

**EPIgenetic mechanisms of Crop Adaptation To Climate cHange**

Training School - 28<sup>th</sup>-30<sup>th</sup> June 2021

**Plant Epigenetics: Basics, Applications and Methodologies**

**Sophie Brunel-Muguet, INRAE**



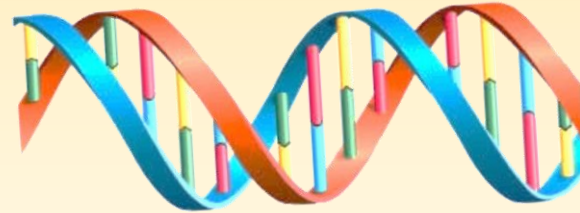
**Crop acclimation to global warming:  
a three-fold lever of action based on agricultural practices,  
genetic improvement and ecophysiological approaches**



- **Introduction: The food security challenge in the context of global warming**
- **Strategies for crop adaptation to global warming**



**Agricultural practices**

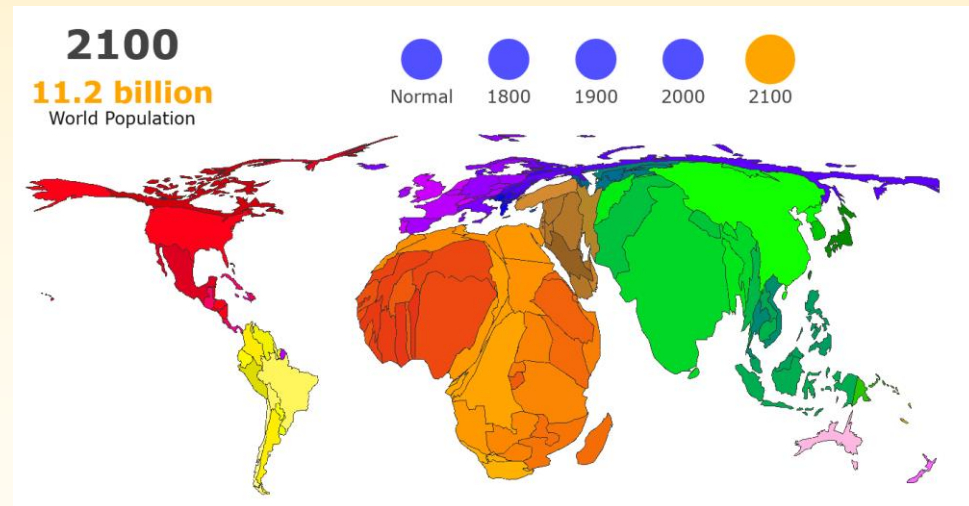
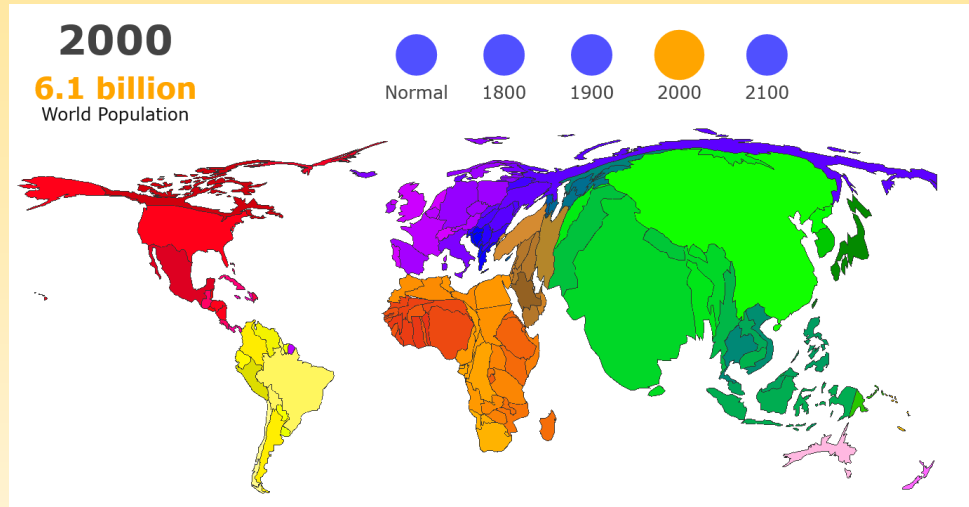


**Crop Genetic Improvement**



**Stress memory  
And priming**

# Expanding human population +2.4 billion people by 2050



<http://metrocosm.com/world-population-history-map/>

# Amongst the 17 sustainable development goals: « No Hunger Zone »



“Agricultural production needs to increase by 70% worldwide, and by almost 100% in developing countries, in order to meet growing food demand”

Tutwiler, 2011 (FAO's Deputy Director-General)



**Expanding human population  
+2.4 billion people by 2050**



**Climate Change**

Higher temperatures, evapotranspiration,  
higher GHG, fluctuating precipitations

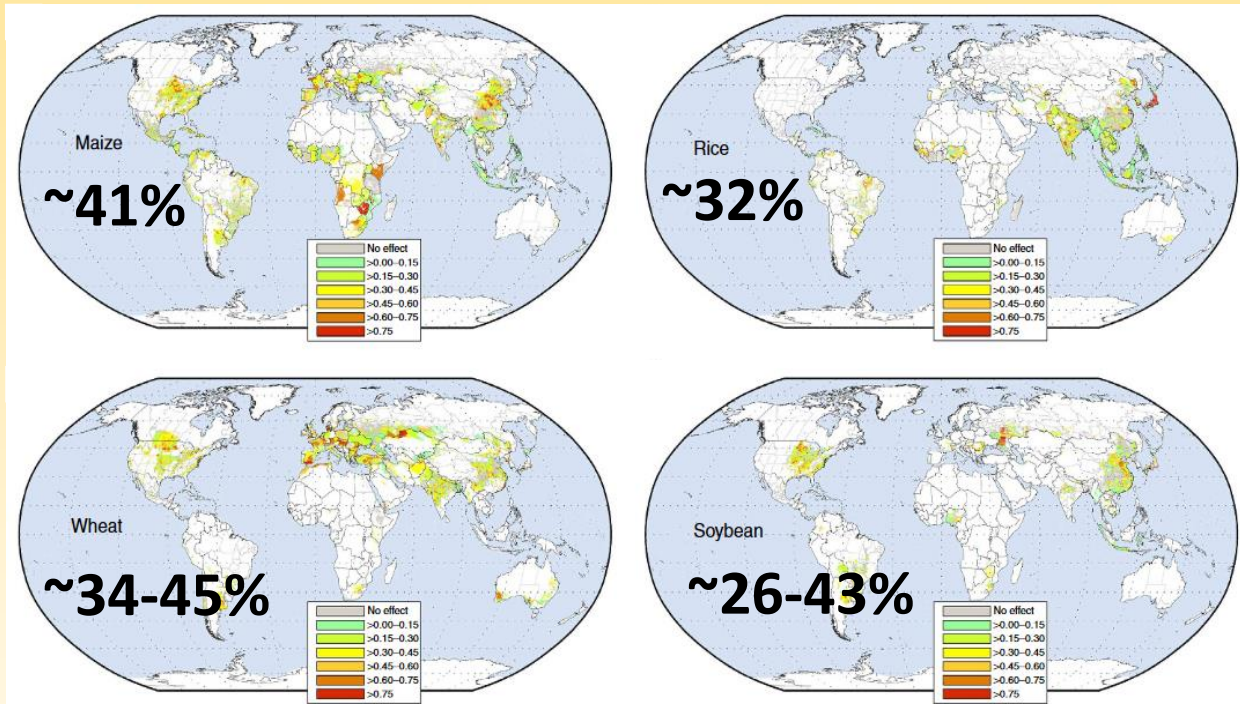
**Food security challenge  
in terms of quantity and quality**

**Degradation**  
**Deforestation**  
prices increase inputs  
**water** increase  
Depeletion agricultural **Soil** quality energy  
**Erosion**  
**resources**

According to the United Nations Framework Convention on Climate Change, **about 14 milliards US\$ will be required annually by 2030** to face adverse effects of **climate change** on **agriculture, forestry and fisheries** sectors (Rötter et al 2011) and other studies point out 2 to 3 times higher estimates.

# Climate variations cause yield and crop quality variability- past observations

Total crop yield variability explained due to climate variability over the last 3 decades.



