3

SALINITY STRESS

SALINITY

- **What is it?**

  Salinity refers to the presence of high concentration of ions (usually Na^+ and Cl^-), primarily in the soil environment.

- **Inherently high salt areas**

  Areas that are enriched with sea water (saline plains and salt marshes).

  Desert soils that accumulate salts because the rate of water evaporation are much higher than precipitation rate (judged from the Pr/PET index).

  High irrigated agricultural lands in which salt accumulation develops due to high evapotranspiration and/or bad quality of irrigation water.

SALINITY

- **Inherently high salt areas**

High salinity soils can be found in extended areas of the world which show high concentrations of salt for various reasons.
A percent of at least 20% of cultivated lands show high salinity.
A much higher extend of saline soils is found in irrigated cultivated lands.
These numbers are growing fast and this outcome appears to be inevitable.

Parameter	**Salt water**	**Good irrigation water**
***Ion contentration* (mM)**		
Na^+	457	<2.0
K^+	9.7	<1.0
Ca^{2+}	10	0.5-2.5
Mg^{2+}	56	0.25-1.0
Cl^-	536	<2.0
SO_4^{2-}	28	0.25-2.5
HCO_3^-	2.3	<1.5
***Osmotic potential* (MPa)**	-2.4	-0.039
***Total ion concentration* (mg L^{-1} or ppm)**	32 000	500
***Electrical conductivity* (dS m^{-1})**	44-55	<2.0

Parameters of salt water compared to good quality irrigation water

SALINITY

- **Effects of salinity (the ‘two-phase inhibition’)**

Soil characteristics become unsuitable, like porosity which affects water drainage and aeration

Reduction of soil water potential which results in **osmotic stress** of plants

High concentration of Na^+ and Cl^- causes **phytotoxicity** due to inhibition of membrane selectivity and impairment of transport proteins and enzymes

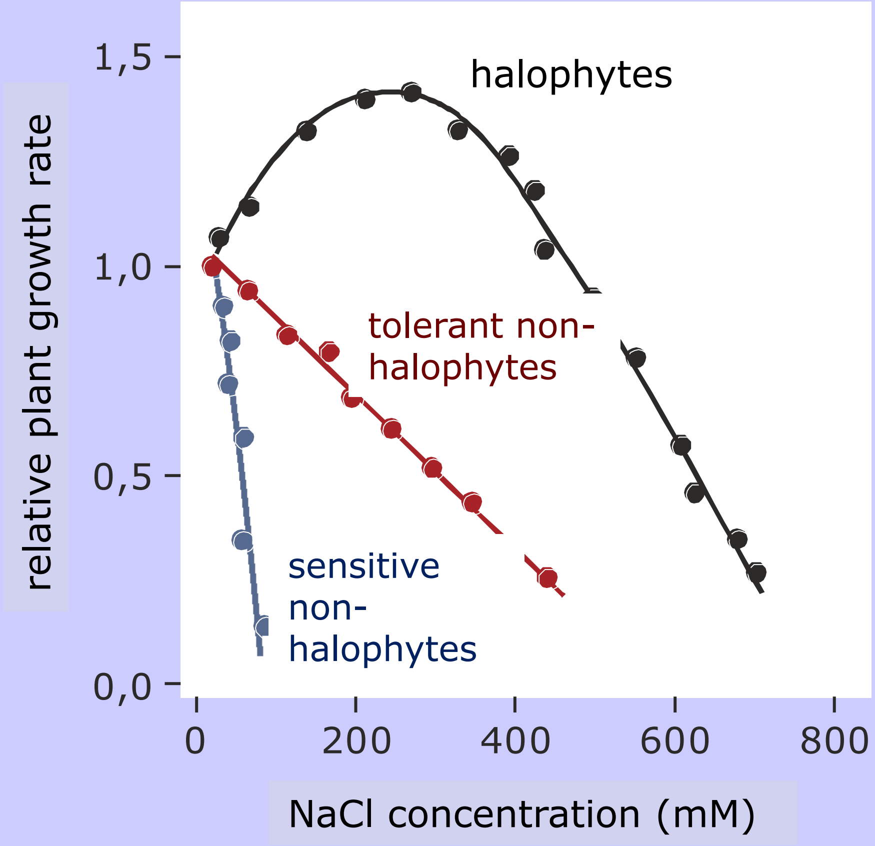
Accumulation of Na^+ and Cl^- in cells threats **cell ionic homeostasis** (the distribution of ions between apoplast, cytoplasm and vacuole which controls electrochemical polarity of plasma membranes).

Cultured plant	Drop of productivity (%) due to salinity increase by 1 dS m^{-1}	Salinity threshold EC_e (dS m^{-1})
apricot	23	1.6
bean	18.9	1.0
carrot	14.1	1.0
orange	15.9	1.7
trifolium	7.3	2.0
cucumber	13.0	2.5
tomato	9.9	2.5
beet	9.0	4.0
soybean	20.0	5.0
wheat	7.1	6.0
cotton	5.2	7.7
barley	5.0	8.0

Tolerance of cultivated species to salinity using two determinant parameters

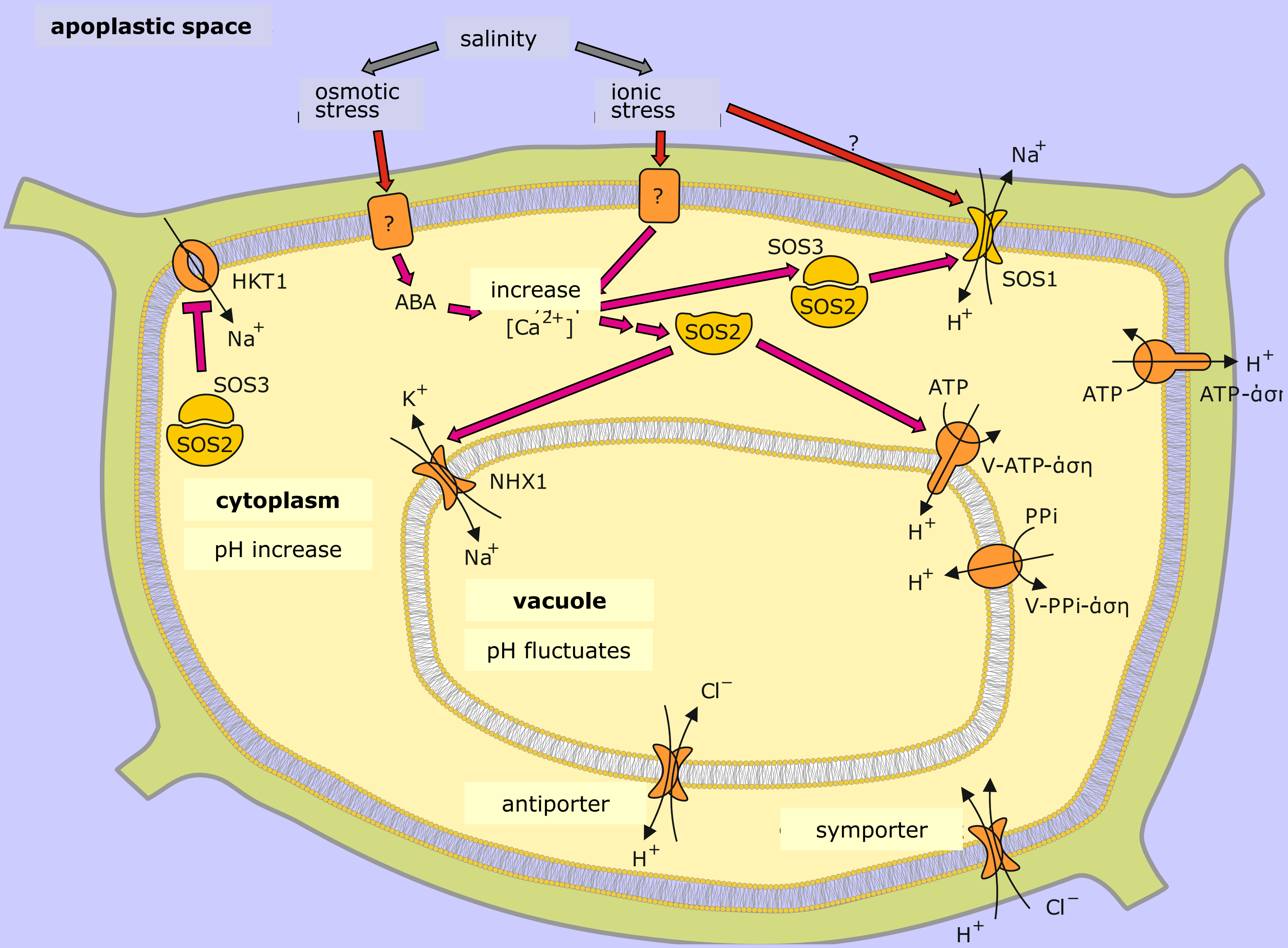
Root substrate water potential (MPa)	**Foliage surface (dm^2 per plant)**	**Photosynthetic rate (mg CO_2 dm^{-2} day^{-1})**	**Respiration rate (mg CO_2 dm^{-2} day^{-1})**
–0.04	30	46	11
–0.64	24	29	16
–1.24	18	23	19

Effects of salinity expressed as water potential in cotton productivity



Dependence of plant growth rate on salt concentration in growth medium for three plant groups

SALINITY SIGNAL PERCEPTION AND TRANSDUCTION



apoplastic space

salinity

osmotic stress

ionic stress

increase $[Ca^{2+}]$

cytoplasm

pH increase

vacuole

pH fluctuates

antiporter

symporter

THREE DIFFERENT STRATEGIES

- **Escape**

  Plants that follow this strategy (**glycophytes**), appear extremely sensitive even in low concentration of salts in soil. They do not colonize saline environments because they are unable to complete their life cycle in the presence of salt.

THREE DIFFERENT STRATEGIES

- **Avoidance**

  The plants that follow this strategy (**salinity regulators**), restrict the entry of ions into the sensitive cells. This strategy shows three variations:

THREE DIFFERENT STRATEGIES

- **Avoidance**

The plants that follow this strategy (**salinity regulators**), restrict the entry of ions into the sensitive cells. This strategy shows three variations:

Salinity regulation by **active exclusion**

Salinity regulation by **salt secretion by specialized cells (salt glands)**

Salinity regulation by **salt distribution**

THREE DIFFERENT STRATEGIES

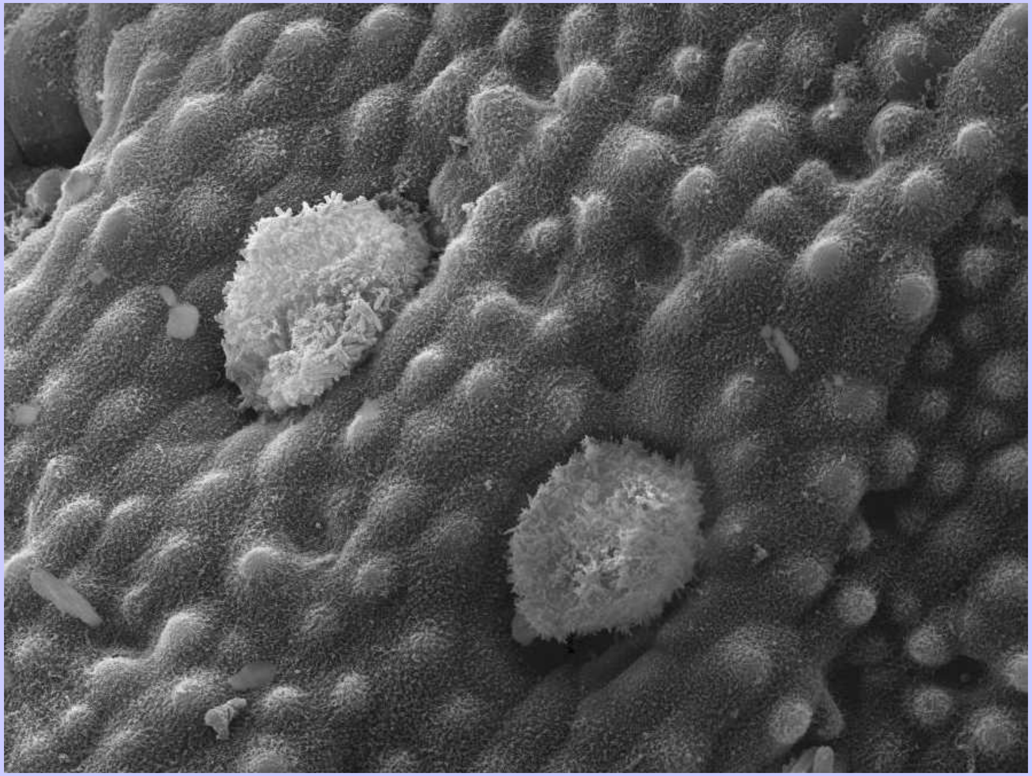
- Salinity regulation by **active exclusion**

Some plant species do not absorb salt, but they actively exclude it in the root medium (e.g. *Rhizophora mangle* in mangrove forests).

