EFB 462 Animal Physiology: Ecological & Environmental
Differential diffusion and solubility pumps

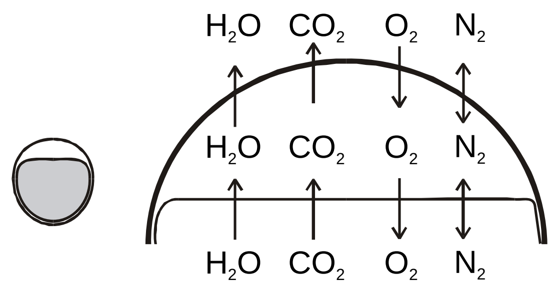
The various gases that animals exchange with the environment differ widely in both their solubilities in both water and air, and in their diffusion coefficients. We have mentioned elsewhere, for example, that nitrogen, oxygen and carbon dioxide differ substantially in their solubilities. These gases also differ in molecular weights, which produces variations in their diffusion coefficients as well.

Many animals have learned to exploit these variations to produce novel mechanisms for exchange of respiratory gases. These come under the general heading of diffusion and solubility pumps. We will consider three:

- Differential diffusion pumps in birds' eggs
- Differential diffusion/solubility pumps in insects
- Differential solubility pumps in bubble gills.

Differential diffusion pumps in birds'eggs

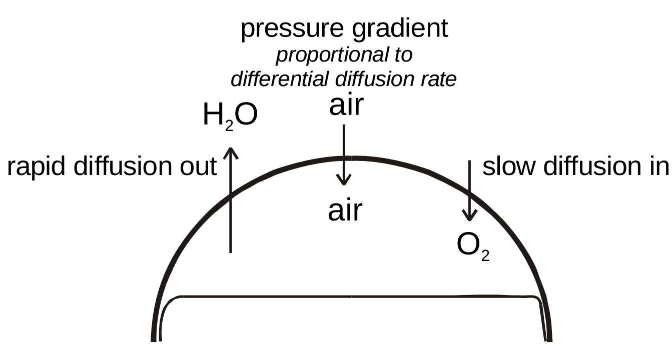
As a bird's egg loses water, an open space called an air cell typically opens up at one end, lined by the outer and inner shell membranes. Because the chorioallantois lines the inner shell membrane, the air cell gas is a close reflection of the embryo's blood gases. This sets up partial pressure gradients for oxygen, carbon dioxide and water vapor that drive a diffusion flux of these gases across the shell.



The various gases in the air cell differ in molecular weight, and hence in their diffusion coefficients:

Gas	MW (g mol^{-1})	*D* (relative)
H_2O	18	highest
N_2	28	↑
O_2	32	
CO_2	46	lowest

Note how the diffusion coefficient for water is greater than the diffusion coefficient for oxygen. This means that water vapor will diffuse out of the air cell faster than oxygen will diffuse in. The consequence will be a slight difference in hydrostatic pressure that will draw air (along with oxygen) into the air cell.



