Plant stress physiology

(what is all that about?)

Marcel Jansen
University College Cork,
Ireland

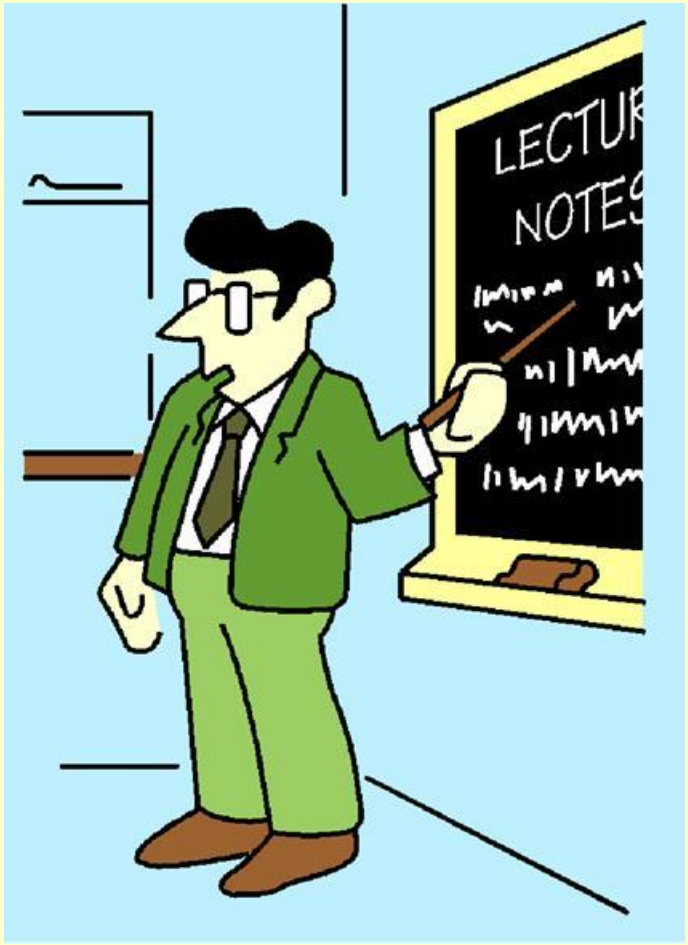
Tato akce se koná v rámci projektu:
Vybudování vědeckého týmu environmentální metabolomiky a ekofyziologie a jeho zapojení do mezinárodních sítí (ENVIMET; r.č. **CZ.1.07/2.3.00/20.0246**) realizovaného v rámci Operačního programu Vzdělávání pro konkurenceschopnost.

Programme

- **Lecture 1; stress biology**
(general terminology & concepts)

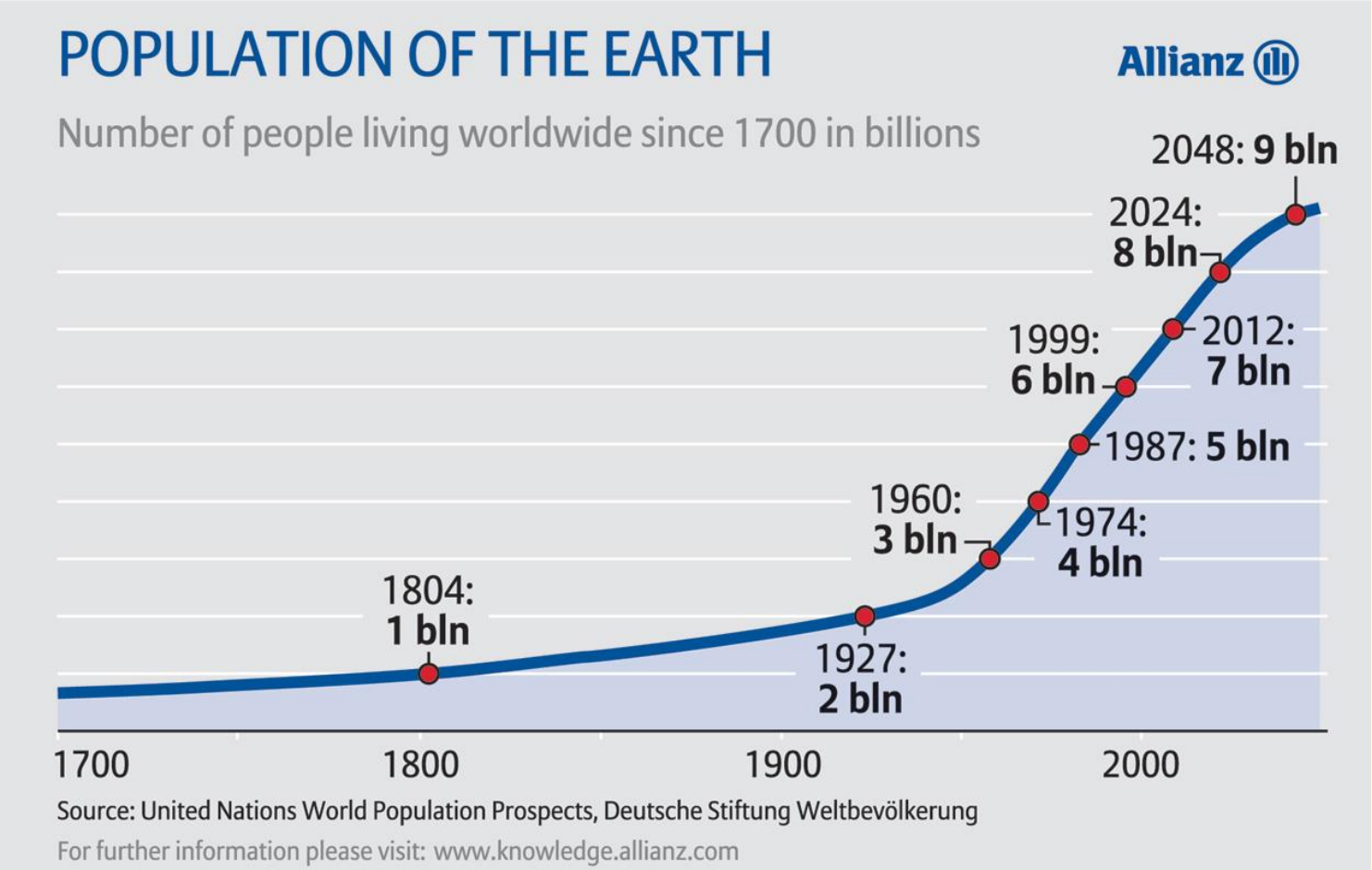
- **Lecture 2; UV-B biology**
(*damaging agent or regulatory factor*)

- **Lecture 3; Lemnaceae biology**
(*from toxicological guinea pig to fast growing food***)**



Why are we interested in plant stress?

Why are we interested in plant stress?



Why are we interested in plant stress?

“Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crops by more than 50%...”

(Wang et al. Planta 2003)

Why are we interested in plant stress?

Depending on the definition!

“Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crops by more than 50%...”

(Wang et al. Planta 2003)

What is plant stress?

How do we define plant stress?

Definitions are vital:

- To facilitate communication
- To facilitate exchange of data
- To improve experimental approaches
- To standardise experimental approaches

What is stress ?

Human stress: strong emphasis on psychological / emotional processes with consequences for physical well being

Plant stress is not psychological!

but what exactly is plant stress?

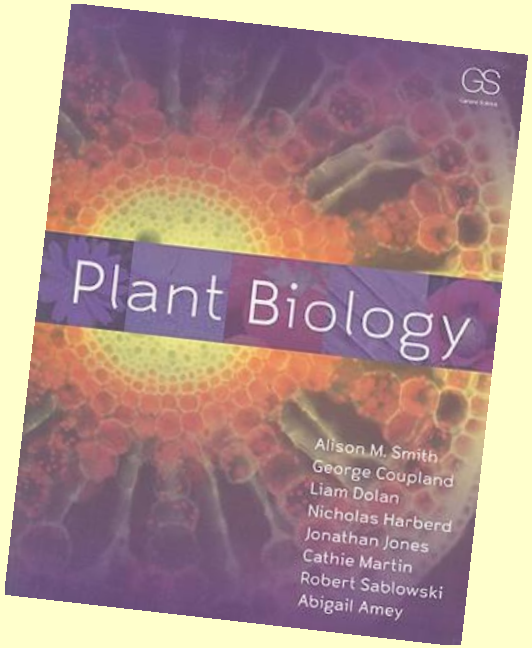
Drought

Storm damage

Insect damage

Acid rain

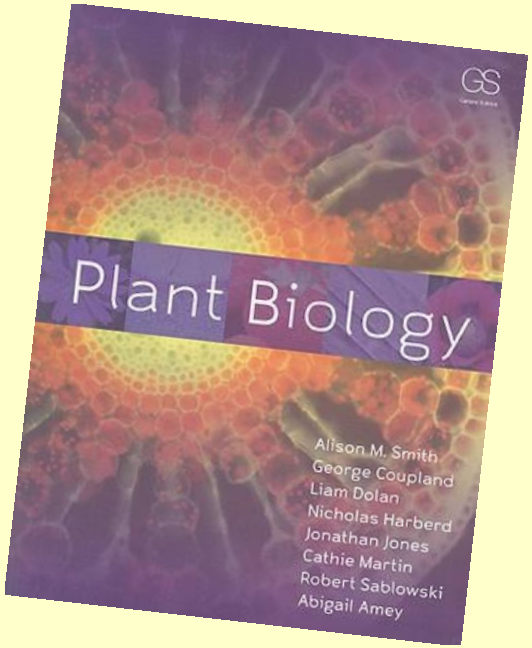
What is plant stress?



Plant Biology by Smith et al., (2010)

“A stressful environment is any environment that is less than optimal for plant growth”

What is plant stress?



Plant Biology by Smith et al., (2010)

“A stressful environment is any environment that is less than optimal for plant growth”

<u>Problems:</u>

Does an “optimal” environment exist?

If so, are plants always stressed?

Non-optimal conditions *versus* plant stress

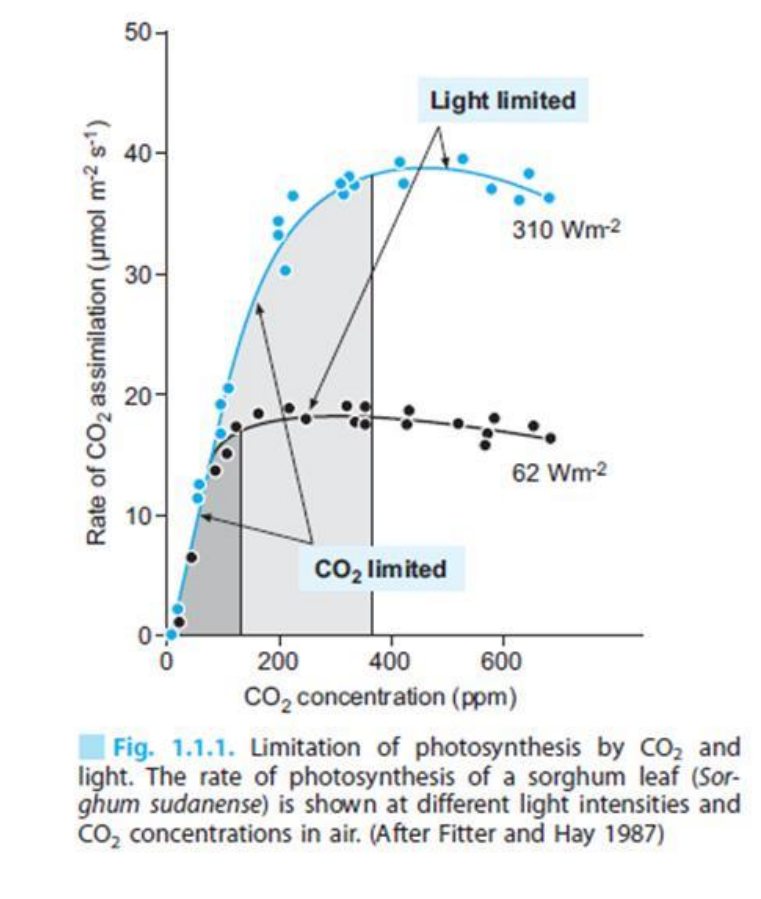


Fig. 1.1.1. Limitation of photosynthesis by CO_2 and light. The rate of photosynthesis of a sorghum leaf (*Sorghum sudanense*) is shown at different light intensities and CO_2 concentrations in air. (After Fitter and Hay 1987)

Blackman; the law of limiting factors

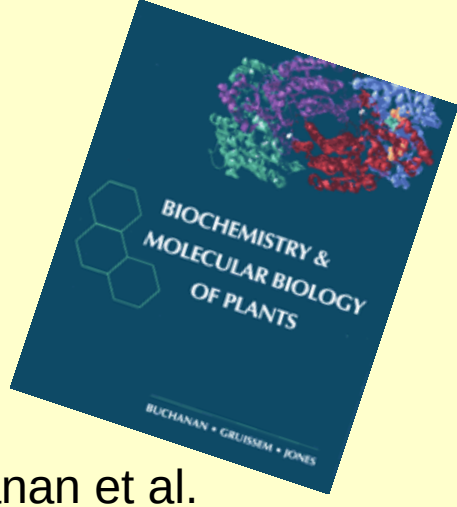
Frederick Frost Blackman FRS (1866 –1947)

There is always a limiting factor

Every change of an environmental factor influences plant growth and development

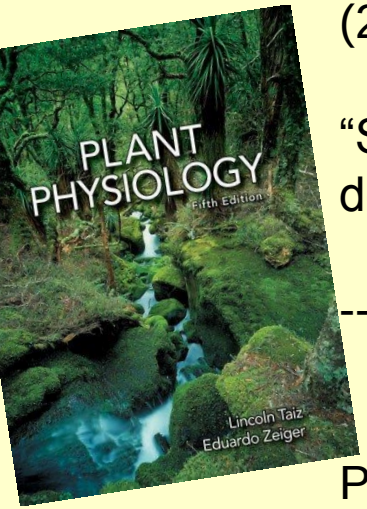
Is this stress?

What is plant stress?



Biochemistry & Molecular Biology of Plants by Buchanan et al. (2000)

“Stresses; external conditions that adversely affect growth, development or productivity”

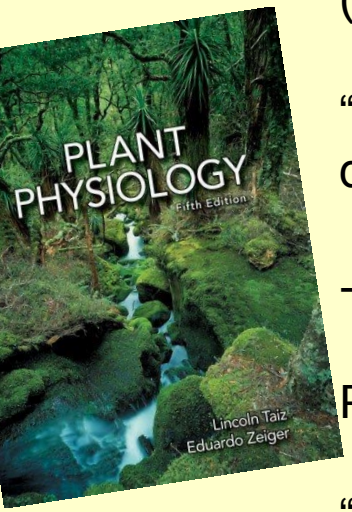


Plant Physiology by Taiz and Zeiger (2010)

“Stress is a disadvantageous influence exerted on a plant by external abiotic or biotic factor(s), such as infection, or heat, water and anoxia.

What is plant stress?

Biochemistry & Molecular Biology of Plants by Buchanan et al. (2000)



"Stresses; external conditions that adversely affect growth, development or productivity"

Plant Physiology by Taiz and Zeiger (2010)

"Stress is a disadvantageous influence"

<u>Question:</u>

Is stress the "external condition" or the "plant response"?

Stress and “external conditions”?

Conditions that comprise a stress for one plant species are not necessarily a stress for another species.