THREE DIFFERENT STRATEGIES

- Salinity regulation by **salt secretion**

  Some plant species allow salt entry but this is eventually secreted through specialized salt glands of leaves (e.g. *Tamarix* species)



THREE DIFFERENT STRATEGIES

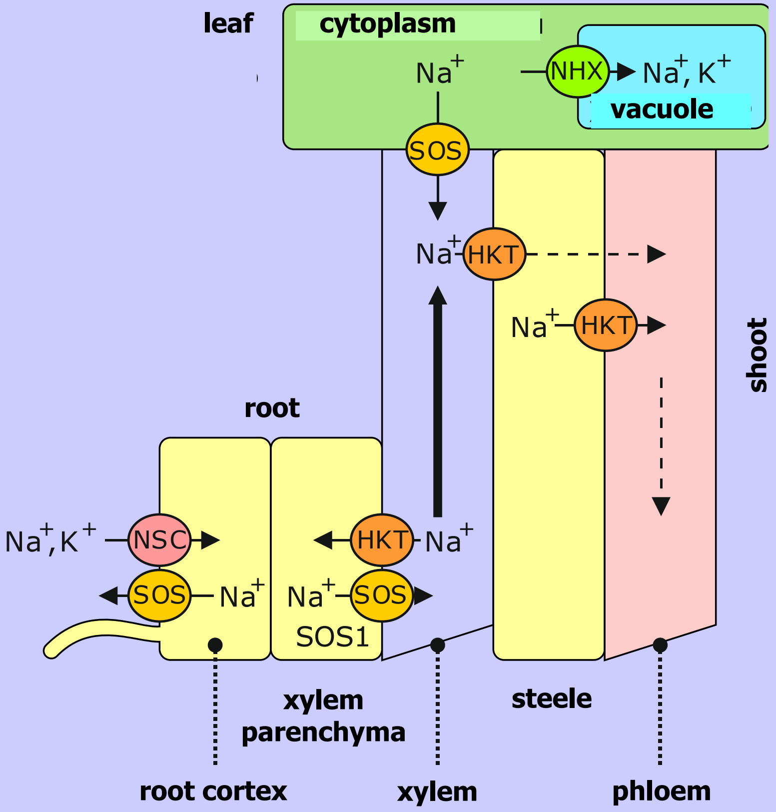
- Salinity regulation by **salt secretion**

  Some plant species allow salt entry but this is eventually secreted through specialized salt glands of leaves (e.g. *Limonium* species)

THREE DIFFERENT STRATEGIES

- Salinity regulation by **active exclusion** and **distribution**

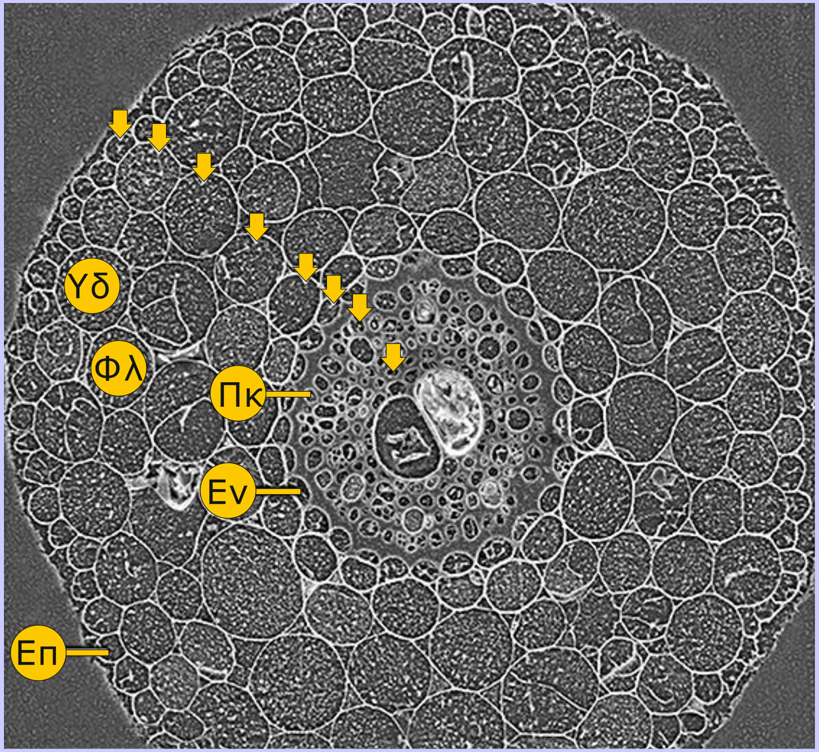
In some species, Na^+ ions are subjected to recirculation between root and shoot. Hence, the dynamic control of salt distribution on a plant level is accomplished.



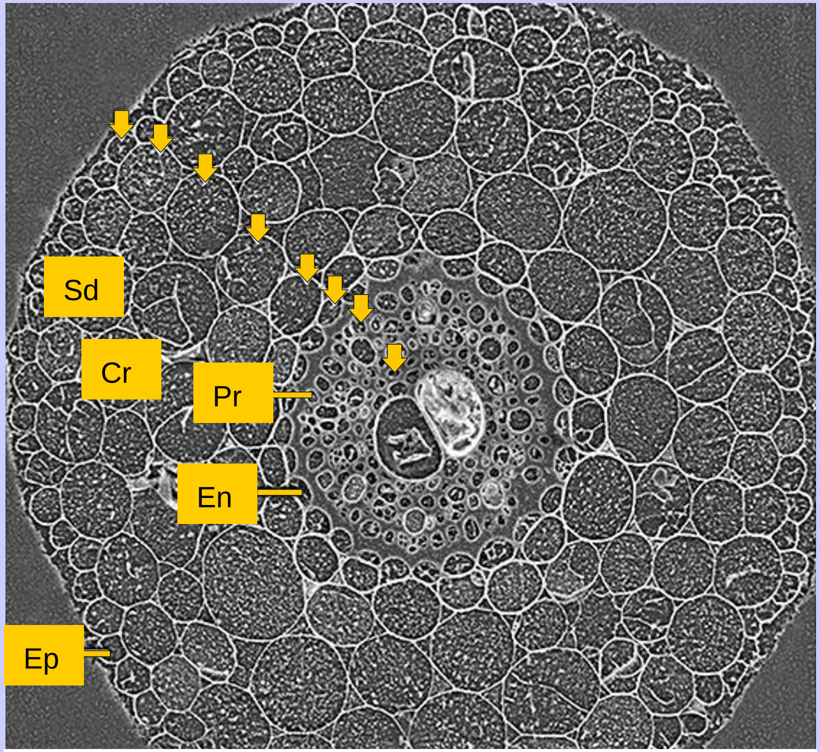
SALINITY TOLERANCE OF DURUM WHEAT

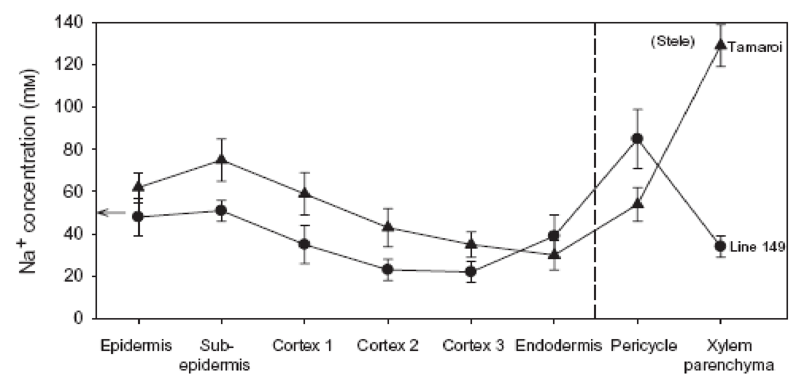
- **Salt control during lateral root transfer**

  Some cereals like wheat (*Triticum turgidum* spp. *durum*) allow salt entry, which is sequestered in the vacuoles and cell walls of specific root tissues

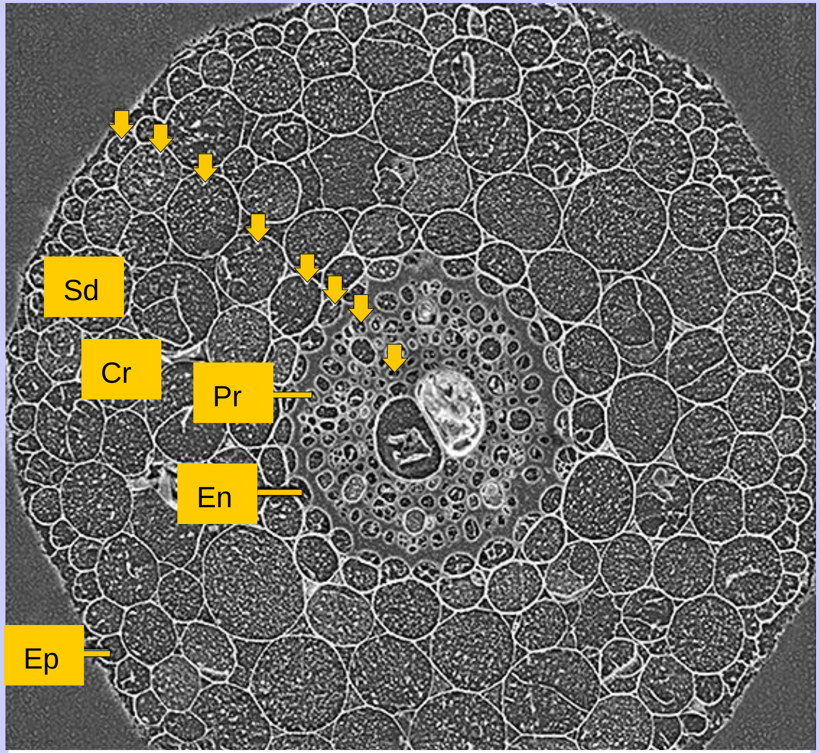


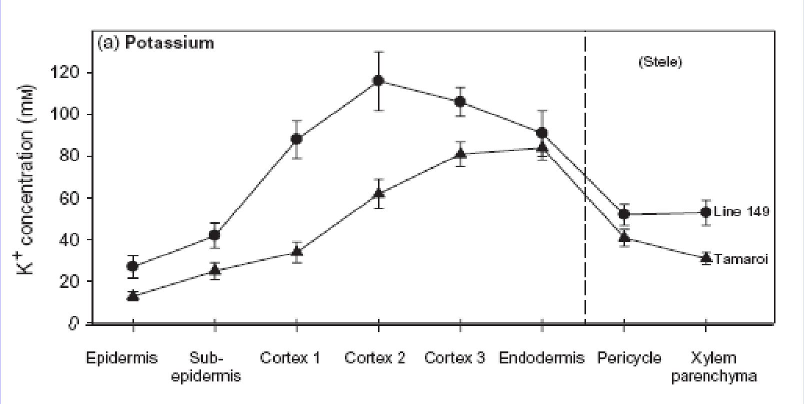
SALINITY TOLERANCE OF DURUM WHEAT





SALINITY TOLERANCE OF DURUM WHEAT





THREE DIFFERENT STRATEGIES

- **Resistance**

Metabolism of these plants (**salt accumulators**) is appropriately adapted to avoid perturbations due to high concentration of salt ions.

Ions accumulate in the vacuole, while concentrations in the cytoplasm remain low. The cytoplasmic water potential is osmotically equilibrated to that of the cytoplasm avoiding dehydration of the latter. Osmoregulation is achieved by the synthesis of compatible solutes.

THREE DIFFERENT STRATEGIES

- **Resistance**

Metabolism of these plants (**salt accumulators**) is appropriately adapted to avoid perturbations due to high concentration of salt ions.

