2

WATER STRESS

WATER STRESS

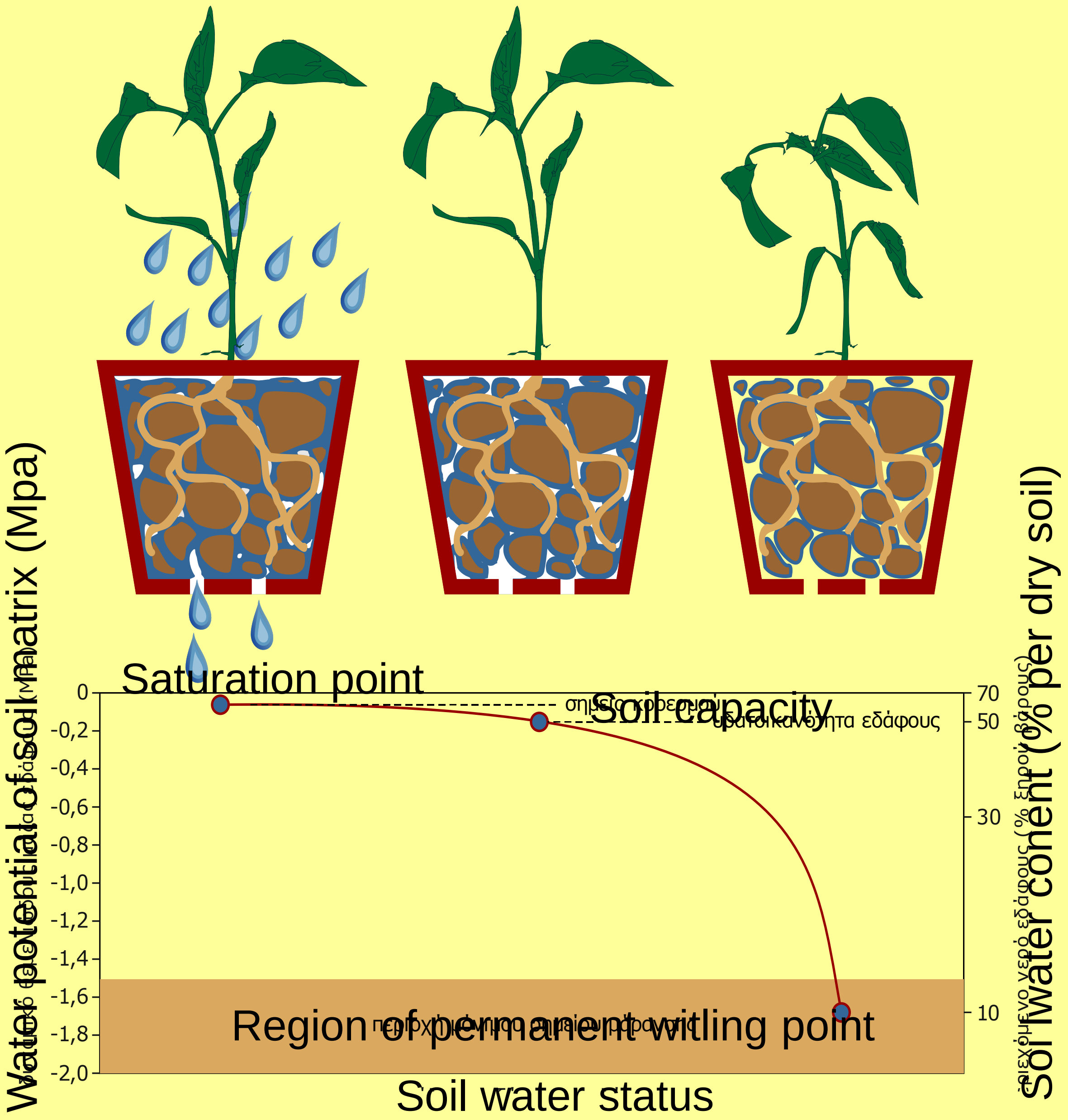
- **What is it;**

  The reduction of water potential of plant cells. Owed to limited water availability in the environment in combination with relation to transpirational needs of plants

- **Drought**

  Is an environmental factor owed to the combination of limited water influx in the soil (usually due to low precipitation) and increased water losses (trough evapotranspiration)

WATER STRESS



WATER STRESS

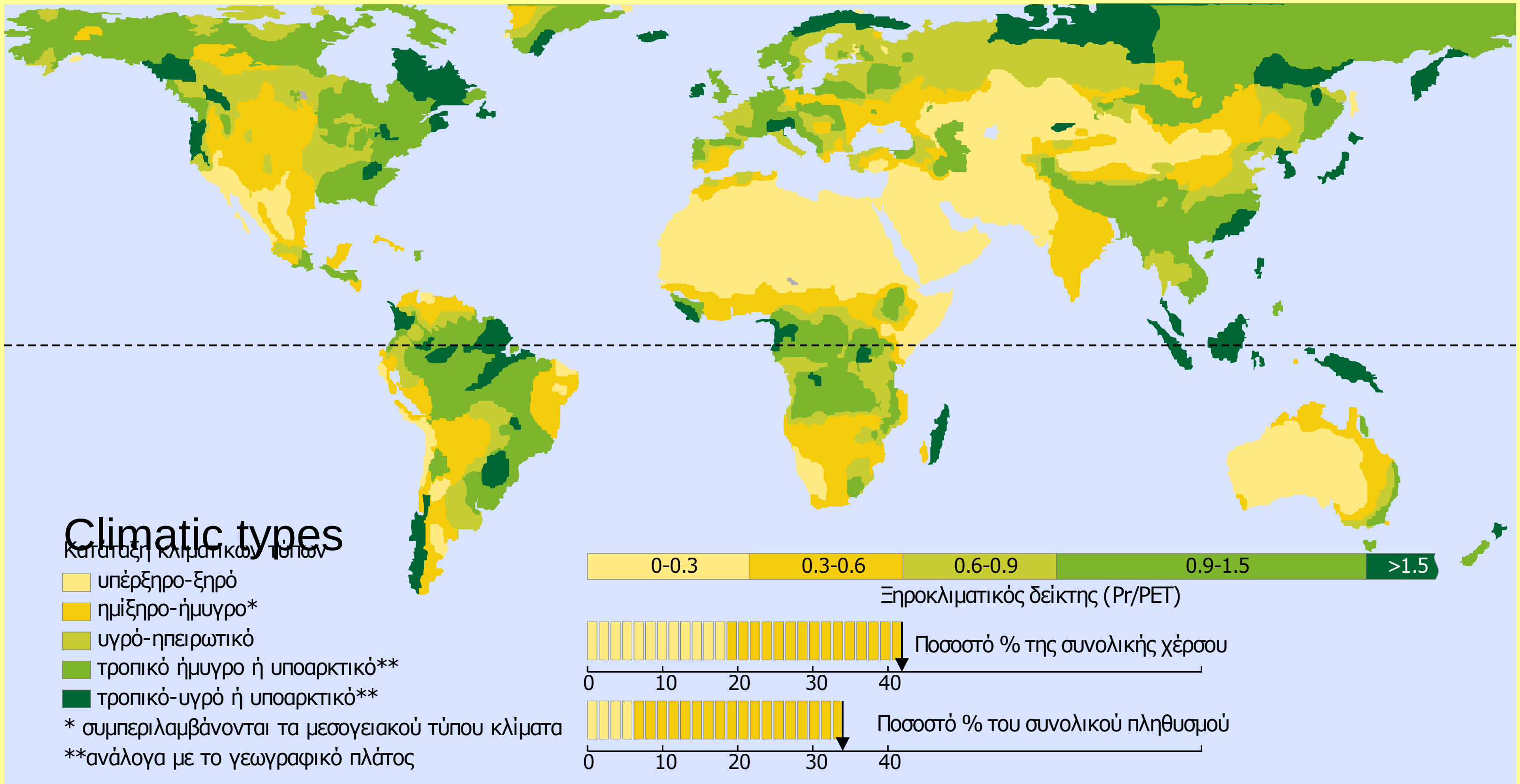
- **Drought distribution**

  Drought conditions prevail in 1/3 of the cultivating land

- **Importance of drought stress**

  Represents the most important, in terms of agricultural product losses, stress factor worldwide

EXTEND OF DROUGHT IN THE PLANET



Distribution of drought regions in the planet using the criterion of the combination of water influx and potential evapotranspiration

Year	**Corn**	**Soybean**
1979	104	106
1980	***87***	***88***
1981	104	100
1982	108	104
1983	***77***	***87***
1984	*101*	*93*
1985	112	113
1986	113	110
1987	114	111
1988	***80***	***89***

Corn and soybean production in the USA (as % of the years 1979-1988 average). *Italics* denote years of extreme drought

PLANT GROUPS DIVIDED BY WATER AVAILABILITY IN GROWTH ENVIRONMENT

- **Aquatic plants**

  Plants of wetlands. They are locates partially or totally underwater

- **Hydrophytes**

  They thrive in environments with constantly high atmospheric and soil humidity

PLANT GROUPS DIVIDED BY WATER AVAILABILITY IN GROWTH ENVIRONMENT

- **Mesophytes**

  They colonize regions characterized by temporarily high or medium levels of atmospheric and soil humidity

