

Ecosystems & Ecophysiology – Lecture 15

Respiration in water – advanced

Objectives

1. Describe modifications of the tracheal system in aquatic insects.
2. Understand the use of air bubbles as physical gills by aquatic insects, and the principle of the plastron gill.
3. Describe adaptations for air breathing in lungfish.
4. Know the structures used by other air-breathing fish, to overcome low oxygen tension in water.
5. Understand the mechanisms used by wetland plants to deliver oxygen to the roots in anoxic soil.

Respiration in water – advanced

Seen aerobic metabolism as the consumption of O₂. Physiology of respiration is uptake of O₂ & excretion of waste product CO₂ – gas exchange

Basic mechanisms of respiration in water & in air covered in Life Processes (Lectures 22-23). Expected to know the principles – brief summary

Major difficulty in water is low O₂. Even when fully saturated, O₂ concentration in water is only 1/30th that of air: 7 ml l⁻¹ vs 210 ml l⁻¹ (i.e. 21% by volume)

Due to low solubility of O₂ in water. In contrast CO₂ has high solubility in water, so excretion of CO₂ generally no problem for aquatic organisms

Volume of gas depends on pressure, given under conditions of Standard Pressure (SP) = 1 atmosphere (760 mmHg)

Partial pressure of a gas in a mixture is proportion in mixture x total pressure. E.g. about 0.21 atm for O₂ at sea level (21% of air, at 1 atm). Tension of gas in solution (doesn't exert a pressure as such) = partial pressure in air

Now look at some advanced topics of respiration in water – insects, air-breathing fish, & wetland plants

Aquatic insects

■ Insects respire through tracheal system (air tubes), opens through spiracles in each segment. For both gas exchange & transport within the body

1. Most of the spiracles are non-functional in many aquatic insects, only the posterior ones open. Insect penetrates water surface with tip of abdomen

Mosquito larva & diving beetle at surface. Appendages at rear of mosquito larva are anal papillae, involved in osmoregulation not respiration (Lecture 16)

2. Small aquatic insects the tracheal system can be completely closed, gas exchange by diffusion through the cuticle. E.g. small chironomid midge larvae. Still need tracheal system for internal O₂ transport

3. Larger aquatic insects have gills, large surface area with thin cuticle, tracheal system extends into these to transport gases to tissues

■ Mayfly nymph *Ecdyurus* (Practical 1) has flat plates (lamellae) & filaments. Stoneflies have smaller gills below the thorax, live in well-oxygenated cool water. Sensitive to pollution by OM so high scores for water quality index

■ Many aquatic insects carry air bubbles, into which the spiracles open. Air held in place by non-wettable surfaces, e.g. diving beetle *Dytiscus*

Gas bubble is not only an oxygen store, but acts as a physical gill; oxygen diffuses into the bubble from the water, & CO₂ diffuses out

Consider an insect in water in equilibrium with air at sea level. Pressure 1 atm (SP), composition (approx) 79% N₂ and 21% O₂. Tensions of N₂ and O₂ in the water will be 0.79 & 0.21 atm, = partial pressures in the air

■ Insect carries a 1 ml air bubble & stays near the surface. Pressure of air in the bubble will still be 1 atm & volume 1 ml. Bubble will contain 0.79 ml N₂ & 0.21 ml O₂ at SP

Partial pressure = proportion of gas in the mixture x the total pressure:

$$N_2 = 0.79/1.0 \times 1.0 = 0.79 \text{ atm}$$

$$O_2 = 0.21/1.0 \times 1.0 = 0.21 \text{ atm}$$

Partial pressures of N₂ & O₂ in the bubble are the same as tension in the water, & there is no net diffusion of gases between bubble & water

■ Now look at the bubble after the insect has been respiring for some time. About half the O₂ has been consumed, now only 0.11 ml at SP

CO₂ has been produced, but this is lost to the water as it is very soluble. So there is now only 0.9 ml of gas in the bubble at SP. Pressure on the bubble is still 1 atm, so volume shrinks to 0.9 ml

Partial pressures of gases in the bubble are now calculated as a proportion of the new volume of the bubble:

$$N_2 = 0.79/0.90 \times 1.0 = 0.88 \text{ atm}$$

$$O_2 = 0.11/0.90 \times 1.0 = 0.12 \text{ atm}$$

Partial pressure of N₂ has increased > tension in water, so it diffuses out.