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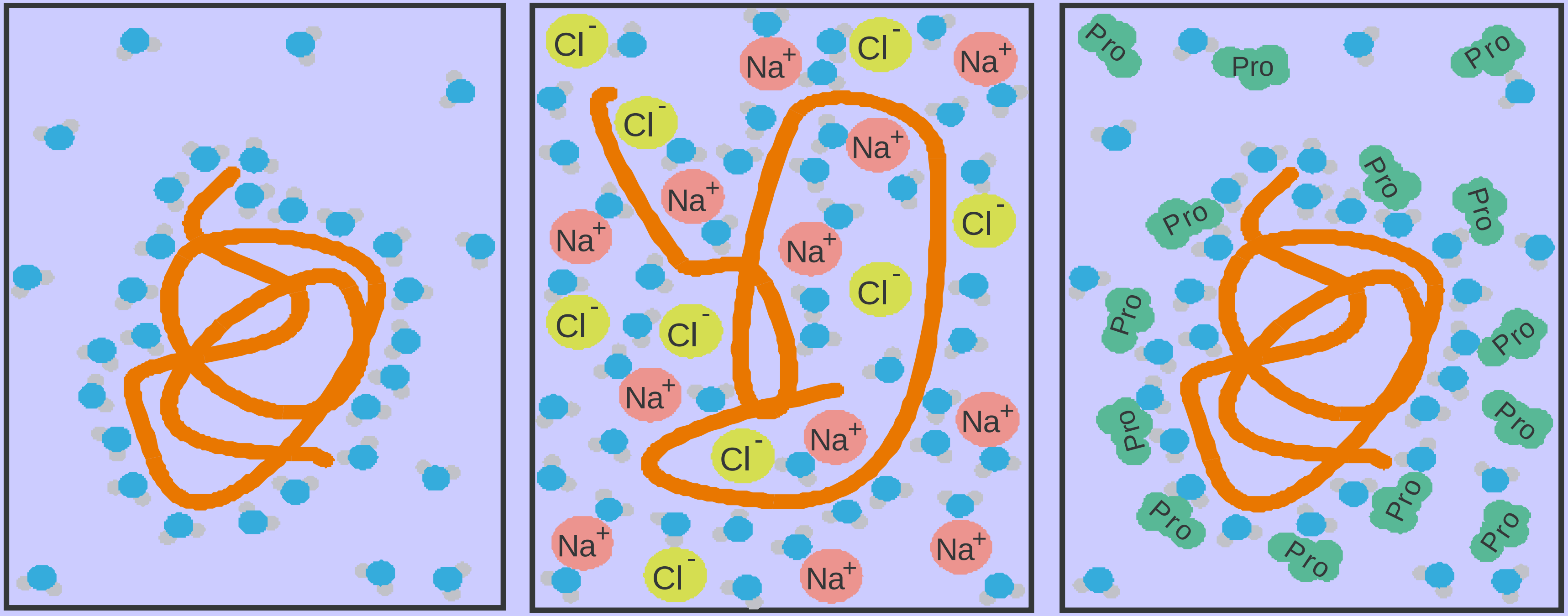
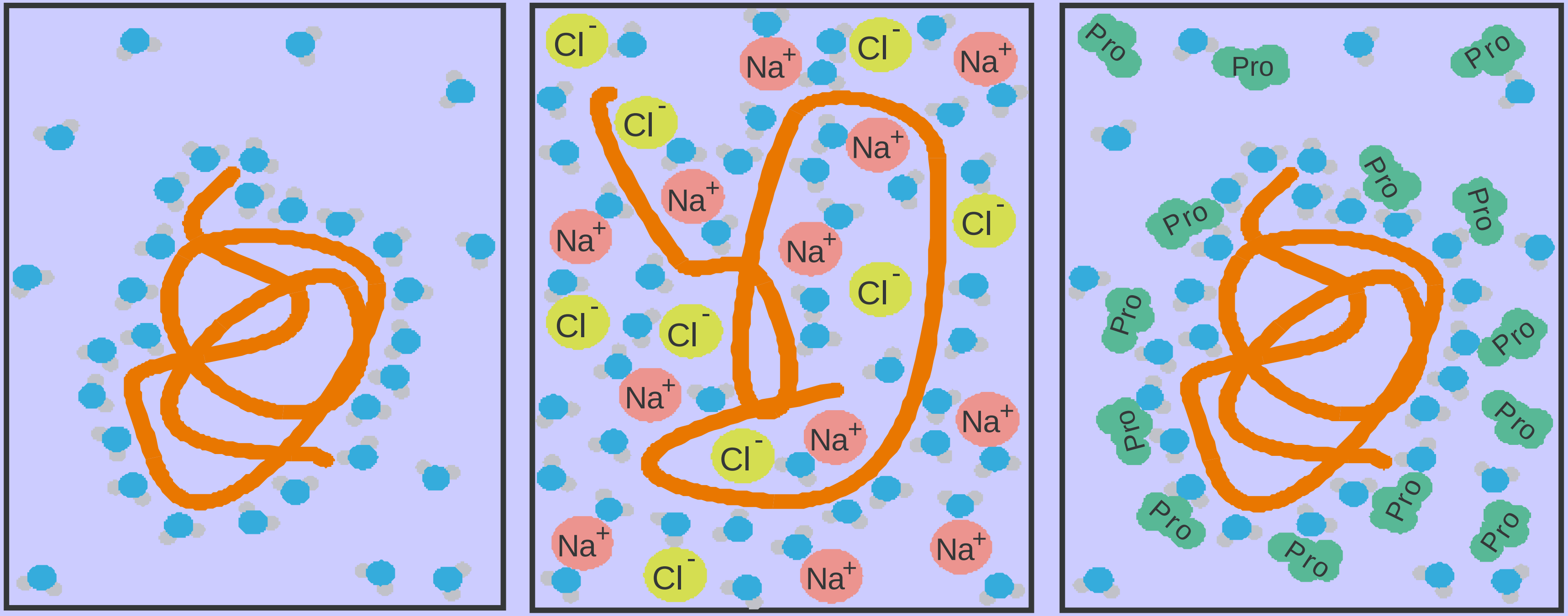
PROTECTIVE FUNCTION OF COMPATIBLE SOLUTES



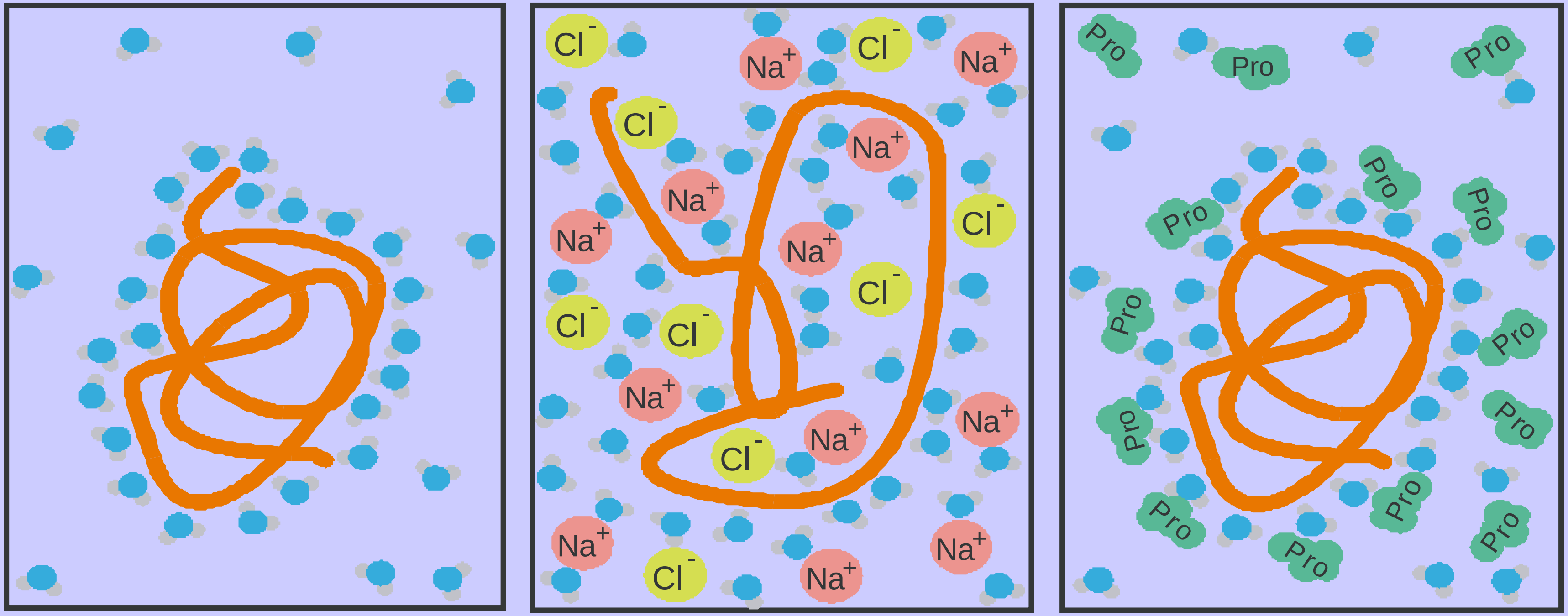
Hydration shell of a protein molecule

PROTECTIVE FUNCTION OF COMPATIBLE SOLUTES



In presence of Na+ and Cl- ions, protein molecule may loose conformation due to disruption of its hydration shell

PROTECTIVE FUNCTION OF COMPATIBLE SOLUTES



Compatible solute molecules stabilize hydration shell of protein and protect it from functional conformation loss

Ion or molecule	**Vacuolar conc (mM)**	**Cytoplasmic conc (mM)**
Glycine betaine	<1	300
Organic acids	100	60
Cl^-	<150	<50
Na^+	200	<50
K^+	150	120
Total	**~600**	**~580**
$[Na^+]_{vac}/[Na^+]_{cyt}$ ratio	~4,0	
$[Na^+]_{cyt}/[K^+]_{cyt}$ ratio	~0,4	
$[Na^+]_{vac}/[K^+]_{vac}$ ratio	~1,3	

Subcellular distribution of molecules or ions in mesophyll cells of spinach under salinity in the growth medium

PROTEOME MODULATIONS

Includes changes in proteome composition that are consisted of *de novo* synthesis of proteins that are necessary for acclimation, e.g. synthesis of compatible solutes

Osmotins, proteins with MW 24-50 kDa accumulate under salinity conditions. They belong to the wide family of pathogenesis proteins

Hydrophilic LEA proteins: The type of dehydrin proteins, work as escorting proteins stabilizing vesicles, proteins and membrane structures under salinity, osmotic stress and dehydration and frost

4

EXTREME TEMPERATURE STRESS

EXTREME TEMPERATURES

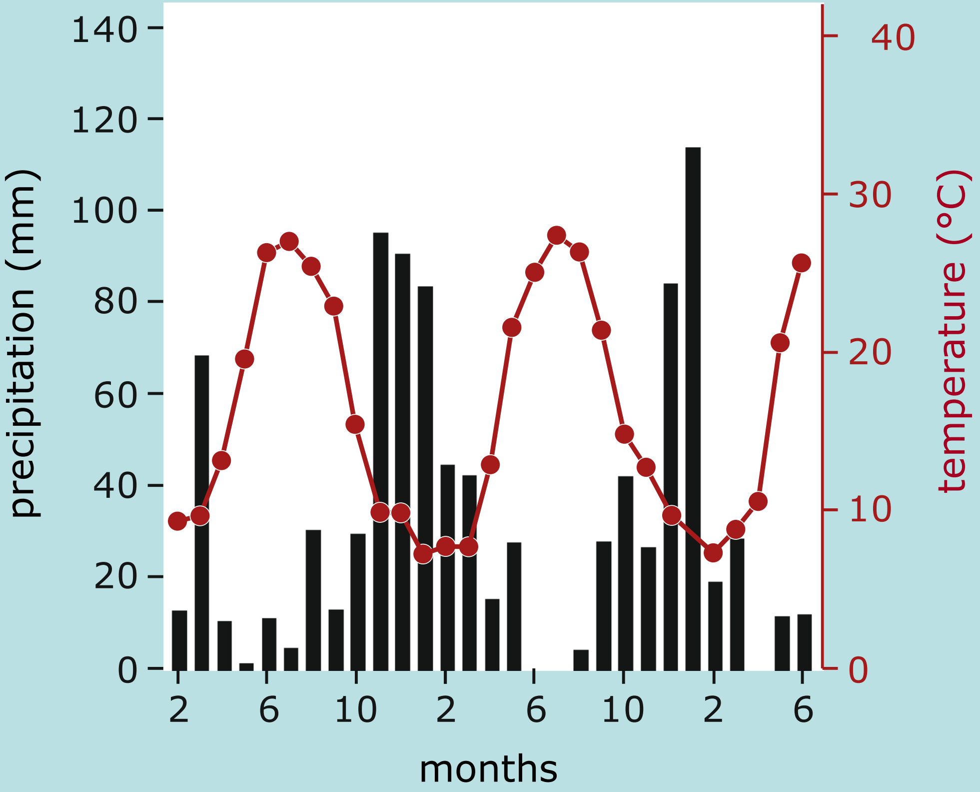
- **Temperature limits of biological activity**

  Beyond these limits a gradual and reversible decrease of biological activity occurs