Ray et al. 2015

Simple measures of growing season temperatures and precipitation (spatial averages based on the locations of each crop) explain **~30% or more of year-to-year variations in global average yields**

**nature**  
COMMUNICATIONS

ARTICLE

Received 1 Sep 2014 | Accepted 28 Nov 2014 | Published 22 Jan 2015

DOI: [10.1038/ncomms6989](https://doi.org/10.1038/ncomms6989) OPEN

## Climate variation explains a third of global crop yield variability

Deepak K. Ray<sup>1</sup>, James S. Gerber<sup>1</sup>, Graham K. MacDonald<sup>1</sup> & Paul C. West<sup>1</sup>

IOP PUBLISHING ENVIRONMENTAL RESEARCH LETTERS

Environ. Res. Lett. 2 (2007) 014002 (7pp) [doi:10.1088/1748-9326/2/1/014002](https://doi.org/10.1088/1748-9326/2/1/014002)

## Global scale climate–crop yield relationships and the impacts of recent warming

David B Lobell<sup>1</sup> and Christopher B Field<sup>2</sup>

# Impacts of heat stress – past observations

**Table 1.** Yield losses due to heat stress in cool and warm season crops

Species	Threshold temperatures for the species <sup>a</sup>	World production in 2017 <sup>b</sup> (kg ha <sup>-1</sup> )	Average yield reduction (%)	Reference
<b>Cool-season crops</b>				
Barley ( <i>Hordeum vulgare</i> L.)	Not reported	3136	15	Weichert <i>et al.</i> (2017)
Chick pea ( <i>Cicer arietinum</i> L.)	15–30 °C for growth, 25 °C for reproductive growth	1015	19–50	Devasirvatham and Tan (2018)
Citrus ( <i>Citrus</i> spp.)	35 °C for vegetative growth	9600	N/A	N/A
Lentils ( <i>Lens culinaris</i> Medik.)	Not reported	1153	38–58	Sita <i>et al.</i> (2018)
Spinach ( <i>Spinacia oleracea</i> L.)	Not reported	29 993	50	Yan <i>et al.</i> (2016)
Wheat ( <i>Triticum</i> spp.)	20–30 °C for vegetative growth, 15 °C for reproductive growth	3531	6	Lobell <i>et al.</i> (2011); Zampieri <i>et al.</i> (2017); Comastri <i>et al.</i> (2018)
<b>Warm-season crops</b>				
Grapes ( <i>Vitis vinifera</i> L.)	Not reported	10 716	35–50	Greer and Weedon (2013)
Maize ( <i>Zea mays</i> L.)	33–38 °C for photosynthesis and pollen viability	5755	7–40	Valdés-López <i>et al.</i> (2016); Zhao <i>et al.</i> (2017); Meseka <i>et al.</i> (2018); Prasad <i>et al.</i> (2018)
Peanut ( <i>Arachis hypogaea</i> L.)	29–33 °C for vegetative growth, 39–40 °C for seed set and yield	1686	6	Prasad <i>et al.</i> (2001)
Potato ( <i>Solanum tuberosum</i> L.)	Not reported	20 111	18–23	Hancock <i>et al.</i> (2014)
Rapeseed ( <i>Brassica napus</i> L.)	About 30 °C for flowering	2195	Up to 85%	Koscielny <i>et al.</i> (2018); Sparks (2018)
Rice ( <i>Oryza sativa</i> L.)	33 °C for biomass, 35 °C limiting for grain formation and yield	4602	3	Zhao <i>et al.</i> (2017)
Sorghum [ <i>Sorghum bicolor</i> (L.) Moench]	26–34 °C for vegetative growth, 40 °C for reproductive growth and yield	1416	17–44	Tack <i>et al.</i> (2017)
Soybean [ <i>Glycine max</i> (L.) Merr.]	26–36 °C for reproductive development, 39 °C lethal	2854	3–7	Valdés-López <i>et al.</i> , 2016; Zhao <i>et al.</i> (2017)
Sunflower ( <i>Helianthus annuus</i> L.)	Not reported	1804	10–70	Debaeke <i>et al.</i> (2017)
Tomato ( <i>Solanum lycopersicum</i> L.)	37 °C for vegetative growth, 28–30 °C for reproductive development	37 600	28	Snider <i>et al.</i> (2012); Lamaoui <i>et al.</i> (2018)

<sup>a</sup> Data from Luo (2011) and Kaushal *et al.* (2016).

<sup>b</sup> Data obtained by world production and world cultivated extension for each crop, from FAOSTAT 2017, <http://www.fao.org/faostat/en/#data/QC/visualize>.

From Janni *et al.* 2020

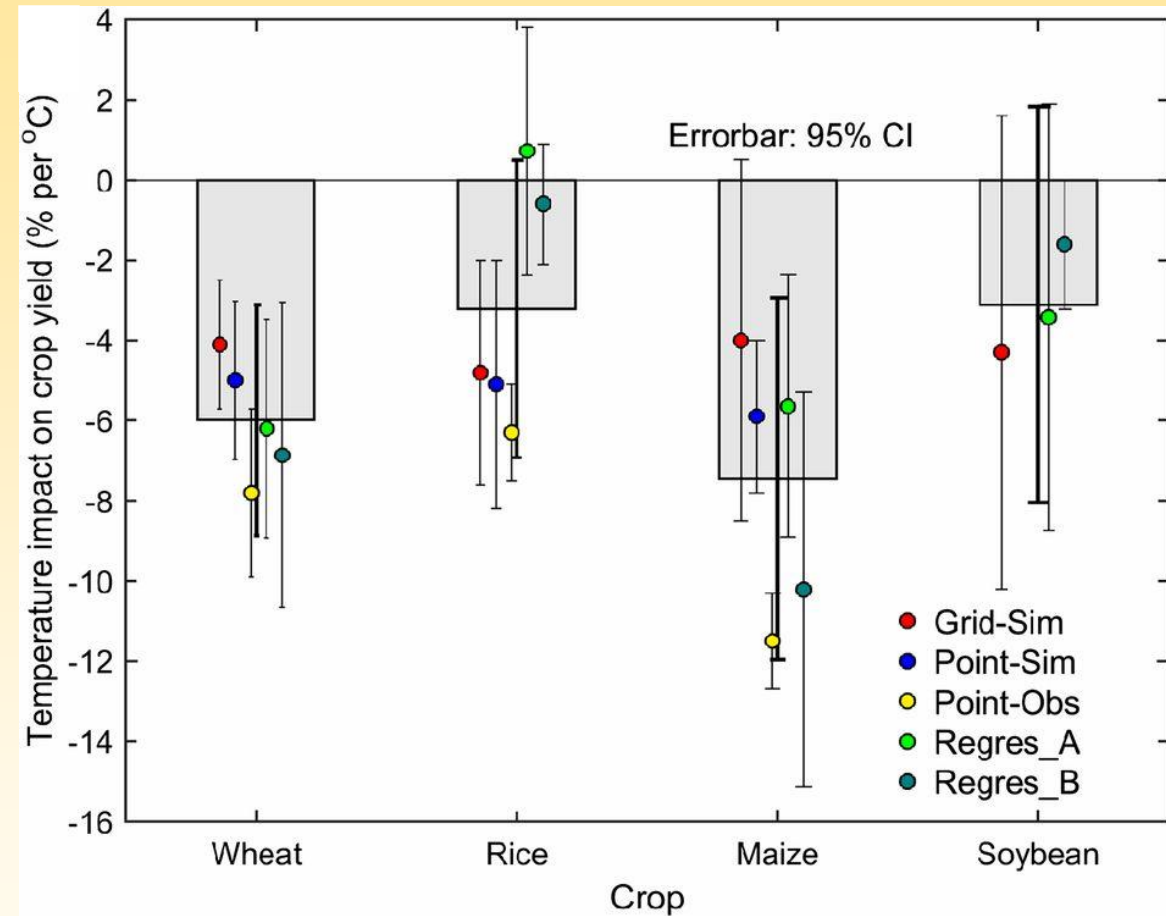
# Expected impacts of temperature increase projections on yield of major crops

Multimethod estimates of global crop yield changes in response to temperature increase.

