5
ANOXIC STRESS

OXYGEN DEFICIENCY

Oxygen is required for both the upper and lower plant parts. I well drained soils, oxygen is diffusing in depth through the gas spaces between soil particles. Therefore, concentrations approach those of the atmosphere.

Under **flooding conditions**, soil air is replaced by water resulting in the inhibition of oxygen diffusion.

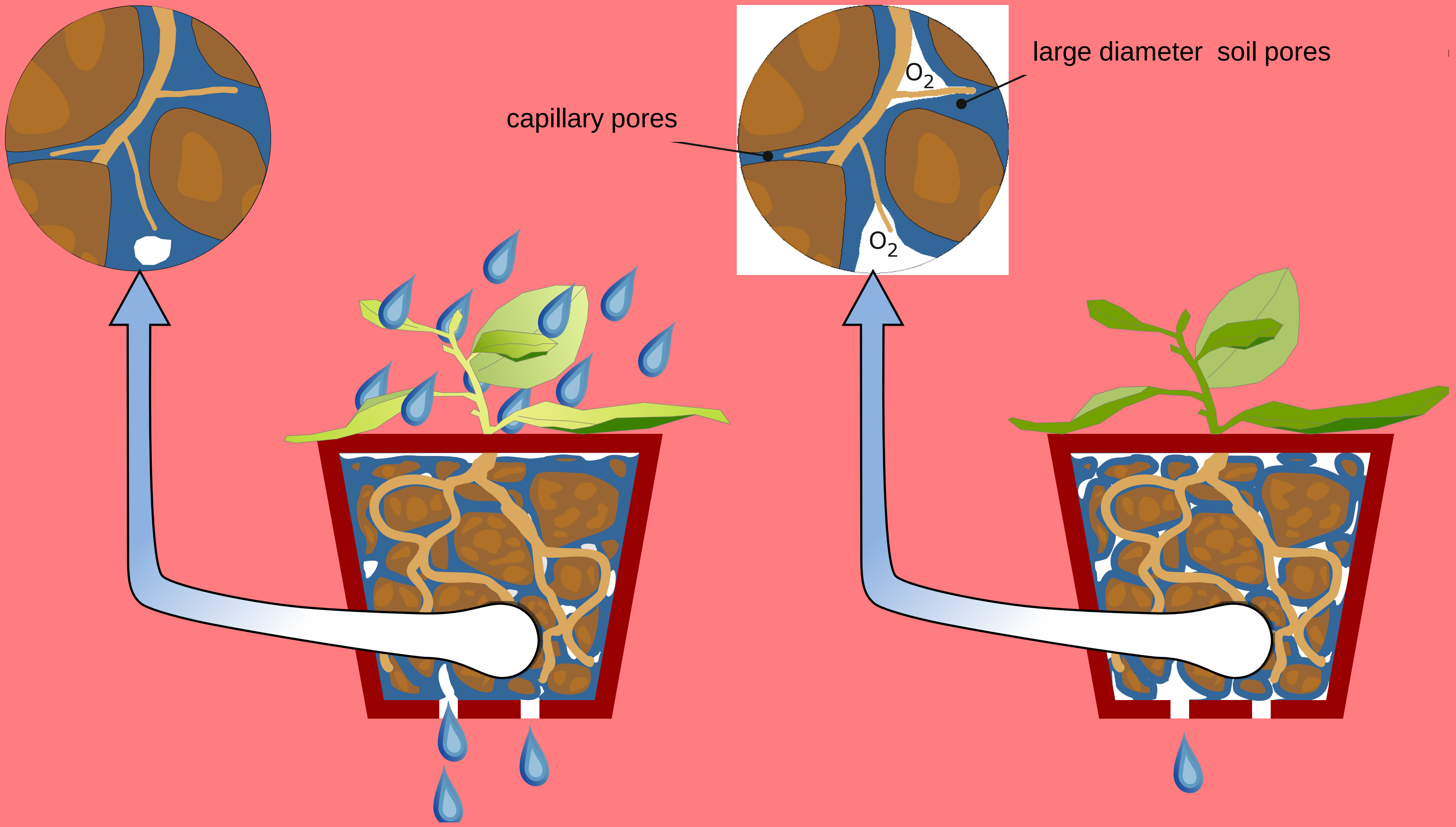
Gas diffusion in liquids is 10.000 times **slower** compared to diffusion in gases.