Saguaro cactus

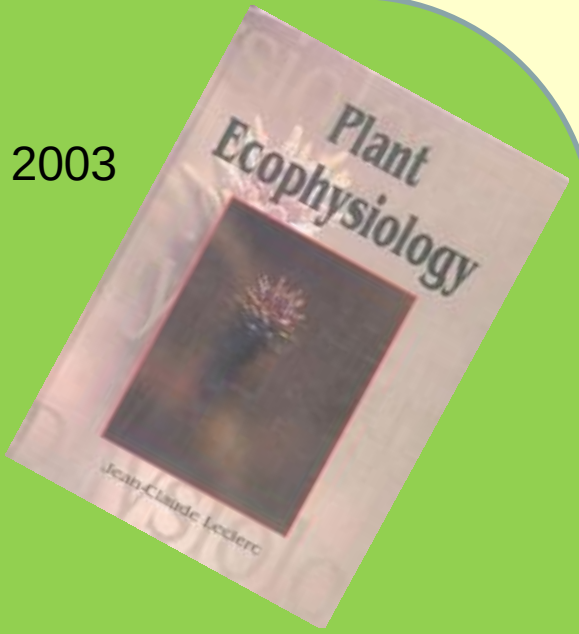
Is a temperature of 5-10°C a stress?

Chilling stress maize

No chilling stress peas

Consequently, stress conditions are very important in terms of biodiversity and plant distribution.

Leclerc, 2003



Terminology

Concept of stress;

“external constraint” or **“stress factor”** or **“stressor”**

and its result

“the state of stress” or **“stress response”** or **“stress”**

which describes the response of the cell, plant or ecosystem,

What is plant stress?

- Hans Selye
- Jacob Levitt
- Reto Strasser

What is (plant) stress?

1907-1982

Hans Selye (**endocrinologist**)

The stress response has two components:

- a set of responses called the "general *adaptation* syndrome"
- a pathological state from destructive, unrelieved stress

The positive, adaptive, stress response triggered by low doses of a stressor is named "**eustress**"

The negative stress response caused by high doses of a stressor is named "**distress**"

Evaluation of plant stress responses

Eustress

- Readjustment metabolism
- Induction repair and protection responses (acclimation)
  - ROS signalling (specific)
  - Changes gene expression
  - Accumulation phytochemicals and antioxidants
  - Morphological and developmental stages

Distress

- Physiological destabilisation
  - Oxidative damage
  - ROS signalling (generic)
  - DNA damage
  - Inactivation photosynthesis
  - Production distress hormones
  - Cell death

In a natural environment, with fluctuating stressors, plants will display mixtures of distress and eustress

Evaluation of plant stress responses

Eustress

- Readjustment metabolism
- Induction repair and protection responses (acclimation)
  - ROS signalling (specific)
  - Changes gene expression
  - Accumulation phytochemicals and antioxidants
  - Morphological and developmental stages

Distress

"state of destructive, unrelieved stress" is too simplistic

- Physiological destabilisation
  - Oxidative damage
  - ROS signalling (ROS, Asc/DHA, GSH/GSSG)
  - Production distress hormones (JA, Ethylene)
  - DNA damage
  - Inactivation photosynthesis
  - Cell death

Eustress; is that stress?

Farmer

Same field of wheat

Plant physiologist

Eustress; is that stress?

Farmer

Same field of wheat

Scientist

Low rain; root/shoot ratio increased

Crop has optimally adjusted to environ

No macroscopic damage

Fv/Fm is normal

This crop is healthy

Eustress; is that stress?

Farmer

Same field of wheat

Scientist

Low rain; root/shoot ratio increased

Yield is lower than hoped for

Non-optimal production!

My crop is stressed

Farming income ↓
World food supply ↓

Crop has optimally adjusted to environ

No macroscopic damage

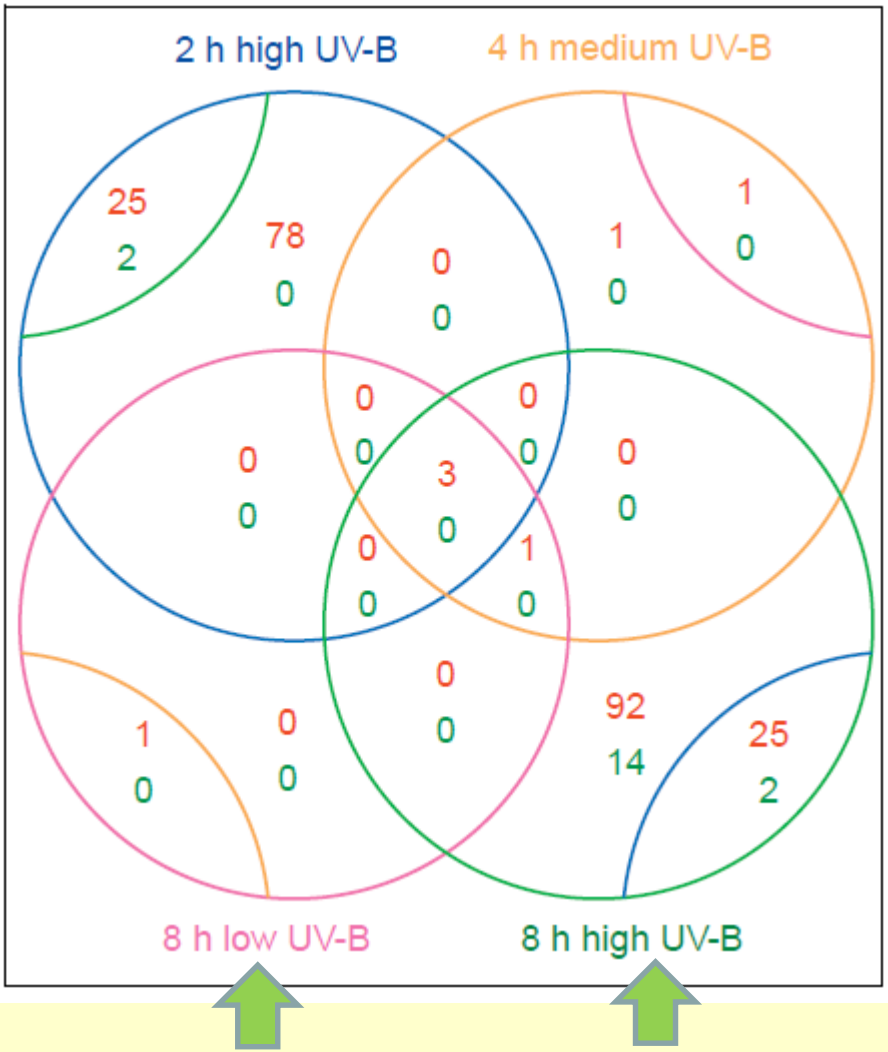
Fv/Fm is normal

This crop is healthy

Dose of a stressor determines whether plant experiences eustress or distress

(thus; different responses depending on the stressor dose)

Distinct gene expression patterns for eustress and distress



UV-induced gene-expression in maize

Low UV-B dose induces different changes in gene-expression than a high dose.

Dose-dependancy of gene-expression

Casati and Walbot, 2004

Distinct responses low and high UV-B

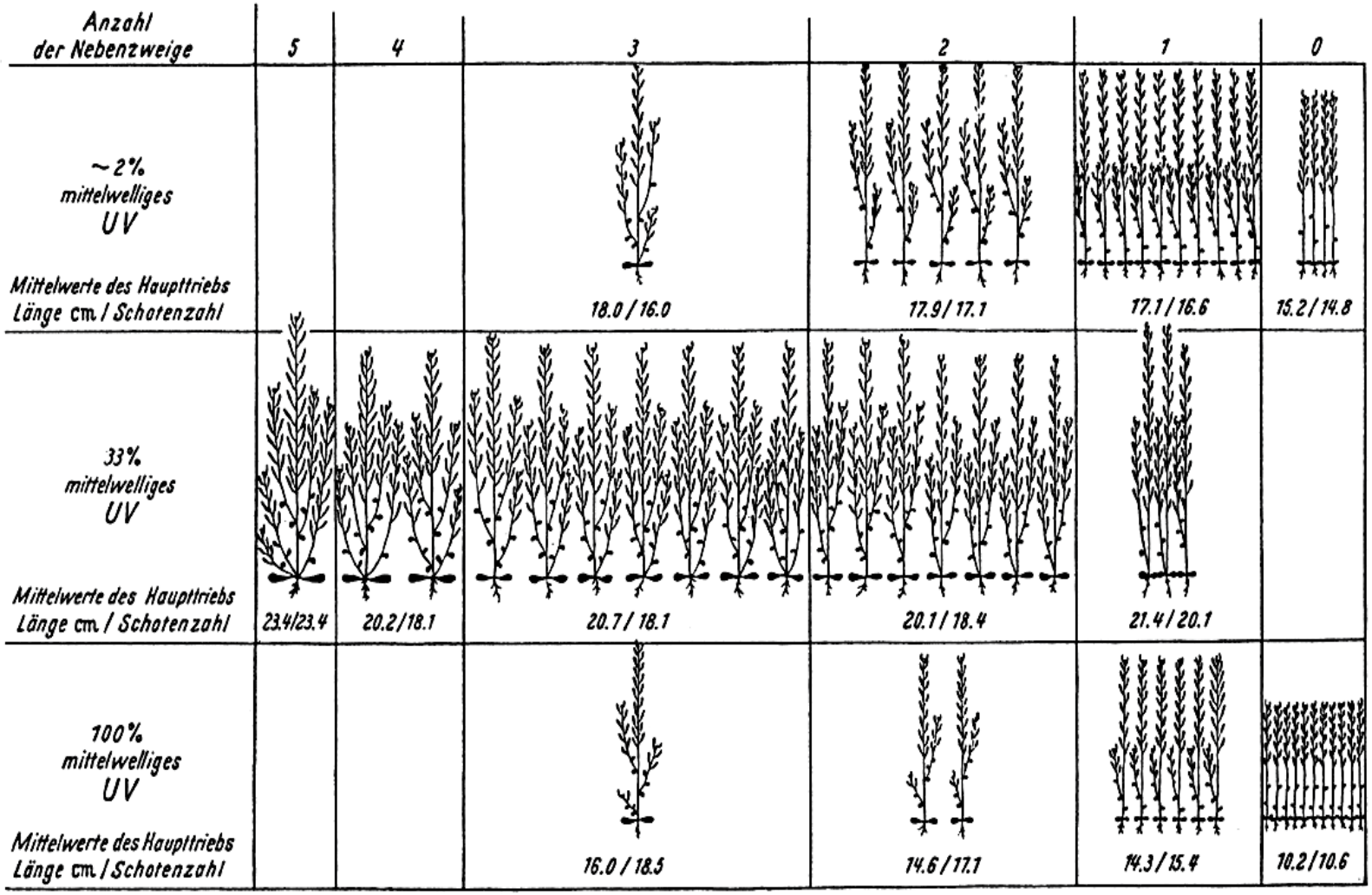
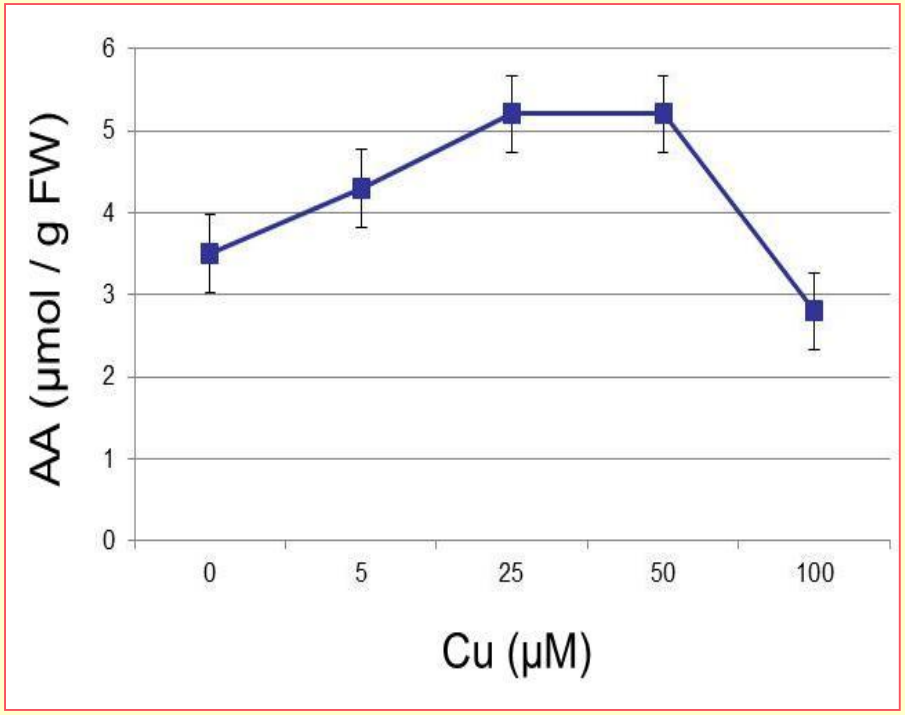


Abb. 14. *Arabidopsis thaliana*, Rasse Catania.

(Brodführer Planta 1955)

Distinct responses low and high Cu



Cu-induced changes in ascorbate acid in Arabidopsis exposed for 1 day

-Low Cu induces increase in AA (Eustress)

-High Cu induces decrease in AA (Distress)

Dose (and time) dependancy of metabolic response

Free after Drazkiewich et al., Plant Science 2003

Take home message!

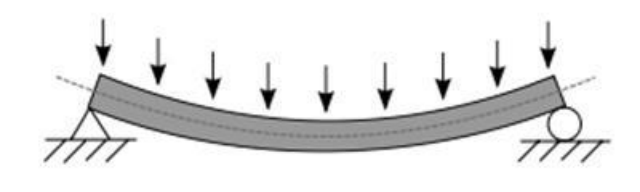
(but you are not yet going home ☺)

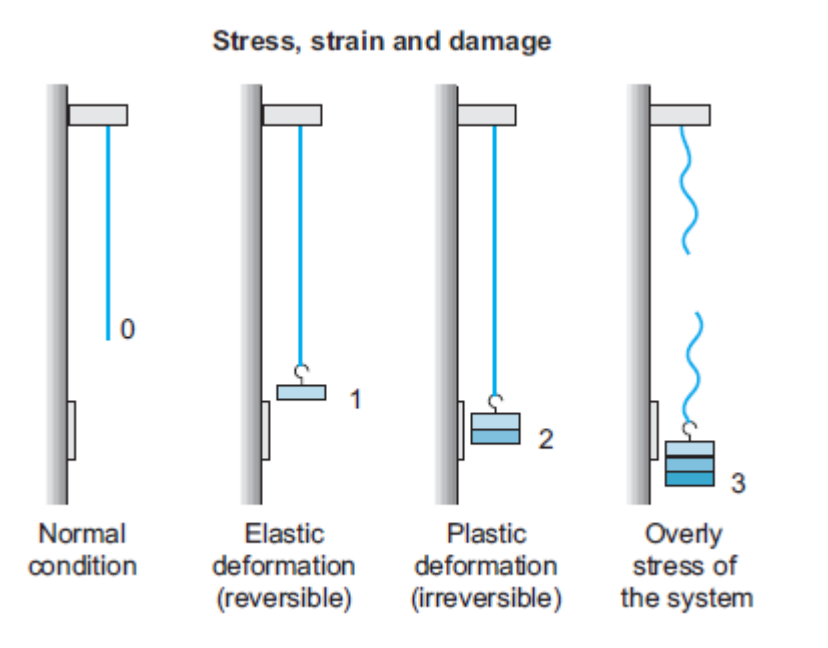
Dose-response curves are **vital** to fully understand the complexity of plant stress responses

Very different results can be obtained depending on whether plants are experiencing eustress / distress!