Scenario	Yield changes (%) due to temperature changes by the end of century				
	Wheat	Rice	Maize	Soybean	Mean
RCP2.6	-6.9 [-15.0, -1.4]	-3.3 [-9.2, 0.8]	-8.6 [-18.6, -1.8]	-3.6 [-11.2, 1.7]	-5.6 [-14.4, -0.1]
RCP4.5	-11.4 [-21.7, -3.9]	-5.5 [-13.8, 1.0]	-14.2 [-27.9, -4.9]	-5.9 [-17.0, 3.1]	-9.2 [-21.2, -0.3]
RCP6.0	-14.0 [-25.7, -5.1]	-6.8 [-16.8, 1.3]	-17.4 [-33.1, -5.8]	-7.2 [-20.2, 3.6]	-11.3 [-25.6, 0.1]
RCP8.5	<b>-22.4</b> [-40.2, -8.5]	<b>-10.8</b> [-25.3, 2.4]	<b>-27.8</b> [-50.4, -9.7]	-11.6 [-31.0, 6.0]	-18.2 [-38.6, -0.7]

RCP8.5 -> -18.2% in average

Even under the less drastic scenario (RCP2.6) -> -5.6%



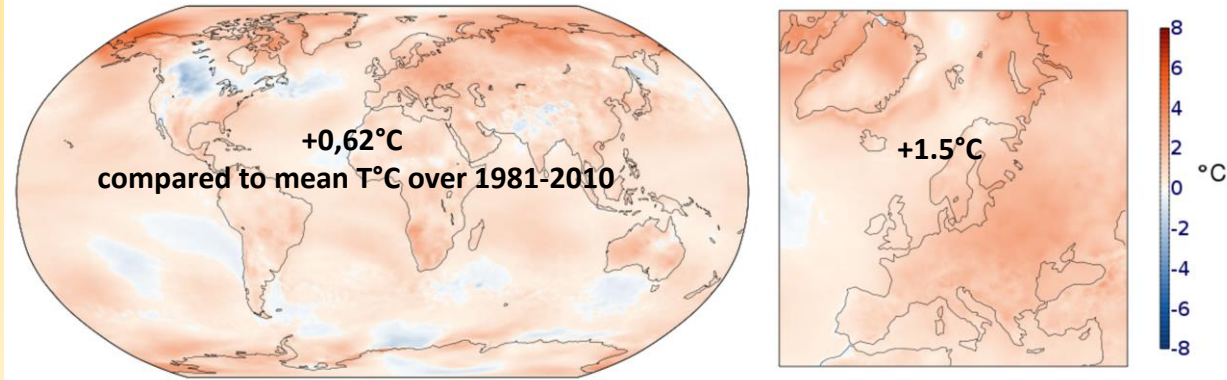
Maize: more impacted crop per unit of degree increase



# Climate projections...more frequent heat waves

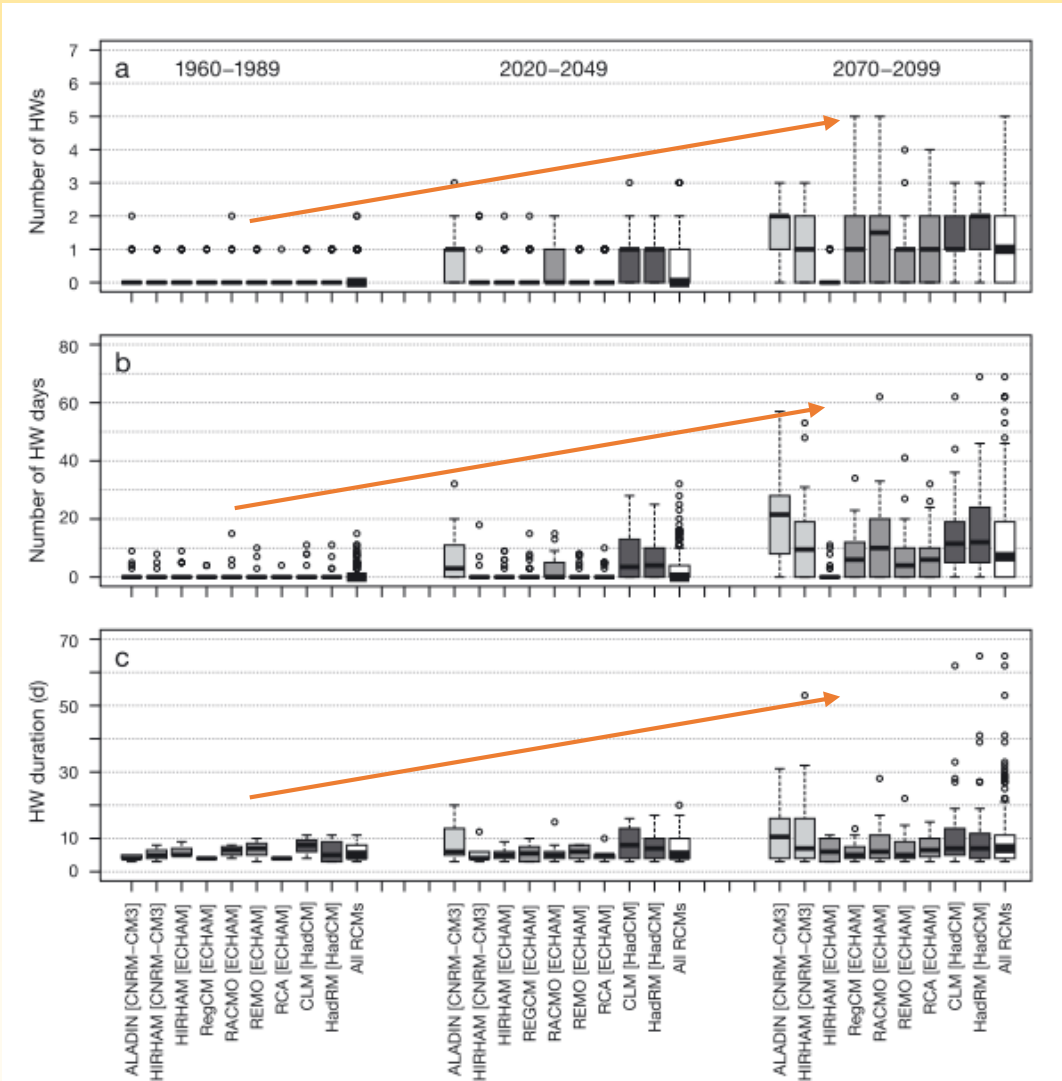
## Frequency of heat waves under several scenarii Lemonsu *et al.* 2014

Surface air temperature anomaly for February 2019 to January 2020 relative to 1981-2010



Surface air temperature anomaly for February 2019 to January 2020 relative to the average for 1981-2010. Data source: ERA5. Credit: Copernicus Climate Change Service/ECMWF.

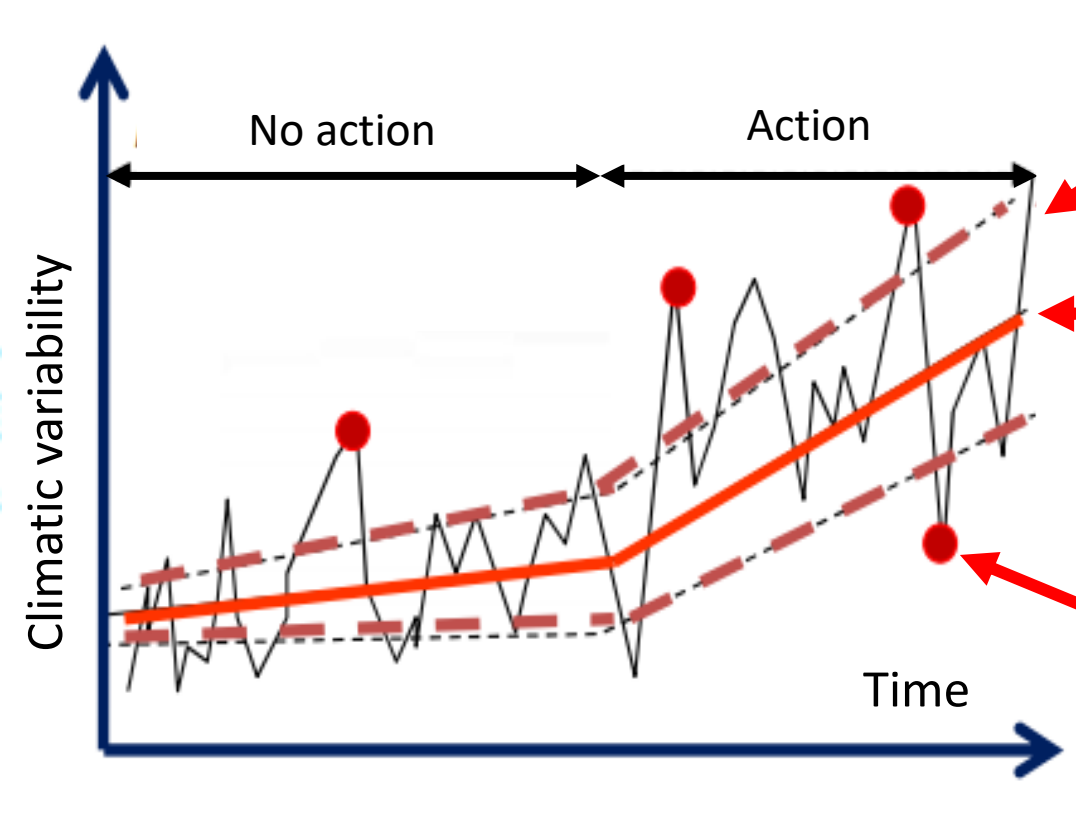
Vol. 61: 75–91, 2014 doi: 10.3354/cr01235	CLIMATE RESEARCH Clim Res	Published September 2
<b>FREE ACCESS</b>		
<b>Evolution of heat wave occurrence over the Paris basin (France) in the 21st century</b>		
Aude Lemonsu*, Anne Lise Beaulant, Samuel Somot, Valéry Masson		



