Physical Principles in Biology
Biology 3550
Spring 2024

Lecture 20:

Rates of Diffusion and a Plant Faces Diffusion

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A Quick Review from the Last Lectures

- Kinetic energy of an object along the x-axis: $E_{\mathrm{k},x} = mv_x^2/2$
- RMS translational kinetic energy of a molecule: $E_{\mathrm{k},x} = kT/2$
- RMS velocity of molecule: $v_x = \delta_x/\tau = \sqrt{kT/m}$
- The diffusion coefficient:

$$D = \frac{\delta_x^2}{2\tau} = \frac{v_x\delta_x}{2}$$

- Calculating δ_x and τ from D and v_x:

$$\delta_x = \frac{2D}{v_x} = \frac{2D}{\sqrt{kT/m}}$$

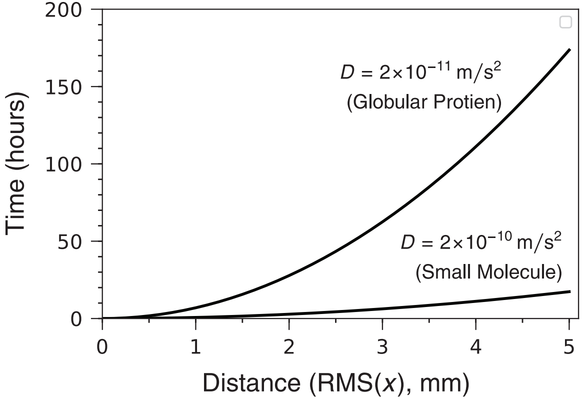
$$\tau = \frac{\delta_x}{v_x} = \frac{\delta_x^2}{2D}$$

Time Required for Diffusion Over a Range of Distances

$$\mathrm{RMS}(x) = \sqrt{2Dt}$$

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

$$t = \langle x^2 \rangle / (2D)$$



- Time required is inversely related to the diffusion coefficient.
- Diffusion is effective over short distances, but not long.

Calculating Diffusion Coefficients

- What determines diffusion coefficient?
  - Velocity of molecules (temperature and mass)
  - Size and shape of molecules
  - How often molecules colide
- Stokes-Einstein equation for spherical particles:

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

$r =$ sphere radius

$\eta =$ viscosity

- A key result from the 1905 Einstein paper on Brownian motion.
- A testable prediction!

Viscosity: Property of a Liquid (or Gas)

Resistance to Motion of Molecules Past One Another

- A molecular property easily observed on the macroscopic scale.

From a 1960s TV ad for Prell Shampoo

https://www.youtube.com/watch?v=91FsrjoLKq0

- Reflects what we commonly think of as the “thickness” of a liquid.
- Units are not straight forward! See the notes.

Some Calculated Diffusion Coefficients

- The Stokes-Einstein equation for spherical particles:

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

- In water at 25°C:
  - Small molecule (1 nm): $2\times10^{-10}\,\mathrm{m^2s^{-1}}$
  - Protein (10 nm): $2\times10^{-11}\,\mathrm{m^2s^{-1}}$
  - Bacterium (1 μm): $2\times10^{-13}\,\mathrm{m^2s^{-1}}$
  - 1 mm sphere: $2\times10^{-16}\,\mathrm{m^2s^{-1}}$

Clicker Question #1

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

A) $\approx 1\,\text{nm}$

B) $\approx 1\,\mu\text{m}$

C) $\approx 1\,\text{mm}$

D) $\approx 1\,\text{cm}$

E) $\approx 1\,\text{m}$

All answers count for now.

Clicker Question #2

Calculate the RMS distance an N_2 molecule travels before changing direction.

A) $\approx 1\,\text{nm}$

B) $\approx 10\,\text{nm}$

C) $\approx 100\,\text{nm}$

D) $\approx 1\,\mu\text{m}$

E) $\approx 10\,\mu\text{m}$

- Diffusion coefficients of gasses (at atmospheric pressure): $\approx 2 \times 10^{-5}\,\text{m}^2/\text{s}$
- From a previous lecture: RMS velocity of N_2: $\approx 300\,\text{m}/\text{s}$.