Careful calibration of stress conditions is necessary in order to be able to compare data between different laboratories

What is stress?





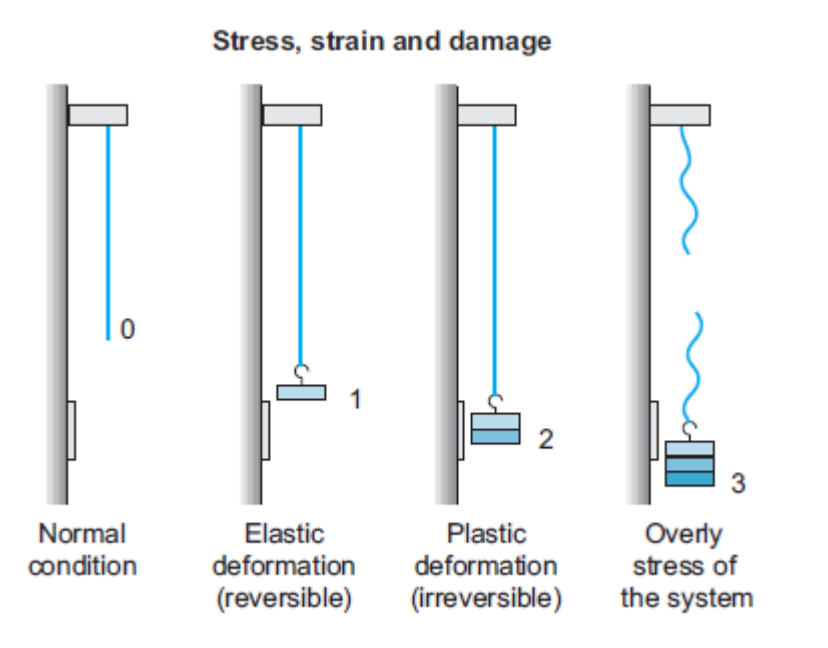
Jacob Levitt (1980)

Stress model based on **<u>mechanics</u>**

Distinction between:

- A reversible component of stress
- An irreversible / permanent component, concept loosely similar to distress (i.e. think cell death)

What is stress?



Jacob Levitt (1980)

Stress model based on mechanics

Distinction between:

- A reversible component of stress
- An irreversible / permanent component, loosely similar to distress (i.e. think cell death)

However plants can repair damage, so this concept is not as clear as in mechanics

Take home message!

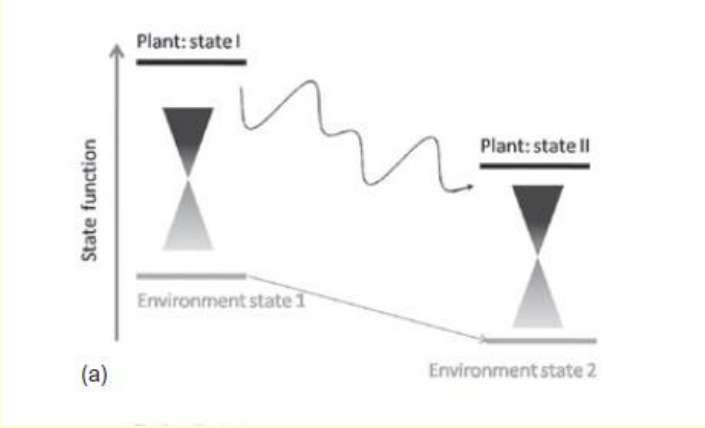
(but you are still not going home ☺)

Dose-response curves are **vital** to fully understand the complexity of plant stress responses

Very different results can be obtained depending on whether plants are experiencing eustress / distress!

Careful calibration of stress conditions is necessary in order to be able to compare data between different laboratories

What is plant stress?

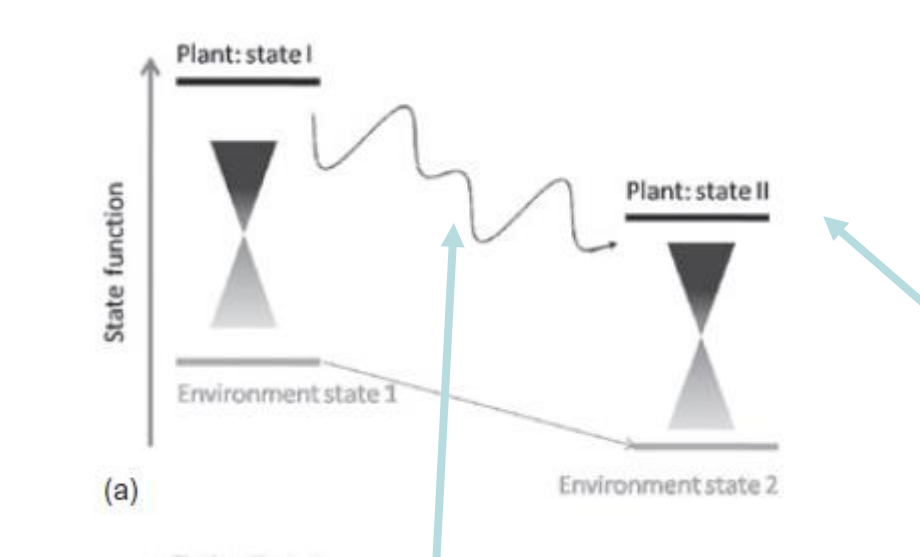


Reto Strasser

Stress model based on existence set of **<u>thermodynamically</u> optimal** states

- Stress is a deviation from the normal, non-stress condition
- Non-stress; when a plant is at a thermodynamically optimal state
- Stress; when the plant is temporarily in a thermodynamically sub-optimal condition, due to environmental change

What is plant stress?

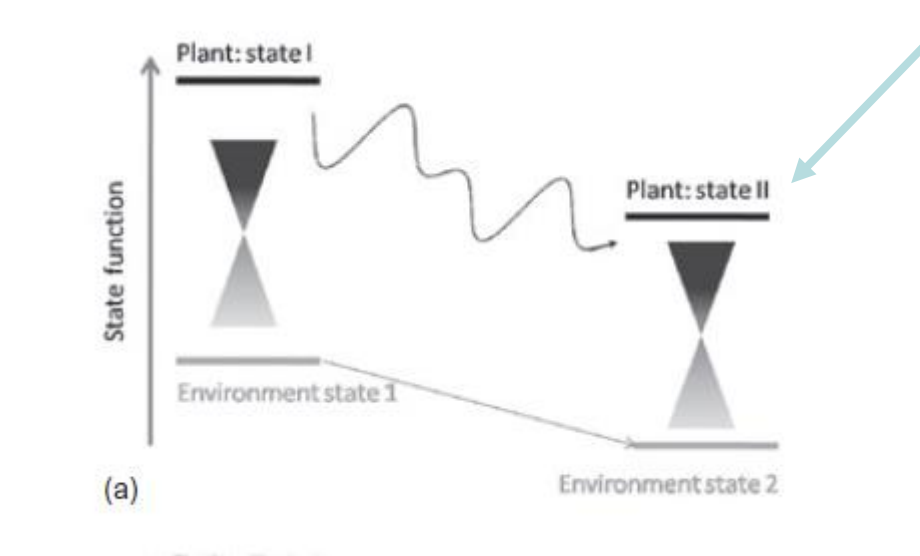


Defined as a new optimised state (Strasser)

Plant stress; a temporary, non-optimal state before plant reaches a new thermodynamically equilibrium (Strasser et al)

"About the perpetual state changes in plants approaching harmony with their environment" (Tsimilli-Michael, Kruger and Strasser, *ARCHIVES DES SCIENCES* (1996)

What is plant stress?



Plant stress defined as a non-optimal state (Selye, Levitt and most authors)

What is plant stress?

- Different concepts,
- Different stakeholders,
- No broadly accepted terminology!

Stress?

What is plant stress?

Terminology

Stress response, *or* state of stress, *or* stress, describes the response of the cell, plant or ecosystem, following exposure to a stressor

- **eu-stress / reversible stress = a mild, acclimative, often specific response to a stressor**

- **distress / irreversible stress = a strong often generic response to a stressor, involving substantial (sub)-cellular damage**

What is stress tolerance?

Stress tolerance

An extension of the range of conditions under which an organism can operate, i.e. prevention of distress

Plants have evolved different strategies

- Stressor escape
- Stressor avoidance
- True stressor tolerance

Stressor escapers

Stress escape via opportunistic growth and reproduction cycles

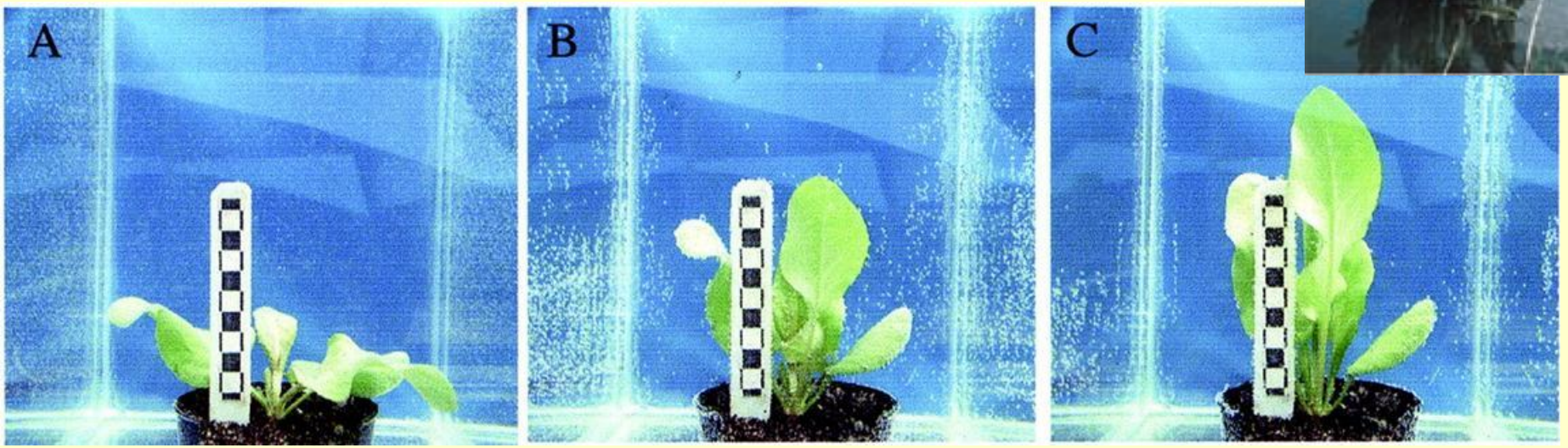
Flowering desert in California

Stressor escapers!

Escape stress-exposure via opportunistic growth and reproduction cycles

Stressor escape

Stress escape via opportunistic growth and reproduction cycles



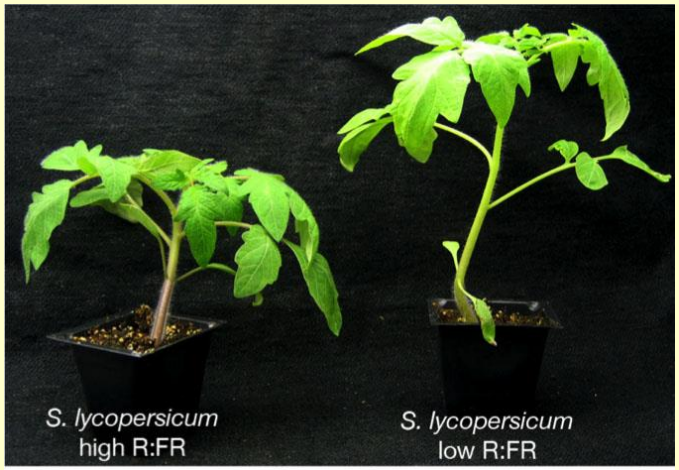
Submergence-induced, ethylene-mediated elongation in *Rumex palustris*.

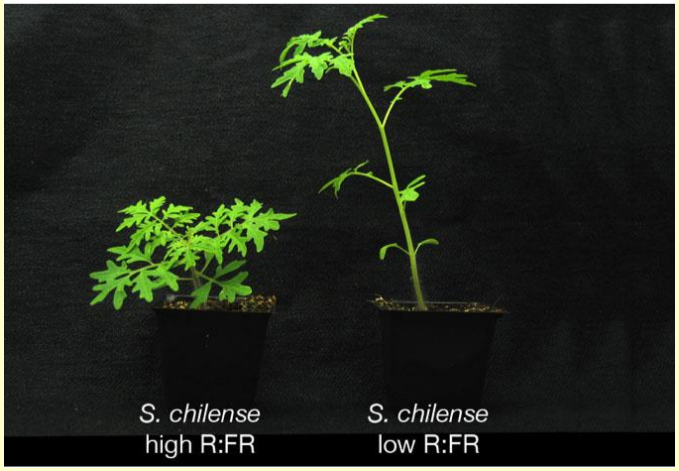
A, Plant submerged for 7 min; B, 8 h; C, 50 h.