- + Number
- + Individual length
- + Sum of lengths



# Challenge to face the features of global warming



**Interannual variability**

→ Ability of species to trigger adequate stress responses and adjust phenology

**Trend**

→ Adaptation to warmer environment

**Extreme event**

→ Adaptation to repeated stress supported by stress memory

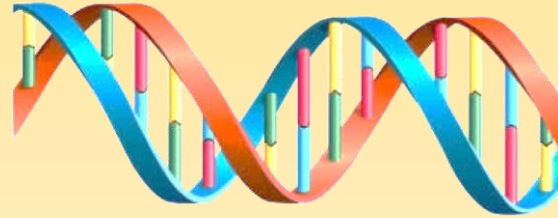
From: P. Bertuzzi, AgroClim, INRAE

**What are the strategies geared towards buffering future crop production from global warming?**

# What are the levers of action for crop adaptation to high temperature stresses?

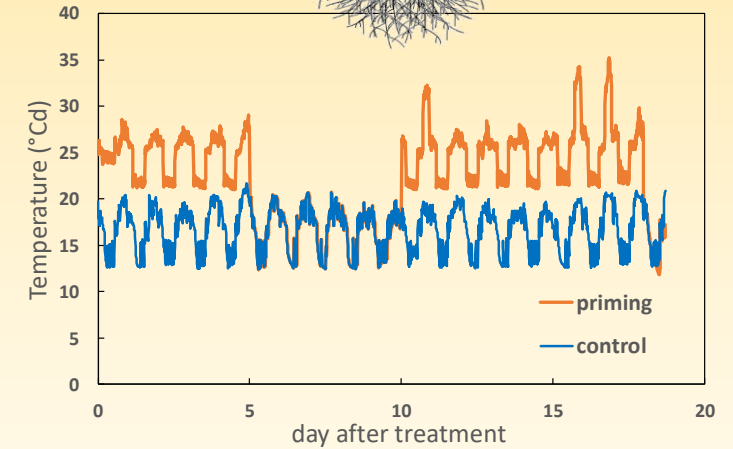
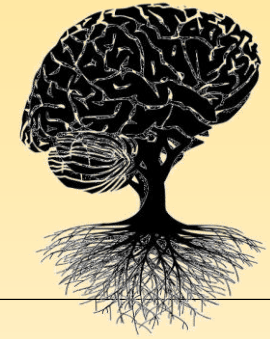


**Agricultural practices**



Nature Review Genetics, 2015

**Crop Genetic Improvement**



**Stress memory  
And priming**



## Agricultural practices

## In the context of global warming

SYSTEM LEVEL

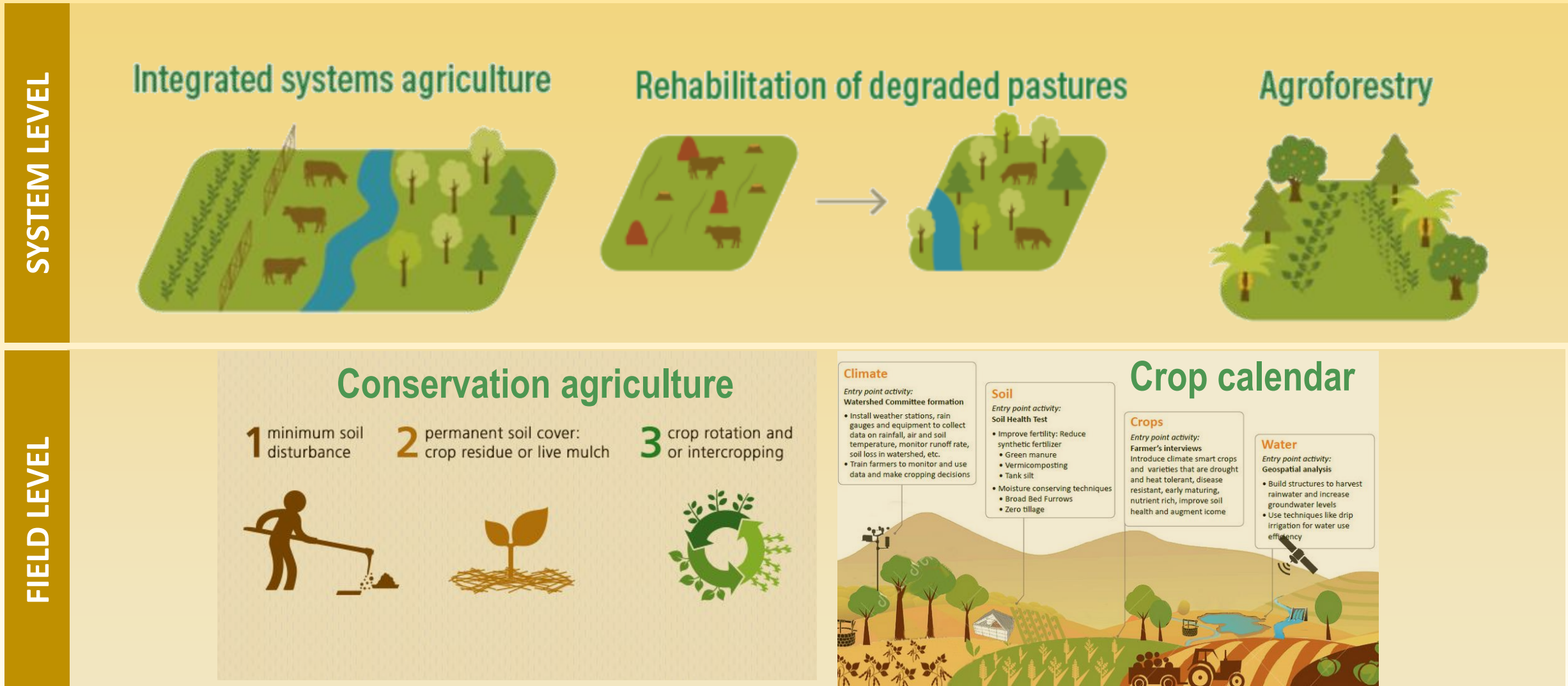
FIELD LEVEL

1. Making agriculture more resilient to climate change
2. Moving location to follow environmental change
3. Adopting protected agriculture

**What are the agricultural practices to target in terms of cropping systems and technical practices ?**



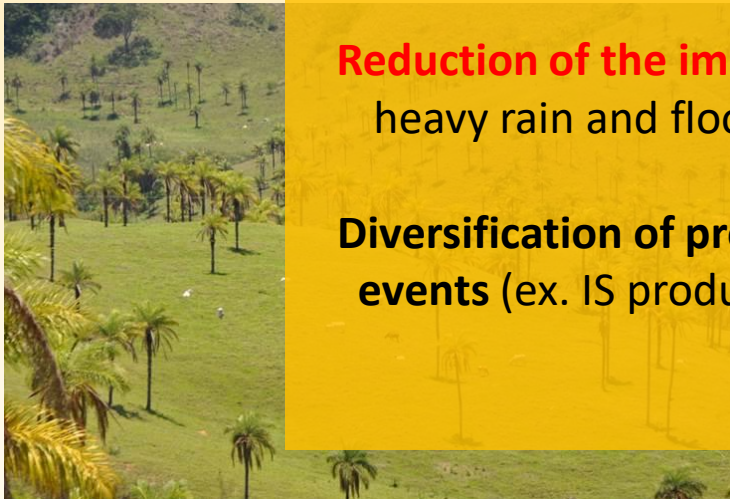
# 1. Making agriculture more resilient to climate change



