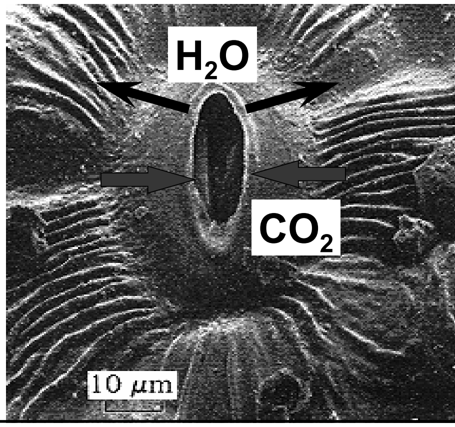
A Fundamental Resource Tradeoff – negotiated by Stomata



Outline

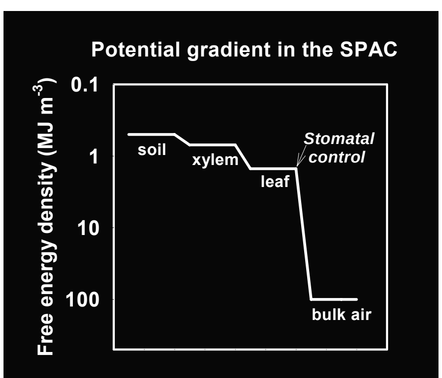
1. Importance of stomata for water relations

2. Physical description of
Stomata, and mechanical drivers for opening and closing

3. The concept of stomatal and leaf
conductance (loosely = stomatal aperture)

4. Economics of carbon gain versus water loss.

Stomata are a critical control point in the soil/plant/atm continuum.



**At 50% humidity, 20 deg c,
Water potential of air = 94 MJ m^{-3}

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Stomatal Anatomy and distribution on leaves

Pair of Guard Cells – either elliptical or ‘dumbell’ shaped

Open stomata cover only 0.5-5% of leaf surface area but are virtually the only exchange port for CO_2 and H_2O

Stomata may occur on both adaxial (‘upper’) or abaxial (‘lower’) surfaces of leaves, but generally are much more prevalent on the abaxial side. (Jones Table 6.1)

Stomatal density: number of stomata per unit area.

Stomatal index:

Number of stomata per number of total epidermal cells.

	Adaxial surface		Abaxial surface		
	ν #/mm2	ℓ um	ν	ℓ	Ref.
Trees:					
Carpinus betulus	0	—	170	13	1
Malus pumila (cv. Cox)	0	—	390	21	2
Malus pumila – variation during season	0	—	230–430	—	2
Malus pumila – variation within leaf	0	—	170–360	—	2
Malus pumila – different cultivars	0	—	350–600	—	3
Pinus sylvestris	120	20	120	20	1
Picea pungens	39	12	39	12	1
Other dicots:					
Beta vulgaris	111	14.6	131	15.3	4
Tomato – low–high light	2–28	—	83–105	—	5
Soybean – range for 43 cultivars	81–174	21–23	242–385	19.5–21.7	6
Soybean – well-watered–stressed	149–158	—	357–418	—	6
Ricinus communis	182	12	270	24	1
Tradescantia virginiana	7	49	23	52	1
Grasses:					
Sorghum bicolor – mean of 6 cultivars	—	22.6	135	23	7
Hordeum vulgare – flag leaf	54–98	17–24	60–89	17	1, 8, 9
Hordeum vulgare – 5th leaf below flag	—	—	27–42	—	9

Stomatal mechanics:

In elliptical stomata, radial microfibrils allow swelling only on the outside of the guard cells.

In dumbbell stomata, ends inflate like balloons and the pore opens across its length. Allows for rapid stomatal movements.