Partial pressure of O₂ has decreased < tension in water, so O₂ diffuses in

N₂ is lost more slowly than O₂ is gained (due to lower solubility of N₂ in water). The bubble gradually shrinks, but while it lasts O₂ diffuses into it

Bubble lasts long enough to give about 8 x as much O₂ by diffusion from the water, as there was originally in the bubble

In fact a bubble of pure O₂ is used faster than a bubble of air, as only 5 x as much O₂ & this is always diffusing out (as partial pressure = 1 atm, > water)

■ What would happen if the volume of the bubble was constant? In this figure half the O₂ has been used & the CO₂ is lost to the water as before. So total of 0.9 ml of gas at S.P. inside bubble

But the volume of the bubble is kept at 1 ml. This means that the pressure in the bubble is reduced by the corresponding amount, to 0.9 atm

Partial pressures are calculated as proportion x pressure as before:

$$N_2 = 0.79/0.90 \times 0.9 = 0.79 \text{ atm}$$

$$O_2 = 0.11/0.90 \times 0.9 = 0.11 \text{ atm}$$

Partial pressure of O_2 is 0.11 atm, < tension in water, so O_2 diffuses in
 Partial pressure of N_2 is 0.79 atm, = tension in water, so there is an
equilibrium with no net diffusion of N_2

Implies that if an insect could keep the volume of the bubble constant, then it
 could be used indefinitely. O_2 would enter as it was used, CO_2 would be lost,
 & the N_2 would be constant

■ System evolved in several insects, also intertidal mites – plastron gill. Can
 be either a dense layer of non-wettable hairs, or perforations in the cuticle

Hemipteran *Aphelocheirus* has a million hairs mm^{-2} . Only high pressure (3-5
 atm) can force water between these hairs, so volume of air is constant

Beetle *Aphrosylus* has a perforated cuticle, small connecting air spaces that
 also resist filling with water

Plastron gill even more of an advantage at depth. E.g. at 10 m the water
 pressure is 2 atm. Does not wet a plastron gill, so equally effective

But air bubble compressed, partial pressure of gases doubled. N_2 will diffuse
 out more quickly, & O_2 will also diffuse out, so bubble lasts much less long

■ Water pressure can be an advantage to insects in fast rivers. Water flow
 creates low pressure downstream of an object, e.g. the insect

This low pressure can prevent an air bubble shrinking, so it is used as a
 permanent physical gill. Air bubble trapped by legs of African river beetle
Potamodytes does not shrink at flows > 2 m s⁻¹

Air-breathing fish

■ Advantage to fish to breathe air if water dries up & they move over land or
 burrow into drying mud – temporary lakes & rivers

Or when O_2 tension in the water is low from decomposition & high
 temperature. Most common in tropical fw fish, this is garpike *Lepisosteus*
 (temperate N. America) breathing at surface

Problem with breathing air is that gill lamellae (gas exchange surface) stick
 together by surface tension, so have a much smaller area & fish suffocates

■ Best-known air breathers are lungfish, 3 genera. African & S. American
 can survive in dry mud, Australian lungfish cannot live out of water

■ Graph of O_2 saturation level in arterial blood as lungfish are moved from
 water to air. African & S. American lungfish can maintain, even increase,
 oxygenation of the blood. But Australian cannot, dies

■ African lungfish *Protopterus* can survive in a burrow in dried mud for several years, breathing air with lungs. Also breathes air when in water, drowns if denied access to air - obligate air breather

Lungs are infolding derived from the gut, with large respiratory surface area & blood supply. Also note partially divided heart, with spiral valve

■ Lungfish needs adaptation of circulatory system, not just lung. Normal fish circulation is single, from heart, through gills, then tissues & back to heart

Problem if circulation to lungs mixed with that from tissues. Oxygenated blood from lung would flow through heart to gills, where O₂ lost to the water

■ Lungfish has functional double circulation. Deoxygenated blood (blue) from tissues passes through heart & gills, then oxygenated in lung (red)

Then back to heart, separate flow to anterior gill arches, lost the lamellae so no loss of O₂ to the water. Oxygenated blood to the tissues where O₂ used

■ Many other fish also breathe air, great variety of organs. Any moist surface can be used for O₂ uptake, just needs access to air & a blood supply

