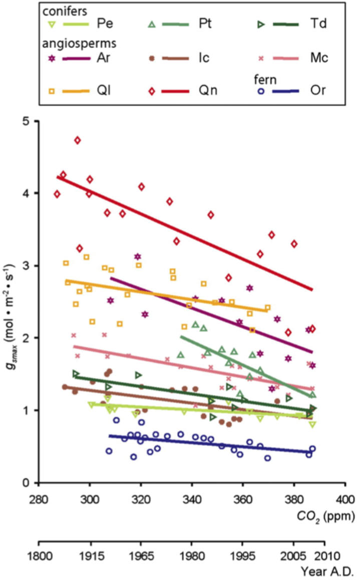
Changes in Stomatal Conductance Since 1880

- g_{smax} = "anatomical maximum stomatal conductance to water vapor"
- Units: $\mathrm{mol \cdot m^{-2} s^{-1}}$, 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.



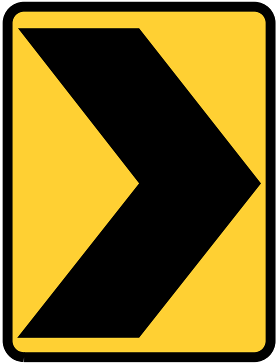
Changes in Stomatal Conductance Since 1880

- 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.

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

$$k = \text{Boltzmann's constant} = 1.38\times10^{-23}\,\mathrm{Kg}\cdot\mathrm{m}^2\mathrm{s}^{-2}\mathrm{K}^{-1}$$

$$T = 300\,\mathrm{K}$$

$$\eta = \text{viscosity} = 1\,\text{centipoise} = 10^{-3}\,\mathrm{Kg}\cdot\mathrm{m}^{-1}\mathrm{s}^{-1}$$

$$D = 2\times10^{-13}\,\mathrm{m}^2\mathrm{s}^{-1}$$

- Compare to $2\times10^{-10}\,\mathrm{m}^2/\mathrm{s}$ 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:

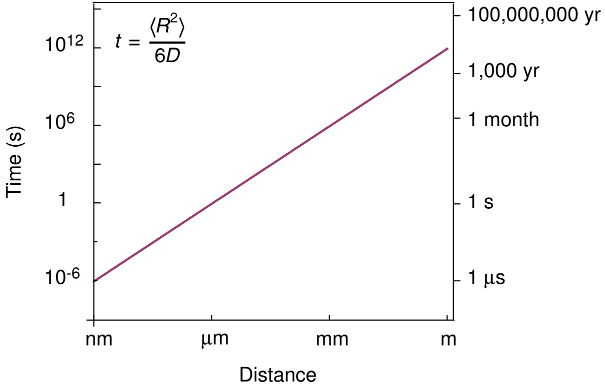
$$\langle r^2 \rangle = \langle x^2 \rangle + \langle y^2 \rangle + \langle z^2 \rangle = 6Dt$$

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 ($\approx 1\,\mathrm{month}$) away?