# 1. Making agriculture more resilient to climate change

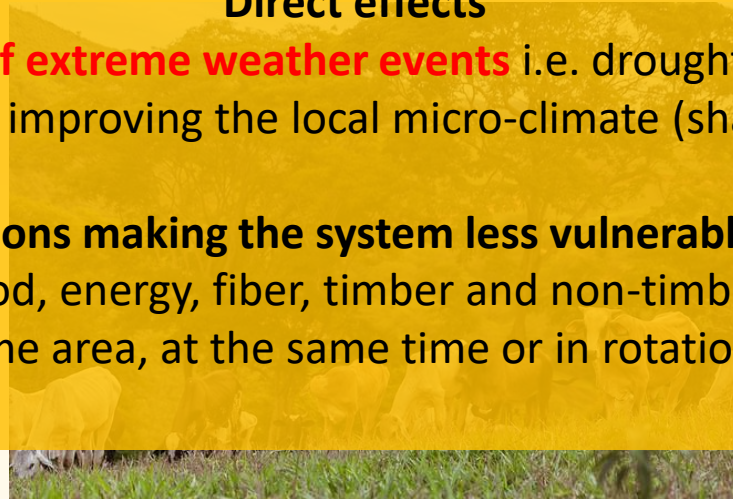
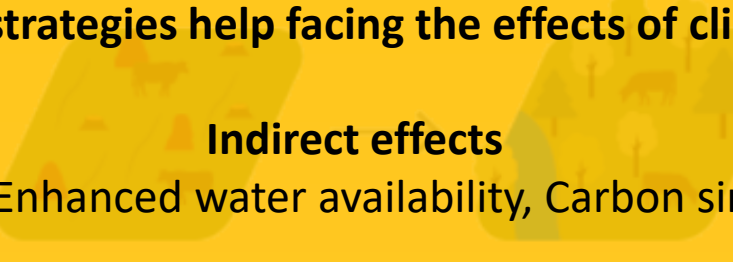
## SYSTEM LEVEL

### Integrated systems agriculture



Integrating pastures with forestry in Brazil

### Rehabilitation of degraded pastures



A farm where the pasture was rehabilitated by Fazenda Ecologica using rotation and trees in the Minas Gerais countryside. Photo by D. Hunter/WRI Brasil

### Agroforestry



Cocoa plants can grow better and be even more resilient under the shade of other trees.

How do these strategies help facing the effects of climate change?

#### Indirect effects

Reduction of soil erosion, Enhanced water availability, Carbon sink, Increased biodiversity

#### Direct effects

**Reduction of the impact of extreme weather events** i.e. drought, heatwaves, cold waves, heavy rain and floods by improving the local micro-climate (shading, downwind edge)

**Diversification of productions making the system less vulnerable to fluctuating stressing events** (ex. IS produce food, energy, fiber, timber and non-timber forest products in the same area, at the same time or in rotation)

<https://www.worldcocoafoundation.org>

<https://www.wri.org/insights/4-ways-farmers-can-adapt-climate-change-and-generate-income>



# 1. Making agriculture more resilient to climate change within the current footprint

## FIELD LEVEL

### Conservation agriculture

- 1 minimum soil disturbance
- 2 permanent soil cover: crop residue or live mulch
- 3 crop rotation and or intercropping



<http://www.fao.org>

**Reduction of evapotranspiration,**

**Reduction of soil erosion,**

**Improvement of water use efficiency and soil fertility**

**-> direct effects of crop adaptation to warming environment**

### Managing agricultural calendar

#### Climate

*Entry point activity:*

**Watershed Committee formation**

- Install weather stations, rain gauges and equipment to collect data on rainfall, air and soil temperature, monitor runoff rate, soil loss in watershed, etc.
- Train farmers to monitor and use data and make cropping decisions

#### Soil

*Entry point activity:*  
**Soil Health Test**

- Improve fertility: Reduce synthetic fertilizer
  - Green manure
  - Vermicomposting
  - Tank silt
- Moisture conserving techniques
  - Broad Bed Furrows
  - Zero tillage

#### Crops

*Entry point activity:*

**Farmer's interviews**

Introduce climate smart crops and varieties that are drought and heat tolerant, disease resistant, early maturing, nutrient rich, improve soil health and augment income

#### Water

*Entry point activity:*  
**Geospatial analysis**

- Build structures to harvest rainwater and increase groundwater levels
- Use techniques like drip irrigation for water use efficiency



<http://www.icrisat.org/Building-climate-smart-farming-communities>

**Adjustments of sowing, planting, harvest, grazing period in relation to soil moisture content, risks of frost events during spring, risks of heat stress over the seed filling period...**



## 2. Moving location to follow environmental change

Relocation of crops to new areas to keep within the current environmental ranges of the current production system is an option but new requirements to adapt to specific feature of the new area (local pests and diseases)

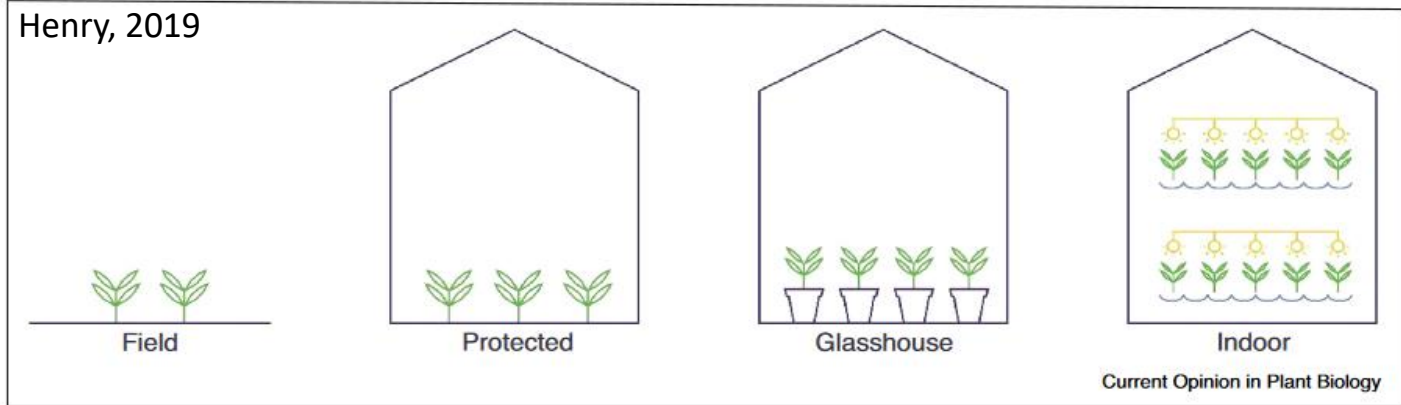
**These options are avoidance strategies as they aim at creating or finding again heat stress-free environments**

Example: Relocation of rice, cotton, vegetables production in Australia, traditionally produced with irrigation in southern areas -> water scarcity -> relocation in northern rain fed areas? (Mushtak et al. 2014, Henry et al. 2019)

## 3. Adopting protected agriculture by partial or completely controlling the environment

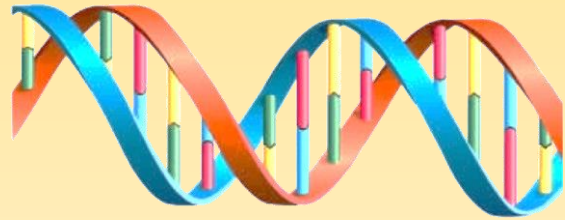
-> trade off between investment in transferring crops into protected systems and financial losses if crops remain growing in the disturbed environment

Henry, 2019



<https://www.bloomberg.com/news/articles/2021-01-16>

Vertical system for high values crops (vegetable and horticultural productions)



#### PERSPECTIVES

##### SCIENCE AND SOCIETY

Protecting crop genetic diversity for food security: political, ethical and technical challenges