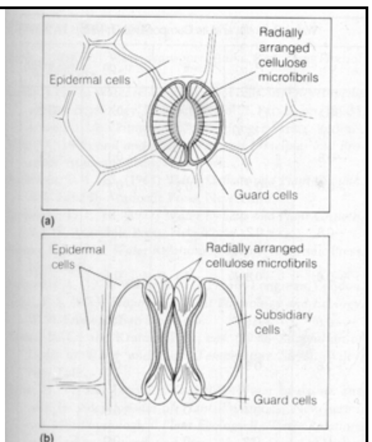
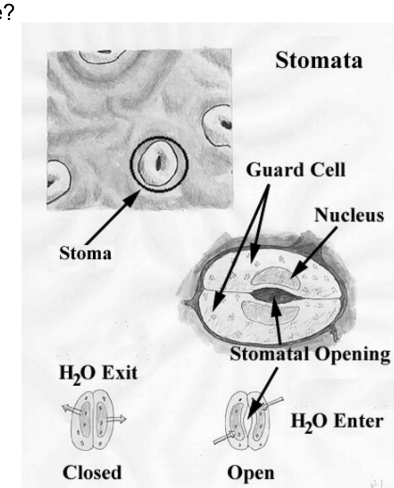
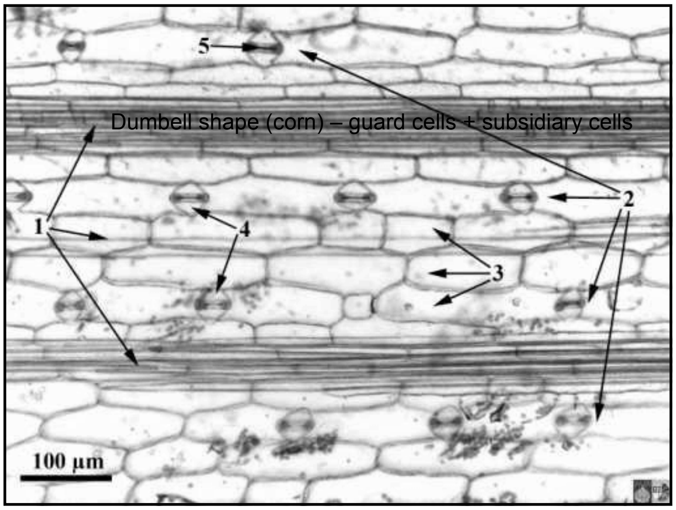


FIGURE 4.14. The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of a kidney-shaped stoma (a) and a grass-like stoma (b). (From Meidner and Mansfield, 1968.)

What do stomata look like?
A shameless web pirate tour…

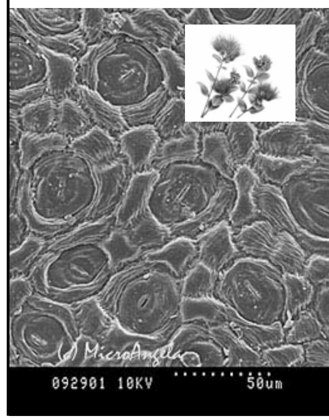
Elliptical shape

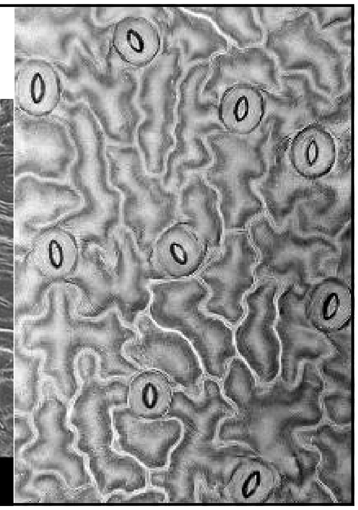




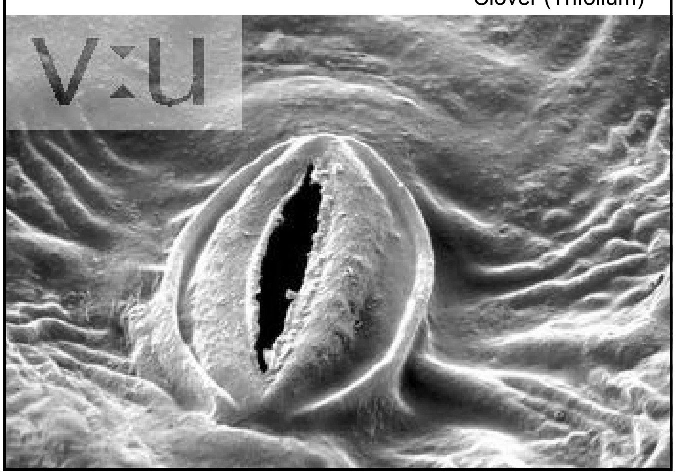
Dumbell shape (corn) – guard cells + subsidiary cells

Ohia leaf
Metrosideros polymorpha





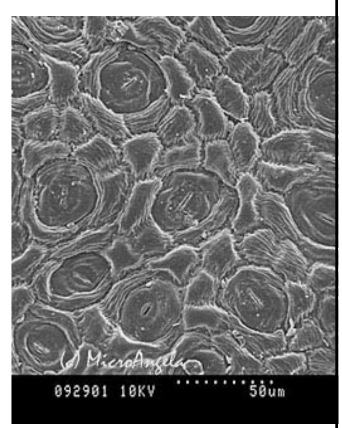
Clover (Trifolium)