Diffusion in Gasses

- Diffusion coefficients of gasses (at atmospheric pressure): $\approx 2 \times 10^{-5}\,\mathrm{m}^2/\mathrm{s}$
- From a previous lecture: RMS velocity of N_2: $\approx 300\,\mathrm{m/s}$.
- $D = \delta_x^2/(2\tau)$, and $v = \delta_x/\tau$

$$\delta_x = 2D/v = 1.3 \times 10^{-7}\,\mathrm{m} = 130\,\mathrm{nm}$$

The “mean-free-path” distance.
Is this the distance between molecules?

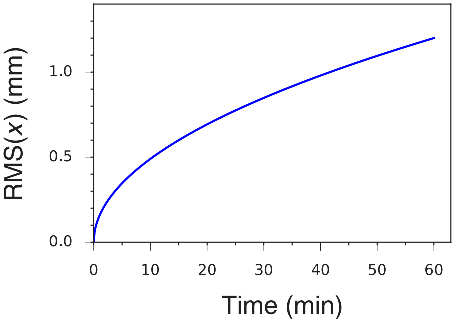
- Time between collisions:

$$\tau = \delta_x/v \approx 4.4 \times 10^{-10}\,\mathrm{s}$$

- Much longer random walk steps than in liquids, but still pretty short.

Diffusion in Liquids vs. Atmosphere

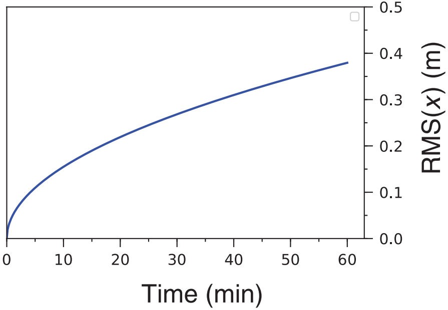
A small molecule in water,
$D = 2 \times 10^{-10}\ \mathrm{m}^2/\mathrm{s}$



$$\delta_x = 6.5 \times 10^{-12}\ \mathrm{m}$$

$$\tau = 10^{-13}\ \mathrm{s}$$

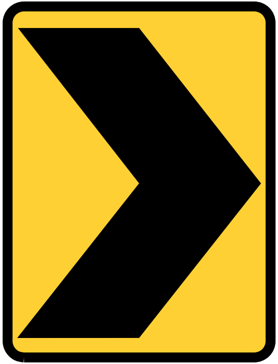
N_2 in atmosphere,
$D = 2 \times 10^{-5}\ \mathrm{m}^2/\mathrm{s}$



$$\delta_x = 1.3 \times 10^{-7}\ \mathrm{m}$$

$$\tau = 4.4 \times 10^{-10}\ \mathrm{s}$$

Warning!



Direction Change

A Plant Faces Diffusion

Growth of a Hypothetical Plant

- 1 kg carbon per year, for net growth and replacement of leaves.
- Where does the carbon come from?

From thin air!

$$6CO_2 + 6H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

An extremely unfavorable reaction, unless coupled to the energy of absorbed light.

Clicker Question #3

How much CO_2 does the plant have to assimilate per second?

(for 1 kg carbon/yr)

A) $\approx 1\,\mu\mathrm{mol}/\mathrm{s}$

B) $\approx 2\,\mu\mathrm{mol}/\mathrm{s}$

[✓ **C)** $\approx 5\,\mu\mathrm{mol}/\mathrm{s}$]

D) $\approx 10\,\mu\mathrm{mol}/\mathrm{s}$

E) $\approx 20\,\mu\mathrm{mol}/\mathrm{s}$

Growth of a Hypothetical Plant

- How much CO_2 (in moles) does the plant have to assimilate per second?