Oxygen solubility in water is **very low**: 0.5 mM O_2 at 25 °C (10 mmol σε 1 l of air)

OXYGEN DEFICIENCY

If soil oxygen is lower than required by plants to grow properly, **hypoxia** conditions develop.
Absolute lack of oxygen is referred as **anoxia**.

OXYGEN DEFICIENCY



Distribution of water and air in the soil under two different regimes

METABOLIC PERTURBATIONS

- **ATP production is reduced considerably**

  Under anaerobic conditions every hexose mole catabolized produces **only 2 moles ATP** instead of **36 produced during aerobic respiration**

  The requirements for energy result in **waste** of respiration substrates

  Final products of anaerobic respiration **accumulate** (**ethanol** και **lactic acid**)

METABOLIC PERTURBATIONS

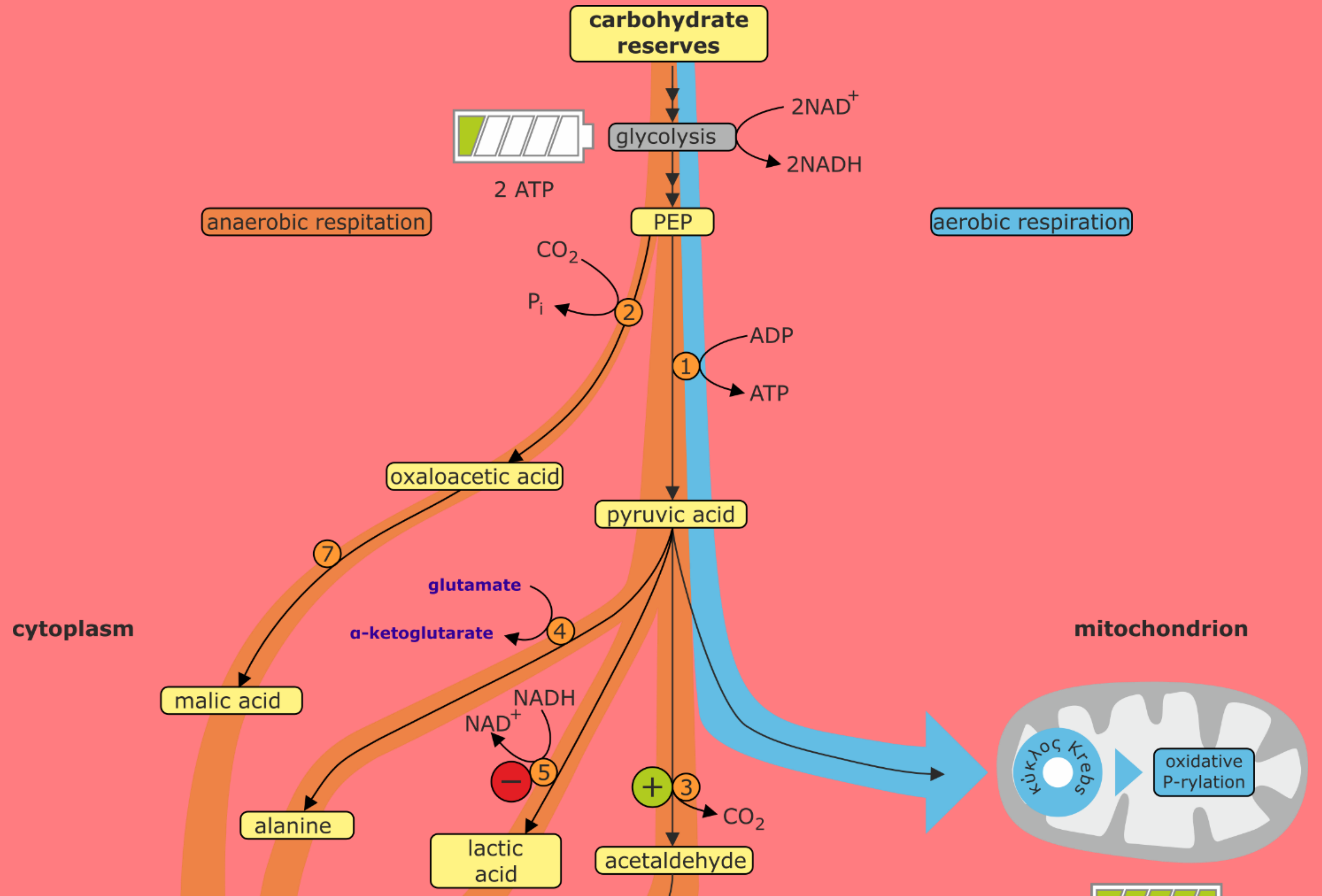
- **Cytoplasm becomes more acidic**

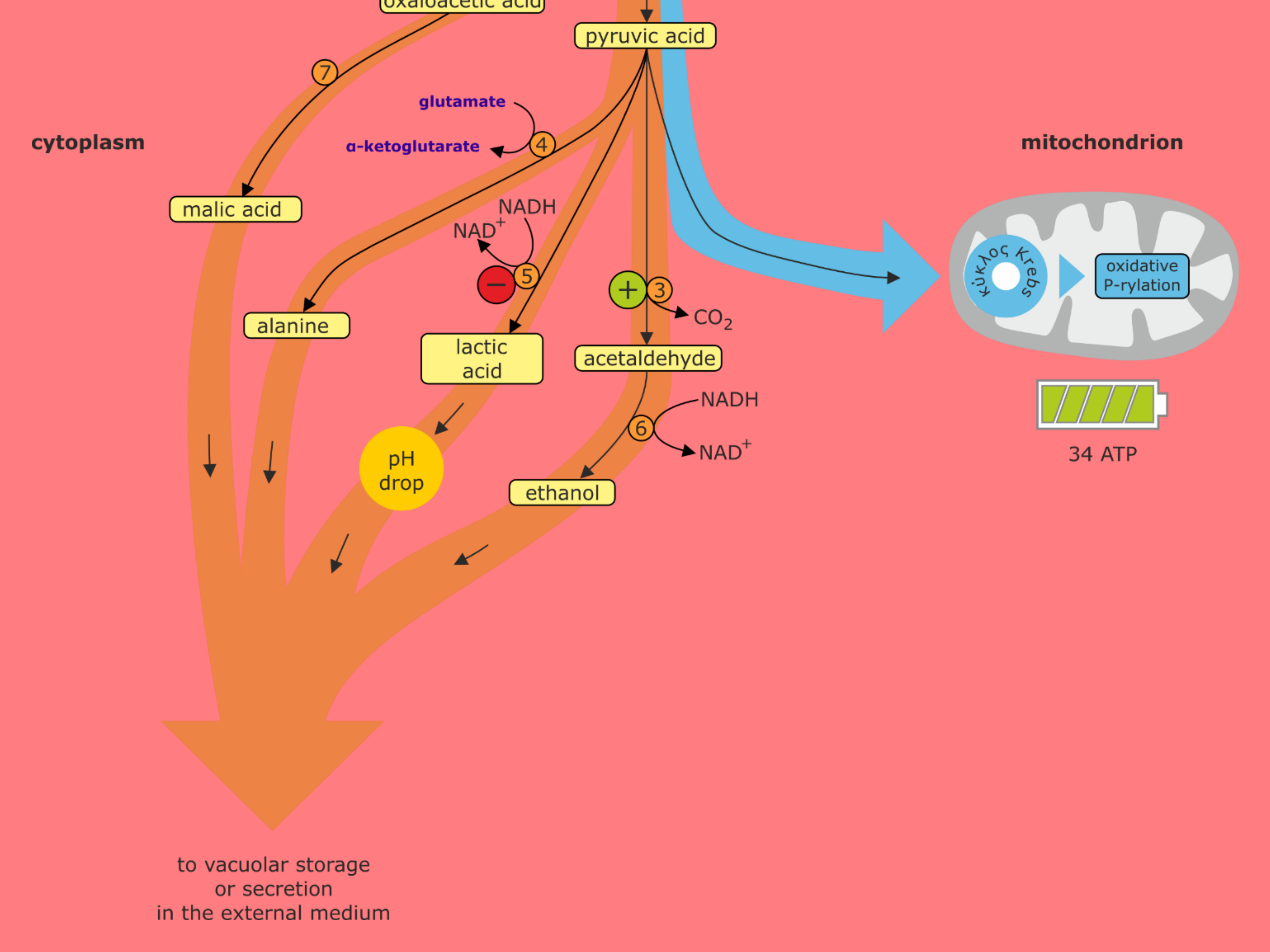
Lactic acid accumulation drives **pH to very low values**. Acidification begins from the **vacuole** and extends to the **cytoplasm**