Voesenek; *Ann Bot (2003)*

Shade-escape syndrome

Stress escape via opportunistic growth and reproduction cycles

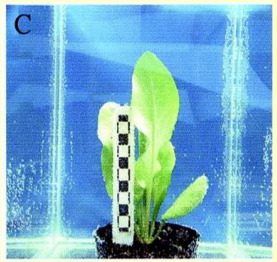


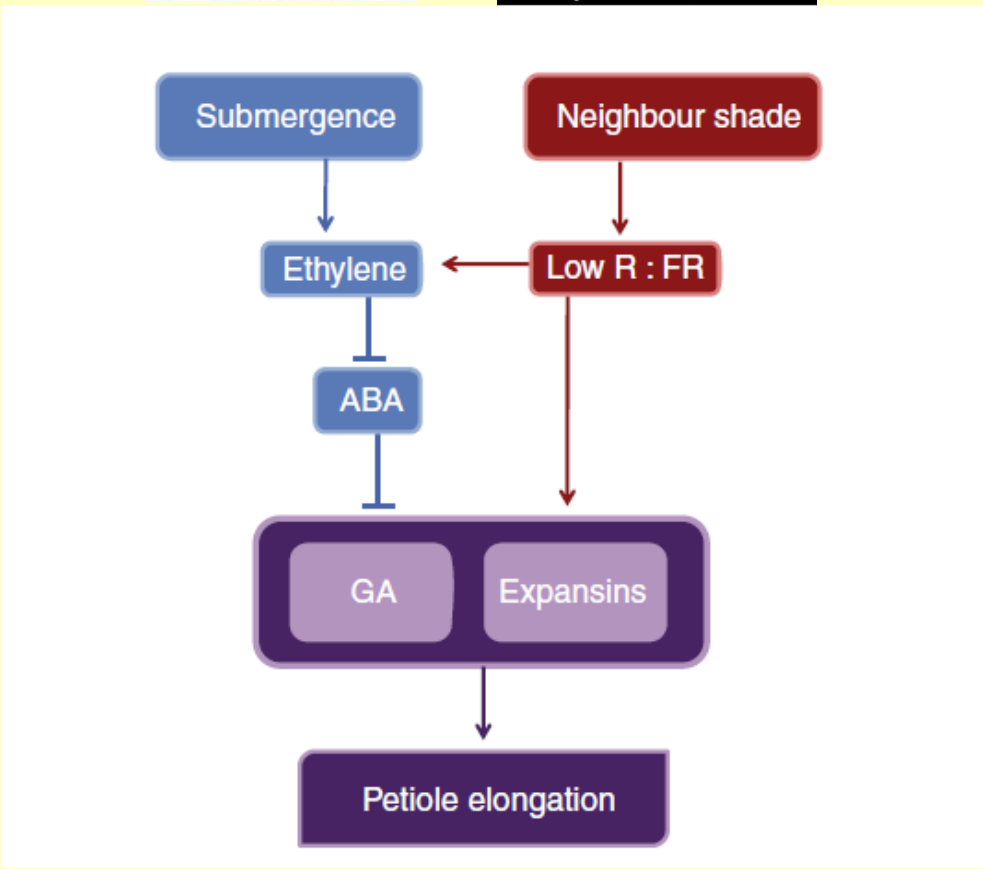


Neighbour (reflection and/or shading) induced R-FR-mediated elongation in *Solanum sp*.

http://solgenomics.net/

Stressor escape

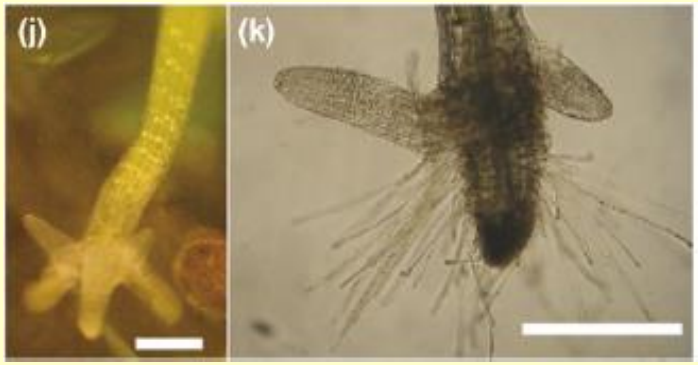




- “Stress escape syndromes”
- Principle rapid cell elongation responses
- GA and expansins play a role in responses to flooding and shade
- Convergence signal transduction pathways?

Pierik, de Wit, Voesenek, 2011

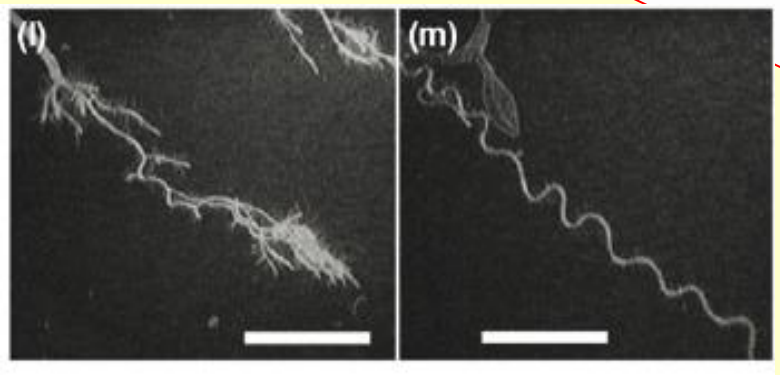
Stressor escape; SIMR



j) Arabidopsis root exposed for 7 days to tert-butyl hydrogen peroxide produces lateral roots (bar 200um)

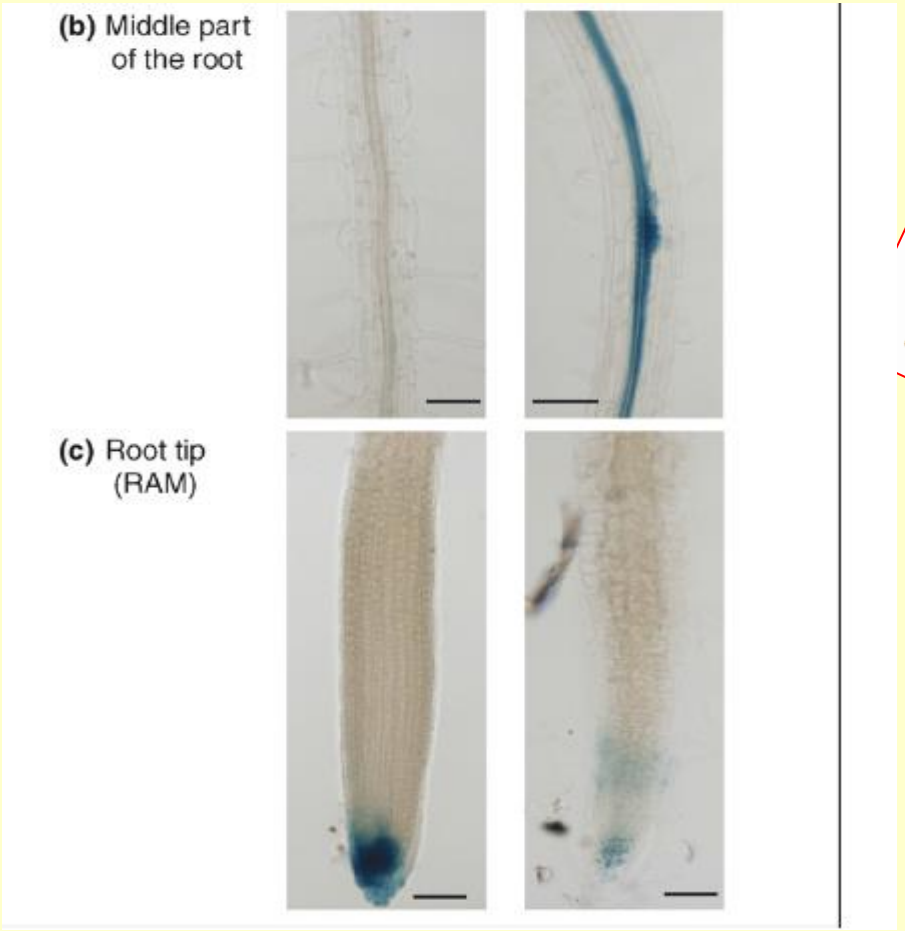
k) Lateral roots formed after exposure to alloxan (bar 200 um)

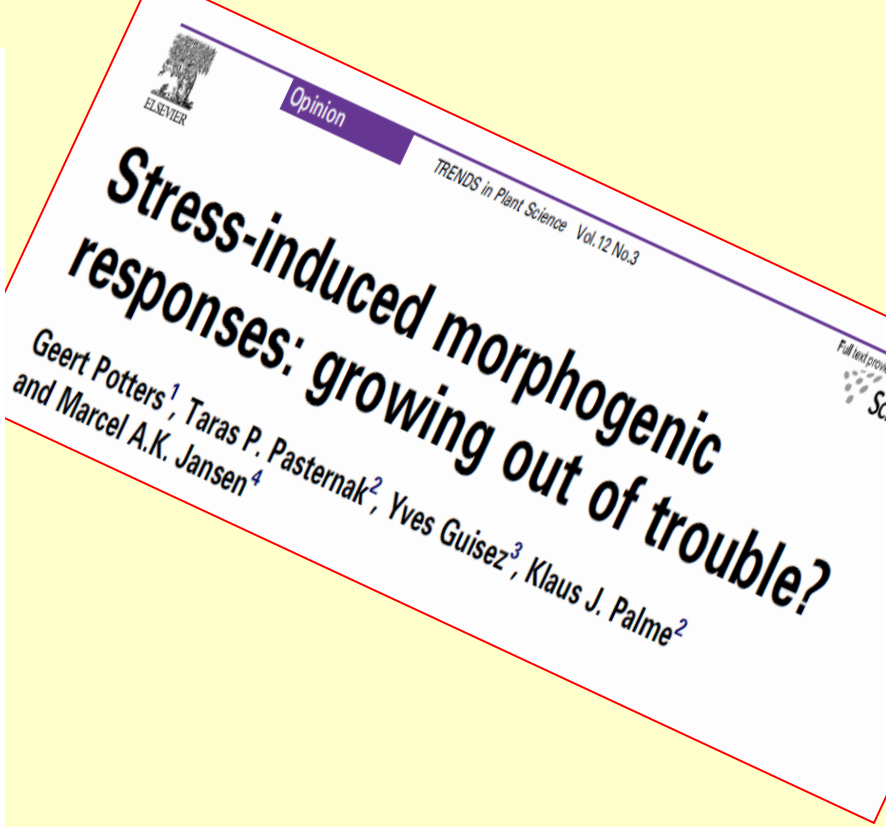
Note; lateral roots & short elongation zone



l) Arabidopsis root on phosphate deficient medium (bar 1 cm)

k) Arabidopsis root on phosphate enriched medium (bar 1 cm)



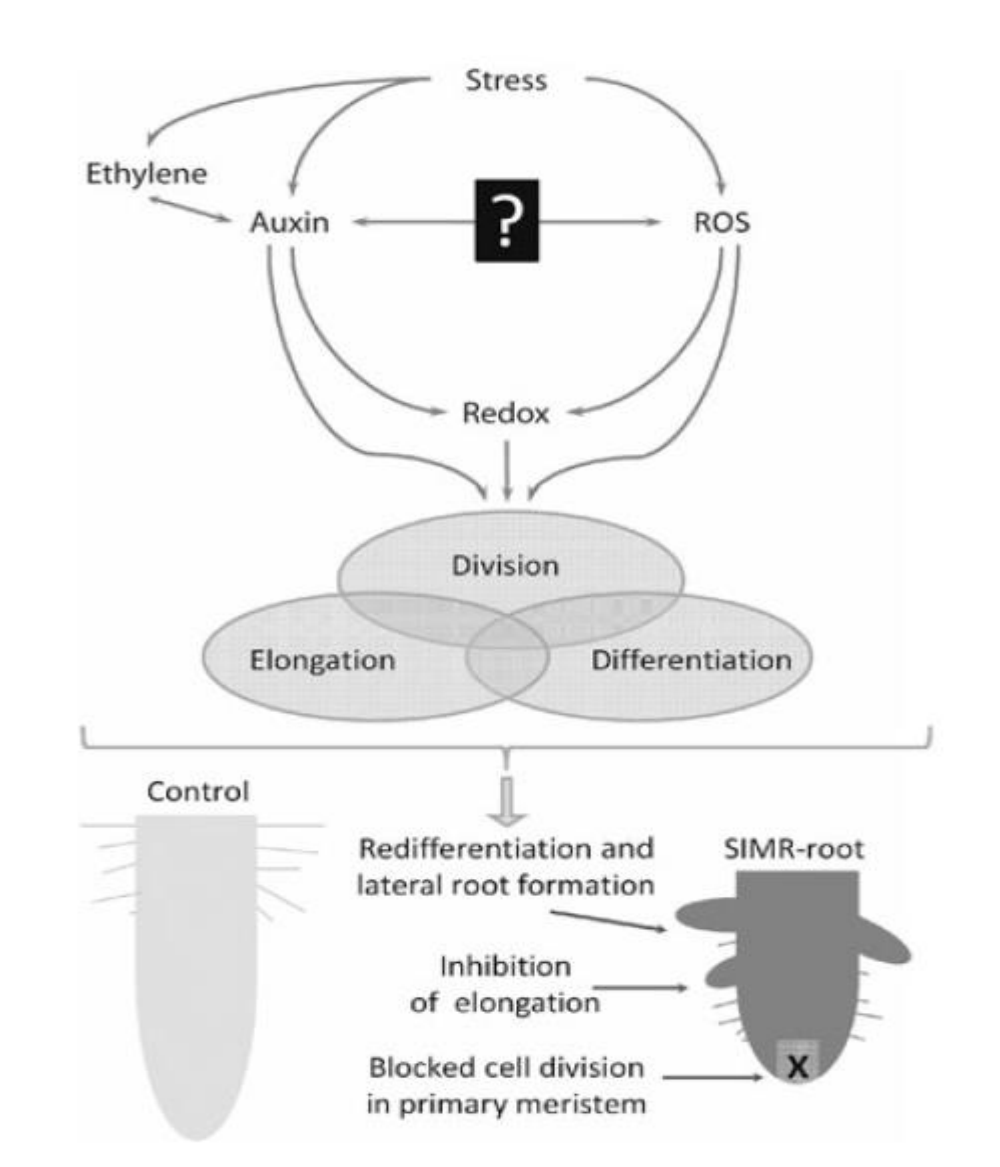


Roots of 6 day old Arabidopsis exposed for 48 hours to 50 uM Cd

Results in redistribution DR5-GUS stain, suggesting auxin redistribution

Low auxin in apex

High auxin in pericycle of middle and upper root zone, coinciding with lateral root formation



Potters et al., PCE, 2009

Model of interactions leading to SIMR

Signals affected by the environment;

- ROS
- Auxin/ethylene

3 response components;

- inhibition cell elongation
- alterations cell differentiation
- local alteration rate of cell division

Stress escape through flowering

Table 1. Some cases of stress-induced flowering

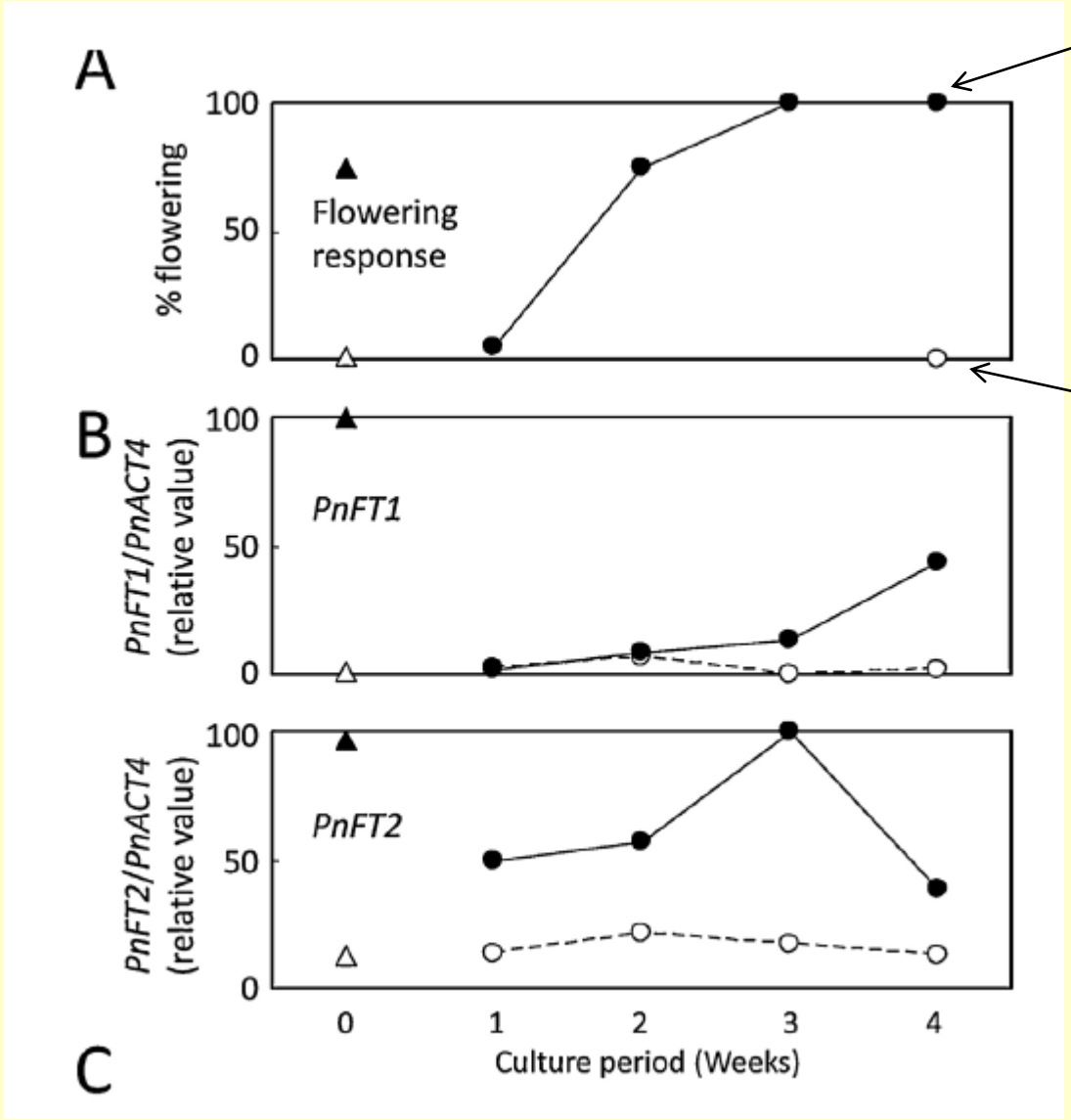
Stress factor	Species	Flowering response
high-intensity light	*Pharbitis nil*	induction
low-intensity light	*Lemna paucicostata*	induction
	Perilla frutescens var. *crispa*	induction
ultraviolet C	*Arabidopsis thaliana*	induction
drought	Douglas-fir	induction
	tropical pasture Legumes	induction
	lemon	induction
	Ipomoea batatas	promotion
poor nutrition	*Pharbitis nil*	induction
	Macroptilium atropurpureum	promotion
	Cyclamen persicum	promotion
	Ipomoea batatas	promotion
	Arabidopsis thaliana	induction
poor nitrogen	*Lemna paucicostata*	induction
poor oxygen	*Pharbitis nil*	induction
low temperature	*Pharbitis nil*	induction
high conc. $GA_{4/7}$	Douglas-fir	promotion
girdling	Douglas-fir	induction
root pruning	Citrus sp.	induction
	Pharbitis nil	induction
mechanical stimulation	*Ananas comosus*	induction
suppression of root elongation	*Pharbitis nil*	induction