- **Xerophytes**

  Plants distributed in semi-dry or dry regions

PLANT SURVIVAL UNDER DROUGHT

- **The ability of plants to cope with drought depends on:**

  The ability to draw water from the soil

  The Water Use Efficiency (WUE) or Transpirational Ratio (TR)

  The ability to preserve water reserves

- **Differences between plant species**

  Differences in adaptation and acclimation capacity differentiate cultivated plant species’ water demands

Species	kg dry matter produced per kg of transpired water (WUE) x 10^3	kg water demand per kg of dry matter produced (transpiration ratio,TR)
Trifolium	1.2	850
Soybean	1.5	650
Oat, potato	1.7	580
Wheat	1.8	550
Sugarbeet	2.6	380
Corn	2.8	350
Sorghum	3.3	300
Representative of *An average CAM* plant	8	125

Water use efficiency of important cultivated plant species

PARAMETERS OF PLANT WATER STATUS

- **Water potential (Ψ)**

  Defined as the amount of free energy per unit of water volume

  It is a measure of the ability of water to produce work

  The difference ΔΨ between two regions determines the intensity and direction of water movement

- **Physical quantity characteristics**

  Water potential of pure water under reference conditions is considered to be equal to 0 Mpa

  Unit of measure is MPa (a unit of pressure)

ΠΑΡΑΜΕΤΡΟΙ ΤΗΣ ΥΔΑΤΙΚΗΣ ΚΑΤΑΣΤΑΣΗΣ ΤΩΝ ΦΥΤΩΝ

- **Relative Water Content (RWC)**

  It is defined as the water content of a plant tissue relatively to its saturated water content

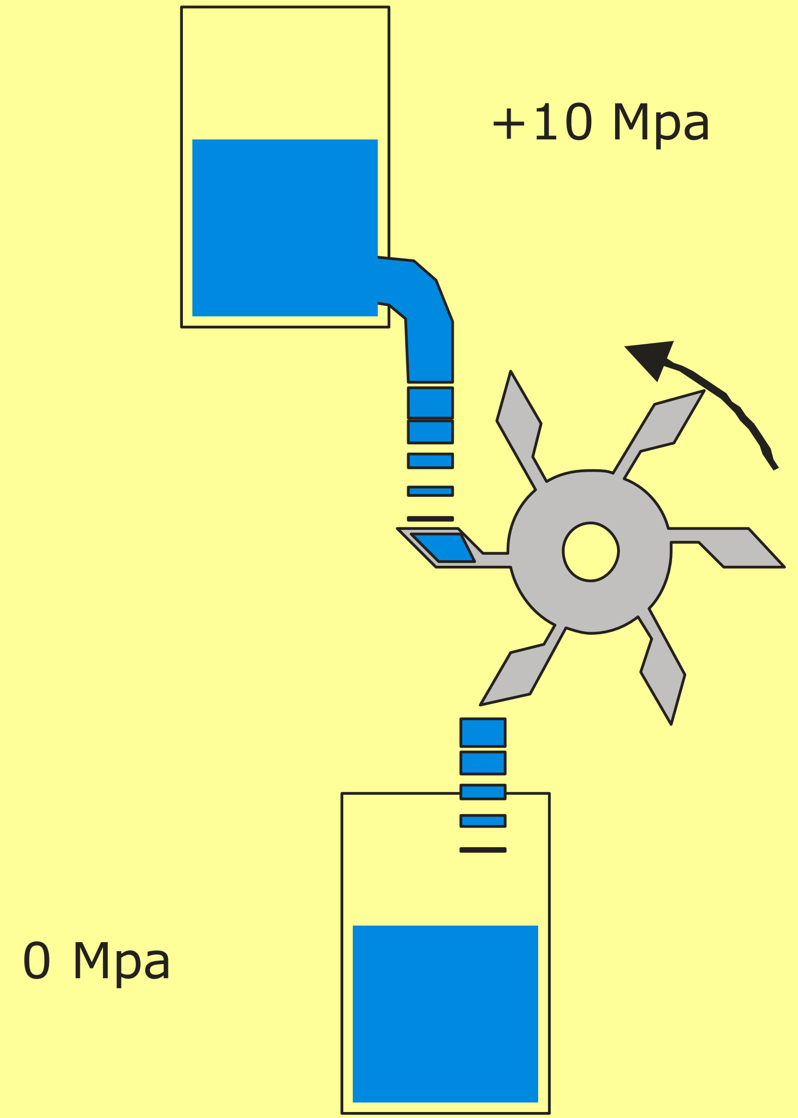
  It is a measure of plant tissues water need coverage

- **Physical quantity characteristics**

  RWC is unitless

  Usually, it is measured in leaf disks weighted as they are and again after full turgor after floating in water for several hours. Finally, the dry weight is taken and the RWC is calculated as below:
  $RWC = (f.w._{current}-d.w.)/(f.w._{saturated}-d.w.)$