- **Fatal temperature limits**

  Beyond these limits plants experience permanent physiological impairments which result in inability to complete the biological cycle

EXTREME TEMPERATURES IN THE MEDITERRANEAN

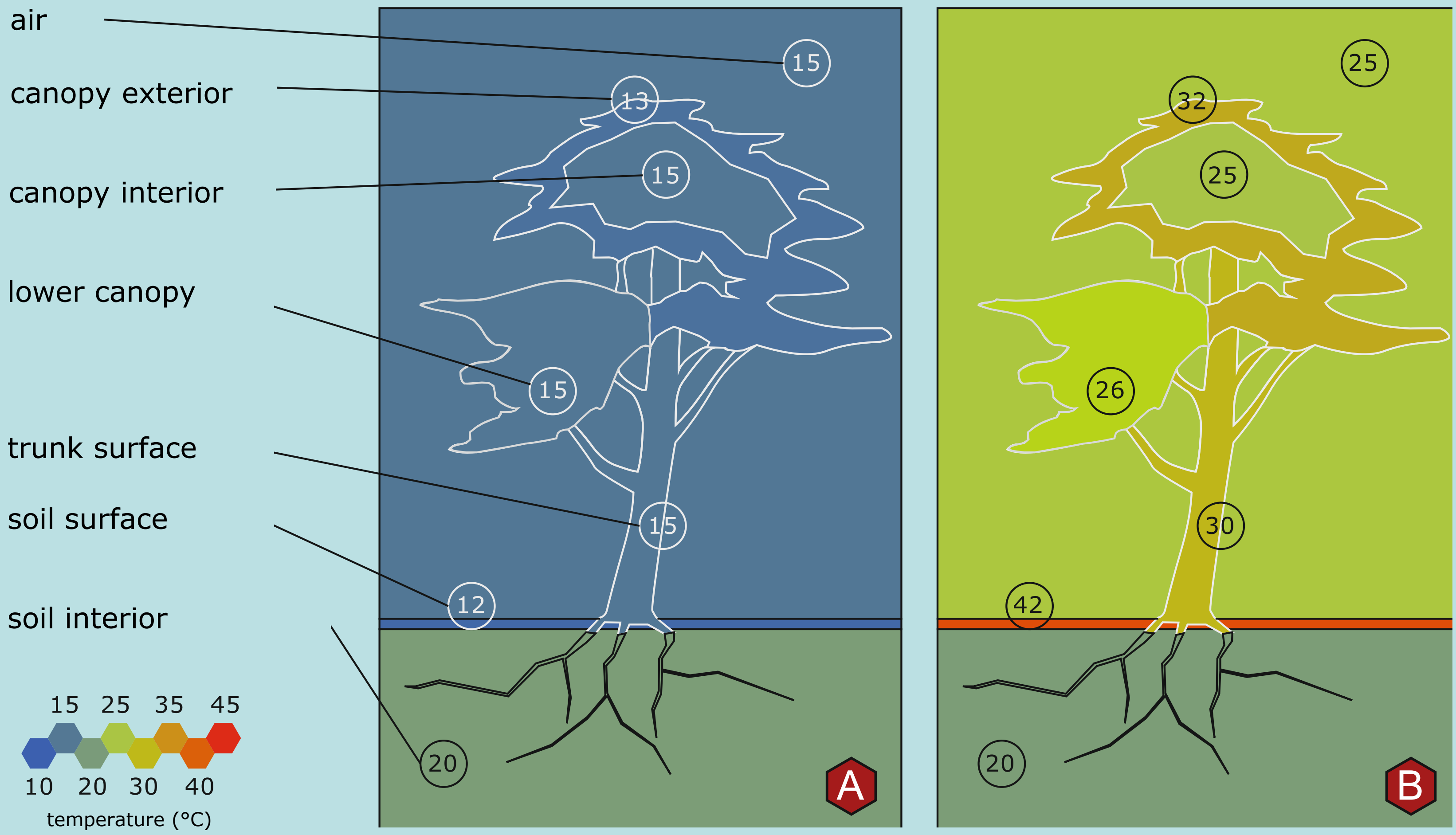


Climate graph of a typical mediterranean climate area

TEMPERATURE LIMITS

Frost is considered for temperatures below 0 ^{o}C

Cold is considered for temperatures between 0 and 15 ^{o}C



Fluctuations in temperature in different parts of a plant

PLANT GROUPS DEPENDING ON TEMPERATURE LIMITS FOR OPTIMAL BIOLOGICAL ACTIVITY

- **Microtherms**

  Optimum growth is observed between 0 and 20 ^{o}C

- **Mesotherms**

  Optimum growth is observed between 10 and 30 ^{o}C

- **Thermophytes**

  Optimum growth is observed between 30 and 65 ^{o}C

Organism/type	**fatal temperature (°C)**	
	hydrated	**dehydrated**
bacteria spores	80-120	up to 160
fungi spores	50-60	beyond 100
temperate lichens	33-46	70-100
polyhydric ferns	47-50	60-100
Ramonda myconi	48	56
Myrothamnus flabellifolius		80

Fatal temperature limits for several polyhydric organisms

EFFECTS OF LOW TEMPERATURES

- **Effect of frost to mesophytes**

Plant adapted to warm climates, including many cultivated plants, are considered as sensitive to low temperatures. Stress symptoms appear if exposed to temperatures below 10 ^{o}C

EFFECTS OF LOW TEMPERATURES

- **Membranes**

  Increased membrane rigidity

- **Biochemical reactions**

  Increase of required activation energy of biochemical reactions

- **Physicochemical changes in the protoplast**

  Change of the physical phase of cell sap affects vital cellular processes and increases the risk of irreversible cell damage

- **Oxidative stress**

  Accumulation of ROS

LEAF WILTING

- **How can cold result in leaf wilting;**

Leaf wilting, despite availability of water, is an early symptom of low temperatures and is caused by two factors:

I. **Low water conductivity**: Under low temperatures, water conductivity of root cell membranes is reduced and transport of water is restricted also due to higher viscosity.

II. **Stomatal movement is inhibited**: This biochemical/osmotic mechanism is inhibited by low temperatures, hence stomatal control is inefficient resulting in water losses.

COLD AND MEMBRANE COMPOSITION

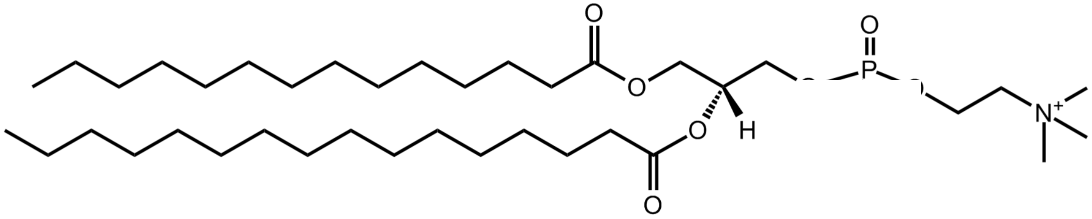
- **Membrane composition is related to temperature stress**

Transition temperature is the temperature point of sudden transition of a membrane from semi-fluid to semi-crystalline / gel phase

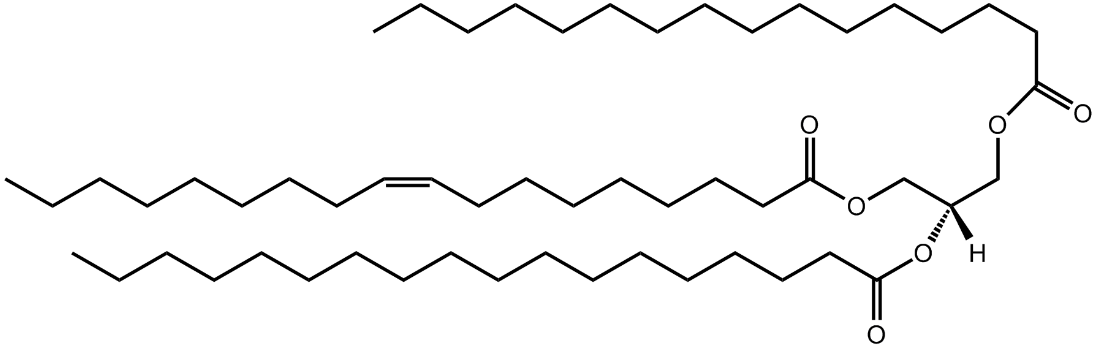
Semi-crystalline membranes lose their intactness and selectivity resulting in **loss of cellular compartmentation** and **dehydration**

COLD AND MEMBRANE COMPOSITION

- **Membrane composition is related to temperature stress**



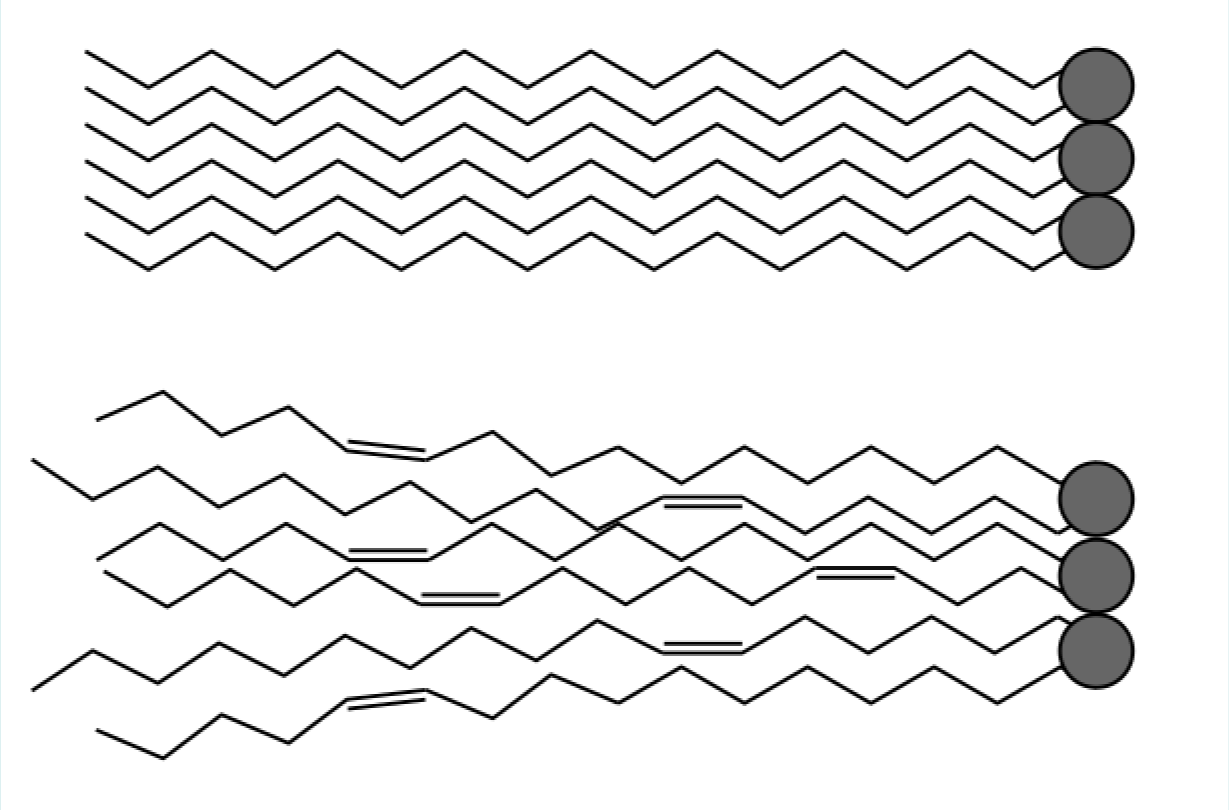
**1-myristoyl-2-palmitoyl-*sn*-glycerophosphocholine
(Glycerophospholipids)**



**1-oleoyl-2-stearoyl-3-palmitoyl-*sn*-glycerol
(Glycerolipids)**

COLD AND MEMBRANE COMPOSITION

- **Membrane composition is related to temperature stress**



COLD AND MEMBRANE COMPOSITION

Fatty acid	Carbon atoms C : double bonds	Structural formula	Freezing point (^{0}C)
Stearic	18:0	$CH_3(CH_2)_{16}COOH$	71
Lauric	12:0	$CH_3(CH_2)_{10}COOH$	44
Oleic	18:1	$CH_3(CH_2)_7CH{=}CH(CH_2)_7COOH$	16
Linoleic	18:2	$CH_3(CH_2)_4CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$	-5
Linolenic	18:3	$CH_3CH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$	-11