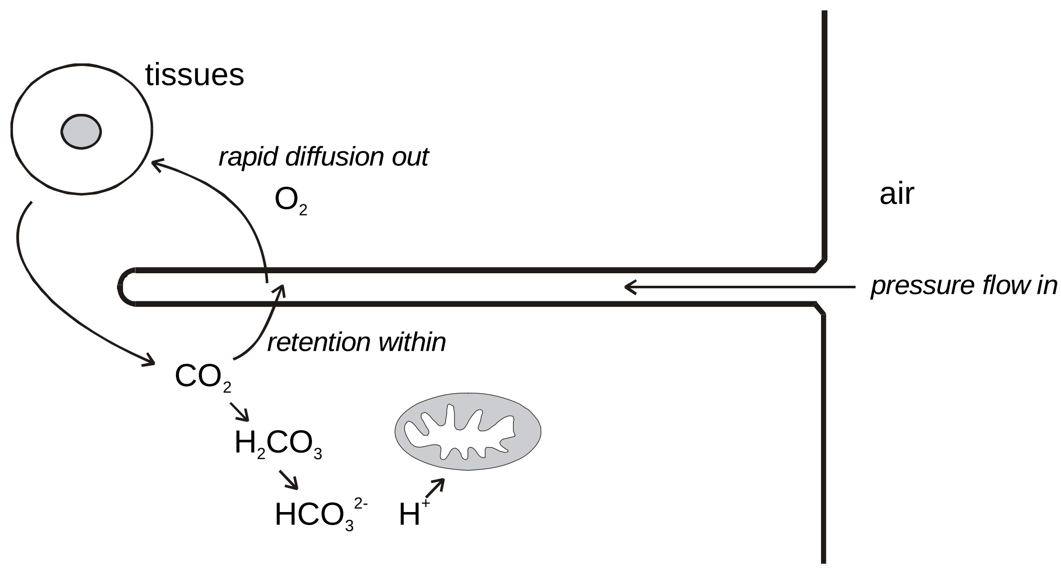
In short, the differential diffusion of oxygen and water vapor establishes a suction pump to draw air forcibly into the air cell.

Differential diffusion/solubility pumps in insect tracheoles

Insects breathe through their tracheoles, a system of finely-divided air-filled tubes that permeate the tissues like capillaries. Most gas exchange by insects is by diffusion only, i.e. there is no convection step as in most gas exchangers. Insects can get away with this because diffusion rates of gases in air are large compared with diffusion rates in water.

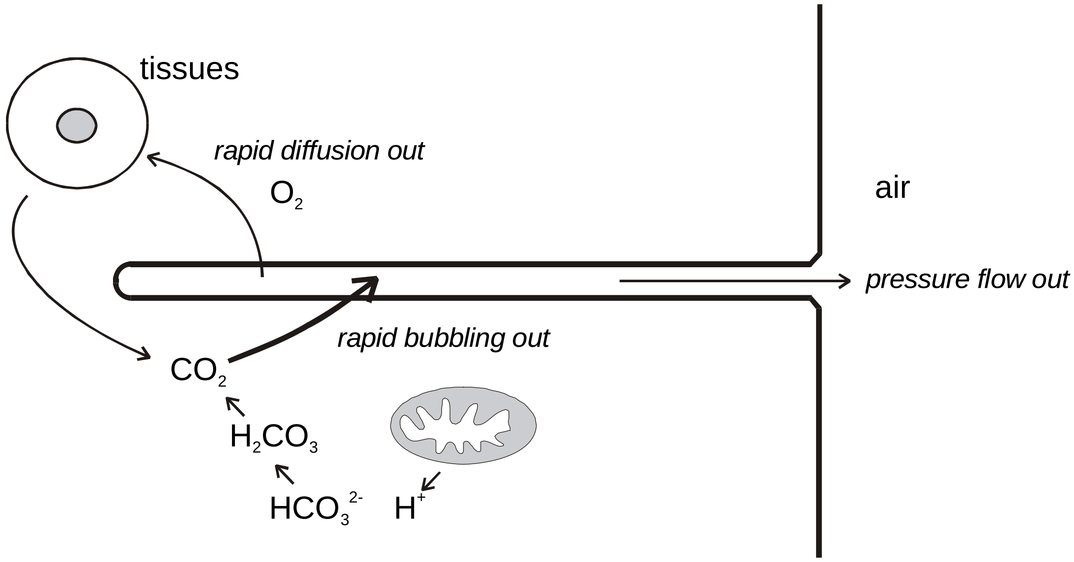
Insect tracheoles also are a differential diffusion pump, but with a twist. Let us see first how they work as differential diffusion pumps. As in a birds' egg, water diffuses out of the tracheole faster than oxygen diffuses in, setting up a slight suction pressure that draws air in. In the tissues, meanwhile, oxygen that is consumed is replaced by an approximately equal quantity of carbon dioxide. Because CO_2 has an apparent solubility many times larger than oxygen's, carbon dioxide tends to be sequestered in the liquids of the body. This means that oxygen can move more readily from gas to liquid across the tracheolar boundary than CO_2 can move the other way. Oxygen removed from the tracheoles is therefore not replaced by CO_2 moving out. This enhances the suction pressure drawing air and oxygen in.