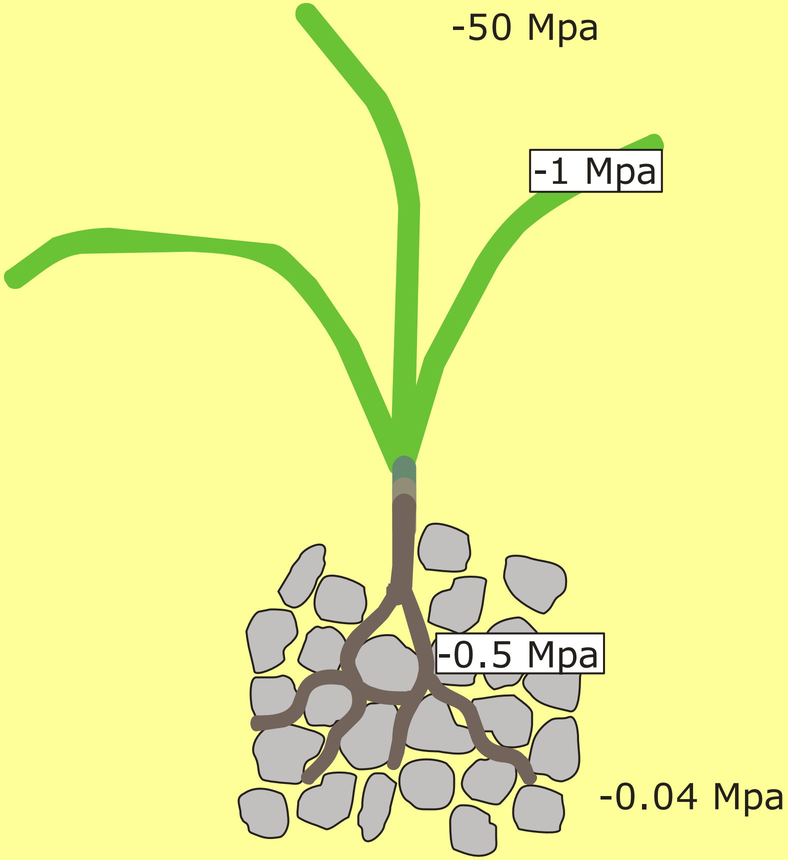
WATER POTENTIAL



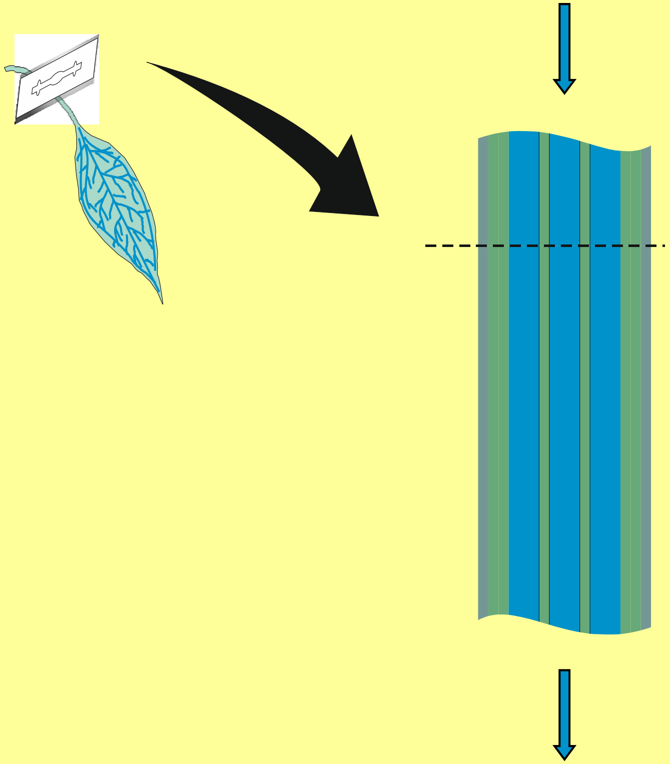
+10 Mpa

0 Mpa

WATER POTENTIAL



WATER POTENTIAL



1

2

from root

section plane

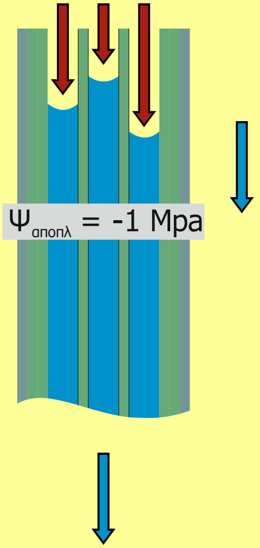
to leaf

WATER POTENTIAL

3

P = 0 Mpa

xylem sap
withdraws;
embolism develops

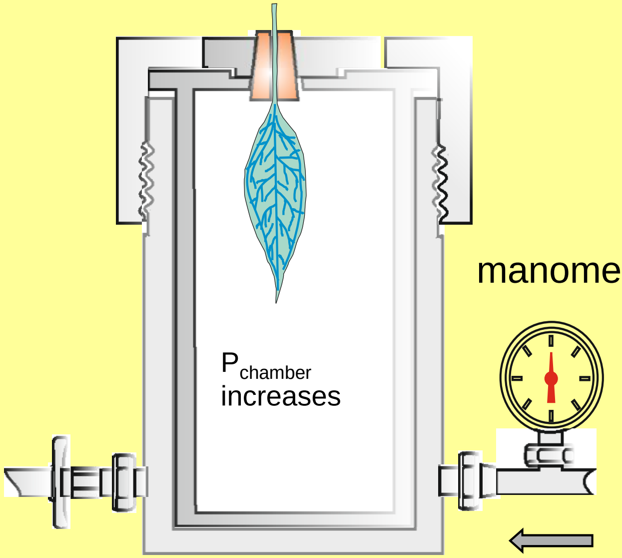


$\Psi_{\alpha\pi o\pi\lambda}$ = -1 Mpa

direction of
xylem sap
movement

to leaf

WATER POTENTIAL



4

$P_{\alpha\tau\mu}$ = 0 Mpa

manometer

$P_{chamber}$ increases

air supply

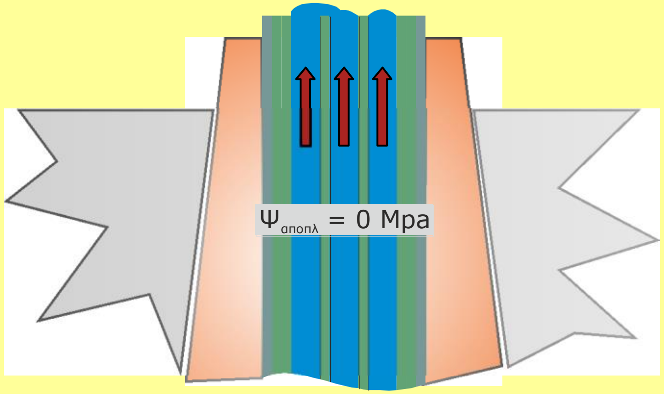
decompression valve (closed during measurement)

WATER POTENTIAL

$P_{\alpha\tau\mu} = 0$ Mpa

5

xylem sap moves back to the section plane due to pressure equalization

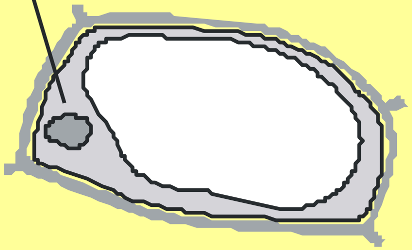


$P_{\theta\alpha\lambda} = +1$ Mpa

WATER POTENTIAL

In plant cells, water potential is primarily determined by two components. The first is osmotic potential (Ψ_s) and the second is pressure potential (Ψ_p). We have:

$\Psi_w = \Psi_s + \Psi_p$



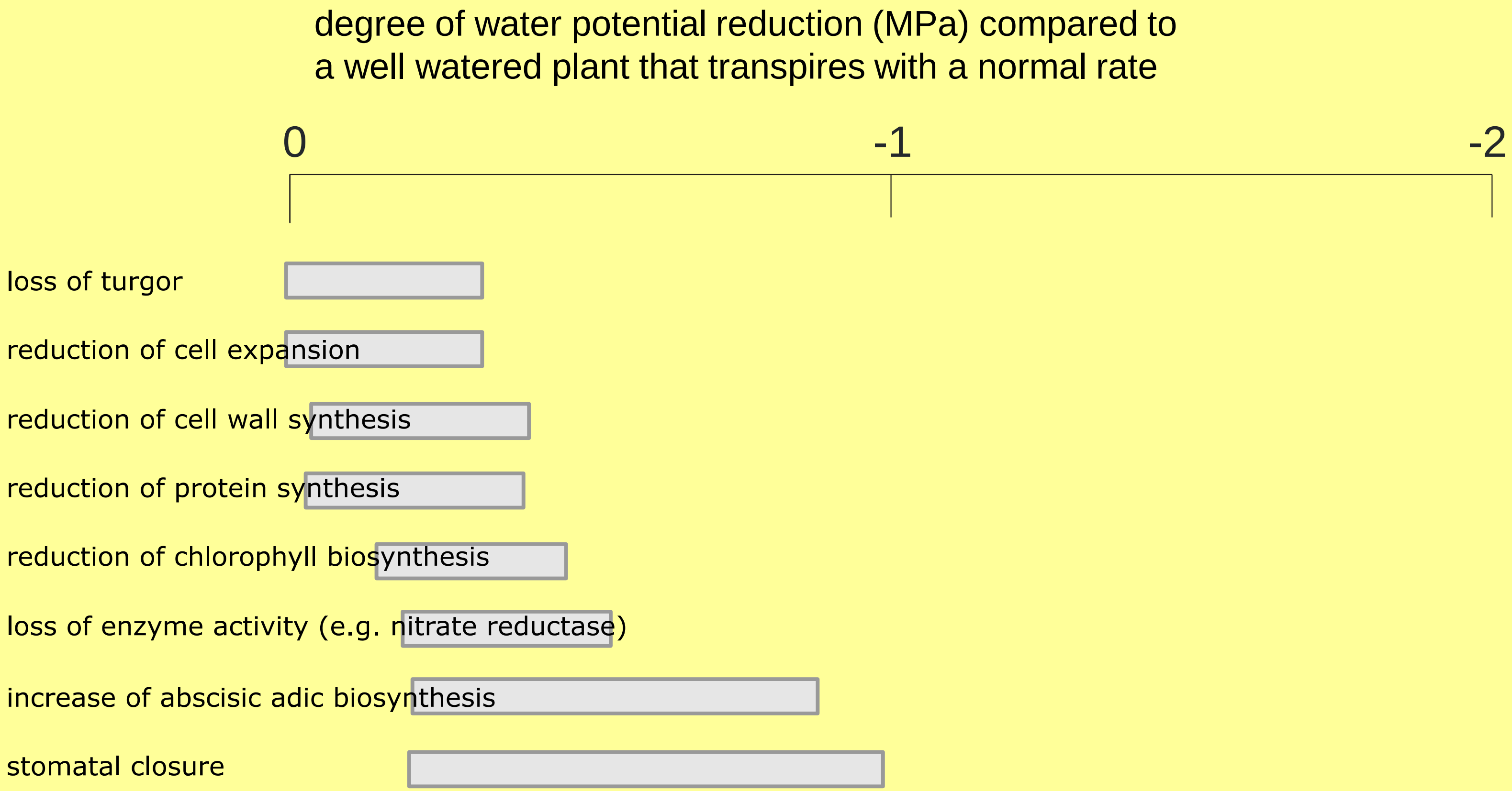
protoplast

$\Psi p = + 0,5$ MPa

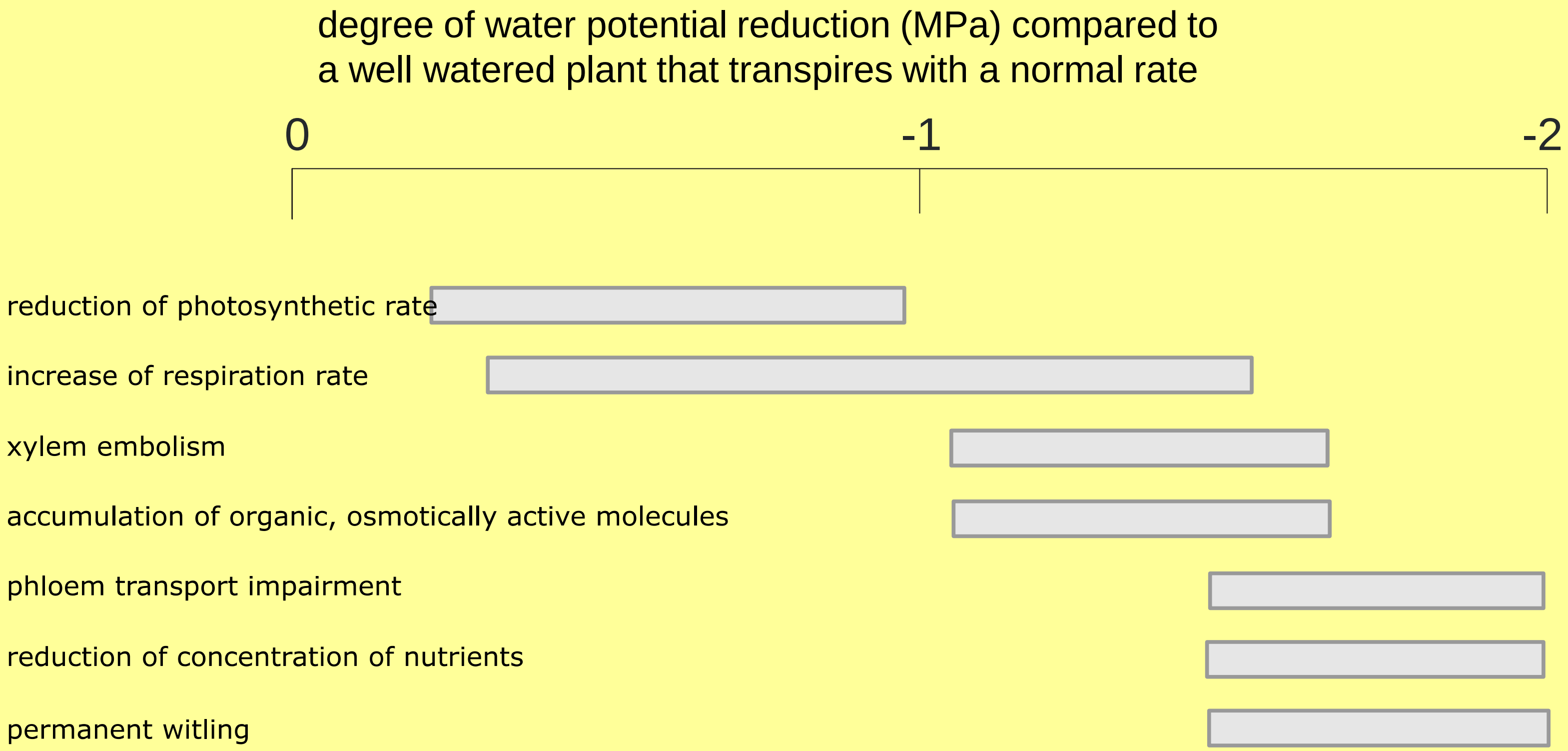
$\Psi s = - 1,5$ MPa

$\Psi w = \Psi p + \Psi s = - 1,0$ MPa

EFFECTS OF WATER POTENTIAL REDUCTION



EFFECTS OF WATER POTENTIAL REDUCTION



degree of water potential reduction (MPa) compared to
a well watered plant that transpires with a normal rate

reduction of photosynthetic rate

increase of respiration rate

xylem embolism

accumulation of organic, osmotically active molecules

phloem transport impairment

reduction of concentration of nutrients

permanent witling

PLANT RESPONSES TO WATER STRESS

- **Plant responses depend on growth stage**

Developed leaves
Their responses are related to the preservation of water reserves and protection against dehydration

Developing leaves
Growth inhibition
Initiation of acclimation processes

GROWTH INHIBITION

- **Cessation of growth of the developing leaves is sudden and represents an important event of the acclimation process under water stress**

The response of developing leaves consists of two stages: a) sudden cell division inhibition and/or cell expansion rate b) growth re-initiation

The inhibition stage is caused by the combined action of three hormonal signals:

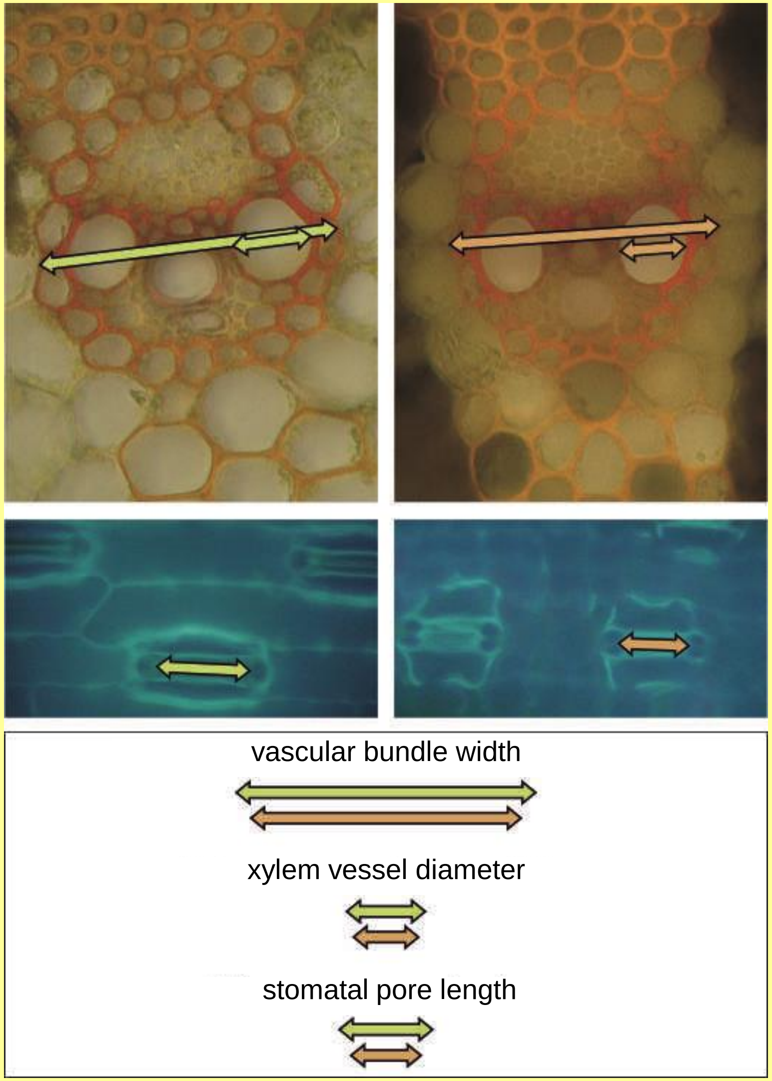
ethylene and ABA>induction of catabolism of GAs>stabilization of growth inhibitors (DELLA proteins) > growth inhibition

RE-INITIATION OF GROWTH OF DEVELOPING LEAVES

- **The re-initiation of growth stage includes the acclimation response and consists of the following:**

  α) metabolic reprograming
  β) reduction of meristematic cells (will result in the production of smaller and, hence, less water demanding leaves; long term acclimation)

RE-INITIATION OF GROWTH OF DEVELOPING LEAVES



RE-INITIATION OF GROWTH OF DEVELOPING LEAVES

- **The re-initiation of growth stage includes the acclimation response and consists of the following:**

    a) metabolic reprograming
    b) reduction of meristematic cells (will result in the production of smaller and, hence, less water demanding leaves; long term acclimation)
    c) modification of the mechanical characteristics of developing cell walls
    d) increase of water conductivity through the synthesis of abundant membrane aquaporins

EFFECTS OF WATER STRESS

- **Effects that are considered as acclimation elements**

  Reduction of leaf surface area

  Modification of the above/below ground plant ratio

  Shedding of older leaves

  Leaf movement

  Increase of water diffusion resistance by stomatal closure

  Induction of CAM

  Proteome alterations related to water transfer and protection of sensitive targets from desiccation

  Osmotic balancing or osmotic adjustment

EFFECTS OF WATER STRESS

- **Effects that are considered as adverse**

  Root system desiccation

  Hypodermis suberization

  Development of embolisms

  Cytoplasm dehydration

  Impairment of cell membrane intactness and selectivity

  Impairment of membrane enzyme activity

  Metabolic perturbations

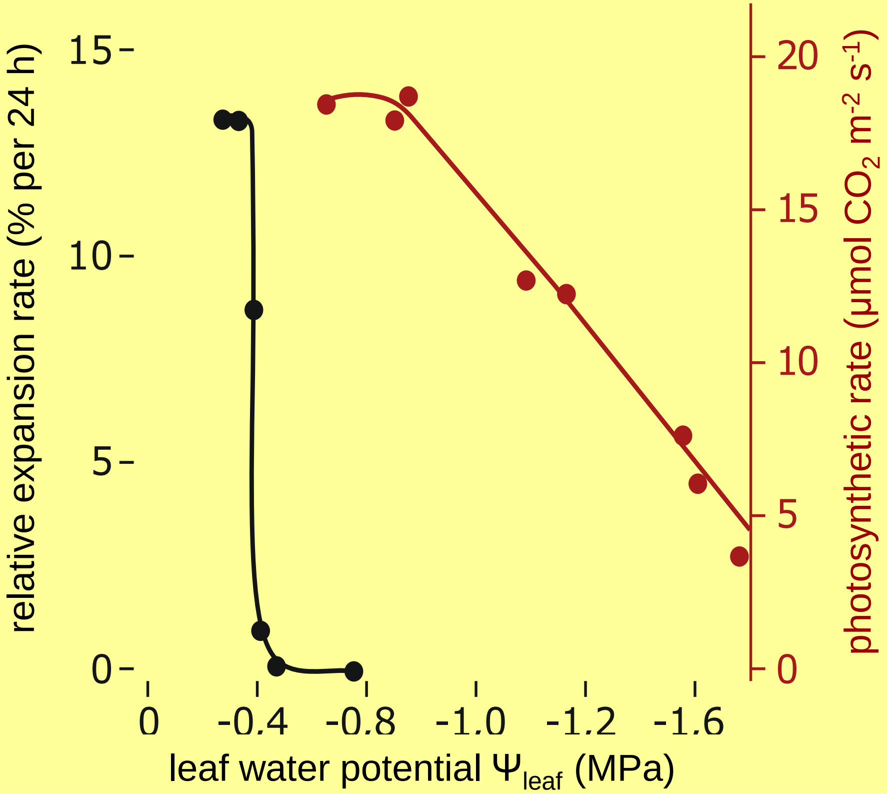
  Perturbation of photosynthesis

  Photoinhibition

  Oxidative damage

REDUCTION OF LEAF SURFACE AREA OF DEVELOPING LEAVES

Cell expansion, of meristem cells in particular, represents a process that is extremely sensitive in water stress, because it depends directly from a adequate turgor pressure. We have $GR = m (\Psi_p - Y)$