Freezing point of representative fatty acids

COLD AND MEMBRANE COMPOSITION

Plant species	**plant organ**	**unsat/saturated ratio**
cold sensitive		
Phaseolus vulgaris	shoot	2.8
Ipomoea batatas	tuber	1.7
Zea mays	shoot	2.1
Lycopersicon esculentum	fruit	2.8
cold tolerant		
Brassica oleracea	bud	3.2
Brassica campestris	root	3.9
Pisum sativum	shoot	3.8

The unsaturated/saturated fatty acid ration of the membrane phospholipids of isolated mitochondria of tolerant and sensitive plant species

FROST EFFECTS

- **Frost results in severe mechanical and water stress in cells**

Temperatures below 0 ^{o}C favor the formation of ice crystals in cells. In this case, cells ultimately die because of mechanical damage

On the other hand, dehydrated forms like seeds can survive temperatures approaching absolute zero (0 ^{o}K), without damage

FROST EFFECTS

Plant species	**Frost damaging temperature (ºC)**		
	shoot growth	*inflorescence*	*fruit set*
Winter wheat genotypes	down to -37		
spring wheat genotypes	-9	-1	-2
barley	-7	-1	-2
lens	-7	-2	-2
bean	-5	-2	-3
sugar beet	-6	-2	
soybean	-3	-2	-2
potato	-2	-1	-1
cotton	-1	-1	-2
rice	-0.5	-0.5	-0.5

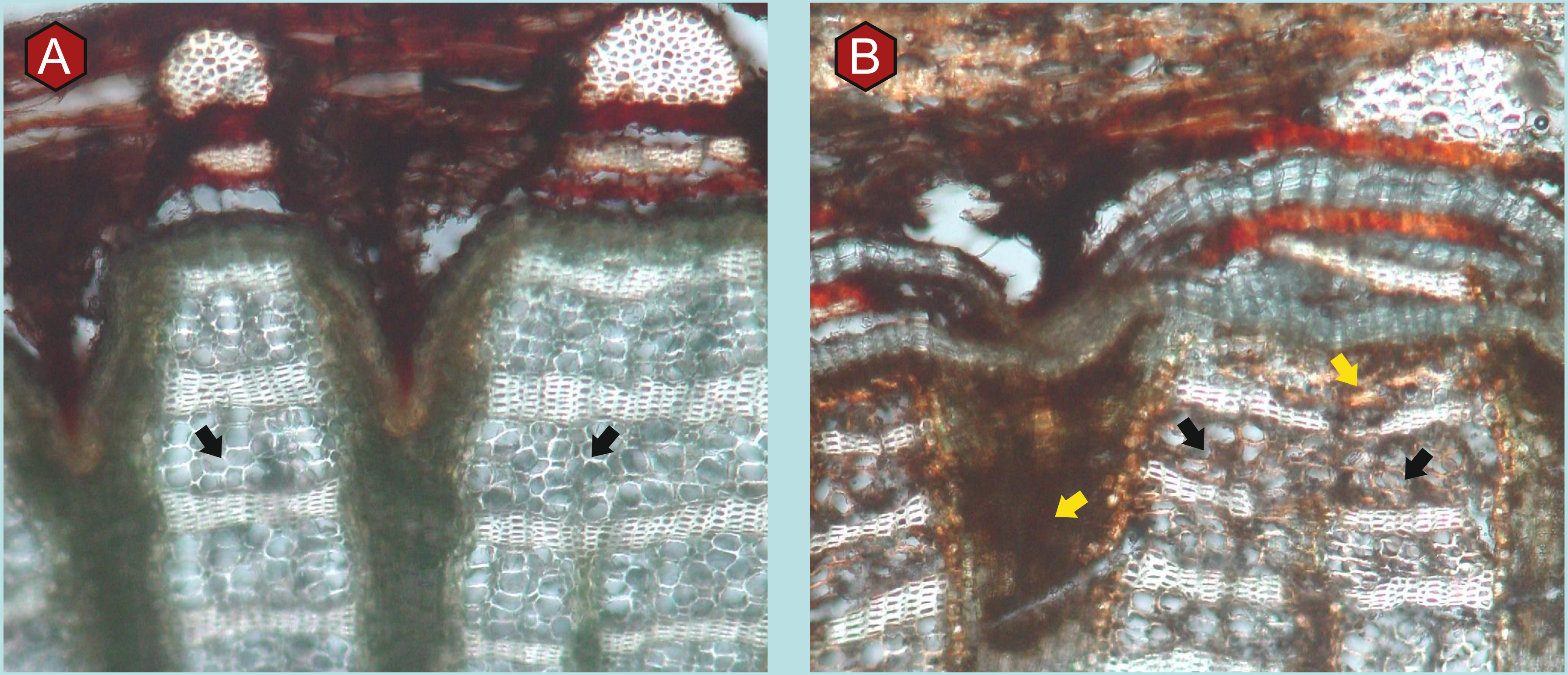
Frost tolerance of selected plant species
in different stages of development

FROST EFFECTS

Plant species	**leaves**	**buds**	**shoot meristem**	**root meristem**
Ceratonia siliqua	-6	-8	-9	
Nerium oleander	-8	-12	-14	
Olea europaea	-12	-12	-16	-6
Quercus ilex	-15	-17	-28	-7

Frost tolerance of plant organs of evergreens from Mediterranean flora during the winter. Temperatures that result in 50% frost damage

FROST EFFECTS



Effects of a frost incidence in grapevine shoot
under optical microscope / polarized light

THERMAL ANALYSIS

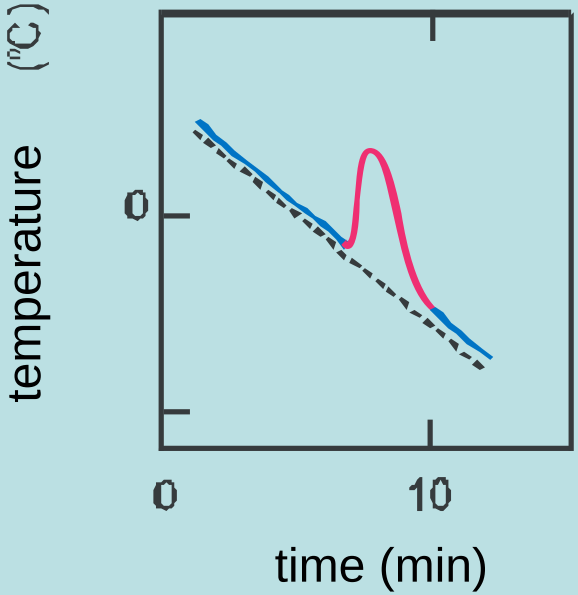
- **Thermal behavior of tissues is not uniform in all temperatures**

  Thermal analysis reveals the thermal behavior of tissues and explains the gradual accumulation of damage from freezing temperatures

  Is based on the measurement of temperature of a plant tissue as the temperature drops and shows the **freezing events** through **exotherms**

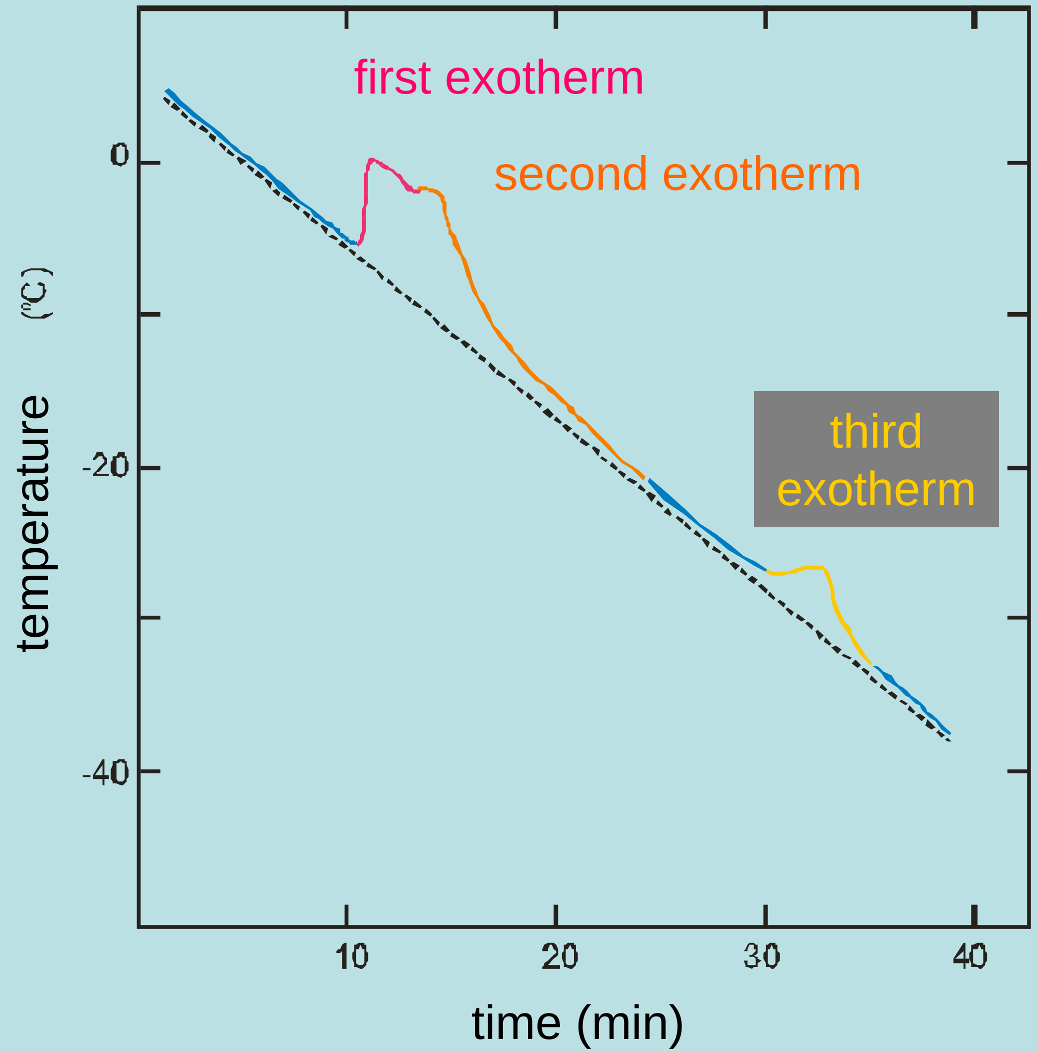
  An exotherm is caused because water transition from liquid to solid state is an **exergonic** event

THERMAL ANALYSIS

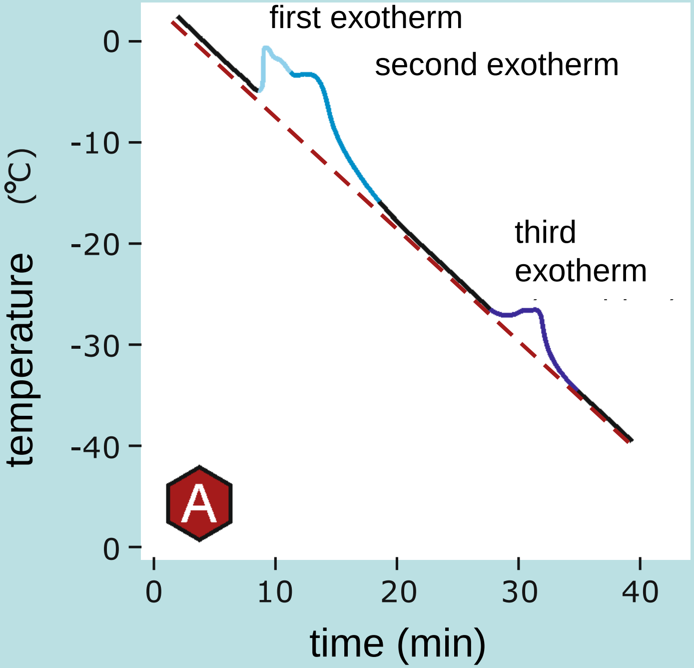


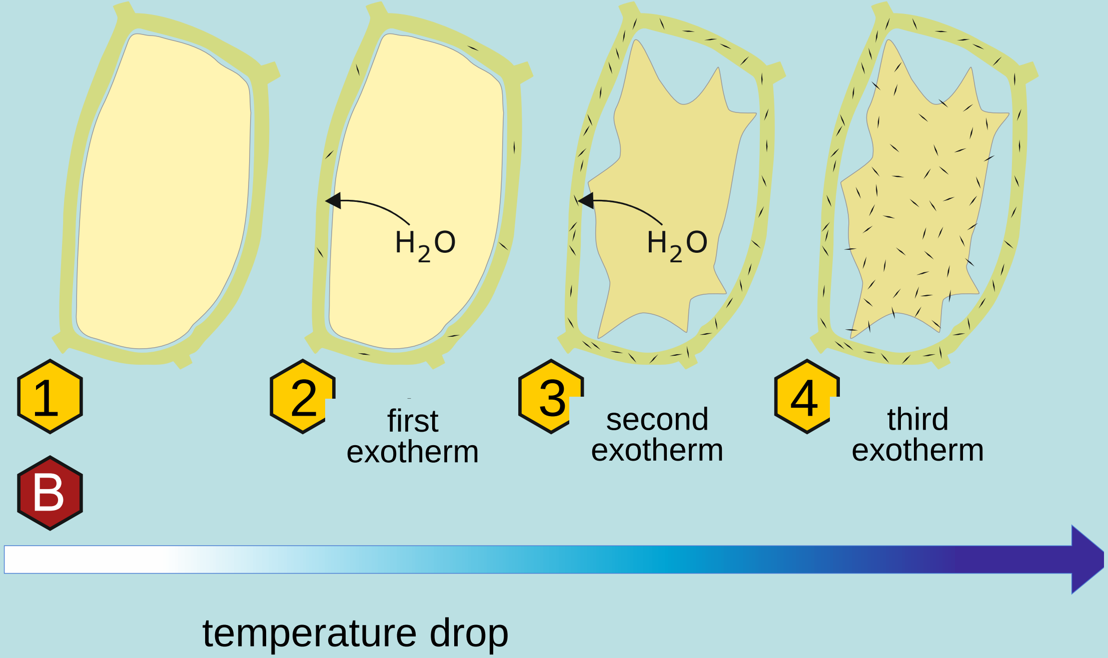
Typical thermal analysis curve. Thermal analysis exotherm shows temperature points that, despite the environmental temperature drop (dotted line), tissue temperature increases temporarily.