Stomatal density:

~10 stomata per
.175 x .175 mm

= 330
stomata/mm2



Mechano-osmotic Control of stomatal aperture

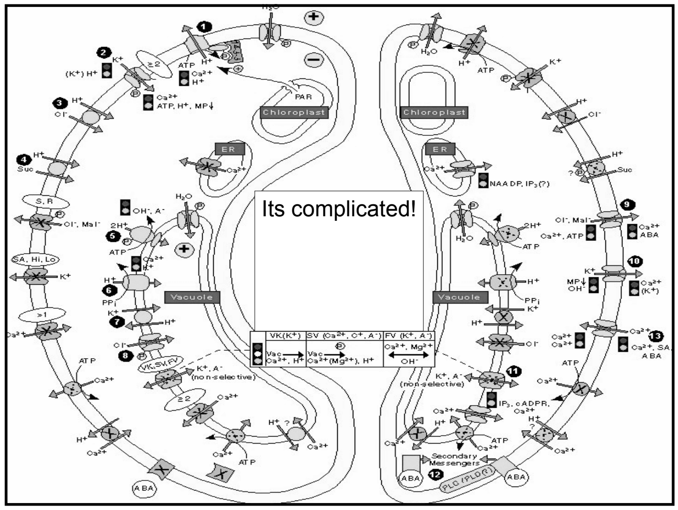
Stomates open with high ion concentrations (K+), and close with low Ion concentrations.

High ion concentrations cause swelling of guard cells due to osmosis – which mechanically cause opening.

Radial microfibrils allow swelling only on the outside of the guard cells

Ion concentrations in guard cells are regulated by membrane bound ion transporters, which are driven ultimately by ATP pumping of H+ out of guard cells.

We know the proximate causes of stomatal movements, but less about the ultimate controls on stomatal movement.



Osmo-mechanical Control of stomatal aperture

Turgor control:

Water potential = Ψ = P + S + G + M

Where P is turgor (hydrostatic pressure), S is osmotic potential, G is gravity, M is matric potential.

Two cells next to each other may be in energetic equilibrium even with turgor differences. Stomatal guard cells may swell next to epidermal cells, if they load solutes.

The osmotic pressure within the other cells of the lower epidermis remained constant at 150 lb/in^2.

Time	Osmotic Pressure (lb/in^2)
7 A.M.	212
11 A.M.	456
5 P.M.	272
12 midnight	191

Environmental Drivers for stomatal movement – can be feedforward or feedback.

•**Blue light** stimulates the ATP pump, leading to ion pumping into guard cells. A “feedforward” (anticipatory) response. Blue light photoreceptor activates K+ channels.

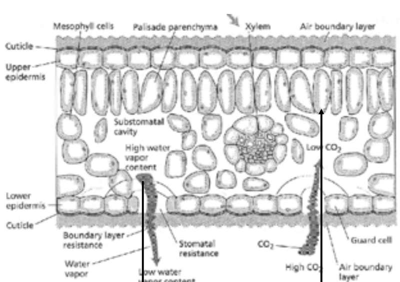
•**CO2 level** – Generally higher CO2 leads to lower stomatal aperture. This makes sense functionally, but the exact direct mechanism is unclear. Stomatal responses to CO2 occur in both light and dark, so it can’t be a photosynthesis feedback alone.

•**Drought** – (1) stimulates Abscisic acid production in roots, stems and leaves. ABA blocks ion pumping into guard cells (K+ transporter). ABA represents a ‘feedforward’ stomatal response. (2) also leads to passive reduction in guard cell turgor pressure – this is a ‘feedback’ response.

•**Humidity** – is there a humidity sensor? Little known, but would be a localized feedback operating as a global feedforward response. May be mediated indirectly by a response to transpiration rate instead.