$$1\,\mathrm{kg} \div 12\,\mathrm{g/mol} \approx 80\,\mathrm{mol}$$

$$1\,\mathrm{yr} \times 365\,\mathrm{days/yr} \times 24\,\mathrm{hr/day} \times 60\,\mathrm{min/hr} \times 60\,\mathrm{s/min} \approx 3 \times 10^{7}\,\mathrm{s}$$

- But, CO_2 is incorporated only during daylight, so the total time available is only about half of this.

$$80\,\mathrm{mol} \div 1.5 \times 10^{7}\,\mathrm{s} \approx 5 \times 10^{-6}\,\mathrm{mol/s}$$

Growth of a Hypothetical Plant

- Total rate of CO_2 assimilation: 5×10^{-6} mol/s
- Assume 1,000 leaves of 1 cm^2 each:

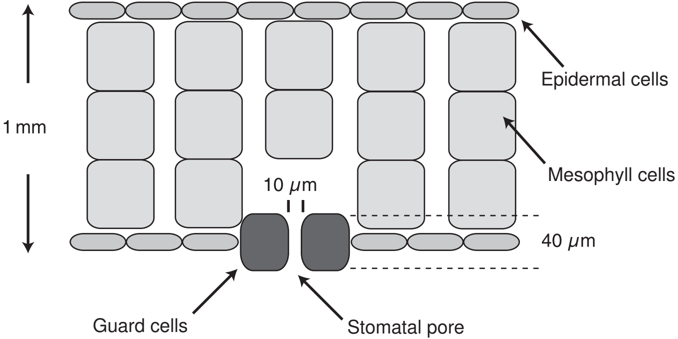
$$1,000\,\text{cm}^2 \times \left(\frac{1\,\text{m}}{100\,\text{cm}}\right)^2 = 0.1\,\text{m}^2$$

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

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

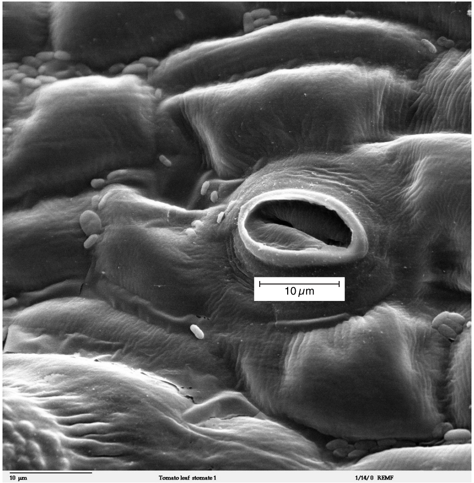
- But, diffusion does not take place across all of the leaf area.

Cross-section of a Plant Leaf



- Photosynthesis takes place in chloroplasts of mesophyll cells.
- Stomata control diffusion of gasses into and out of leaves.
- Diffusion through the stomata takes place in gas phase.

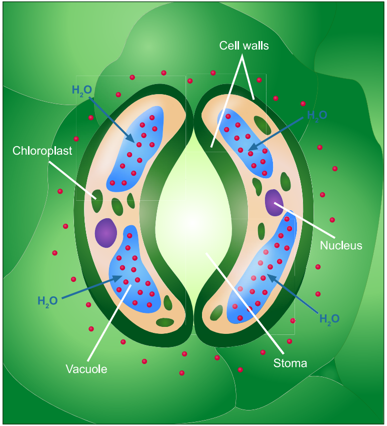
Scanning Electron Micrograph of a Tomato Leaf Stoma



Micrograph by Louisa Howard.
http://remf.dartmouth.edu/images/botanicalLeafSEM/source/16.html

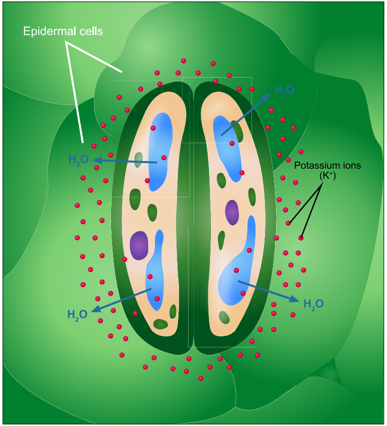
Opening and Closing of Stomata

Guard cells (swollen)