Loss of homeostasis is due to the **inability of proton transfer** from cytoplasm to the vacuole via the ATPase proton pumps of the tonoplast due to lack of ATP

Cytoplasmic acidification results in metabolic modulations towards the production of ethanol via **alcoholic fermentation**

METABOLIC PERTURBATIONS





oxaloacetic acid
pyruvic acid
cytoplasm
mitochondrion
7
glutamate
α-ketoglutarate
4
malic acid
NADH
NAD+
5
alanine
lactic acid
3
CO2
acetaldehyde
κύκλος Krebs
oxidative P-rylation
34 ATP
NADH
6
NAD+
pH drop
ethanol
to vacuolar storage
or secretion
in the external medium

METABOLIC PERTURBATIONS

- **Soil toxicity conditions**

The activity of soil **anaerobic microorganisms** increases

Their activity results in the development of **reducing chemical conditions** in the soil

Some anaerobic microorganisms reduce sulfates to hydrogen sulfide (H_2S). H_2S is a **respiration inhibitor**

Trivalent iron (Fe^{3+}) is reduced to divalent iron (Fe^{2+}), which **may accumulate in toxic levels** after a prolonged period of anoxia (e.g. *rice iron toxicity*)

METABOLIC PERTURBATIONS

- **Soil nutrient availability is reduced**

  Anaerobic microorganisms reduce nitrates to nitrites or nitrogen oxide and molecular (gas) nitrogen. Hence, this process results in **significant nitrogen losses** to the atmosphere

METABOLIC PERTURBATIONS

- **Above ground plant part perturbations**

  Hypoxic roots cannot respond to plant requirements.

  Active absorption of nutrients from the roots and their transfer to the shoot are considerably reduced resulting in **nutrient deficiency symptoms in leaves**

  Remobilization of several nutrients (N, P, K) from mature to young-developing organs usually causes **early senescence** of mature organs

METABOLIC PERTURBATIONS

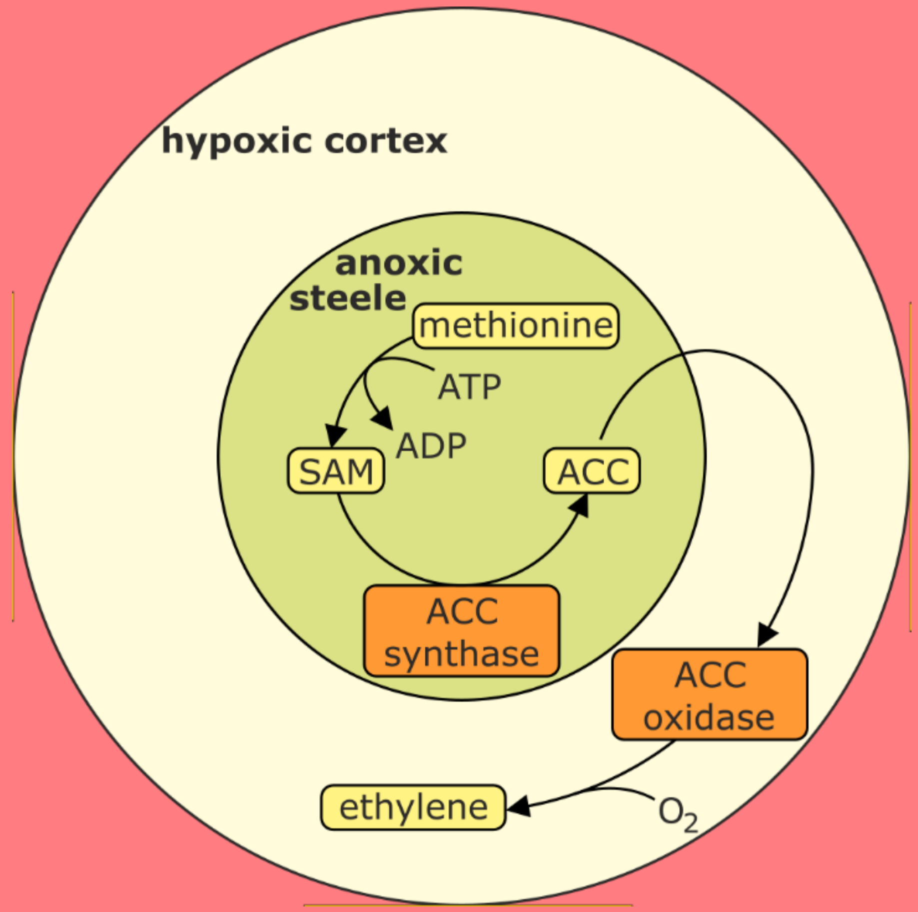
- **Above ground plant part perturbations**