THERMAL ANALYSIS



THERMAL ANALYSIS





CELL THERMAL BEHAVIOR

- **Results of the thermal behavior of plant cells**

Plant tissues can have temperatures far below zero without transition from liquid to solid. This phenomenon is called **supercooling** (**hyper-freezing**).

During the **first exotherm** ice is only formed in the **apoplast**. This freezing event is not damaging for the cells.

CELL THERMAL BEHAVIOR

- **Results of the thermal behavior of plant cells**

Due to water potential difference (caused by freezing of the apoplast) protoplasmic water moves (continuously) to the apoplast. This continues during the **second exotherm**. Results:

1. protoplast sap gradually becomes more concentrated. This causes the **depression of the freezing point**, so the protoplast stays liquid.

2. Continuous water movement results in cell dehydration (**freezing plasmolysis**). This results in a special case of **water stress**.

CELL THERMAL BEHAVIOR

- **Results of the thermal behavior of plant cells**

3. The **third exotherm** represents the eventual formation of ice crystals in the protoplast. This freezing incident is usually lethal for the cells.

THREE DIFFERENT STRATEGIES

- **Escape**

  This is followed by mesophytes and thermophytes that are not exposed during the low winter temperatures.

  A variation of this strategy is followed by overwintering plants that have shed their leaves before winter.

THREE DIFFERENT STRATEGIES

- **Avoidance**

Tissues avoid freezing by reducing thermal losses to the environment. Suitable anatomical and morphological traits favor this strategy.

Buds are covered with multiple scales (cataphylls), cryptophytes remain below litter or below soil surface to reduce exposure.

Appropriate leaf movements prevent heat loss or allow gain of heat from sunlight (heliotropic leaf movements).

THREE DIFFERENT STRATEGIES

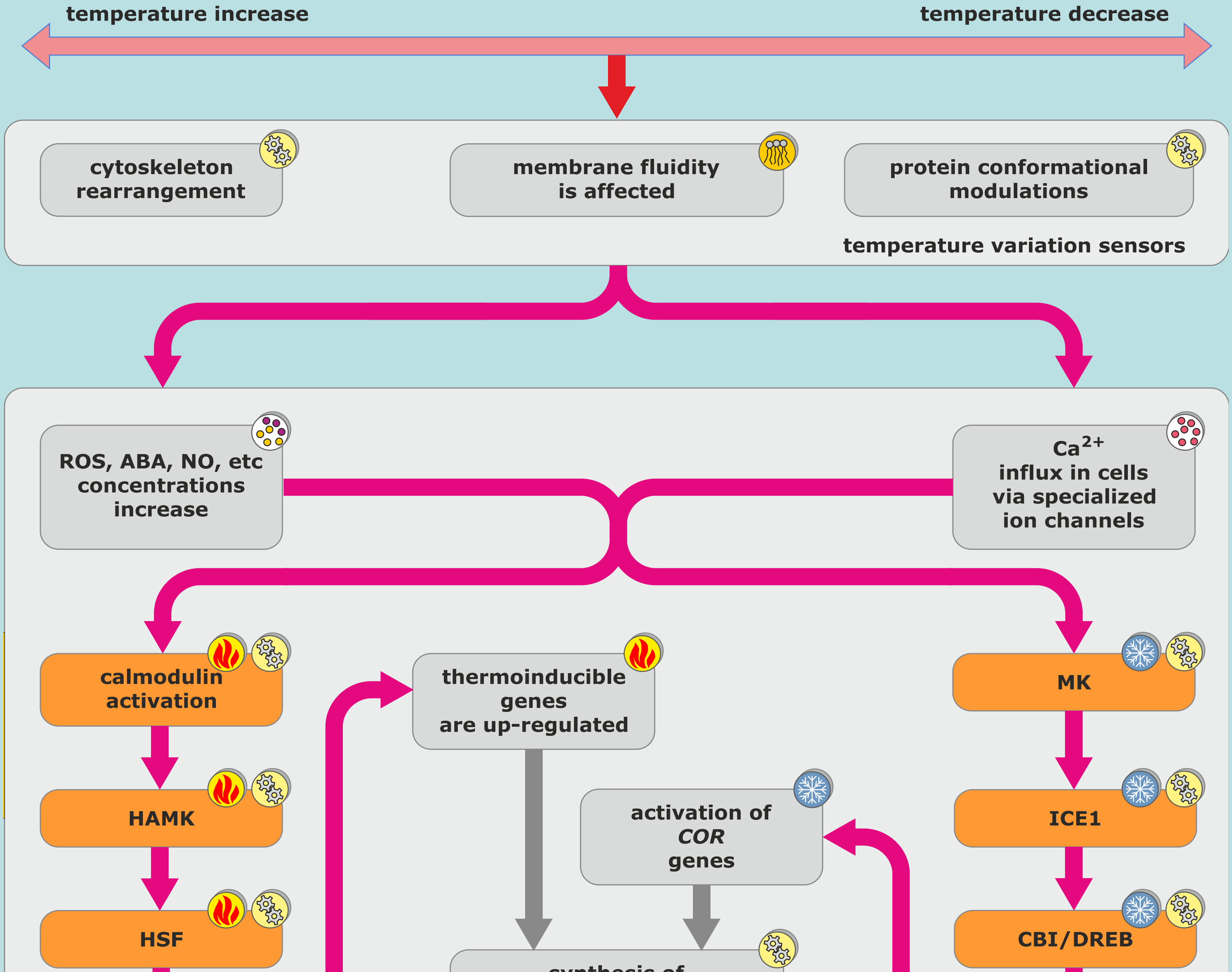
- **Resistance**

Cells or resistant plants take advantage of **supercooling**.

These cells do not contain many **freezing nuclei**, which are necessary to initiate ice crystal formation at higher temperatures. **Small cells** also help avoid formation of ice crystals at higher temperatures.

Woody tissues may freeze below -15°C. Shoot buds may supercool even at -40°C without formation of ice crystals.

PERCEPTING TEMPERATURE EXTREMES



temperature increase

temperature decrease

cytoskeleton rearrangement

membrane fluidity is affected

protein conformational modulations

temperature variation sensors

ROS, ABA, NO, etc concentrations increase

Ca^{2+} influx in cells via specialized ion channels

calmodulin activation

HAMK

HSF

thermoinducible genes are up-regulated

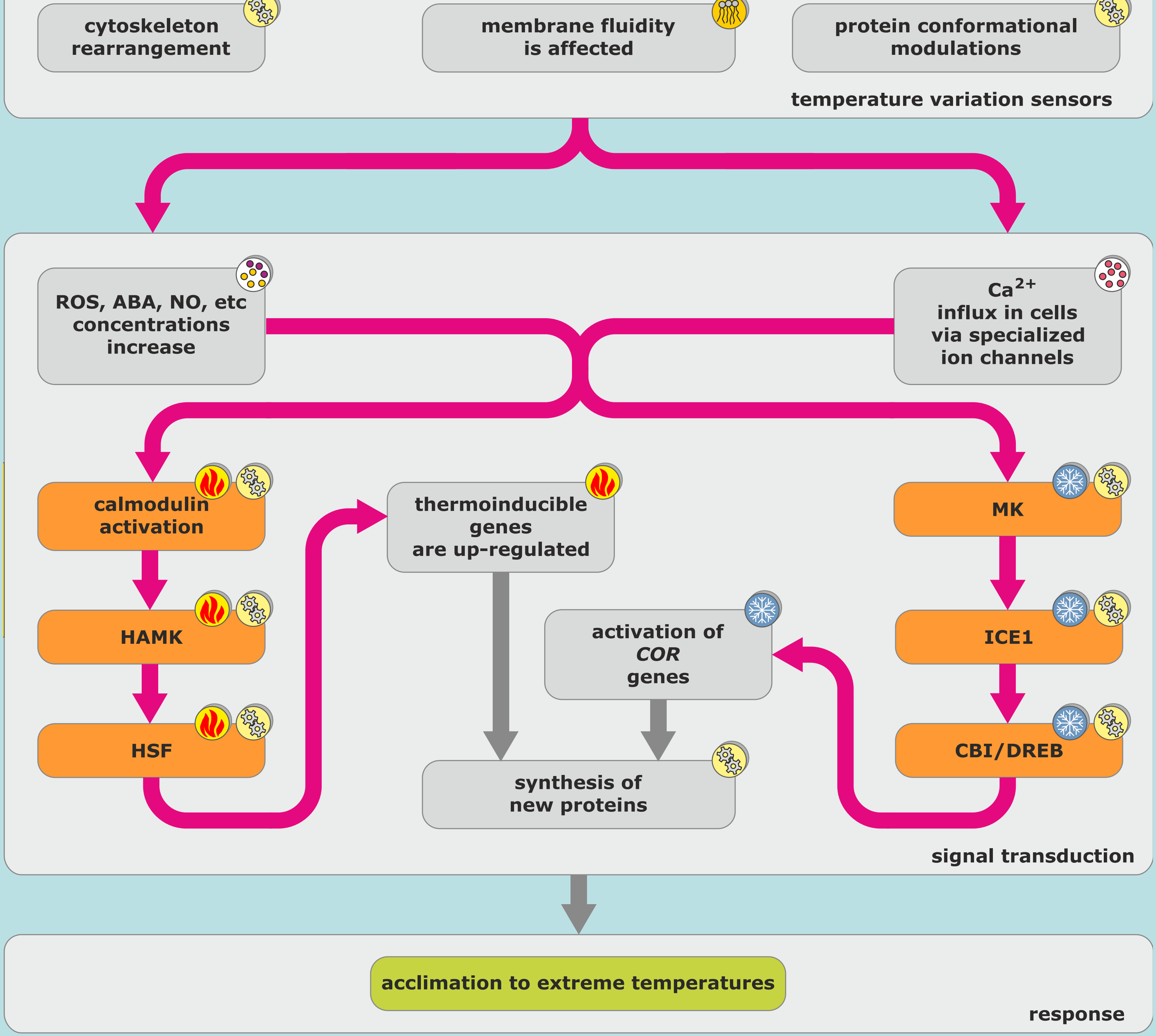
activation of *COR* genes

synthesis of

MK

ICE1

CBI/DREB



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MK

ICE1

CBI/DREB

activation of *COR* genes

synthesis of new proteins

signal transduction

acclimation to extreme temperatures

response

ACCLIMATION AND RESISTANCE

- **Resistance to low temperatures is dramatically improved after proper acclimation to cold (cold hardiness)**

Deciduous trees near the Arctic, birch (*Betula* sp.), poplar (*Populus* sp.) and willow (*Salix* sp.) survive at extremely low temperatures as they acclimate gradually, a process resulting in **cold hardiness**.

ACCLIMATION AND RESISTANCE

- **Resistance to low temperatures is dramatically improved after proper acclimation to cold (cold hardiness)**

Acclimation to low temperatures involves **two discrete stages**. The **first** takes place in autumn, before leaf fall and is induced by photoperiodic stimuli. The sensory mechanism is sensitive to short days (photoperiods) and is controlled by the phytochrome system.