MODIFICATION OF ABOVE/BELOW GROUND RATIO

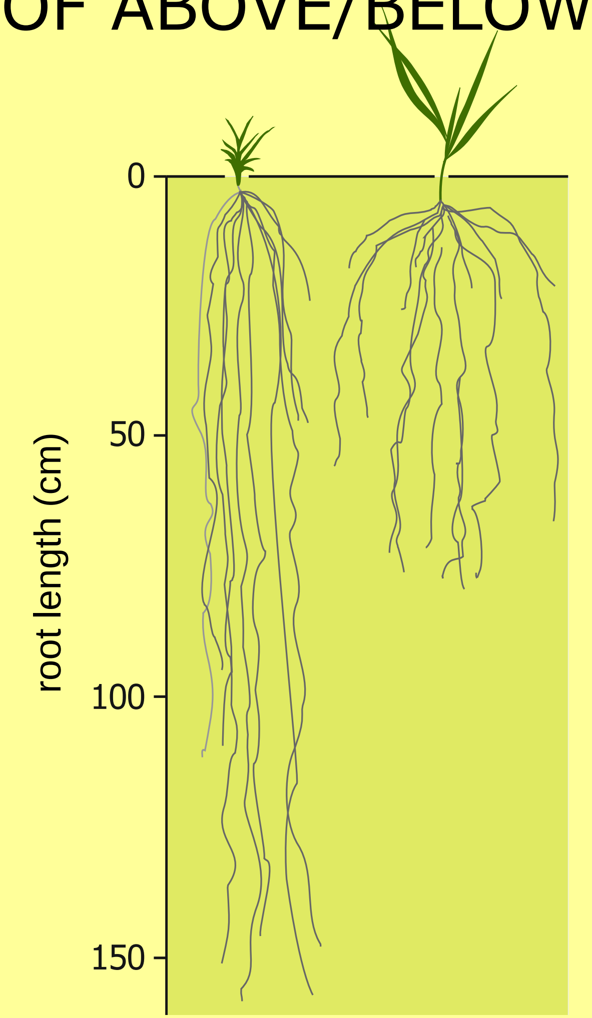
Root development under water stress is less sensitive compared to that of the shoot and, especially, the leaves.

This is due to osmotic equilibration of the root cells, that can cause a considerable reduction of the osmotic potential (in levels much more negative than the levels of soil water potential).

Root cells can maintain cell expansion under a much lower water potential compared to the leaf cells.

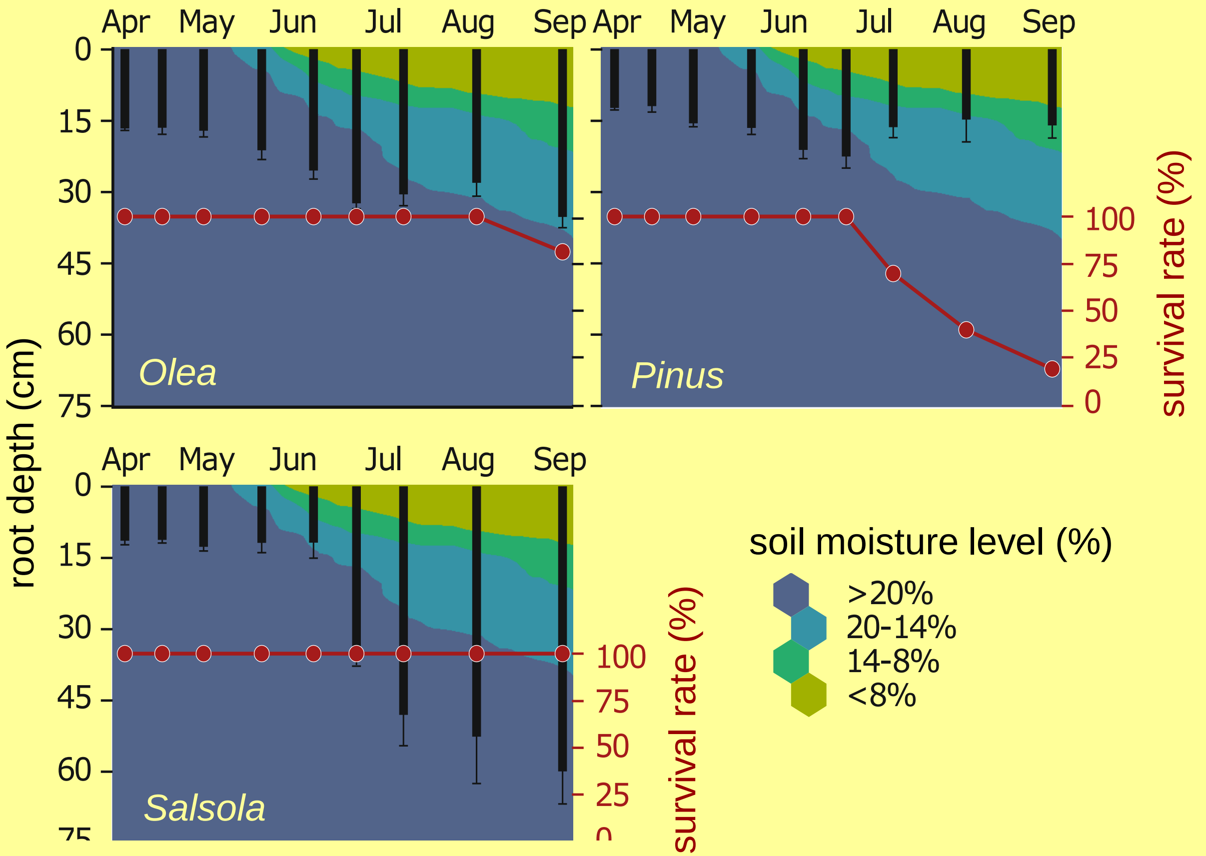
A much larger portion of the photosynthates may be allocated to the root part due to intrinsic restrictions in leaf growth compared to the inhibition of photosynthesis on a whole plant scale

MODIFICATION OF ABOVE/BELOW GROUND RATIO



Acclimation of *Agropyron smithii* in dry soil. The plant to the left is grown in a relatively dry soil compared to the plant to the right that is grown in a much more wet soil.

RELATION BETWEEN PLANT SURVIVAL RATE AND ROOT DEPTH



Maximum root depth (black bars), isobaric lines of soil moisture and time-course of survival rate of seedlings (red line).

LEAF MOVEMENTS

They alter the energy balance of the leaf

Leaf energy balance (and temperature) depends on the relative magnitudes of incoming and outgoing energy:

$Q >=< Q_1 + Q_2 + Q_3$

Q_1: reemission of energy to the environment as radiation and heat transfer

Q_2: incoming radiation energy and heat transfer

Q_3: energy loss through water evaporation maintained through transpiration

LEAF MOVEMENTS

Leaf movements aim to reduce energy influx (Q) through the reduction of leaf surface exposed to the sunlight

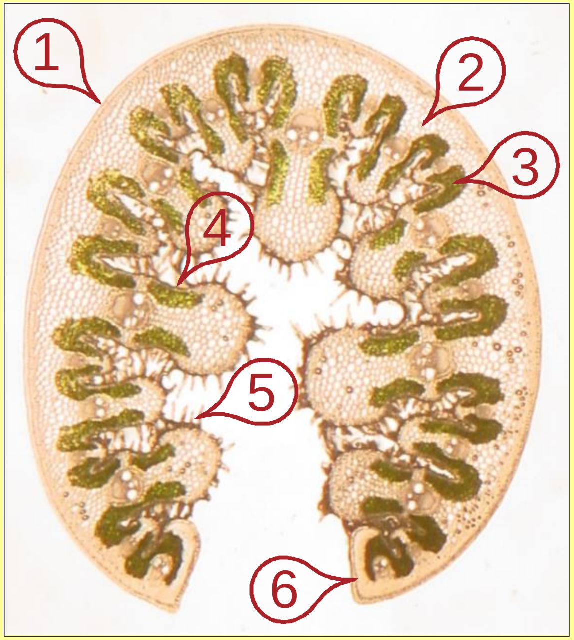
They include paraheliotrpic movements, change in lamina inclination and leaf curling

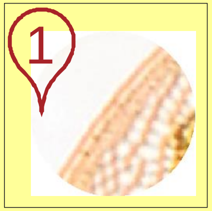
STUDYING THE EXTREMES

How many mechanism of water saving are present?

STUDYING THE EXTREMES

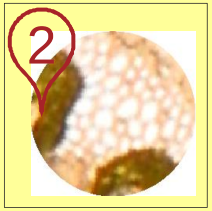
How many mechanism of water saving are present?