  Due to stomatal closure, **transport of nutrients through the transpiration stream** is significantly reduced

  Some **hormonal preturbations** result in impairment of shoot growth and development

  Root ACC accumulation is observed under hypoxial or anoxia conditions while, **ABA is produced** in other cases. **Conversion of ACC to ethylene** is inhibited in the roots because the ACC oxidase needs oxygen

METABOLIC PERTURBATIONS



Root ethylene production: ACC synthesis may occur in other tissues and transferred to the root through the stele. Due to anoxia in the stele, ACC oxidation takes place in the cortex

THREE DIFFERENT STRATEGIES

- **Escape**

  Plants that follow this strategy, grow in soils that **flood very rarely**. Seeds of plants following this strategy **do not germinate** under hypoxia or anoxia conditions

THREE DIFFERENT STRATEGIES

- **Avoidance**

Plants following this strategy are able to supply their tissues with adequate amounts of oxygen, despite that the surrounding environment may be anoxic

This strategy requires **suitable morphological and anatomical modifications in the shoot**, leaf petioles and root in order to ensure unhampered supply of oxygen to cells

These modifications may be a result of adaptation or acclimation

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

- **Aerial roots**

  Roots of many hydrophytes **are grown near the soil surface** and avoid deeper anoxic layers

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AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

- **Leaf emergence in water surface**

In some hydrophytes (e.g. in *Nymphoides peltata*) the residence of developing leaves into the water results in endogenous ethylene accumulation that **induces petiole cell expansion**

As a result, the petiole is extended so that the leaf is able to **emerge to water surface** in order to gain access to the air

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

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AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

- **Aerenchyma: a path for oxygen**

In most hydrophytes, but also in many plants that are able to acclimate in soil flooding conditions, the shoot and the root possess or are able to create a network of air conducting elements called **aerenchyma**. These vertical air spaces are interconnected horizontally.

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

- **Aerenchyma: a path for oxygen**

In most marsh hydrophytes, aerenchyma is formed in the root **regardless of anoxia** or hypoxia conditions.