ACCLIMATION AND RESISTANCE

- **Resistance to low temperatures is dramatically improved after proper acclimation to cold (cold hardiness)**

The **second** stage is induced by low temperatures. Takes place during the first freezing incident. During this stage, metabolic modulations which include changes in the profiles of phosphorylated metabolites, conversion of starch to oligosaccharides, accumulation of glycoproteins and an overall increase of protoplast freezing tolerance.

ACCLIMATION AND RESISTANCE

- **Resistance to low temperatures is dramatically improved after proper acclimation to cold (cold hardiness)**

Cold hardiness requires extensive changes in gene expression and a considerable metabolic cost. The hormone ABA is implicated in the process. Exogenous ABA application in young seedlings induces cold resistance.

ACCLIMATION AND RESISTANCE

- **Cold acclimation of *Arabidopsis***

  A number of gene expression regulation proteins, CBF (COR (COld Regulated) Binding Factors)/DREB (Dehydration Responsive Element Binding (proteins)) is involved. These transcription factors bind in specific targets, the regulatory elements DRE/CRT (C-RepeaT).

  Gene expression patterns share common elements with other stressors, like osmotic or water stress, which are all related to dehydration.

HIGH TEMPERATURES

- **High temperature effects on mesophytes**

Most plant species show a high temperature threshold located around 50-55 ^{o}C. This limit also depends on the hydration level of organs and tissues.

Plants in xerothermic environments are frequently exposed to extremely high temperatures. Concurrently, high temperatures are combined with water stress and high intensities of solar radiation.

HIGH TEMPERATURES

- **High temperature effects on mesophytes**

High temperature stress is very frequent in greenhouses due to absence of air currents, high relative air humidity. These conditions do not favour the cooling mechanisms of plants such as passive cooling and transpiration.

HIGH TEMPERATURES

- **High temperature effects on mesophytes**

High temperature stress is very frequent in greenhouses due to absence of air currents, high relative air hu
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cooling and tr

HIGH TEMPERATURES

- **Resistance mechanisms of thermophytes**

  Desert plants may tolerate temperatures up to 60 ^{o}C, while they can be exposed for short time intervals to temperatures even higher than 70 ^{o}C.

EFFECTS OF HIGH TEMPERATURES

- **Membranes**

  Increase in membrane fluidity may affect selectivity and catalytic properties.

- **Biochemical reactions**

  The possibility of conformational changes and irreversible denaturation of proteins is increased.

EFFECTS OF HIGH TEMPERATURES

- **Photosynthesis**

  Functional integrity of PSII is quite sensitive to high temperatures. The oxygen evolving complex is deactivated under high temperatures resulting in inhibition of electron flow from PSII to PSI. Photophosphorylation is impaired. Energy excess in photosystems is increased.

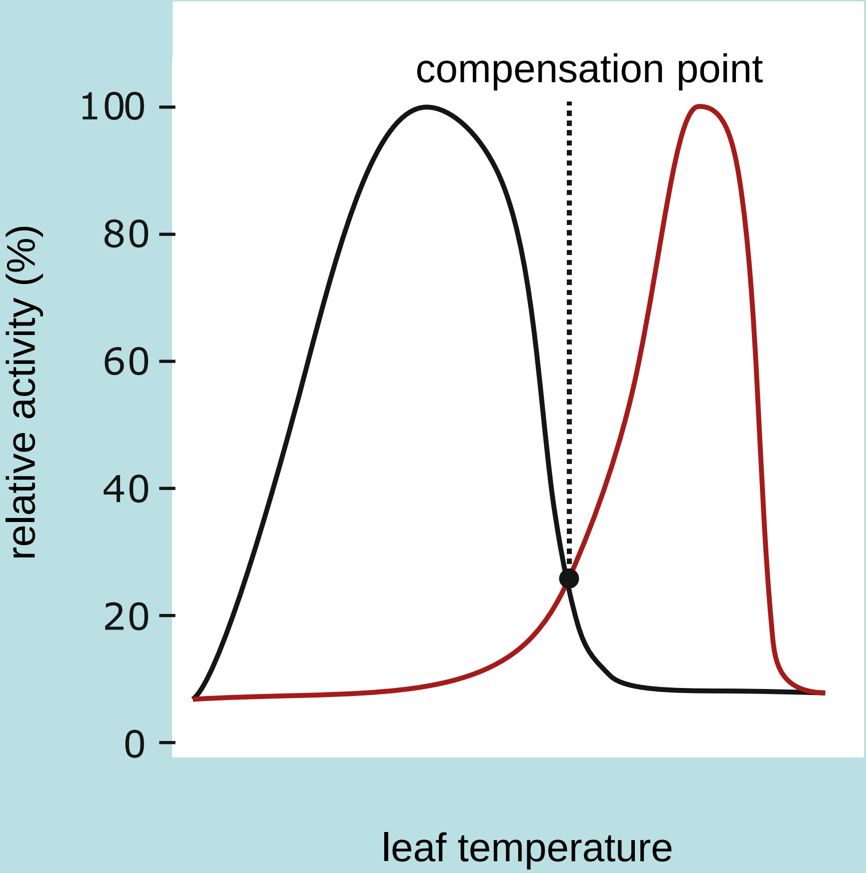
EFFECTS OF HIGH TEMPERATURES

- **The photosynthetic compensation point may appear under high temperatures**

  Photosynthesis is inhibited more severely than respiration under high temperatures. The CO_2 assimilation rate (through photosynthesis) / CO_2 emission (through respiration) balance is gradually reversed. At a certain temperature rates of assimilation and emission of CO_2 equalize and the compensation point is recorded. Further increase in temperature results in an increase of CO_2 emission.

EFFECTS OF HIGH TEMPERATURES

- **The photosynthetic compensation point may appear under high temperatures**



EFFECTS OF HIGH TEMPERATURES

Plant species	**Tissue or organ**	**lethal temperature (°C)**	**Exposure (min)**
	cultivated plant species		
Zea mays	leaves	49-51	10
Solanum tuberosum	leaves	42,5	60
Olea europaea	leaves	57	30
Hordeum vulgare	fruit	65	8
Lycopersicum esculentum	fruit	45	-
Malus domestica	fruit	49-52	-
Vitis vinifera	mature fruit	63	-
Medicago sativa	seeds	120	30
Triticum sp.	dehydrated seeds	90,8	8

Lethal temperatures for some organs of cultivated plant species

HIGH TEMPERATURES AND MEMBRANE COMPOSITION

- **Membrane composition is related to temperature stress**

Membranes of thermophytes show higher percent of phospholipids with saturated fatty acids allowing stronger hydrophobic interactions between aliphatic chains.

This results in reduced fluidity of the membrane which appears more stable under higher temperatures.

THREE DIFFERENT STRATEGIES

- **Escape**

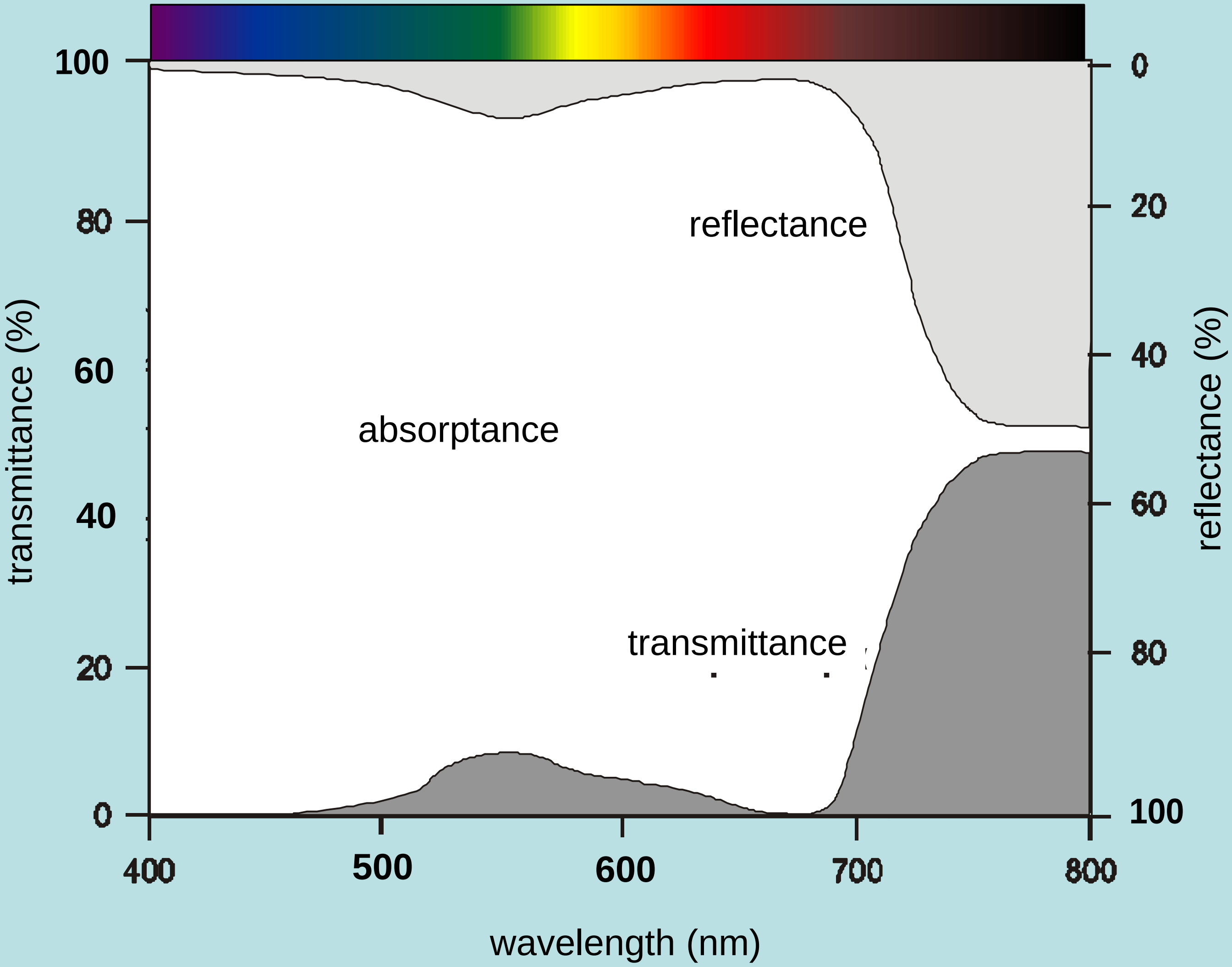
  This is followed by microtherms which do not expand to warm climatic zones. A variation of this strategy refers to shedding of sensitive organs before the period of high temperatures or the existence of the organism in a lethargic form (like rhizomes, tubers, etc.).