Retention of CO_2 within the tissues is enhanced by mitochondria, which tend to sequester protons. As the CO_2 produced by cells forms carbonic acid, the reaction tends strongly toward bicarbonate:



Although oxygen is flowing in, virtually no CO_2 is moving out.

Every so often, the proton load in the mitochondria builds to a critical level, at which time they vigorously dump protons into the extracellular fluid. This pushes the reaction between CO_2 and water strongly toward CO_2 and water. Eventually, the concentration of CO_2 exceeds its true solubility, and carbon dioxide comes bubbling out into the tracheoles:

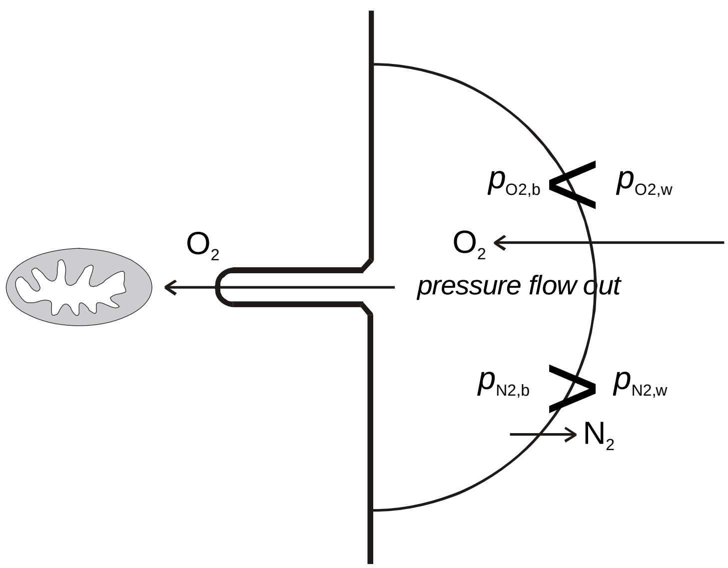


Emerging as a burst of CO_2 emission out the spiracles. This clever exploitation of the differential solubility of carbon dioxide is the basis of the intermittent respiration of insects.

Differential solubility pumps in bubble gills

Despite being obligate air-breathers, many insects live either permanently or semi-permanently under water. They are able to do so because they use "bubble gills", bubbles retained on the surface. These bubbles are not simply oxygen stores, but act as tiny aqualungs, extracting oxygen from the water. Their ability to do so depends upon the differential solubilities of nitrogen and oxygen in water.

A bubble attached to a spiracle can draw oxygen from the water. As oxygen is consumed by the insect, the oxygen partial pressure in the bubble declines to less than that in the water. The resulting partial pressure drives a diffusion flux of oxygen from the water into the bubble.



Nitrogen's partial pressure in the bubble, meanwhile, tends to be elevated above that in the water, through a combination of hydrostatic pressure (proportional to depth) and surface tension in the bubble (proportional to the inverse square of bubble radius). Nitrogen therefore diffuses out of the bubble into the water, causing the bubble to shrink.

Because solubility of nitrogen in water is less than solubility of oxygen in water, oxygen more readily moves from the water into the bubble than nitrogen moves from the bubble to the water. The differential solubility therefore tends to prolong the bubble's life, and hence its ability to extract oxygen from the water.

This differential solubility explains a puzzling phenomenon about bubble gills, and points to a surprising function.

- *The puzzling phenomenon:* If an insect carries down a bubble filled with pure oxygen, it will quickly drown. This is because the bubble contains no nitrogen, and hence no 'filler gas' to maintain the bubble's volume. The bubble therefore rapidly shrinks, and its ability to extract oxygen diminishes with it.
- *The surprising function:* When an insect comes up to replenish its bubble, it is not coming up for more oxygen, but more nitrogen!