Thick cuticle and epidermis

Limiting water loss



Extensive sclerenchyma

Mechanical strengthening,
light transfer,
water economy

Limited photosynthetic tissue

Rationalization of photosynthesis

Stomata inside crypts

Limiting water losses,
imminent supply of CO_2

Leaf hairs

Limiting water loss

Cylindrical lamina

Limiting water loss

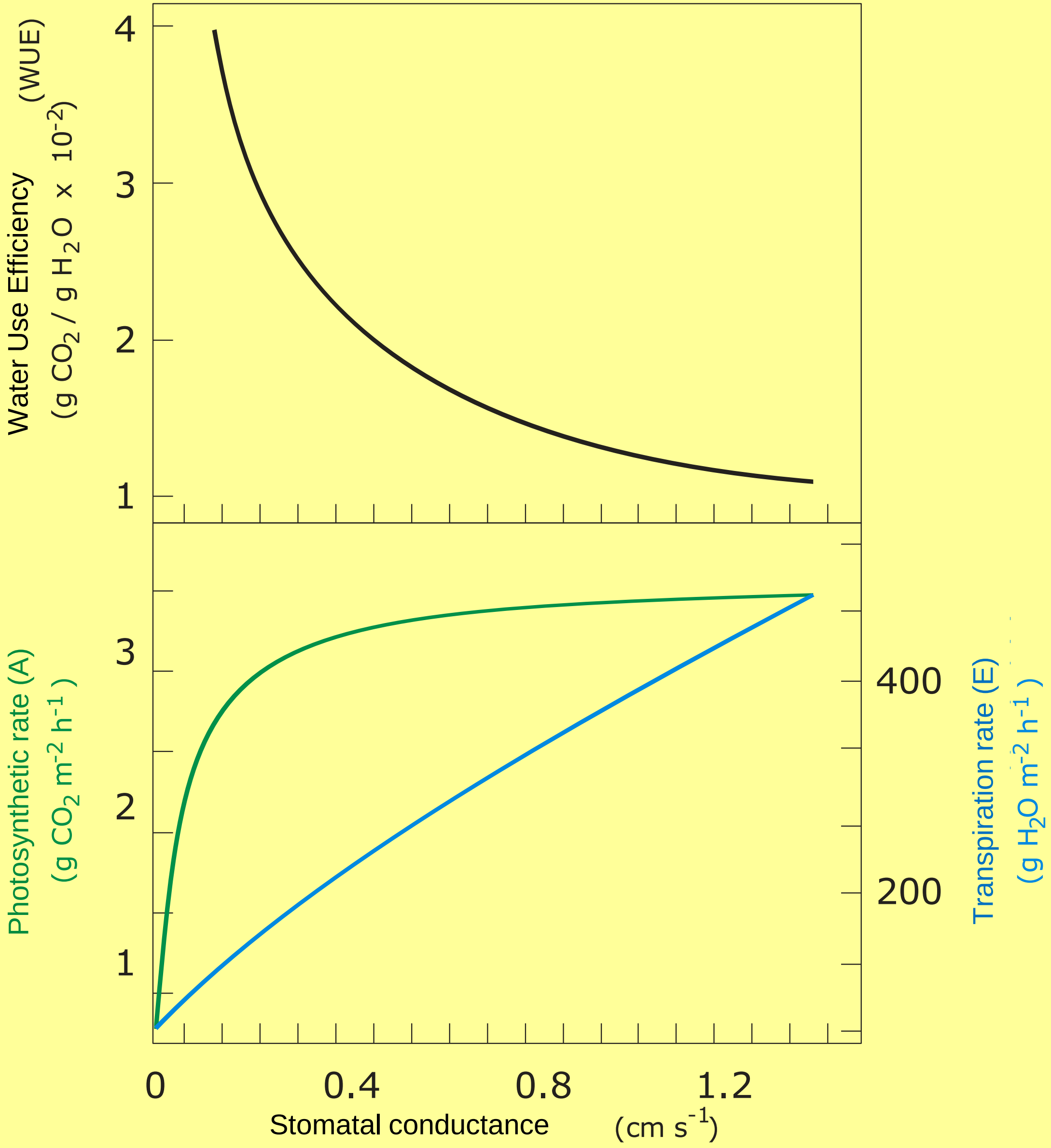
STOMATAL CLOSURE

Results in the in crease if water vapor diffusion resistance to the atmosphere aiming to water economy

Stomatal closure may be passive (because of loss of turgor of the guard cells) or active (because of the metabolically dependent accumulation of osmotically active molecules form guard cells after an abscisic acid signaling)

Abscisic acid may be originating from the leaves of from the root vial the xylem vessels

STOMATAL CLOSURE

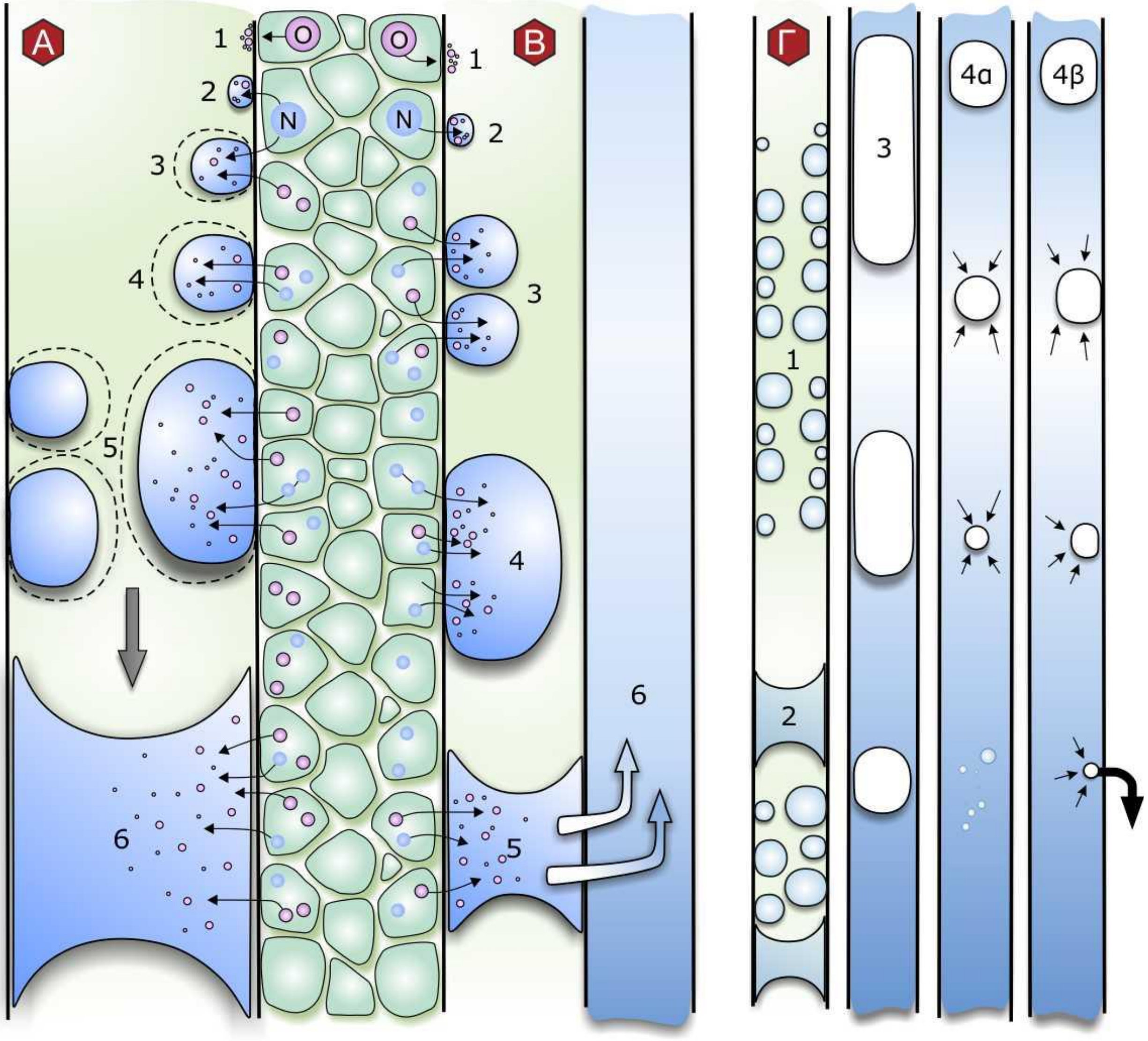


OTHER MODIFICATIONS OF WATER CONDUCTIVITY

Root hypodermis suberization

Development of xylem vessel embolism

RECOVERY FROM EMBOLISM



OTHER MODIFICATIONS OF WATER CONDUCTIVITY

Root hypodermis suberization

Development of xylem vessel embolism

Changes in aquaporin distribution (MIPs)
PIPs: this group is related to intercellular transport of water, hence to its distribution on a plant level, and to water economy
TIPs: this group is related to intracellular distribution of water and osmoregulation ability

INDUCTION OF CAM

Results in increase of the water use efficiency through the maintenance of CO_2 assimilation under closed stomata

Under normal water conditions, optional CAM plants restore their normal C_3 carbon metabolism

TRANSCRIPTOME MODIFICATIONS

Proteins and hormones act as transcription factors in transcription regulatory sequences in target genes

Four signal cascades exist: two ABA-dependent and two ABA-independent signal cascades for regulation of gene expression

ABA-dependent : MYC/MYB and AREB/ABF
ABA-independent : CBF/DREB and NAC/ZF-HD

PROTEOME MODIFICATIONS

Protein and enzyme activities change. New proteins are synthesized *de novo*.