Stress-induced flowering

Channelling resources into reproduction to survive stressfull conditions

Wada and Takeno, 2010

Stress escape through flowering



15ºC

Low temperature (15ºC) induced flowering

25ºC

Induction “Flowering Locus T” (FT) by low temperature *or* nutrient deficiency

Flowering Locus T best known for role in photoperiodic flowering (Florigen)

Integration stress in regulatory network that controls flowering

Yamada and Takeno 2014
Using *Pharbitis nil*

True- stressor tolerance

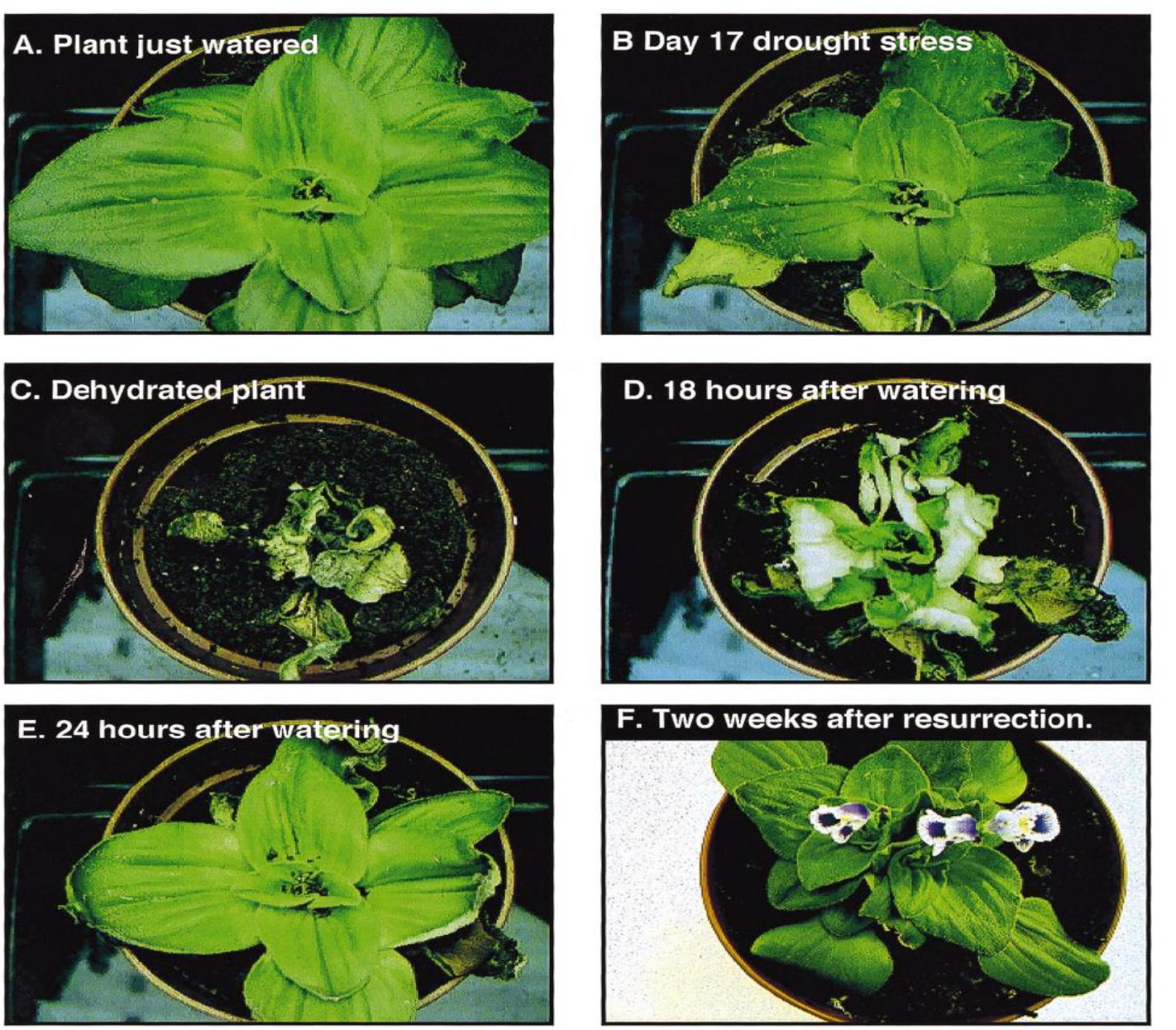
A relatively rare phenomenon whereby plants are able to survive exposure of physiological systems to a stress.

Selaginella sp.

water

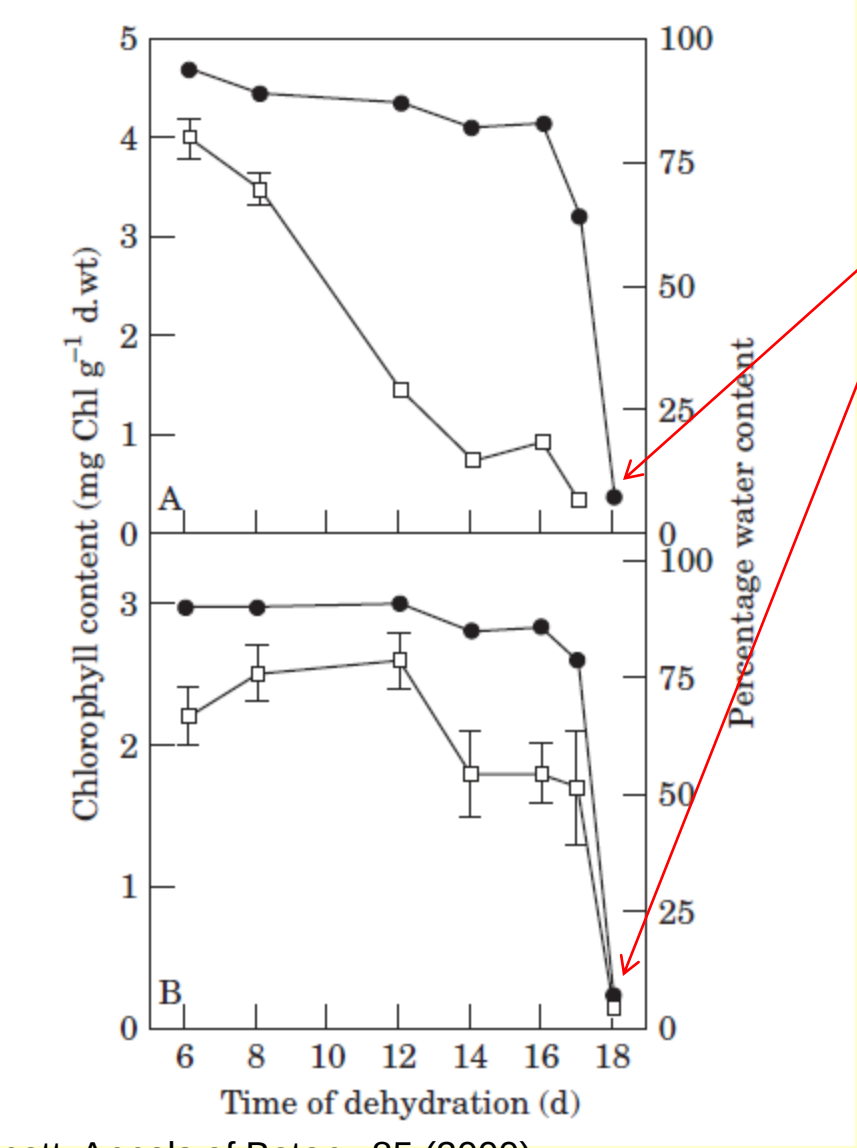
Mosses and other resurrection plants scattered throughout the Plant Kingdom

Craterostigma plantagineum dehydration and rehydration



Scott, Annals of Botany 85 (2000).

True- stressor tolerance



- Water content young (A) and mature (B) *Craterostigma sp* leaf.

  Full photosynthetic recovery can occur in < 24 hours

Scott, Annals of Botany 85 (2000).

“True stressor tolerance” mosses and “resurrection” plants

- Capability to re-imbibe and restart growth
- Central role ABA
- Accumulation compatible solutes and other stabilising compounds (proline, glycine-betaine, but also sugars)

Similarities “true stressor tolerance” mosses and “desiccation tolerance” seeds

- Capability to re-imbibe and restart growth
- Central role ABA
- Accumulation compatible solutes and other stabilising compounds (proline, glycine-betaine, but also sugars)
- Accumulation homologues of “LEA” and “HSP” genes

LEA; late embryogenesis abundant
HSP; heat shock protein

Similarities “true stressor tolerance” mosses and “desiccation tolerance” seeds

- Capability to re-imbibe and restart growth
- Central role ABA
- Accumulation compatible solutes and other stabilising compounds (proline, glycine-betaine, but also sugars)
- Accumulation LEA and HSP
- Many drought responsive genes induced in resurrection plants are homologues of angiosperm genes expressed during seed development
- *Desiccation tolerance has become restricted within the reproductive stages of plant development (pollen & seed)*

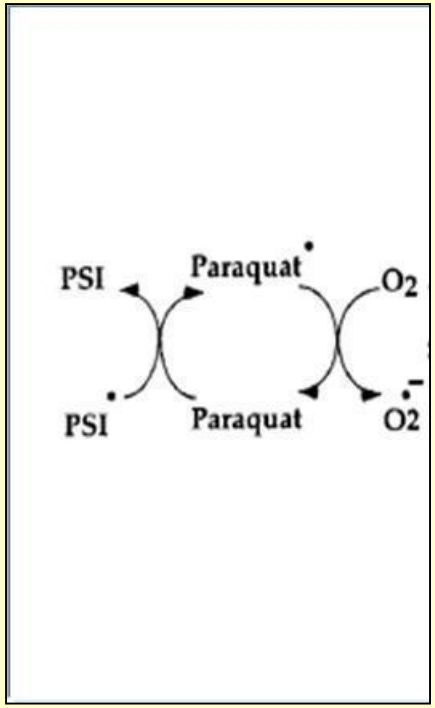
True- stressor tolerance

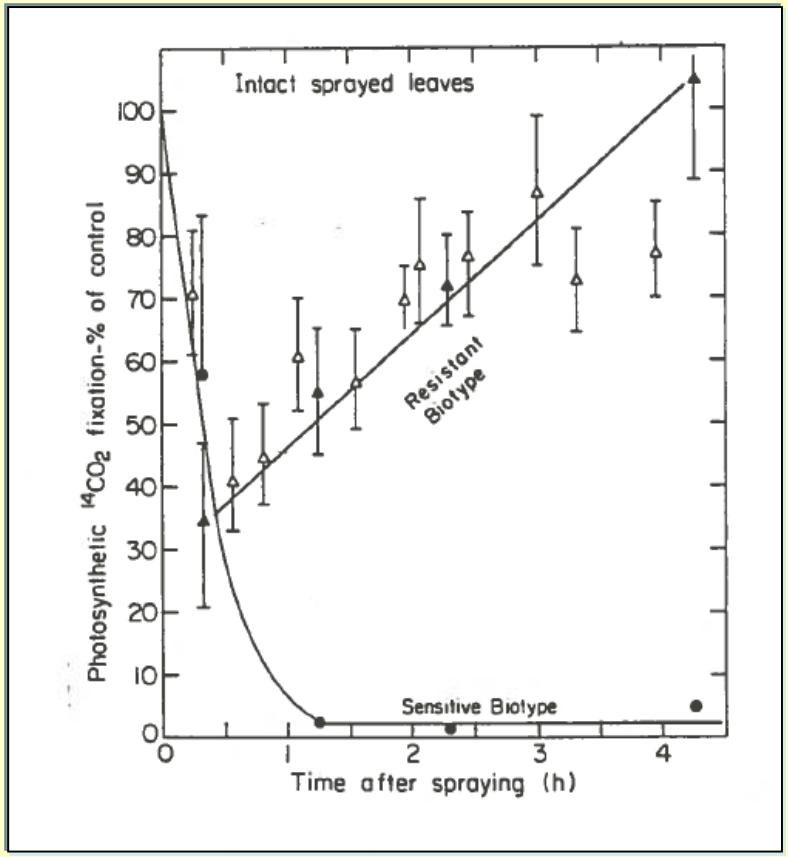
Vascular plants have developed extensive morphological (roots, cuticle, reduced leaf area) and physiological systems to prevent cellular dehydration stress

Evolution from “true-stressor tolerance” to “avoidance tolerance”

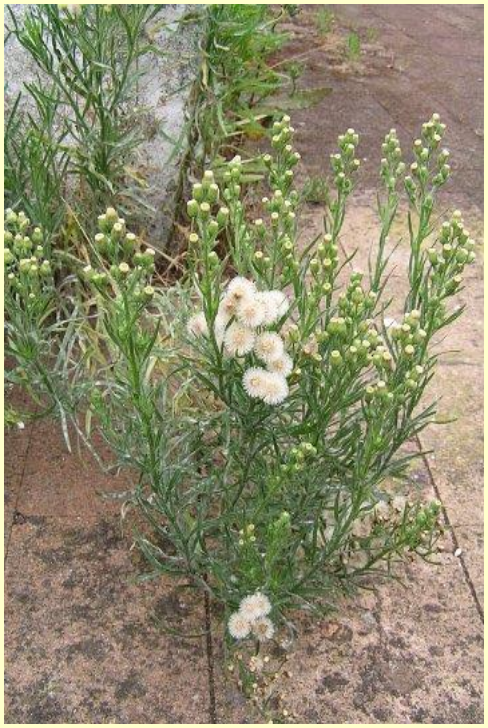
True- stressor tolerance; Paraquat resistance