THREE DIFFERENT STRATEGIES

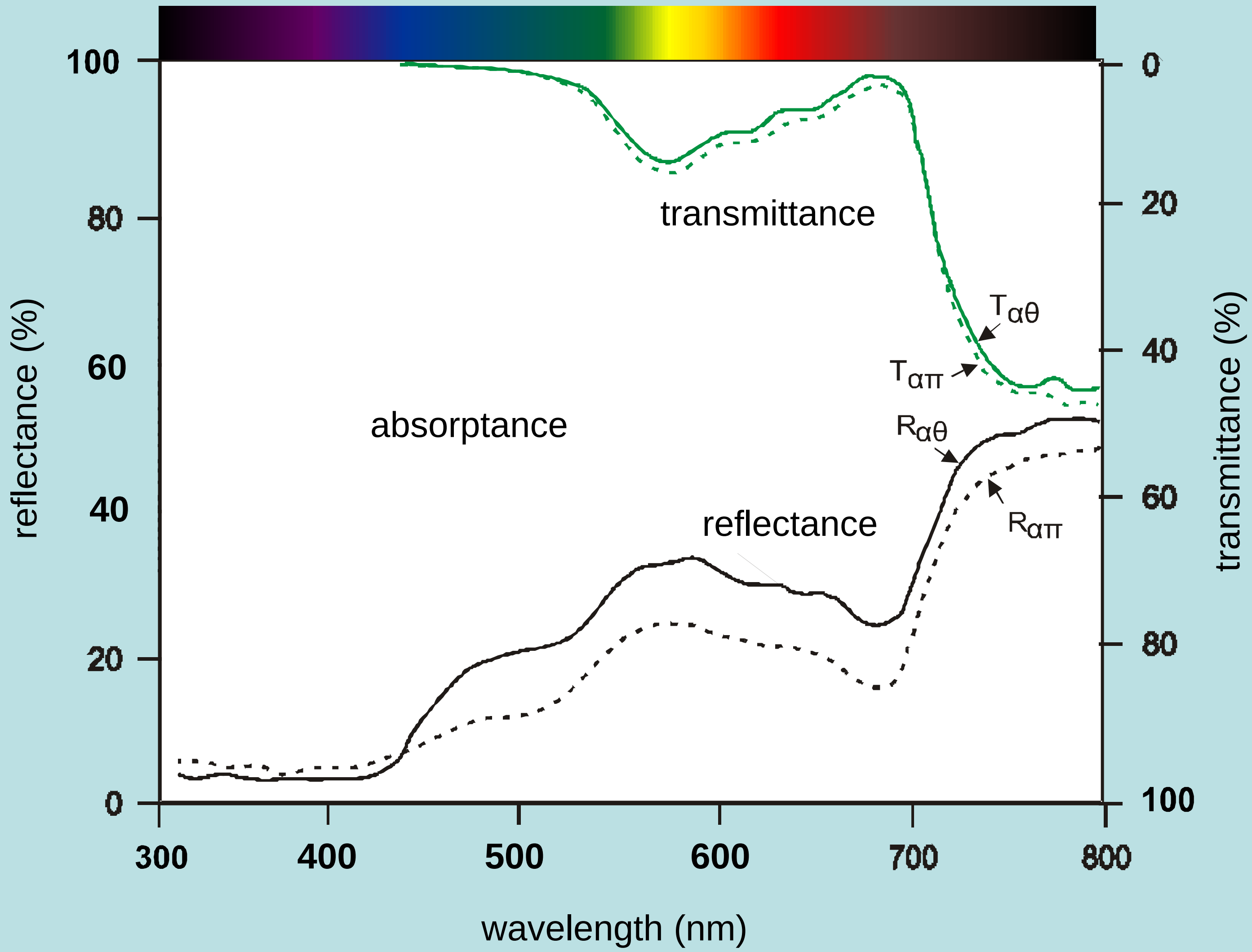
- **Avoidance**

Some plant traits that contribute to overheating avoidance:
1. Leaf curling
2. Vertical leaf lamina arrangement
3. Highly reflective / scattering leaf surface due to trichome layers or specific epicuticular layer arrangements resulting in glabrous leaves
4. Small leaf size that reduces the thickness of the boundary layer and increases heat
5. Seasonal leaf dimorphism which involves leaves that show increased tolerance for high temperatures.

AVOIDANCE – LEAF OPTICAL PROPERTIES



AVOIDANCE – LEAF OPTICAL PROPERTIES



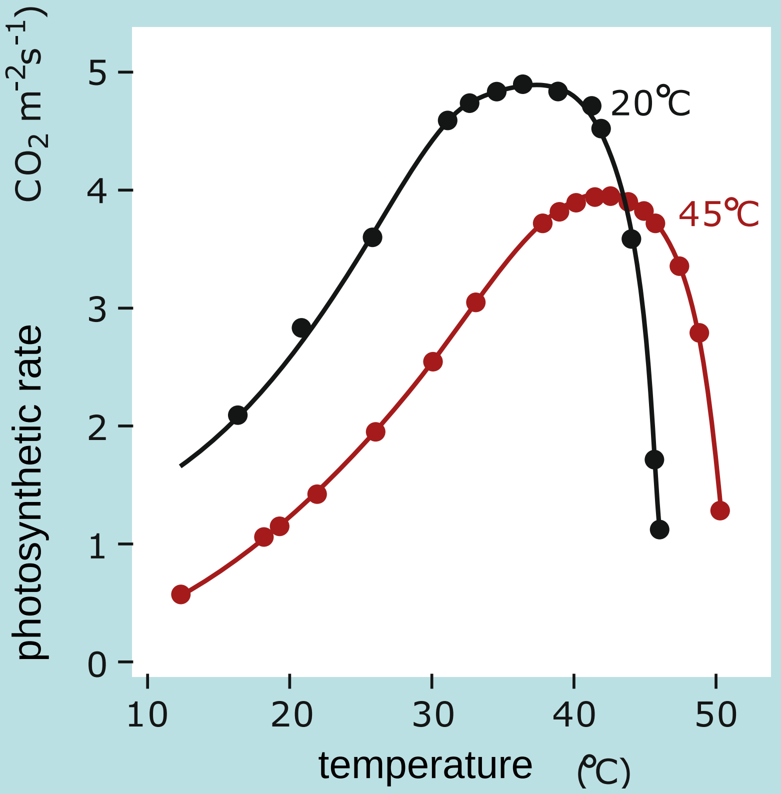
THREE DIFFERENT STRATEGIES

- **Resistance**

  Resistant plants are exposed to high temperatures that could be lethal to other, non-resistant, species.

  The *de novo* protein synthesis (primarily during the acclimation stage), offers protection to cell vital processes.

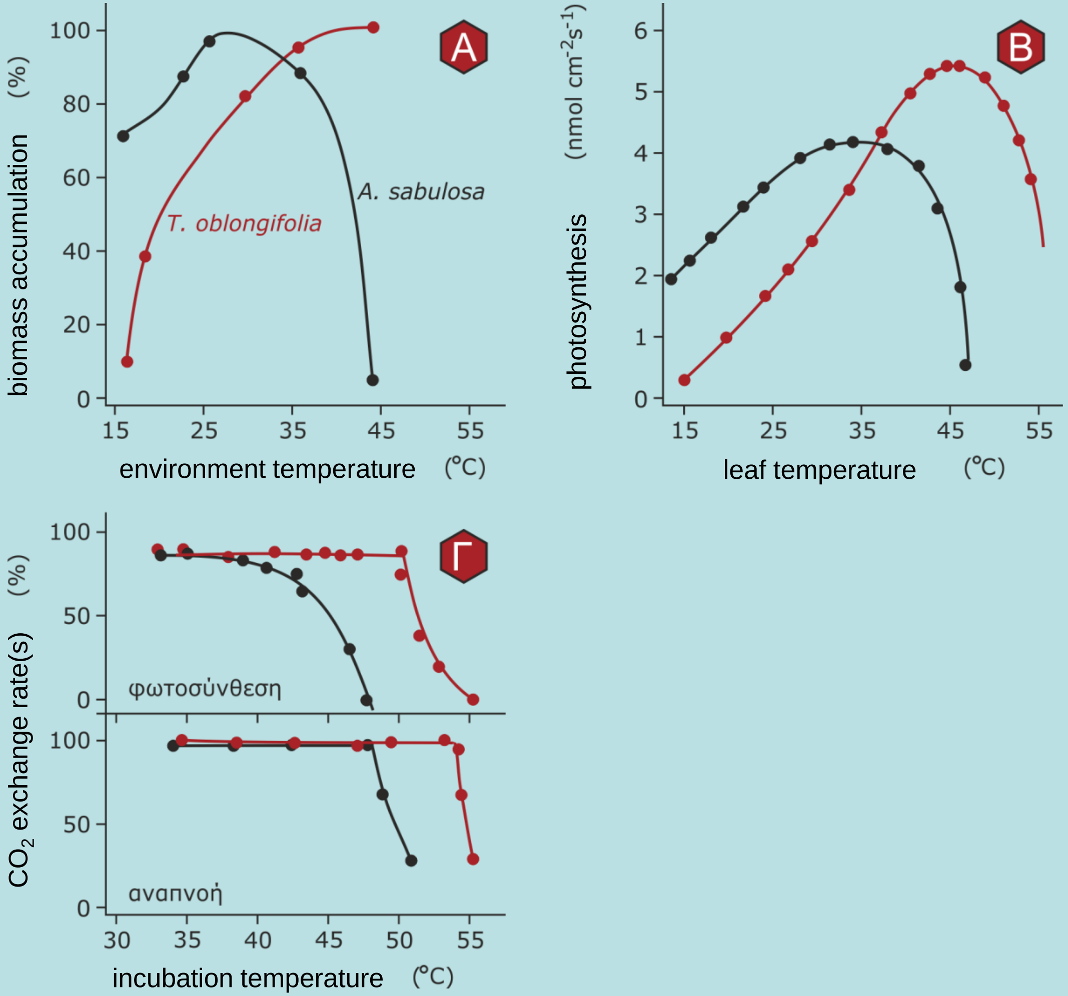
RESISTANCE
ACCLIMATION TO DIFFERENT THERMAL REGIMES



Acclimation of photosynthesis of leaves of *Nerium oleander* in different growth temperatures

RESISTANCE

ACCLIMATION TO DIFFERENT THERMAL REGIMES



Tidestromia oblongifolia colonizes hot desert areas, while *Atriplex sabulosa* cold coastal areas in the USA

RESISTANCE AND PROTEOME

- **The role of Heat Shock Proteins**

Short exposure to high temperatures inhibits usual protein synthesis. However, the synthesis of low MW proteins known as **Heat Shock Proteins** (HSP) is induced.

Induction of **synthesis is rapid**, mRNAs appear within 3 to 5 min and respective HSPs **within 30 min** from initial exposure to high temperatures.

Sharing **many similarities between plans species**, HSPs play significant roles in plant survival under high temperatures.

RESISTANCE AND PROTEOME

- **Groups of Heat Shock Proteins**

  Distinguished based on MW: HSP100 , HSP90, HSP70, HSP60 and very low MW HSPs between 17 and 28 kDa.

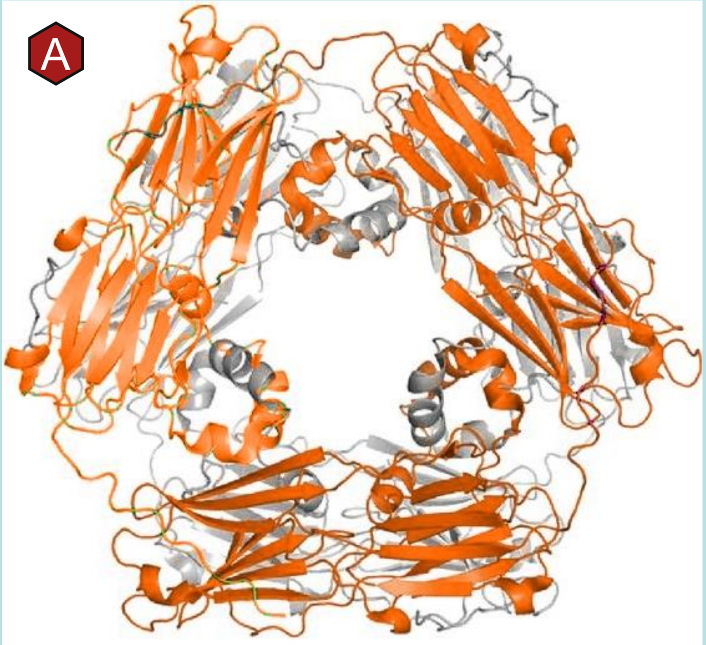
  HSP40,60,70 groups act as **chaperons**. They contribute to protein protection, folding of newly synthesized proteins and refolding of proteins that have lost correct conformation due to stress.

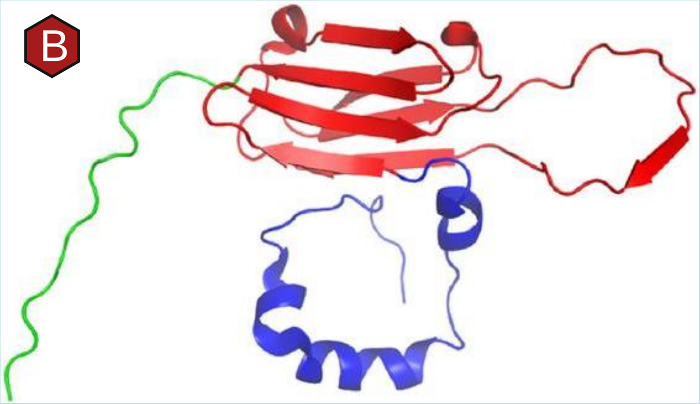
  Ubiquitin (8 kDa) also shares chaperone functionality and is inducible together with other HSPs to tag unneeded or denaturated proteins for decomposition through the proteasome.

RESISTANCE AND PROTEOME

HPS group	location	Possible function
HSP 110		unknown
HSP 90		Protein protection
HSP 70	Cytoplasm, mitochondria, chloroplasts	Protein unit assembly or disassembly of enzymes or multienzyme complexes.
HSP 60	Cytoplasm, mitochondria, chloroplasts	As HSP70
LMW HSP (17-28 kDa)	Aggregates in cytoplasm and chloroplasts	Unknown
Ubiquitin		Tags proteins for decomposition

RESISTANCE AND PROTEOME





RESISTANCE AND PROTEOME

- **Other proteins**

  DREB2 transcription factors
  Expansins
  Oligosaccharide metabolism enzymes
  Antioxidative metabolism enzymes
  LEA family of proteins / dehydrins