Key-enzymes of basic metabolic paths
Aquaporines
Ubiquitin and proteases
LEA proteins/dehydrines

OSMOTIC REGULATION/ADJUSTMENT

Causes a reduction of the osmotic potential of cells through the accumulation of osmotically active molecules

Reduction of Ψ_s should not be confused with passive reduction of the same parameter due to desiccation. Osmoregulation is an **active increase** of the concentration of osmotically active molecules due to **biosynthesis** or **accumulation from other source** (i.e. from depolymerization of starch).

OSMOTIC REGULATION/ADJUSTMENT

- **Benefits of osmoregulation for the plant**

The cell osmotic potential (Ψ_s) is reduced
This results in a reduction of the water potential of the cell (Ψ_w)

This reduction results in the maintenance of the ability of cells to **absorb water under drought conditions** (conditions that favor the reduction of the soil matrix water potential)

Secondly, water absorption occurs in a state of **maintenance of a sufficient cell turgor** of the cells and avoidance of desiccation

OSMOTIC REGULATION/ADJUSTMENT

- **Which molecules can participate in osmoregulation;**

Easy for the cell to acquire them, synthesize, etc.

Compatible for cell metabolism in high concentrations

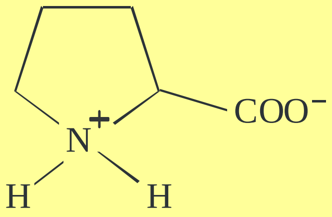
Should be polar molecules, soluble in the cell sap, attract many molecules of water while at the same time protecting valuable protein and other biomolecules from denaturation

Most common compatible solutes: Proline, glutamate, betains, polyols, fructans, trehalose, glucose and oligosaccharides.

OSMOTIC REGULATION/ADJUSTMENT

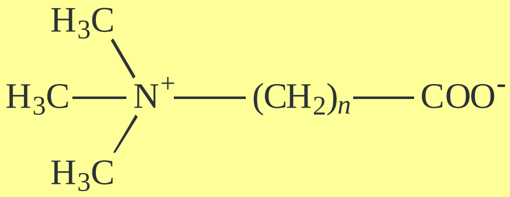
- **Most common compatible solutes**

amino acids



proline

betains

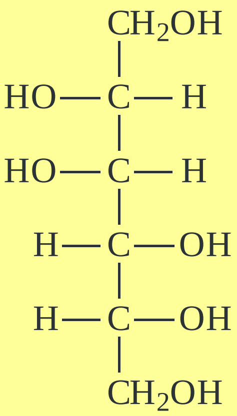


$$(H_3C)_3N^+-(CH_2)_n-COO^-$$

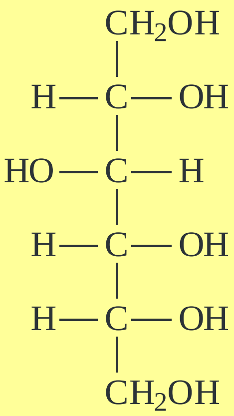
n = 1, glycine betain

n = 2, alanine betain

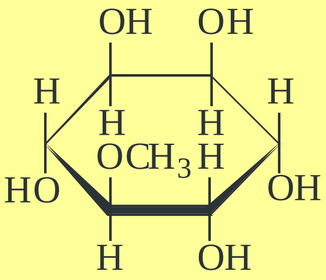
polyols



mannitol

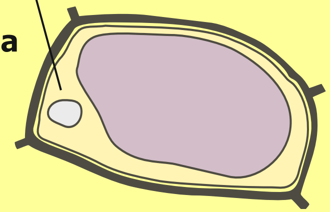


sorbitol



pinitol

OSMOTIC REGULATION/ADJUSTMENT

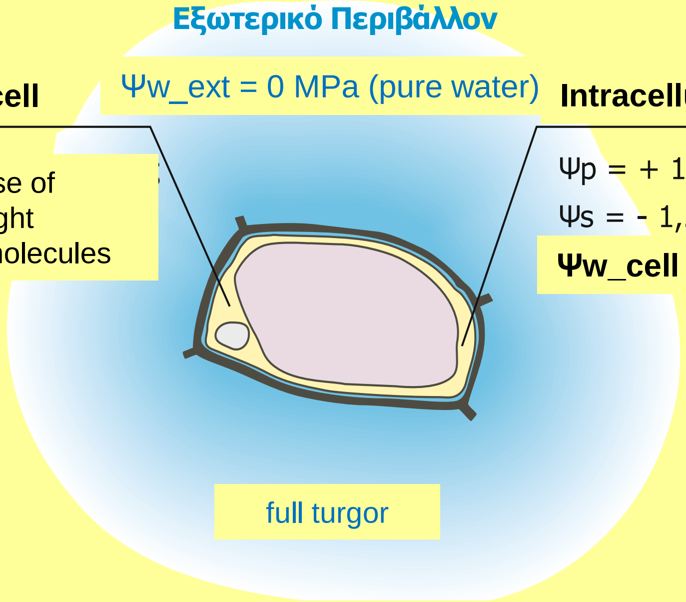


Intracellular environment

Ψp = + 0,5 MPa

Ψs = - 1,5 MPa

$\Psi w = \Psi p + \Psi s$ = - 1,0 MPa



Εξωτερικό Περιβάλλον

Ψw_ext = 0 MPa (pure water)

$\Psi w\_ext > \Psi w\_cell$

water entry, increase of turgor pressure, slight dilution of diluted molecules

Intracellular environment

Ψp = + 1,2 MPa

Ψs = - 1,2 MPa

Ψw_cell = 0 MPa = Ψw_Ext

full turgor

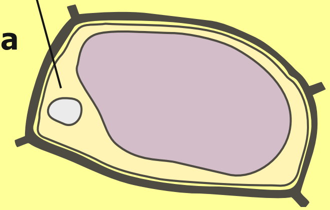
OSMOTIC REGULATION/ADJUSTMENT

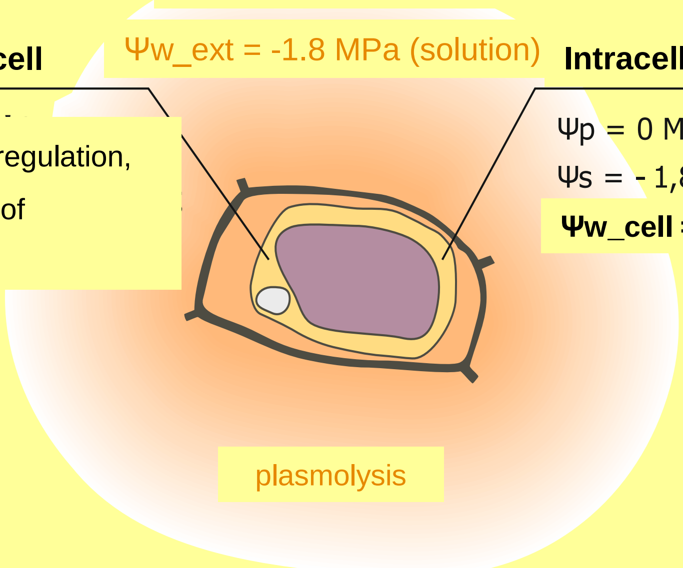
Intracellular environment

$\Psi p = +\ 0{,}5\ \text{MPa}$

$\Psi s = -\ 1{,}5\ \text{MPa}$

$\boldsymbol{\Psi w = \Psi p + \Psi s = -\ 1{,}0\ \text{MPa}}$





External environment

$\Psi w\_ext = -1.8\ \text{MPa}$ (solution)

$\Psi w\_ext > \Psi w\_cell$

inability for osmoregulation,

passive increase of

dilute substances

Intracellular environment

$\Psi p = 0\ \text{MPa}$

$\Psi s = -\ 1{,}8\ \text{MPa}$

$\Psi w\_cell = -1.8\ \text{MPa} = \Psi w\_Ext$

plasmolysis

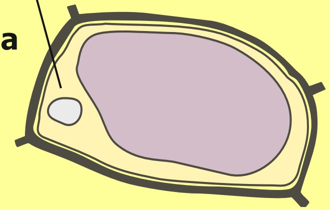
OSMOTIC REGULATION/ADJUSTMENT

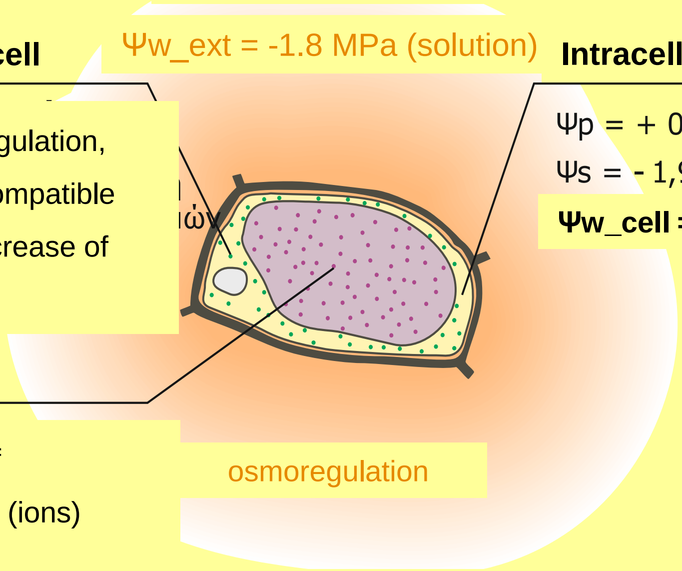
Intracellular environment

Ψp = + 0,5 MPa

Ψs = - 1,5 MPa

Ψw = Ψp + Ψs = - 1,0 MPa





External environment

Ψw_ext = -1.8 MPa (solution)