Upregulated, cellular anti-oxidant defences to give a broad stress tolerance





Shaaltiel and Gressel, 1987

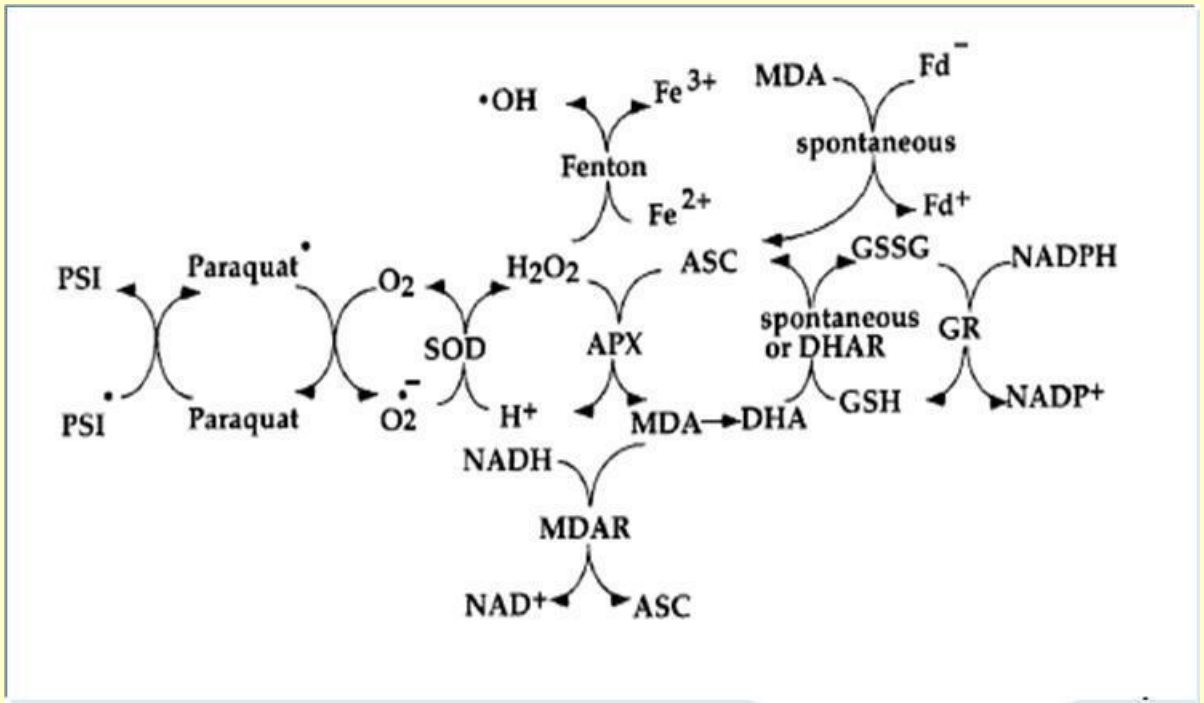


Conyza bonariensis

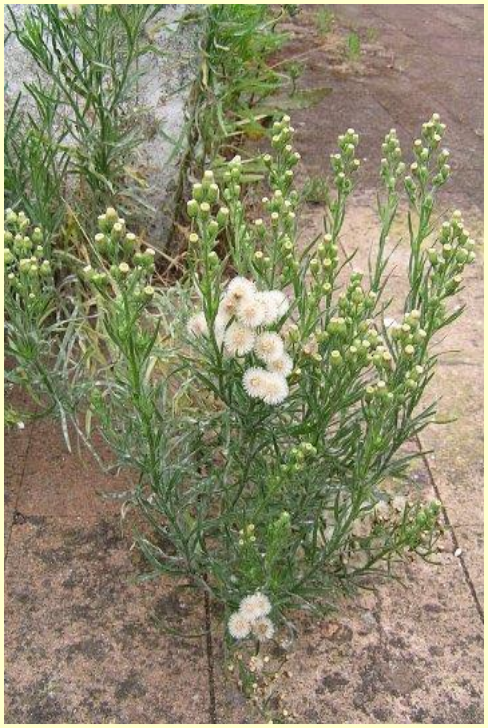
True- stressor tolerance

Paraquat resistance

Upregulated, cellular anti-oxidant defences to give a broad stress tolerance



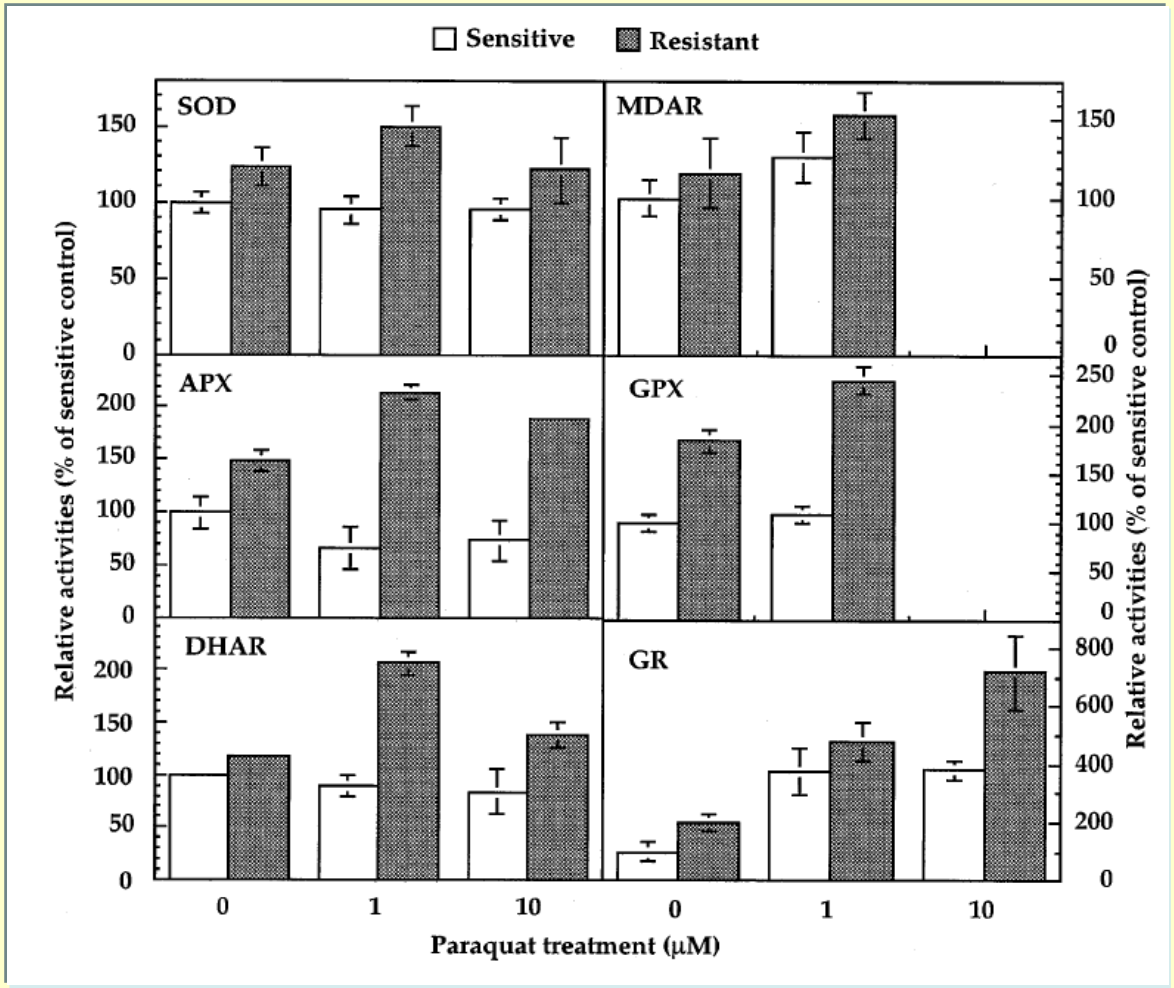
Ye and Gressel, Plant Science, 1994

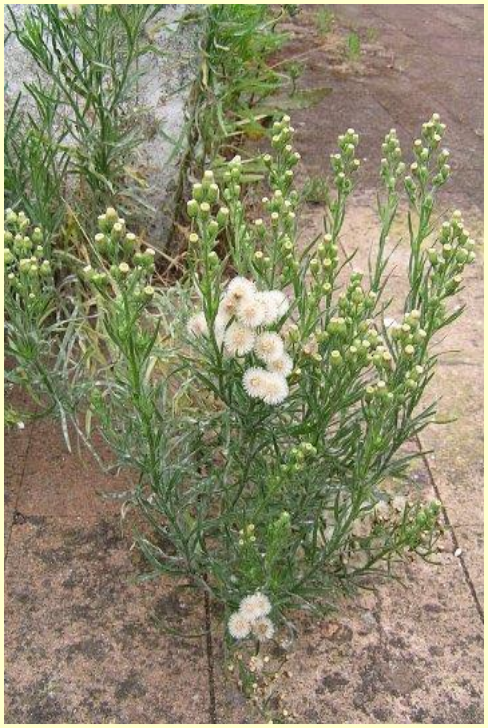


Conyza bonariensis

Paraquat resistance

Upregulated, cellular anti-oxidant defences to give a broad stress tolerance



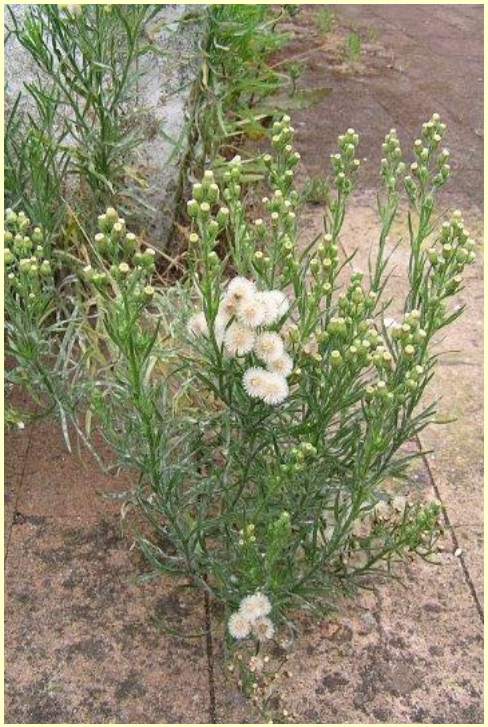


Conyza bonariensis

- Superoxide dismutase
- Ascorbate peroxidase
- Dehydroascorbate peroxidase
- Monodehydroascorbate reductase
- Glutathione peroxidase
- Glutathione reductase

Ye and Gressel planta 2000

Paraquat resistance



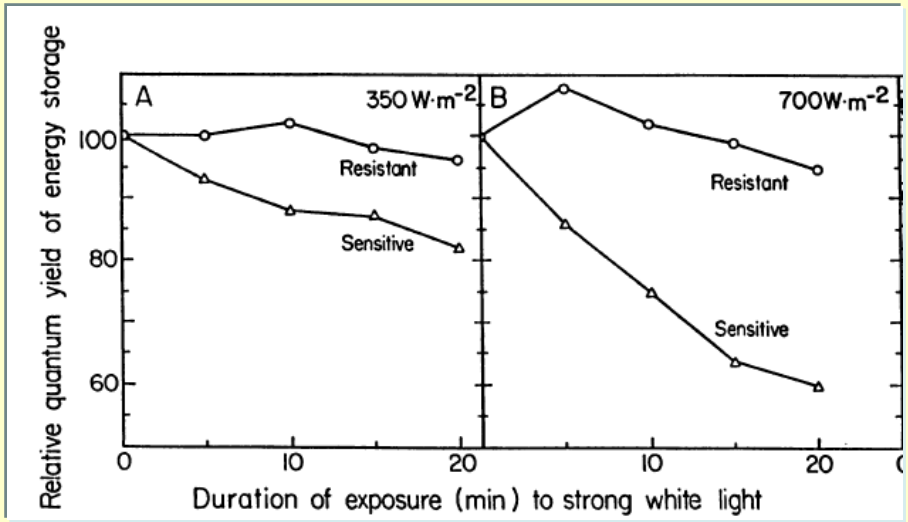
Conyza bonariensis

Upregulated, cellular anti-oxidant defences to give a broad stress tolerance

Cross tolerance to:

- Paraquat
- Atrazine
- Acifluorfen
- SO_2
- Photoinhibition
- Drought

Photoinhibition

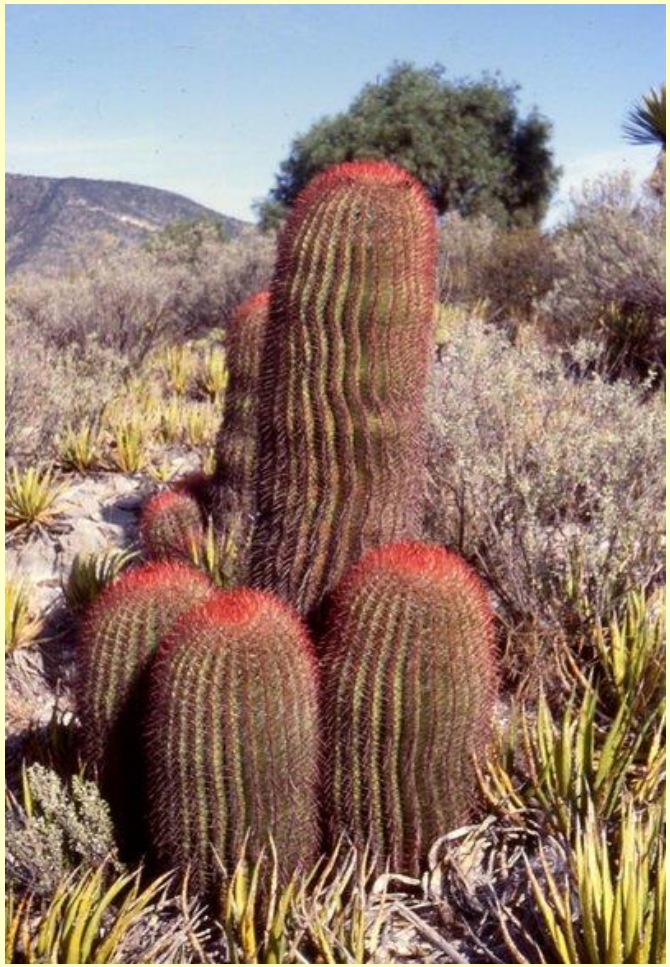


Jansen et al., Plant Physiol 1989

Stressor avoidance

Stress avoidance; tolerance based on mechanisms that prevent exposure of the cell content to stressors

Species have evolved mechanisms that can hasten, retard, or decrease the action of a stressor on cellular systems