*José Esquinas-Alcázar*

Nature Review Genetics, 2015

## Crop Genetic Improvement

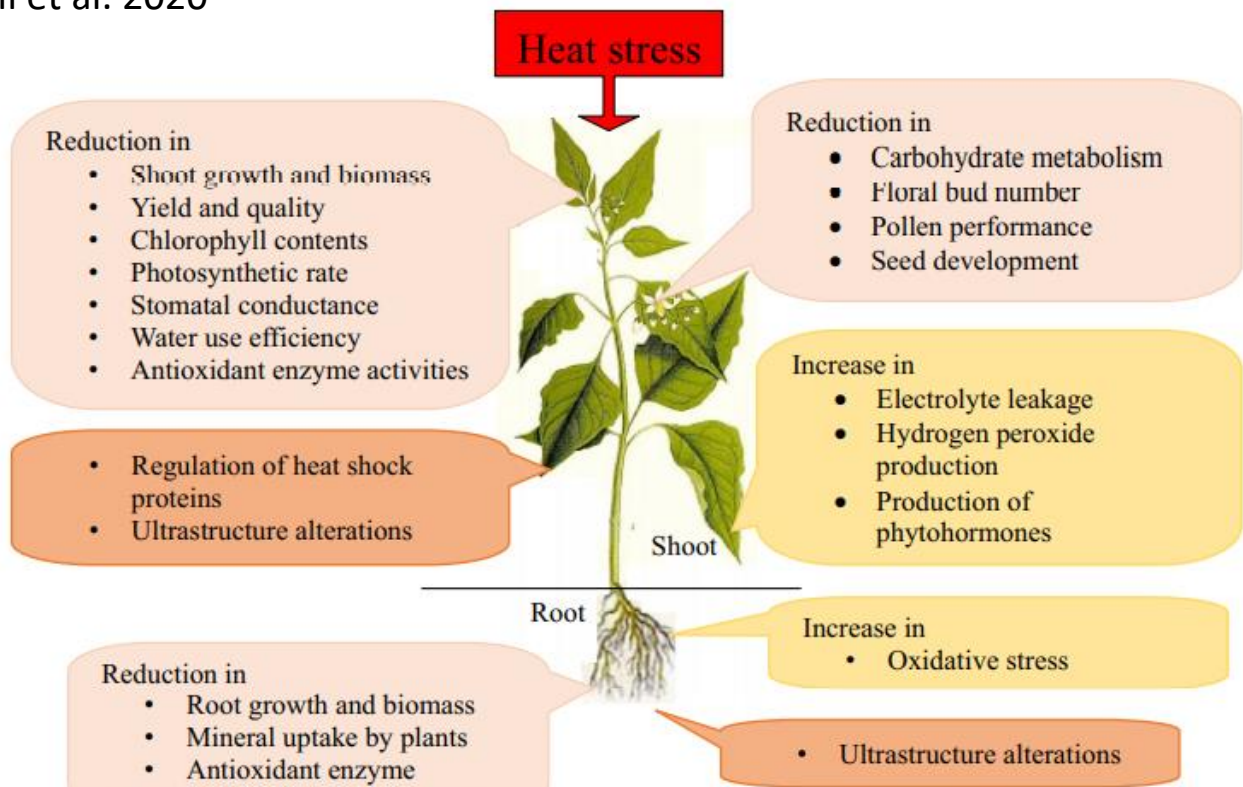
# Crop Genetic Improvement

*The science of applying genetic and plant breeding principles and biotechnology to improve plants (Univ. Illinois)*

Crop breeding for heat stress tolerance requires a deep understanding of the **metabolic, physiological and developmental processes** which impairment affects the ability of plants to cope with heat stress (HS).

## What are the main effects of HS on plant metabolism, physiology and development?

Ali et al. 2020



Wahid et al. 2007, Prasad et al. 2017, Valdés-Lopez et al. 2016, Seghal et al. 2017, Cho et al. 2018

### Molecular level:

**HS-responsive genes** are involved in primary and secondary metabolism, regulation of processes such as  $\text{Ca}^{2+}$ , phytohormone, lipid and sugar signaling or protein modifications (Jha et al. 2014)

### HS responses involve HSFs and HSPs

HSFs regulate the transcription of HSP genes while HSPs act as molecular chaperones to prevent the misfolding and denaturation of other proteins and help stabilize them under HS (Serrano et al. 2019)

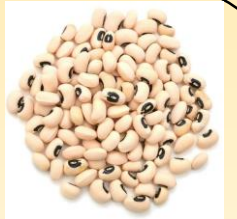


## What are the desired characteristics for heat tolerant varieties?

- Higher photosynthetic rates (e.g. stay green leaves)
- Enhanced membrane thermostability (which interferes with cell signaling, and molecular transport)
- Stable pod set or grain production...

### Examples of selected traits target for HS tolerance

**In Cowpea:** selection for abundant flower production, greater pod set (Ehlers et al. 2000)



**In Wheat:** selection for traits involved in **light interception, radiation use efficiency, partitioning of assimilates** (Cossani and Reynolds, 2012)



**In Maize:** selection for traits associated with **reproductive success** (anthesis-silking interval, pollen viability, stigma receptivity...) and **other morpho-physiological traits** (senescence, chlorophyll content) (Alam et al. 2017)



# Genetic diversity is required for crop genetic improvement

The pre-requisite for breeding for heat tolerance is to **identify/create genotypic variability** on traits involved in HS

**This genotypic variability** can be **naturally found** or **artificially created**

Natural  
genetic  
variability

Diversity found in agricultural species: domesticated gene pools and in gene banks

Close relatives of domesticated species  
“Crop Wild Relatives”

Artificial  
genetic  
variability

Mutations by chemical, radiation

# Expanding the gene pool for crop HS tolerance based on naturally occurring genetic diversity

Natural genetic  
variability

Diversity found in agricultural  
species: domesticated gene  
pools and in gene banks



Close relatives of  
domesticated species  
“Crop Wild Relatives”

Prior breeding programs have resulted in **genetic erosion**.  
Barely more than 150 species are now cultivated.  
(Esquinas-Alcázar, 2005)

**Traditional farmers’ varieties have provided many individual traits that have been introduced into existing, improved breeding lines**

**Example of a primitive Japanese dwarf wheat variety**, which had a key role in the genetic improvement of wheat during the ‘Green Revolution’. It was used as a donor of the genes that are responsible for dwarfism, which allow increased nitrogen uptake (Esquinas-Alcázar, 2005)



**Wild forms of Beta collected as a source of resistance to rhizomania.** It was found that the collections also show Erwinia root-rot resistance, sugar-beet root maggot tolerance, and moderate leaf-spot resistance (Esquinas-Alcázar, 2005)

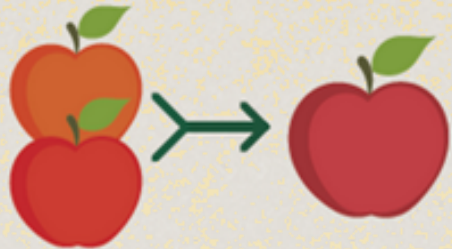


# Breeding approaches for heat tolerance

The screening and incorporation of the genetic variability into new cultivars can be done using different approaches (Janni et al. 2020):

## Conventional breeding

### Traditional Crossbreeding



Based on phenology and/ or SAM

## New Breeding Techniques

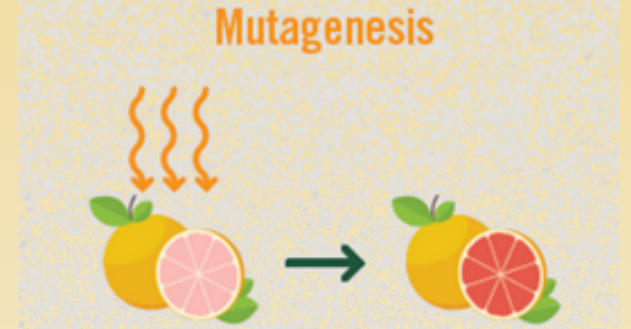
### Gene Editing



GMO

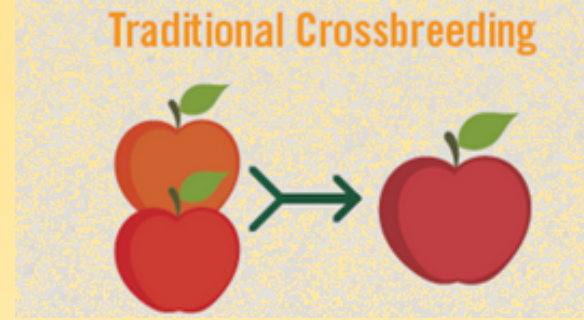
## Mutational breeding

### Mutagenesis



## Conventional breeding approach Janni et al. 2020

The conventional breeding approach encompasses the screening of natural genetic variability and the incorporation of portions of genes or genes of interest into new cultivars.



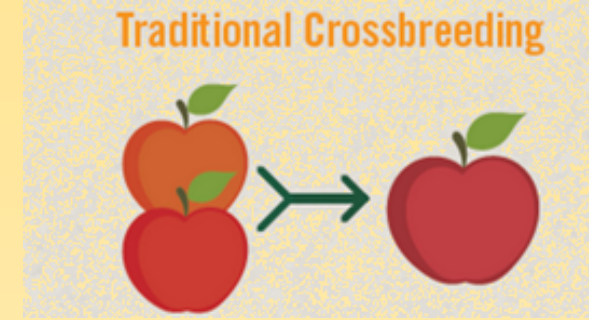
What are the underlying techniques?

- **QTL mapping** -> large DNA portions which can contain many candidate genes.
- **Genotyping-by-sequencing (GBS)** -> which has allowed an increase in the number of markers, making **precise mapping of QTL and candidate gene identification possible.**
- **Genome-wide-association-studies (GWAS)** permits narrowing down the candidate regions to explore specific haplotypes in natural population and wild species.