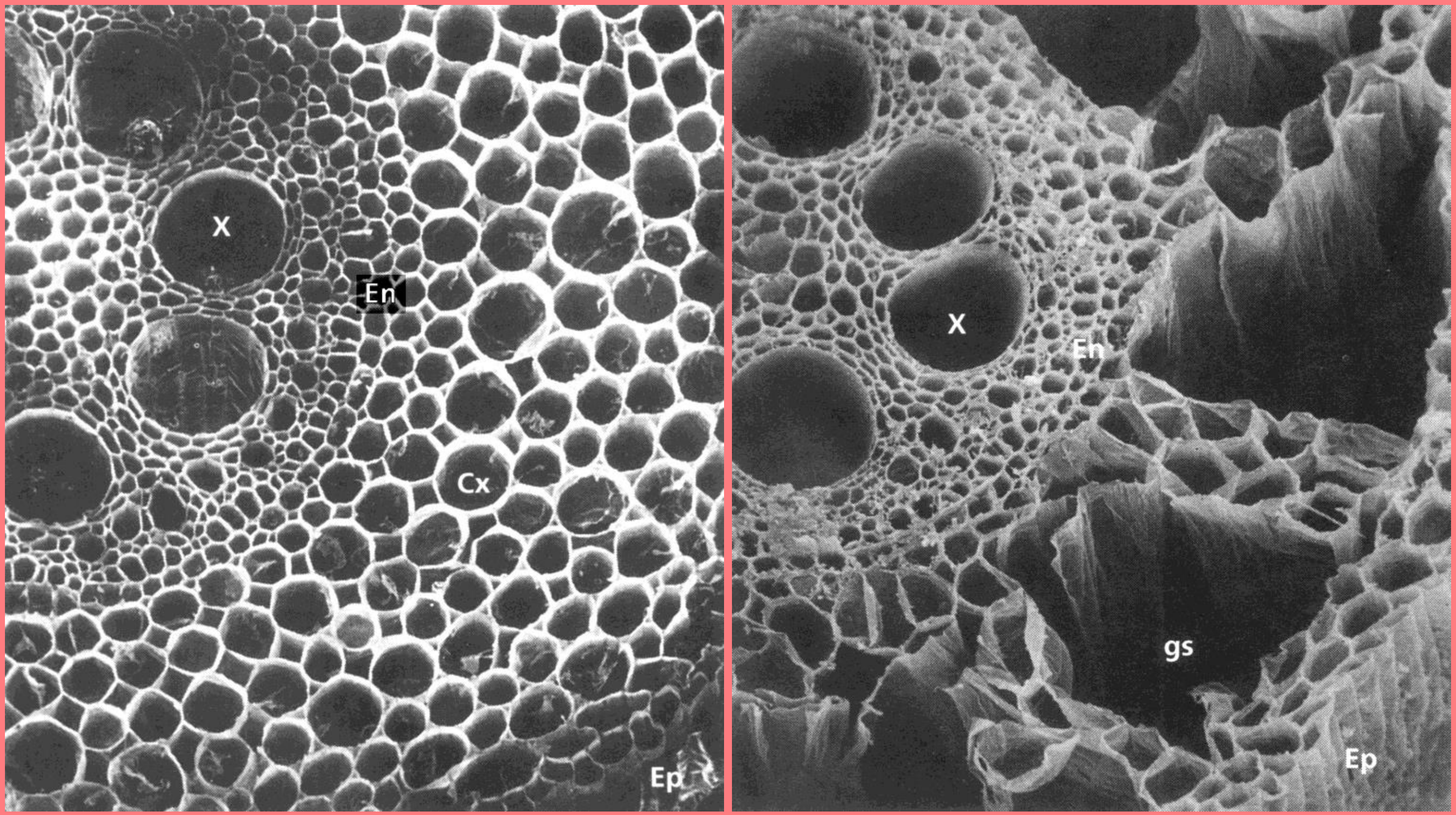
However, in several non-hydrophytes (e.g. in corn) proper **acclimation by anoxic conditions** in the substrate induces aerenchyma formation.

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

- **Aerenchyma formation**

  Anatomically, in corn, aerenchyma formation is induced in the base of the stem and also, in young roots.
  Schizogenous and **lysigenous air spaces** form in the cortex parenthyma. These will eventually form the aerenchyma network.
  Lysigenous spaces form by lysis of several cells that are responsive (sensitive) to ethylene.

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS



Aerenchyma formation in corn root

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

Pneumatophores (breathing roots) exit through sand in a mangrove tree

AVOIDANCE: SUITABLE ANATOMICAL MODULATIONS

Pneumatophores in a mangrove remains

THREE DIFFERENT STRATEGIES

- **Resistance**

  Plants following this strategy are able to maintain (at least in some tissues/cells) a **basic level of metabolic activity** in an environment of **hypoxia** or **anoxia** for prolonged time periods

  This group includes **rhizomes** of plants such as *Schoenoplectus lacustris*, *Sciprus maritimus*, *Typha angustifolia*, the **embryo** and **coleoptile** of rice and also **those of its weed** *Echinochloa crus-galli* var. oryzicola