Ferocactus-Mexico

Stressor avoidance; drought tolerance

Stressor avoidance; insulation

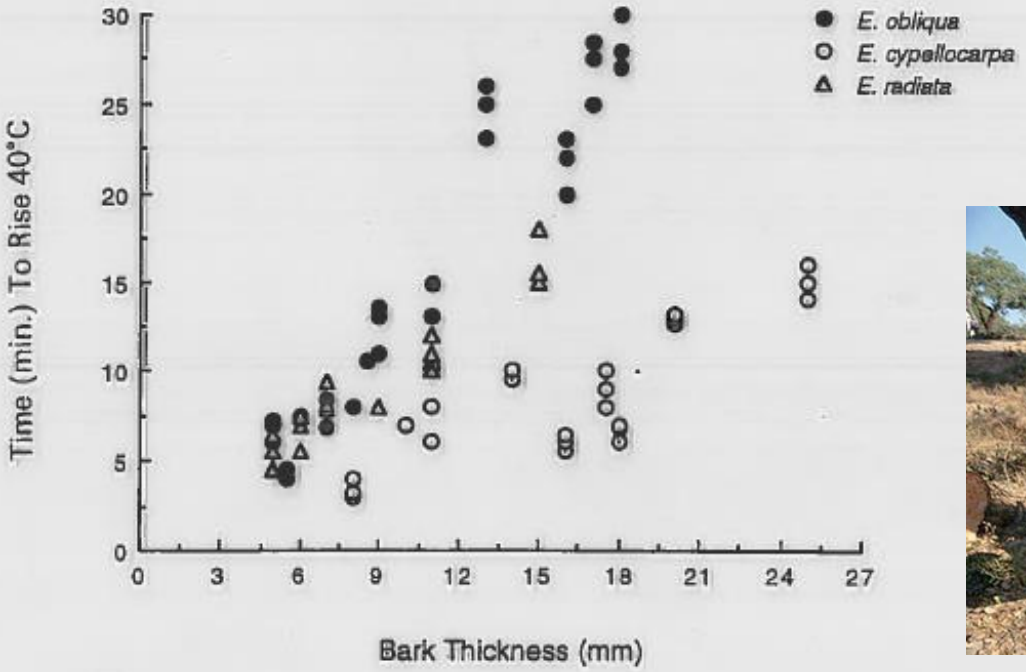
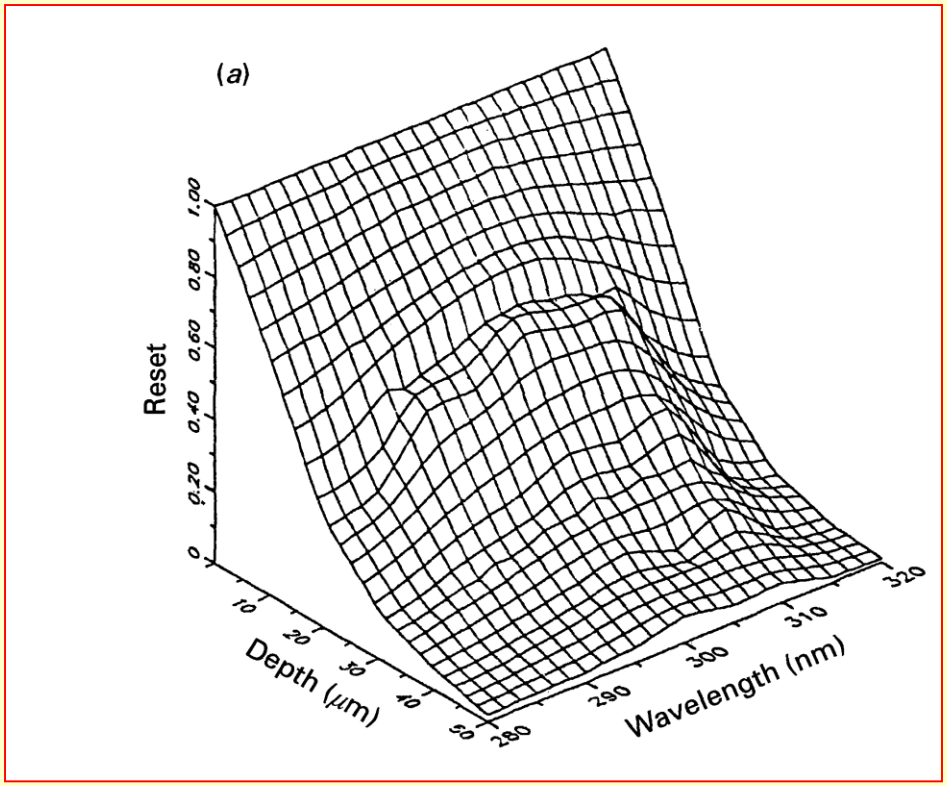


Figure 3.4 The influence of bark as an insulator of the cambium in Australian *Eucalyptus* species is essentially similar to that for the North American species (see Fig. 3.3): with thicker bark, the cambium takes longer to rise through 40 °C (data from Gill and Ashton 1968). However, the quantitative nature of the relationship varies among species. For a given bark thickness, *E. obliqua* (solid circles) takes longer to heat up than either *E. cypellocarpa* (open circles) or *E. radiata* (triangles).

Stressor avoidance; UV-screening

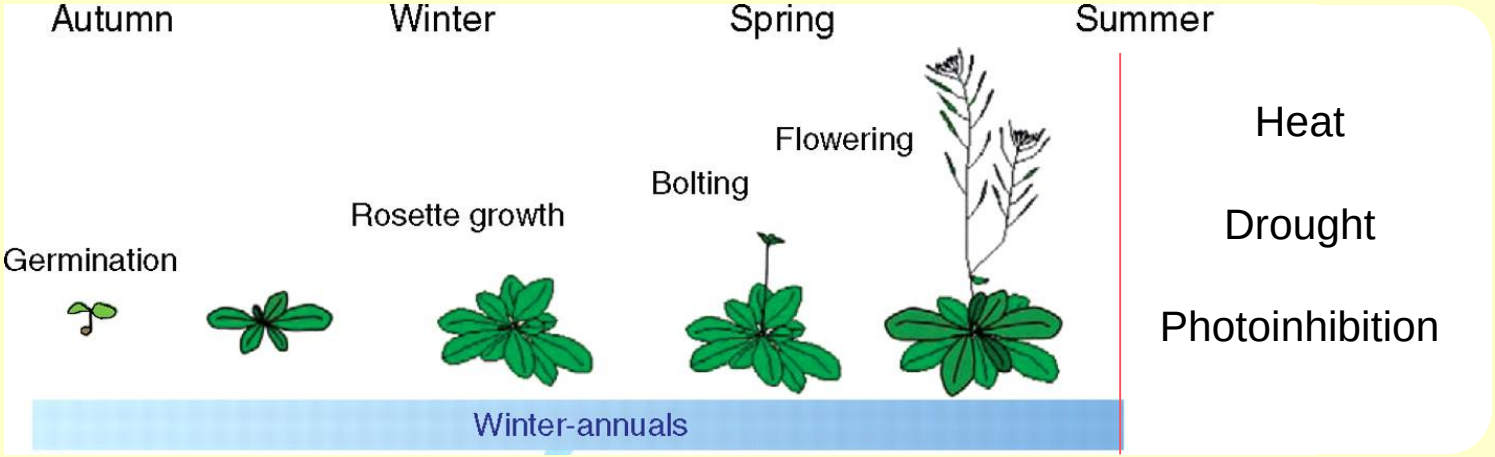


Alenius, Vogelmann & Bornman (1995), New Phytologist, 131, 297-302

Different plant species use different strategies to defend against the same stressor

Don’t search for avoidance tolerance in a species using stress escape!

Arabidopsis thaliana (winter type) as a stressor escaper



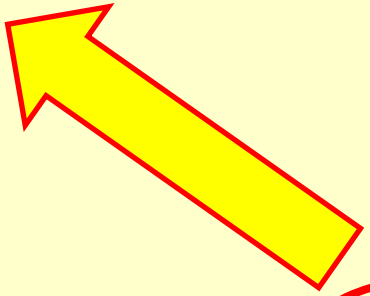
Shindo C et al. Ann Bot **2007;99:1043-1054**

What happens when a plant is exposed for the first time to a stressor?

Stress tolerance

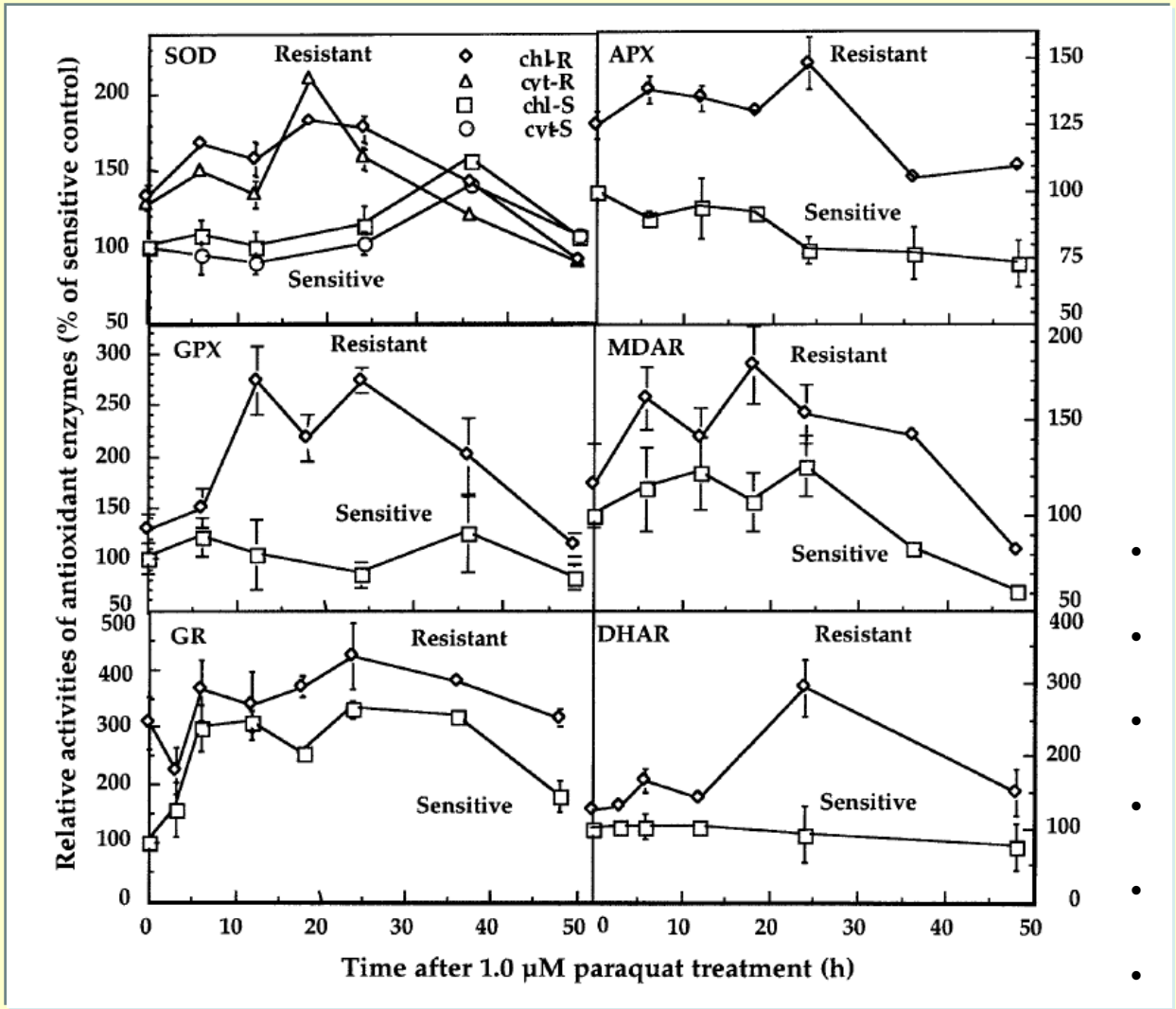
- Stress **acclimation** is a non-heritable / physiological / biochemical response leading to increased tolerance

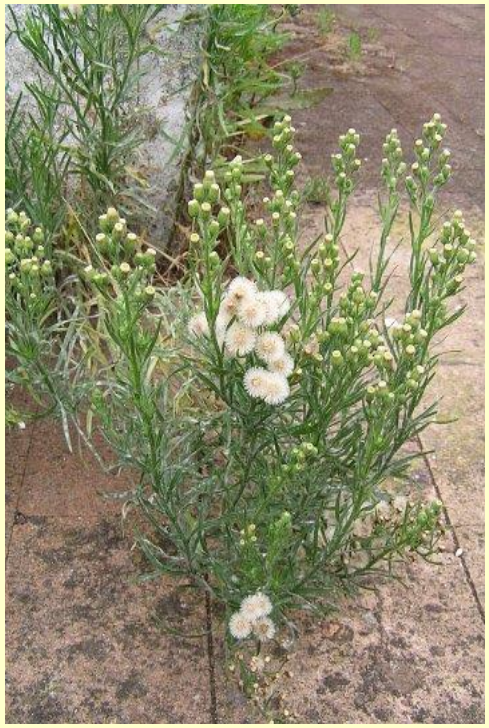
- Stress **adaptation** is an evolutionary / genetic process leading to increased tolerance



Term widely misused in literature

Stress acclimation is a dynamic process





- Superoxide dismutase
- Ascorbate peroxidase
- Glutathione peroxidase
- Monodehydroascorbate reductase
- Glutathione reductase
- Dehydroascorbate peroxidase

Ye and Gressel, Planta 2000

Integration plant stress responses

Acclimative responses can be comprised of multiple components, which vary with time