Stoma opening

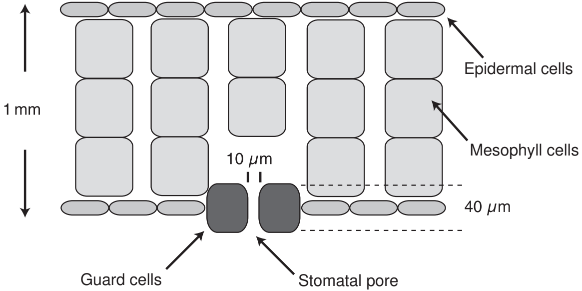
Guard cells (shrunken)



Stoma closing

Illustration by Ali Zifan
https://en.wikipedia.org/wiki/Stoma

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.

Clicker Question #4

What is the concentration gradient, $\frac{dC}{dx}$, across the stomatal pore?

- Diffusion coefficient of CO_2 at atmospheric pressure and 298 K: $D = 1.5 \times 10^{-5}\,\text{m}^2/\text{s}$.
- Atmospheric CO_2 concentration: $15\,\mu\text{M}$ (≈ 400 ppm)
- CO_2 concentration in leaf airspace: $7.5\,\mu\text{M}$
- Length of stomatal pore: $\approx 40\,\mu\text{m}$

A) $\approx 2\,\text{mol}\cdot\text{m}^{-4}$

B) $\approx 20\,\text{mol}\cdot\text{m}^{-4}$

C) $\boxed{\approx 200\,\text{mol}\cdot\text{m}^{-4}}$

D) $\approx 2000\,\text{mol}\cdot\text{m}^{-4}$

Diffusion of CO_2

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

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

Clicker Question #5

What is the flux, J, of CO_2 through the stomata?

- Diffusion coefficient of CO_2 at atmospheric pressure and 298 K: $D = 1.5 \times 10^{-5}\,\mathrm{m}^2/\mathrm{s}$.
- Atmospheric CO_2 concentration: $15\,\mu\mathrm{M}$ (≈ 400 ppm)
- CO_2 concentration in leaf airspace: $7.5\,\mu\mathrm{M}$
- Length of stomatal pore: $\approx 40\,\mu\mathrm{m}$

A) $\approx -3 \times 10^{-4}\,\mathrm{mol} \cdot \mathrm{m}^{-2}\mathrm{s}^{-1}$

[✓ **B)** $\approx -3 \times 10^{-3}\,\mathrm{mol} \cdot \mathrm{m}^{-2}\mathrm{s}^{-1}$]

C) $\approx -3 \times 10^{-2}\,\mathrm{mol} \cdot \mathrm{m}^{-2}\mathrm{s}^{-1}$

D) $\approx -3 \times 10^{-1}\,\mathrm{mol} \cdot \mathrm{m}^{-2}\mathrm{s}^{-1}$

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:

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

How Many Stomata Does Our Plant Need?

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

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

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

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

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

- If total leaf surface area is $0.1\,\mathrm{m}^2$ and each leaf is $\approx 1\,\mathrm{cm}^2 = 1 \times 10^{-4}\,\mathrm{m}^2$
  - Stomatal pores 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.

    Number varies with plant species and environmental conditions.

The Big Problem

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

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

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

- Flux:

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

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

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

$$
\begin{aligned}
&\text{flux } (\mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1}) \times \text{surface area } (\mathrm{m}^2) \times \text{time (s)} \\
&= 0.4\,\mathrm{mol}\cdot\mathrm{m}^{-2}\mathrm{s}^{-1} \times 0.002\,\mathrm{m}^2 \times 1.5 \times 10^7\,\mathrm{s} \\
&= 1.2 \times 10^4\,\mathrm{mol} \times 18\,\mathrm{g/mol} \\
&= 2 \times 10^5\,\mathrm{g} = 200\,\mathrm{kg} \\
&\approx 50\,\mathrm{gal}
\end{aligned}
$$

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