Ψw_ext > Ψw_cell

ability for osmoregulation, biosynthesis of compatible solutes, active increase of dilute substances

active increase of dilute substances (ions)

osmoregulation

Intracellular environment

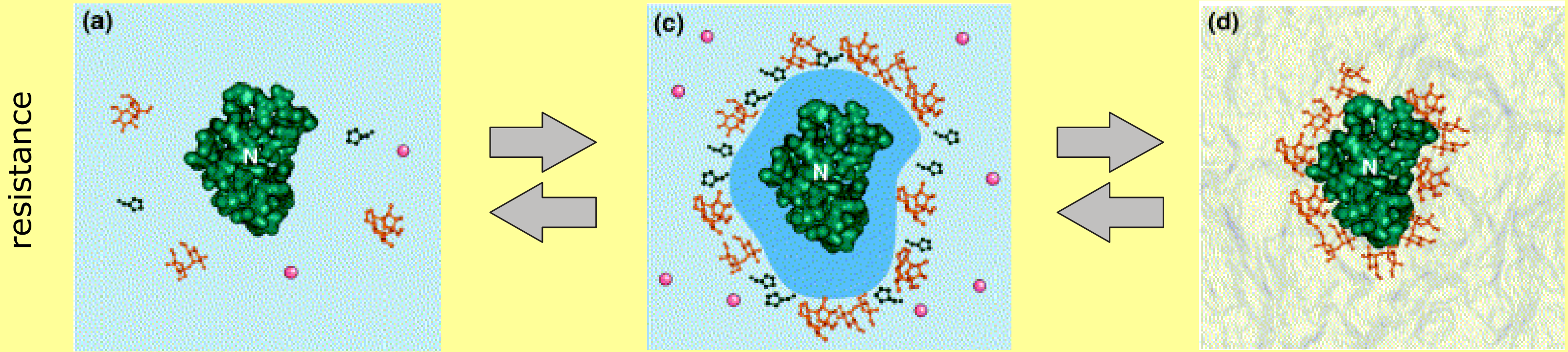
Ψp = + 0,1 MPa

Ψs = - 1,9 MPa

Ψw_cell = -1.8 MPa = Ψw_Ext

OSMOTIC REGULATION/ADJUSTMENT

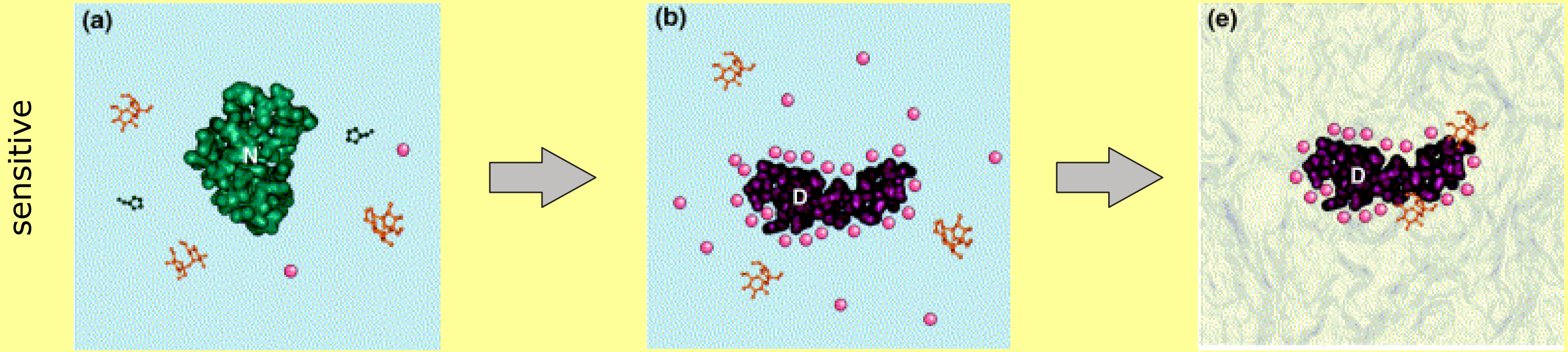
- **Protection of sensitive target molecules**



full hydration

partial desiccation

full desiccation (vitrified cytoplasm)



full hydration

partial desiccation

full desiccation (vitrified cytoplasm)

THREE DIFFERENT STRATEGIES

- **Escape**

  Plants (usually annuals) complete their life cycle within the favorable season. During the unfavorable season they exist in lethargic forms (e.g. seeds).
  Other plants shed their leaves (like *Euphorbia*) or the whole above part (e.g. *Asphodelus*) during the unfavorable season.

THREE DIFFERENT STRATEGIES

- **Avoidance**

  Annual or perennial species. In the presence of water stress, these plants manage to maintain a sufficient water potential. Their cells do not experience stress nor they are resistant to it.
  Plants like evergreen sclerophylls and phrygana (bushwoods) follow the strategy of avoidance against water stress.

THREE DIFFERENT STRATEGIES

- **Avoidance through water economy**

  These plants can considerably limit their transpirational water losses, keeping CO_2 assimilation at reasonable rates (WUE is high).
  Priority is given to water saving and conservation of water reserves. During the unfavorable season, cells still maintain quite high water potential. A good example of plants of this group are the CAM plants.

THREE DIFFERENT STRATEGIES

- **Avoidance through water economy**

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THREE DIFFERENT STRATEGIES

- **Avoidance through water consumption**

  i. Ability to develop very low root water potential, in order to allow high rates of water absorption from the soil.
  ii. The ratio below/above ground plant part is increased. In some deep root plants, roots may reach considerable depths, gaining access to the deep groundwater.
  iii. Water conductivity is high.
  iv. Water can also be absorbed from aboveground organs (leaves, stems, epiphyte roots).

THREE DIFFERENT STRATEGIES

- **Avoidance strategy is very common in plants of the Mediterranean biome**

  Many plants are evergreen shrubs and small trees

  Leaves share common characteristics against water stress:

  - Reduced surface / volume ratio
  - Extensive sclerenchyma/collenchyma tissues
  - Strengthened epidermises and epidermal accessories
  - Small stomata, often high stomatal density
  - Midday depression of photosynthesis

THREE DIFFERENT STRATEGIES

- **Avoidance strategy is very common in plants of the Mediterranean biome**

  Many plants are phrygana, bushwoods (semi-deciduous woody shrubs with soft hairy leaves)

  Leaves share common characteristics against water stress:
  - Dense trichome layer (especially on young leaves)
  - Partial defoliation at the end of the wet period
  - Seasonal leaf dimorphism
  - Existence of leaf glands with essential oils

THREE DIFFERENT STRATEGIES

- **Resistance**

  Plants characterized by this strategy have the ability to maintain elemental metabolic activity even under very low levels of cytoplasmic water potential. Some, under conditions of prolonged and intense dehydration, go into the so-called resurrection mode characterized by conditions of near-complete dehydration of the cells.

THREE DIFFERENT STRATEGIES

- **Resurrection plants**

  These are polyhydric organisms, whose cells may survive during a prolonged time, even if the water content drops to atmospheric levels.

  They include unicellular photosynthetic organisms, lichens and higher plants (*Ramonda* and *Haberlea* are quite common in the Southern Europe).

  Resurrection plants are included in known plant families: Scrophulariaceae, Lamiaceae, Cyperaceae, Poaceae and Liliaceae

THREE DIFFERENT STRATEGIES

- **Resurrection plants**

  The resurrection state at the cell level is a nearly totally desiccated cytoplasm. Sensitive targets (like membranes, proteins, nucleic acids) are protected through the accumulation of oligosaccharides (like raffinose and trehalose).

MULTIPLE STRATEGIES IN THE SAME PLANT

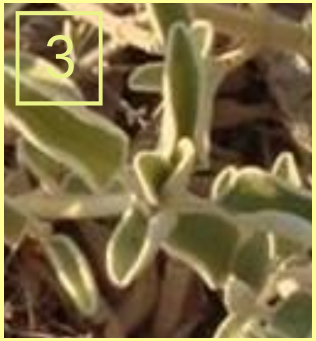
MULTIPLE STRATEGIES IN THE SAME PLANT

Partial defoliation

Escape at the plant organ level

Dessication avoidance

Avoidance in the leaves that remain



New leaf emergence

These leaves show traits of **resistance**