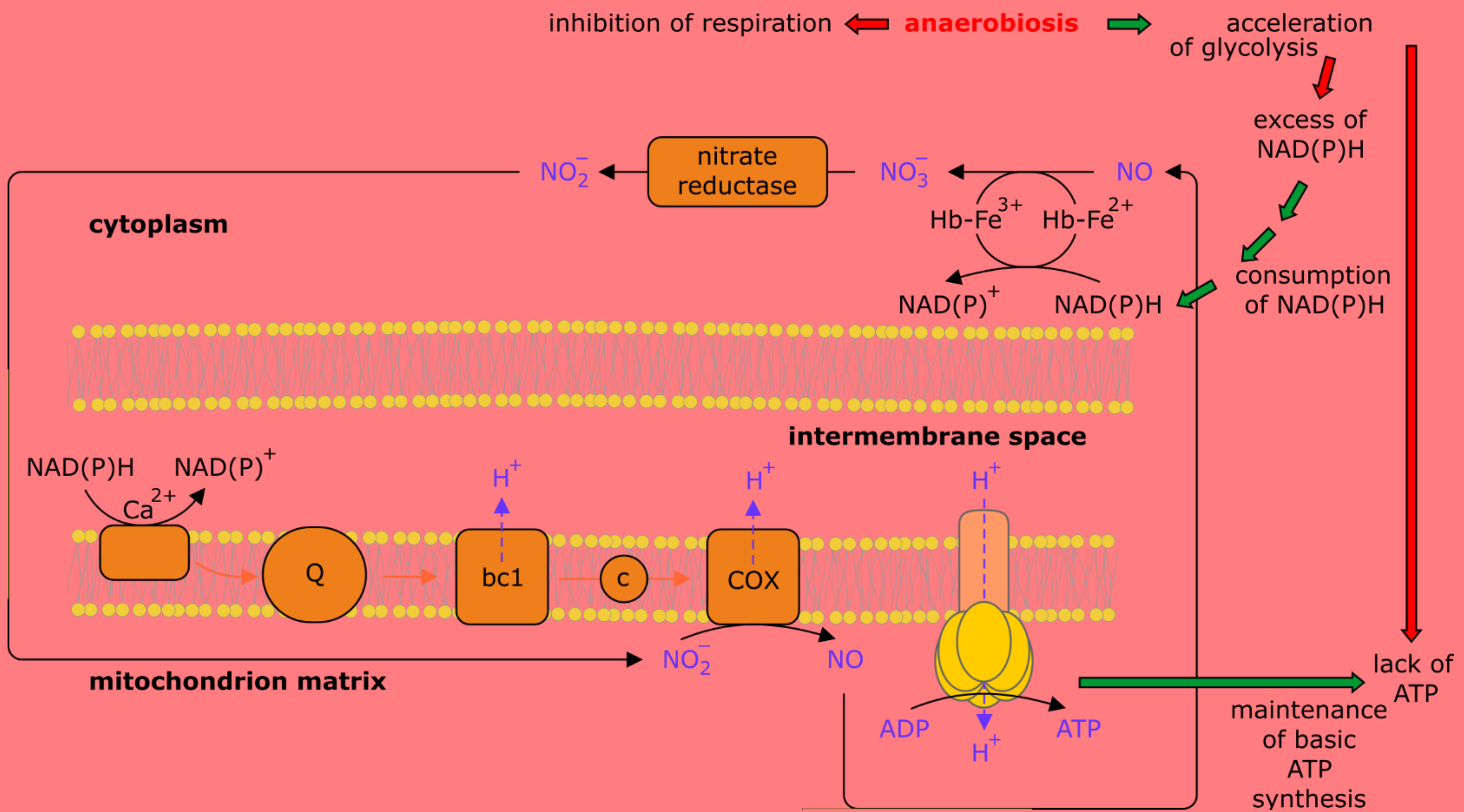
THREE DIFFERENT STRATEGIES

- **Resistance**

  Traits that determine survival under these conditions are related to the **control of cytoplasmic pH**. **Constant ATP synthesis** through the glycolysis and anaerobic respiration, combined with **enough respiratory substrate reserves** to cover this energetically expensive metabolism are also important.
  In some resistant plants, mitochondria maintain the ability to perform oxidative phosphorylation through the use of **alternative oxidases** and **different types of cytochromes**.

THREE DIFFERENT STRATEGIES

- **Resistance**



THREE DIFFERENT STRATEGIES

- **Resistance**

  Some plants (e.g. some *Limonium* species) are able to **secret lactic acid**, formed by anaerobic respiration, in the rhizosphere. This process helps avoid cytoplasm acidification and cell metabolic perturbation, **however results in considerable carbon loss**

THREE DIFFERENT STRATEGIES

- **Resistance**

  Rhizomes of plants that overwinter under anoxia conditions inside the alluvium of the shore of marshes, lakes, etc., during spring they emerge leaves that **come in contact with the atmosphere**. These leaves **transfer oxygen through the aerenchyma to the rhizomes**, whose the anaerobic respiration **shifts to aerobic**

THREE DIFFERENT STRATEGIES

- **Resistance**

The shift from anaerobic to aerobic respiration results in an additional type of metabolic stress (**post-anoxic stress**), due to reactive oxygen species that form after the beginning of oxygen supply

Anoxic resistant rhizomes, are equipped with mechanisms to cope with **sudden increase of ROS production**. Antioxidant enzymes such as SOD are **induced before the normoxic shift** to provide protection