Organs used: lungs, swim bladder, skin (*Anguilla* – eel), mouth & opercular cavities, air sacs, stomach, intestine, or modified gill extensions

Several of them obtain most of their O₂ from air even when in well oxygenated water (but most CO₂ is lost to water by gills or skin as it is so soluble):

		% O ₂ from air	Organ
<i>Lepidosiren</i>	S. American lungfish	96	Lung
<i>Protopterus</i>	African lungfish	89	Lung
<i>Arapaima</i>	S. American teleost	78	Swim bladder
<i>Lepisosteus</i>	Garpike	73	Swim bladder
<i>Trichogaster</i>	Asian teleost	40	Gill extension
<i>Neoceratodus</i>	Australian lungfish	0	Lung

■ Electric eel *Electrophorus* uses mouth & opercular cavities, folded lining & highly vascular – also obligate air breather

Breathes when O₂ content of air in mouth falls by 1/3, every few minutes. CO₂ is lost through skin & does not build up as fast as O₂ is lost

■ African catfish *Clarias* has two specialised organs for breathing air:

1. Respiratory fan. Fan-like structures, modified gill filaments, stiff enough to prevent collapse in air.
2. Arborescent organs. Complex branching extensions of two gill arches.

So air breathing physiologically simple, repeated evolution. See other adaptations to low O₂ (hypoxia) & absence (anoxia) in water in Lecture 17

Wetland plants

■ Waterlogged soils have pore spaces filled with water. O_2 used by roots & microbial metabolism, & slow diffusion through water, so soils become anoxic

Oxidation shown by redox potential in mV, measured with platinum electrode. Potential indicates the reactions occurring in the soil:

>300	Oxygenated
200 to 300	Denitrification, bacteria reduce NO_3^- to N_2
100 to 200	Fe^{3+} reduced to soluble Fe^{2+} (toxic)
-200 to -100	Sulphate & CO_2 reduced to sulphide & CH_4 (toxic)

■ Microorganisms can use anaerobic metabolism (Lecture 17), but plant roots need O_2 . Supplied by air pathways in root tissue – aerenchyma

O_2 diffuses through shoots & aerial roots to supply the flooded tissues. O_2 in roots may diffuse out into nearby soil & oxygenate it

■ Roots of rush *Phragmites* grown in anoxic culture medium, oxidised the stain methylene blue around them

Also seen in soil at different distances from roots of mangrove *Rhizophora*:

	3 mm	0.5 m	
Redox potential (mV)	-80	-203	
Sulphide (nM)	0.17	1.70	(x 10)

Oxygenation may be ecologically significant, protects roots from toxic reduced heavy metal ions & sulphide, also reduce loss of nitrate by denitrification

E.g. reduced Fe^{2+} and Mn^{2+} are soluble & toxic, oxidised to Fe^{3+} & Mn^{4+} , insoluble (manganese dioxide MnO_2) & non-toxic

■ Aerial roots of mangroves & fw swamp trees have pores (lenticels) above the water, air enters & passes along aerenchyma to underground roots

Air spaces in *Rhizophora* make up to 6% of volume of aerial roots, 22-40% under water, & 42-51% in mud, for increased O_2 supply

■ Most tree roots branch from the trunk underground. *Rhizophora* roots branch off up to 2 m above ground, for support & O_2 supply. Up to 1/4 of above-ground biomass may be these stilt roots

Avicennia mangrove roots are underground, pneumatophores emerge at intervals of 15-30 cm, 30 cm tall – may be 10,000 of these per tree, aerenchyma up to 70% of their volume

Swamp cypresses (*Taxodium*) in fw swamps also have pneumatophores. Marsh & saltmarsh plants also have aerenchyma tissue in roots, e.g. saltmarsh grass *Spartina*, papyrus rush *Cyperus*

■ Underground roots die if no connection to air. Experiment with *Rhizophora* with greased lenticels, O₂ decreases within roots & CO₂ accumulates

Especially at night, more stable in day as photosynthesis provides some O₂. Lower air space in roots in light (22-29%) than those in shade (35-40%)

Most O₂ supplied simply by diffusion along aerenchyma. May also be bulk flow of air into roots. Not due to pressure from tides, as pressure in aerenchyma lowest when roots covered by water

Lenticels are hydrophobic, open under water but not flooded. CO₂ from root metabolism dissolves in water, so pressure in aerenchyma decreases. Air sucked in at low tide when lenticels above water