Stomatal control of gas exchange

- Stomatal conductance
- Water use efficiency



At the same time, H_2O vapor moves out of the leaf by diffusion

CO_2 moves from the air to the leaf to the chloroplast by diffusion

The diffusive movement of CO_2 and H_2O into and out of a leaf can be described by **Fick’s Law**:

Net flux = Δ concentration / resistance

Net flux = Δ concentration * conductance

Fick's law is a special case of the more general Flux/Gradient relationship:

Ohm's Law: Electrical Current/Voltage

Fourier's Law: Heat conduction/Temperature Gradient

Poiseuille's Law: Liquid water flow/Pressure gradient

The units of conductance and resistance:

In the 1980's and before, people commonly used cm s^{-1} (or m s^{-1}) for conductance (and the inverse for resistance)

Why? Flux (kg/m2s) = driving force (kg/m3) x cond. (m/s)

This was motivated primarily by hydrologic studies because Flux is easily converted to units like mm/d

However, these units are cumbersome when dealing With biochemical reactions such as photosynthesis, which are usually expressed in molar units.

Today, the most common units for conductance are mol m^{-2} s^{-1}

Hydrologists still sometimes use m/s though

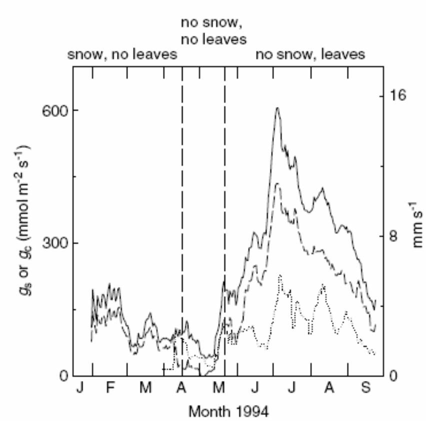
The choice of units depends on the units used to describe

CO_2 concentration. Today we use "mole fractions" (or ppm or partial pressure) to describe gas concentration, and molar fluxes (mol/m2s) for Photosynthesis or Transpiration.

The concentration units are moles/moles – i.e. the value is "unitless"

HYDROLOGICAL PROCESSES
Hydrol. Process. **18**, 1561–1578 (2004)
Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/hyp.1406

The cano **st, Prince**



So, going back to the formula for Fick's law:

Net flux = Δconcentration * conductance

If the "net flux" is the rate of photosynthesis, described in units of mol m^{-2} s^{-1}, and if the concentration difference for CO_2 is unitless, then conductance must also have units of mol m^{-2} s^{-1}

'molar' and 'mass' units for Conductance/Resistance are inter-convertible

This can be seen from considering the gas law:

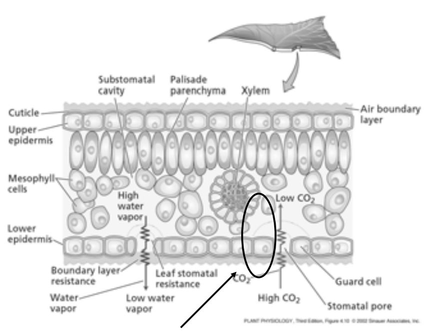
PV=nRT

n/V = P/RT Units on either side are [mol/m3]

Then, g (mol/m2s) = g(m/s)* P/RT (mol/m3)

@ atmospheric pressure and 25^{O}C, g(mol/m2s) = 0.04g(mm/s)

"Stomatal" conductance is different from (but a part of) "leaf conductance



Total leaf resistance to is made up of (at least) two separate resistances, the stomatal resistance (r_s) and the boundary layer resistance (r_b). Diffusive resistances "sum" just like electrical resistances, so $r_{total} = r_s + r_b$ (or 1/gtot = 1/gs + 1/gb)

Recall stomatal Conductance to CO2 is directly convertible to stomatal conductance to H2O

$g_{s,carbon} = g_{s,water}/ 1.6$

1.6 is the ratio of diffusivities of H2O/CO2

H2O is lighter and diffuses faster than CO2

see Section 2.2.2 Lambers Chapin Pons for more details

Similarly, *Leaf* Conductance to CO2 is directly convertible to *Leaf* Conductance To H2O

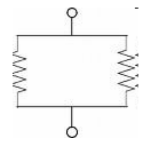
Stomatal alone: $1/g_{s,carbon} = 1.6/g_{s,water}$

But it includes an additional difference between water and CO2 movement in the leaf boundary layer caused by differential diffusion AND turbulence

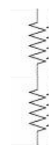
Total (stomatal+boundary): $1/g_{L,carbon} = 1.37/g_{a,water} + 1.6/g_{s,water}$

OR, $R_{L,carbon} = 1.37R_{a,water} + 1.6R_{s,water}$

Examples of when we want to use g, and when r



Parallel – use g
(gtot = g1 + g2)



Series – use r
(rtot = r1 + r2)