**These techniques allow the identification of markers (microsatellites, SNPs) used in Markers-Assisted Selection (MAS)**

-> known to be the most efficient methods when working on complex traits having hereditary characteristics such as HS tolerance (Tayade et al. 2018)

# Examples of gene/QTL identification for to heat stress tolerance



Species	Techniques	HS reponsive genes/QTL	References
Wheat	GWAS and GBS	Genomic regions associated to heat tolerance	Vijayalaskshmi et al. 2010 Acuña-Galindo et al. 2015 Maulana et al. 2018
Sorghum	GWAs	key genomic regions (specific alleles) under heat stress	Chopra et al. 2017
Cowpea	QTLs	Two dominant genes controlling heritable tolerance to heat at pod set QTLs associated to pod set number per peduncle that include HSP and HSF genes	Marfo and Hall 1992 Lucas et al. 2013 Pottorff et al. 2014
Rice	QTLs	Heat tolerance at flowering	Ye et al. 2012, 2015 Kilasi et al. 2018



# New Breeding Techniques (NBTs) Janni et al. 2020

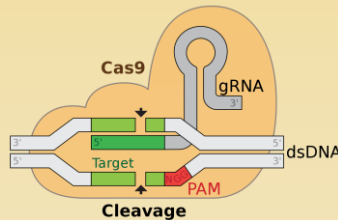
## Creation of transgenic plants

e.g. transgenic cotton plants overexpress an HSP in pollen-  
-> increased pollen germination and pollen tube growth  
under high temperature resulting in overall heat tolerance  
of reproductive tissue and reduced yield losses (Burke and  
Chen, 2015)

Availability of genomic sequences owing to genome  
editing techniques such as CRISPR-cas9

-> used in ~20 crops

e.g. potato, tomato, rice, cotton, soybean, maize,  
sorghum, wheat...



Crop	Target gene	Stress or trait
Maize	ARGOS8	Improved yield under drought stress condition
Rice	OsPDS, OsMPK2, OsBADH2	Abiotic stress tolerance
Rice	OsMPK2, OsDEP1	Yield under stress
Rice	GS3, Gn1a	Grain size and number increase
Rice	GW2, GW5, TGW6	Grain weight increase
Rice	Gn1a, DEP1, GS3	Grain size and number Increase in dense, erect panicles
Wheat	TaDREB2, TaERF3	Abiotic stress tolerance

Genome editing approaches used for heat stress breeding



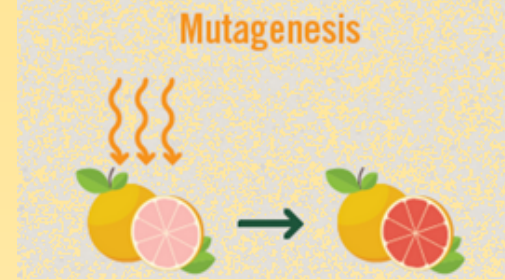
Crop	Target gene or protein/sources	Promoter	Stress or trait
Maize	OsMYB55/rice	Maize ubiquitin Ubi1 promoter/ overexpression	Increased drought and <b>HS tolerance</b>
Maize	ZmNF-YB2/maize	Rice actin 1 constitutive promoter/overexpression	Enhanced drought tolerance and <b>photosynthetic capacity</b>
Potato	HSc70 allelic variant/ potato	HSc70 native promoter	<b>Greater tolerance to HS</b> as determined by improved yield
Rice	HSP70/rice	CaMV 35S	Overexpression manifested enhanced <b>tolerance to HS</b>
Rice	Athsp101 /Arabidopsis	CaMV 35S promoter	Increased <b>tolerance to high temperature</b>
Rice	OsRab7	CaMV 35S	<b>Greater tolerance to HS</b> as determined by improved yield
Rice	TaMBF1c/wheat	Maize ubiquitin 1	<b>Higher thermotolerance</b> than control plants at both seedling and reproductive stages
Soybean	P5CR/Arabidopsis		Enhanced <b>HS tolerance</b>
Tobacco (Nicotiana tabacum L.)	HSP70-1/tobacco	CaMV 35S	Transgenics possessed <b>enhanced tolerance to HT stress</b>
Tobacco	HSP70-1/brassica		<b>Enhanced tolerance to HT stress</b>
Tomato	HSP21/tomato	CaMV 35S	<b>Overexpression protected PSII</b> from temperature-dependent oxidative stress; early accumulation of carotenoids noted
Wheat	Hsf6A /wheat	Barley HVA1s promoter/ drought inducible, up-regulated	<b>Improved thermotolerance</b>
Wheat	EF-Tu/maize	Maize ubiquitin 1 promoter/ overexpression	<b>Improved thermotolerance</b>

List of selected heat stress- (HS) tolerant transgenic plants

**General public concerns and complex legislation -> limiting applications**

## Mutational breeding Janni et al. 2020

Generation of new variability in plants by chemicals or radiation



Development of TILLING (Targeting Induced Local Lesions IN Genome, 2000 Arabidopsis) which requires a population of EMS induced mutants (random mutations) and a screening method to identify individuals with mutations in the target gene (Wang et al. 2010)

**More commercially competitive than precise genome editing approaches  
(not seen as transgenic crops in most jurisdictions)**

**In rice**, screening of a TILLING population for mutations in HSP genes  
-> several lines were shown to display enhanced HS tolerance (Yona et al. 2015)

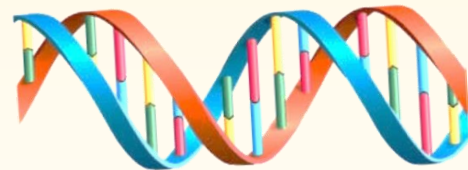
**In Durum wheat**, identification of small HSP alleles suitable for enhancing HS tolerance using TILLING approach (Comastri et al. 2018)

# Genetic approaches to cope with Heat Stress: Conclusions

**In the past, genetics has mainly been used to enhance yield and product quality but it can be equally applicable to alternative objectives such as contributing to adaptation to climate change**

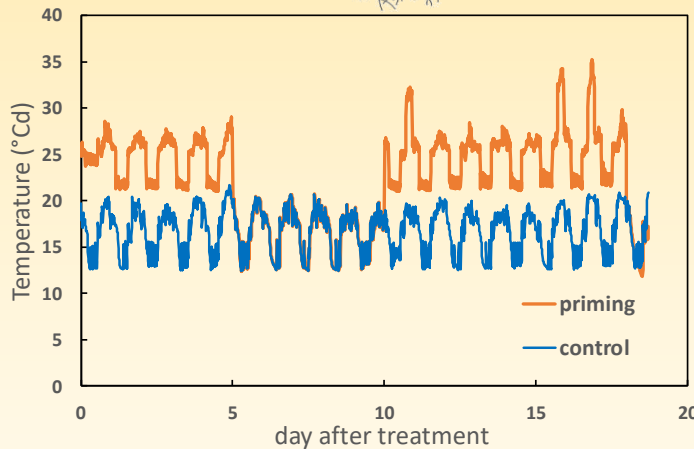
Three challenges to increase crop production under global warming:

- to **modify our selection criteria** to focus on efficiency or tolerance to stress(es) in addition to total yield
- to **determine** whether such **efficiency/stress-tolerance alleles are still present** and exploitable in our elite material and wider breeding germplasm
- to accelerate the development of **genomic tools for screening** genetic diversity



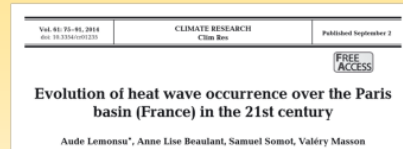


# Stress memory and priming: a key lever for thermosensitization in the context of increased frequency of heat waves?

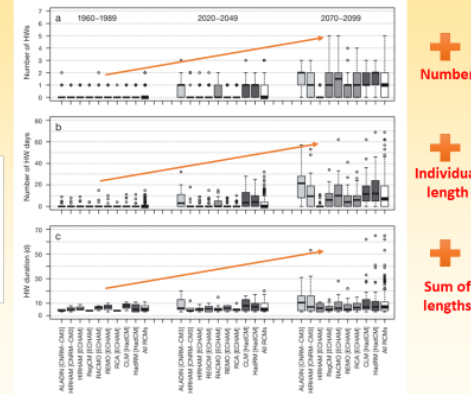


**Stress memory and priming**

## Climate projections...more frequent heat waves



## Frequency of heat waves under several scenarios Lemonso et al. 2014



+ Number

+ Individual length

+ Sum of lengths

## LETTERS nature climate change

## Dramatically increasing chance of extremely hot summers since the 2003 European heatwave

Nikolaos Christidis<sup>a</sup>, Gareth S. Jones and Peter A. Stott

Features of global warming

Journal of Integrative Agriculture 2017, 16(12): 2709–2716

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

ScienceDirect

ELSEVIER

REVIEW

Priming: A promising strategy for crop production in response to future climate

WANG Xiao<sup>1</sup>, LIU Fu-la<sup>2</sup>, JIANG Dong<sup>1</sup>

frontiers in Plant Science

ORIGINAL RESEARCH published: 14 April 2016 doi: 10.3389/fpls.2016.00501

Heat Priming Induces *Trans*-generational Tolerance to High Temperature Stress in Wheat

