Physical Principles in Biology Biology 3550 Spring 2025

Lecture 21:

#### Diffusion in Plants and Bacterial Locomotion

Wednesday, 26 February 2025 ©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.
- Rate of CO<sub>2</sub> assimilation: 5×10<sup>-6</sup> mol/s
- Assume 1,000 leaves of 1 cm<sup>2</sup> each.
- Atmospheric  $CO_2$  concentration:  $15 \,\mu M$
- Diffusion coefficient of CO<sub>2</sub> in atmosphere:  $1.5 \times 10^{-5} \text{ m}^2/\text{s}$

### Cross-section of a Plant Leaf



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

# Diffusion of CO<sub>2</sub>

■ Diffusion coefficient of CO<sub>2</sub> at atmospheric pressure and 298 K:

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

Concentration gradient:

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

Flux:

$$J = -D\frac{dC}{dx} = -1.5 \times 10^{-5} \,\mathrm{m^2/s} \times 175 \,\mathrm{mol} \cdot \mathrm{m^{-4}}$$
$$= -2.6 \times 10^{-3} \,\mathrm{mol} \cdot \mathrm{m^{-2}s^{-1}}$$

#### How Many Stomata Does Our Plant Need?

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

$$5 \times 10^{-6} \text{ mol/s} = J \pmod{\text{mol} \cdot \text{m}^{-2} \text{s}^{-1}} \times \text{area} (\text{m}^2)$$
  
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:  $pprox \pi (5 imes 10^{-6} \, {
  m m})^2 pprox 10^{-10} \, {
  m m}^2$
- Number of stomata:

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

 $2\times 10^4\, stomata/cm^2$ 

# The Big Problem

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

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

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

Flux:

$$J = -D\frac{dC}{dx} = -2.4 \times 10^{-5} \text{ m}^2/\text{s} \times 1.5 \times 10^4 \text{ mol} \cdot \text{m}^{-4}$$
$$= -0.4 \text{ mol} \cdot \text{m}^{-2}\text{s}^{-1}$$

Compare to  $-2.6\times 10^{-3}\,\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$  for CO\_2.

### Water Loss Through Stomata

- From requirement for CO<sub>2</sub> diffusion, total average surface area of open stomata: 0.002 m<sup>2</sup>
- Total water diffusion (transpiration) in a year:

flux (mol  $\cdot$  m<sup>-2</sup>s<sup>-1</sup>) × surface area (m<sup>2</sup>) × time (s) = 0.4 mol  $\cdot$  m<sup>-2</sup>s<sup>-1</sup> × 0.002 m<sup>2</sup> × 1.5 × 10<sup>7</sup> s = 1.2 × 10<sup>4</sup> mol × 18 g/mol = 2 × 10<sup>5</sup> g = 200 kg ≈ 50 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!

### Water Flow in Plants



Modified from: Nagwa.com, Tyree and Zimmermann 2002, and Organismal Biology

Figure from Jaycie Fickle (University of Utah), adapted from M.T. Tyree and M. H. Zimmerman, Xylem Structure and the Ascent of Sap, 2002, Springer.

#### 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<sub>2</sub> is fixed as malate and stored in vacuoles.
- During daylight, CO<sub>2</sub> 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, and almost all cacti species.

#### What Happens When Atmospheric CO<sub>2</sub> 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<sub>smax</sub> = "anatomical maximum stomatal conductance to water vapor"
- Units: mol  $\cdot$  m<sup>-2</sup>s<sup>-1</sup>, 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.

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

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

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

• 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 (x<sup>2</sup>) (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

 $\bullet \langle r^2 \rangle = 6Dt$ 

Solve for t for RMS(r) = R (a specified value) and,

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

 $R^2 = 6Dt$ 

- $t=R^2/(6D)$
- For 1- $\mu$ m 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



- It looks like a random walk! (with variable step size)
- Step sizes are larger than the bacterium ( $\approx 1\,\mu\text{m}$ ) 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).



#### Clicker Question #2

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