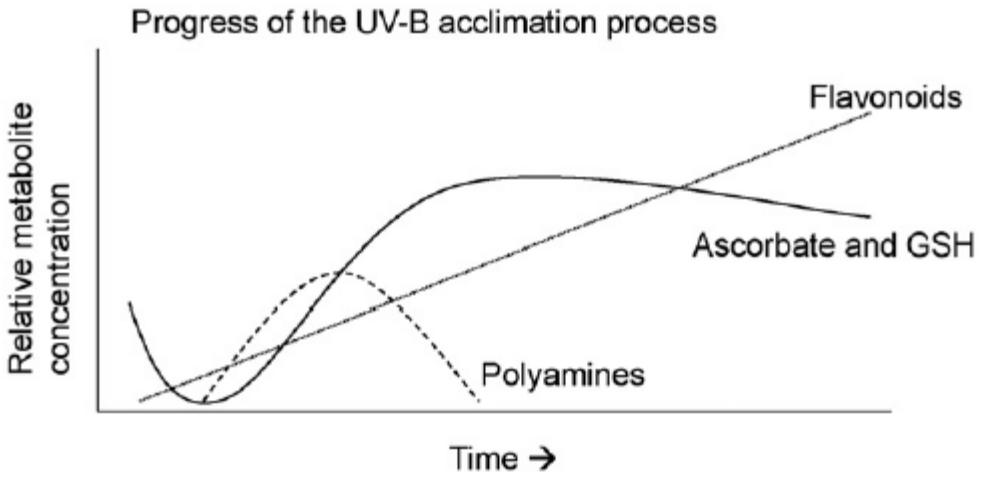
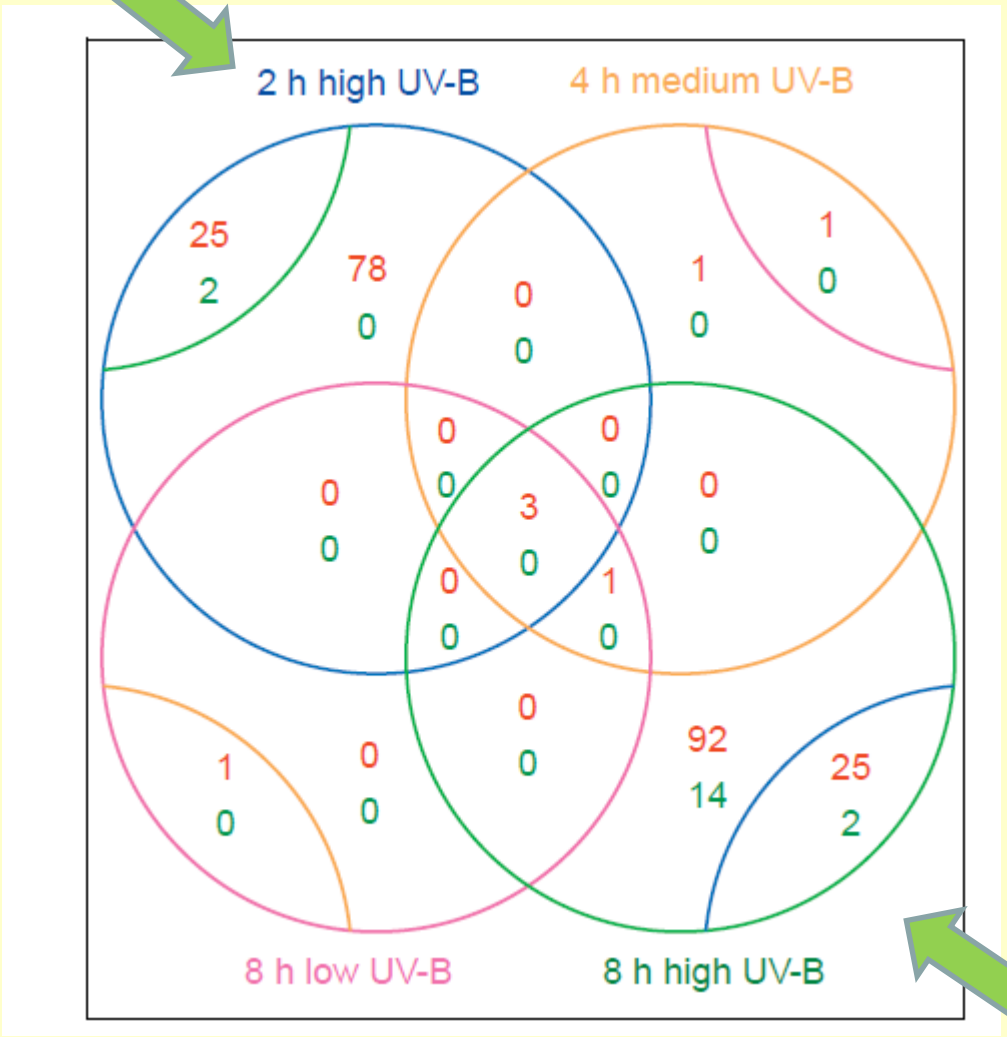


Fig. 2. Schematic model showing the changes in metabolite levels that occur in plants during the UV-B acclimation process. Levels of ascorbate and glutathione initially decrease during exposure to acute UV-B stress, with the extent of this decrease depending on the severity of the imposed oxidative stress (Table 1). Following an initial decrease, antioxidant levels increase in plants acclimated to chronic UV-B conditions. Polyamines transiently accumulate during early stages of the acclimation process (Table 2), whilst levels of flavonoids increase gradually during UV-B acclimation (Table 3).

Jansen et al., (2008) Plant Science

Dynamics of plant stress responses



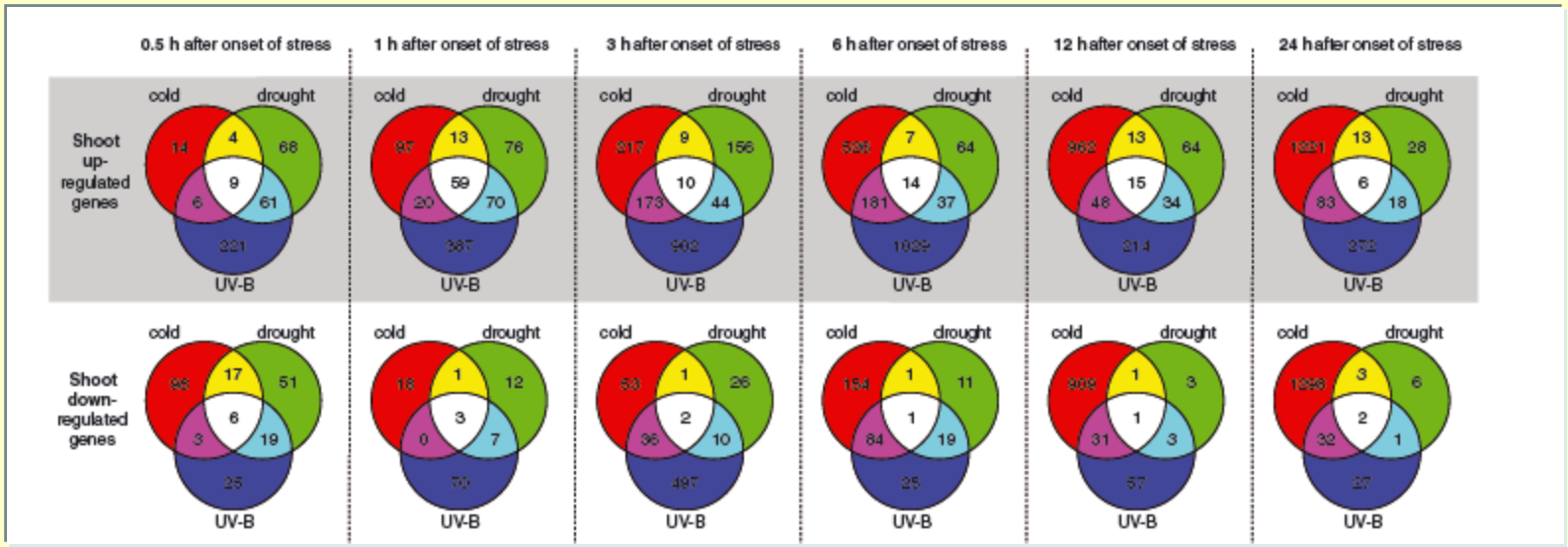
UV-induced gene-expression in maize

2 h high UV-B induces different changes in gene-expression than 4 h high UV-B

Dynamics of gene-expression

Casati and Walbot, 2004

Global gene-expression pattern Arabidopsis



1) Initially induction of a relative high number of generic genes

2) Subsequently, emphasis more on stressor specific genes

Kilian et al., The plant Journal 2007

Take home message!

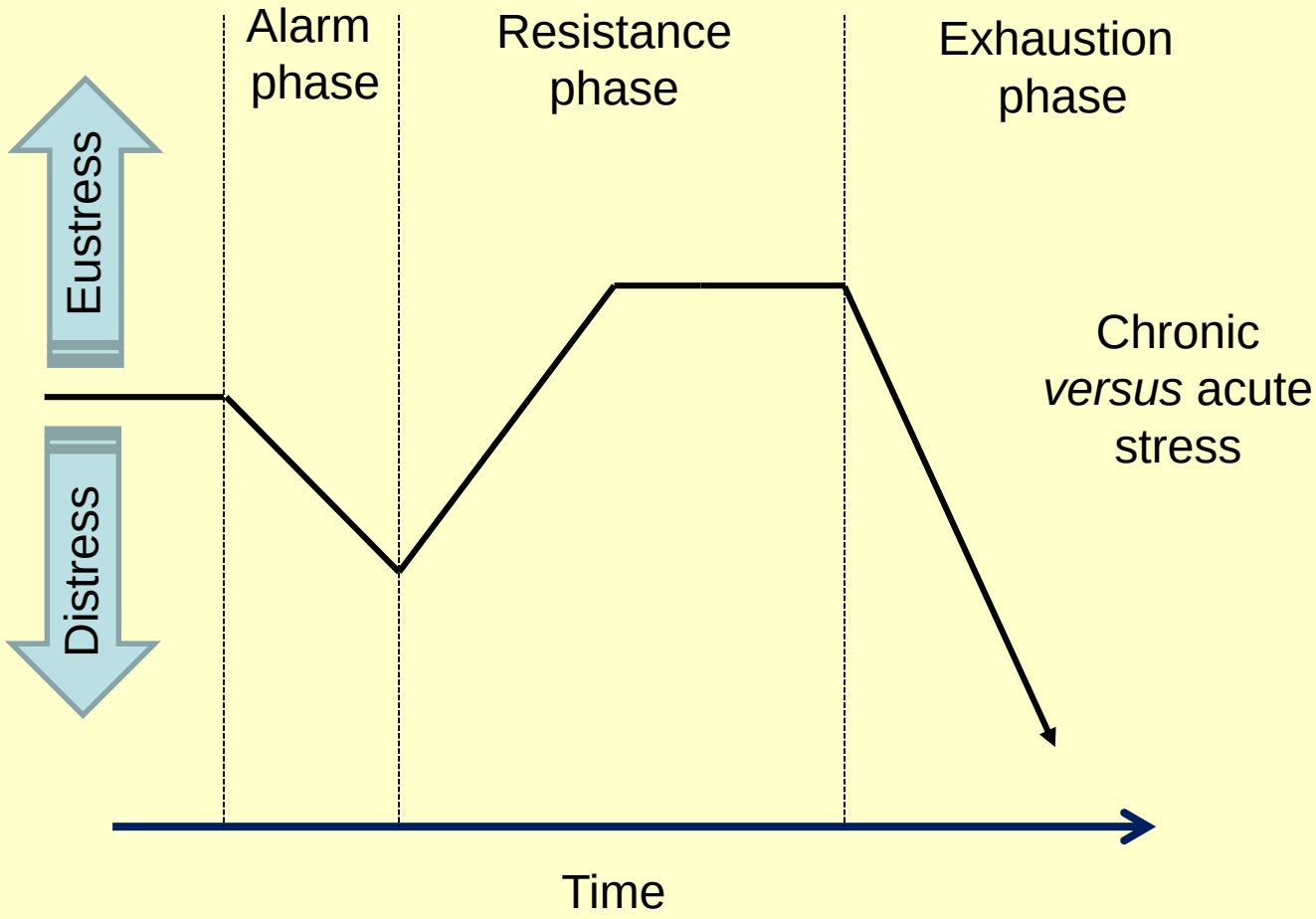
Response kinetics are **vital** to fully understand the complexity of plant stress biology

Different results can be obtained depending on whether plants have been

- primed,
- newly exposed to a stressor, or
- are already at a new steady state!

Careful calibration of stress conditions is necessary in order to be able to compare data between different laboratories

What happens when a plant is first exposed to a stressor?



Free after Selye

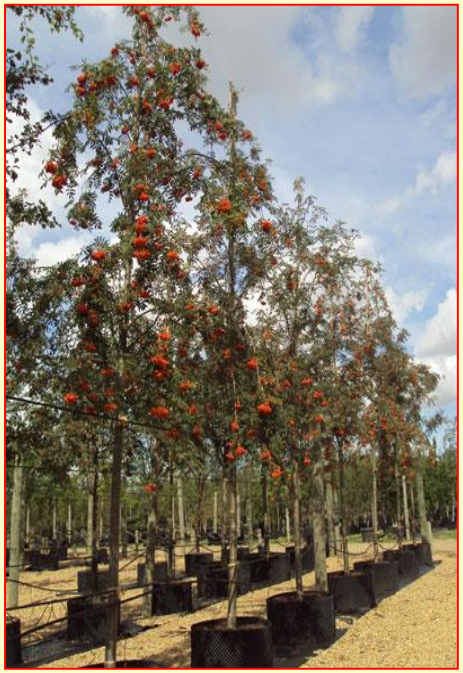
Acute versus chronic stress

Acute stress responses are <u>not a good model</u> for chronic stress responses

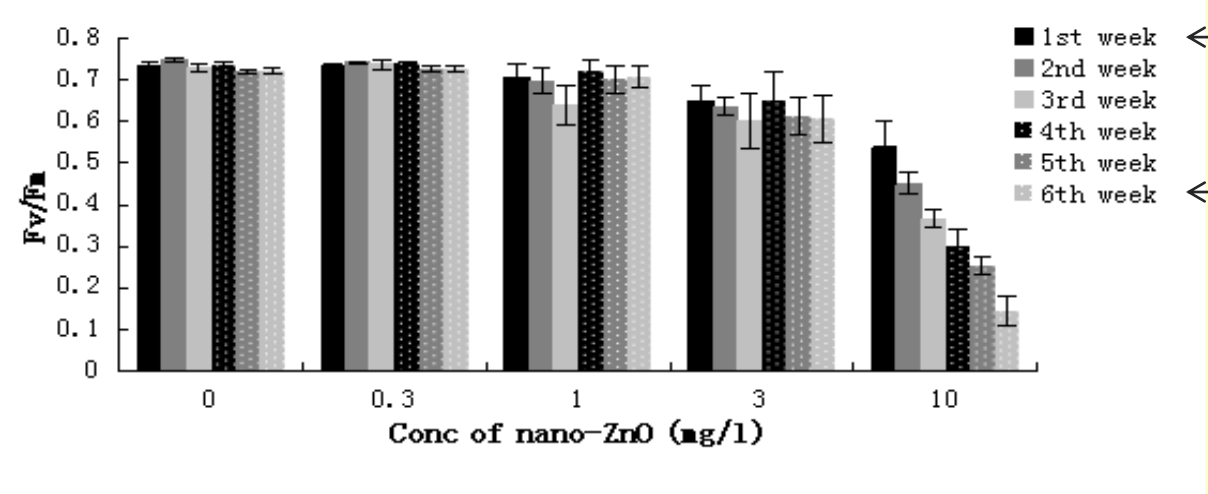
This Sorbus-trees will be exposed for 20-30 years

Silvermines Tipperary

These “laboratory” Sorbus-trees will be exposed for 1 or 2 years



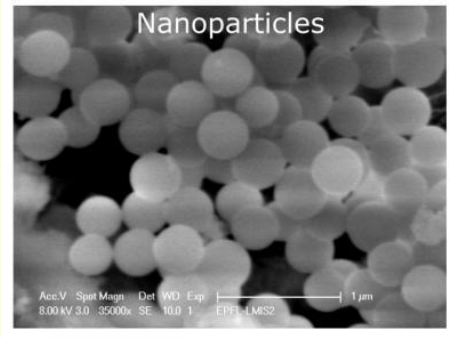
Growth rate of *Lemna minor,* exposed to nano-ZnO (0, 0.3, 1, 3, 10 mg/l)



"Acute"

"Chronic"

Chen and Jansen, 2014



Take home message!

(but you are still not going home ☺)

By selecting a specific time-point for analysis, a researcher pre-determines the outcome of a study!!!!!!!!!

Few molecular (micro-array), metabolic, or morphological studies of stress acclimation consider the dynamic character of the stress response

In conclusion:

- Abiotic plant stress is important
- We are not all speaking the same “stress-language” (concepts & terminology)
- The dose of a stressor does matter (eustress *versus* distres)
- Kinetics do matter (Selye; alarm, resistance & exhaustion phase)
- Different strategies for dealing with stress (escape, avoidance and true tolerance)
- Stress responses are complex (specific and non-specific components), but not enough is known about integration

The end!