Xiao Wang<sup>1</sup>, Caiyun Xin<sup>1,2</sup>, Jian Cai<sup>1</sup>, Qin Zhou<sup>1\*</sup>, Tingbo Dai<sup>1</sup>, Weixing Cao<sup>1</sup> and Dong Jiang<sup>1\*</sup>

Contents lists available at [ScienceDirect](http://ScienceDirect)

Plant Physiology and Biochemistry

journal homepage: [www.elsevier.com/locate/plaphy](http://www.elsevier.com/locate/plaphy)

Research article

Multiple heat priming enhances thermo-tolerance to a later high temperature stress *via* improving subcellular antioxidant activities in wheat seedlings

Xiao Wang<sup>a,b</sup>, Jian Cai<sup>a</sup>, Fulai Liu<sup>c</sup>, Tingbo Dai<sup>a</sup>, Weixing Cao<sup>a</sup>, Bernd Wollenweber<sup>b</sup>, Dong Jiang<sup>a,\*</sup>

nature COMMUNICATIONS

ARTICLE

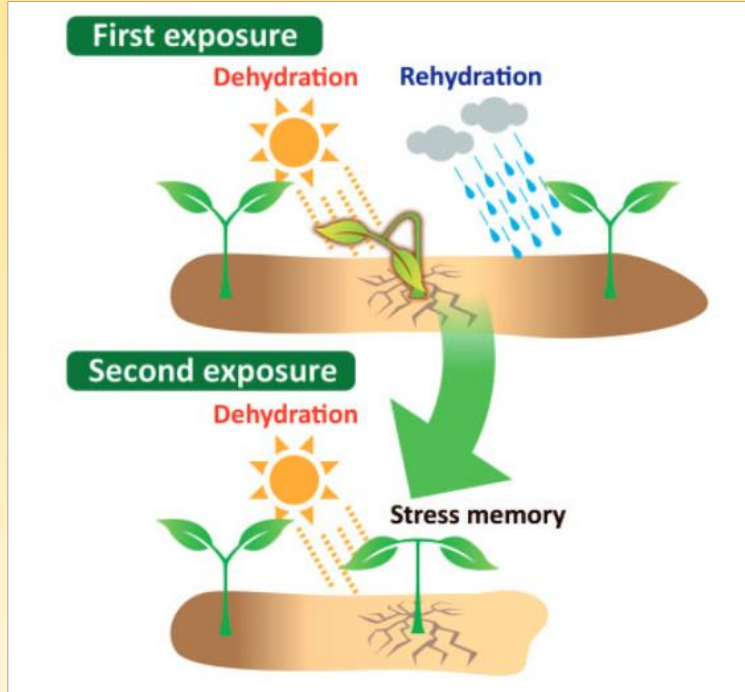
Received 27 Oct 2011 | Accepted 6 Feb 2012 | Published 13 Mar 2012

DOI: 10.1038/ncomms1732

Multiple exposures to drought 'train' transcriptional responses in *Arabidopsis*

Yong Ding<sup>1</sup>, Michael Fromm<sup>2</sup> & Zoya Avramova<sup>1</sup>

# Beneficial effect of stress memory for heat stress acclimation



Kinoshita and Seki, 2014

**1st stress exposure**

Storage and retrieval of stress-triggered information

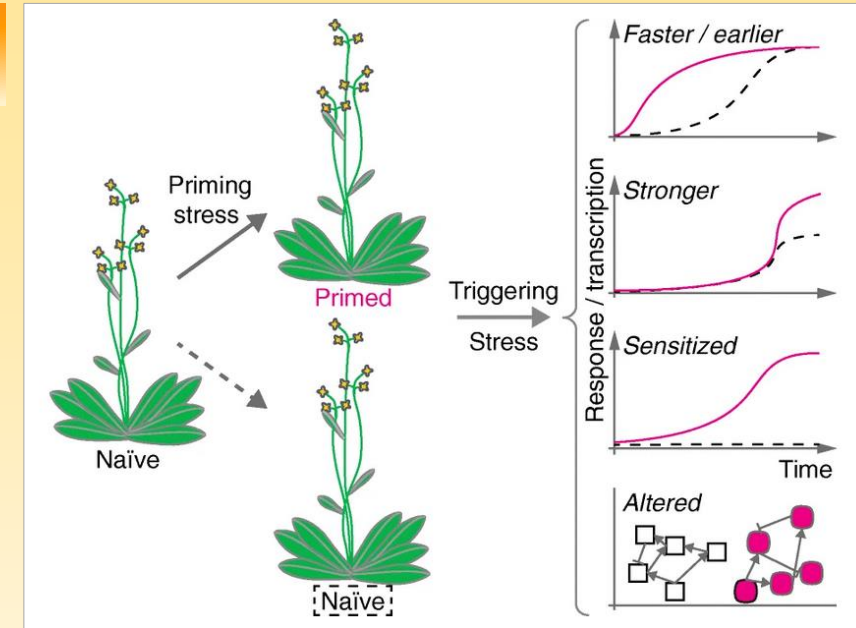
**Priming/Sensitization**

**2<sup>nd</sup> stress exposure**

**Earlier, more rapid, intense and/or sensitive response**

**How long does the stress memory last?**

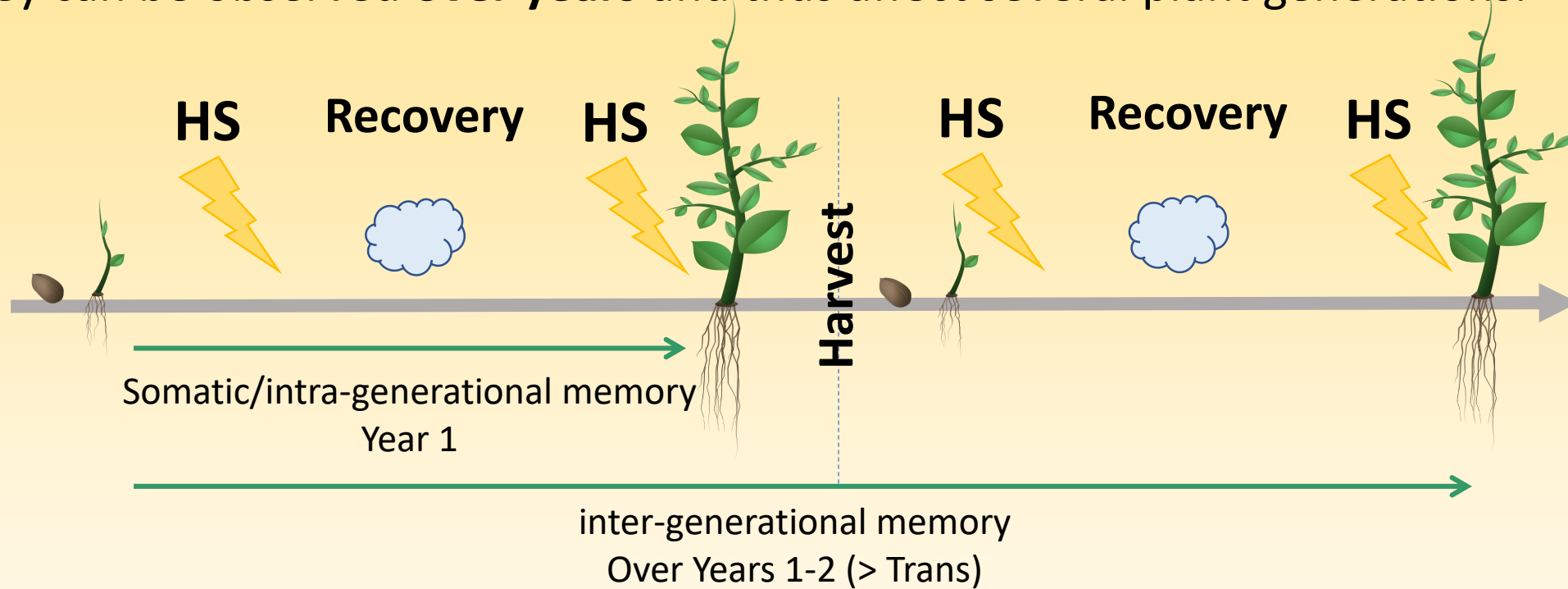
**What are the mechanisms that contribute to memory?**



Lamke and Baurle, 2017

Originally described for herbivory attacks  
Conrath et al., 2002

Stressing events can recur **during the crop season** and affect the plant during its crop cycle or they can be observed **over years** and thus affect several plant generations.



The definition of stress memory distinguishes **somatic memory that is intra-generational memory** from **inter/transgenerational memory** when we talk about memory that is transmitted to the offsprings.

# Somatic or intra-generational memory

Persistence of stress induced-metabolites (Pastor et al. 2014, Balmer et al. 2015, Hu et al. 2016)

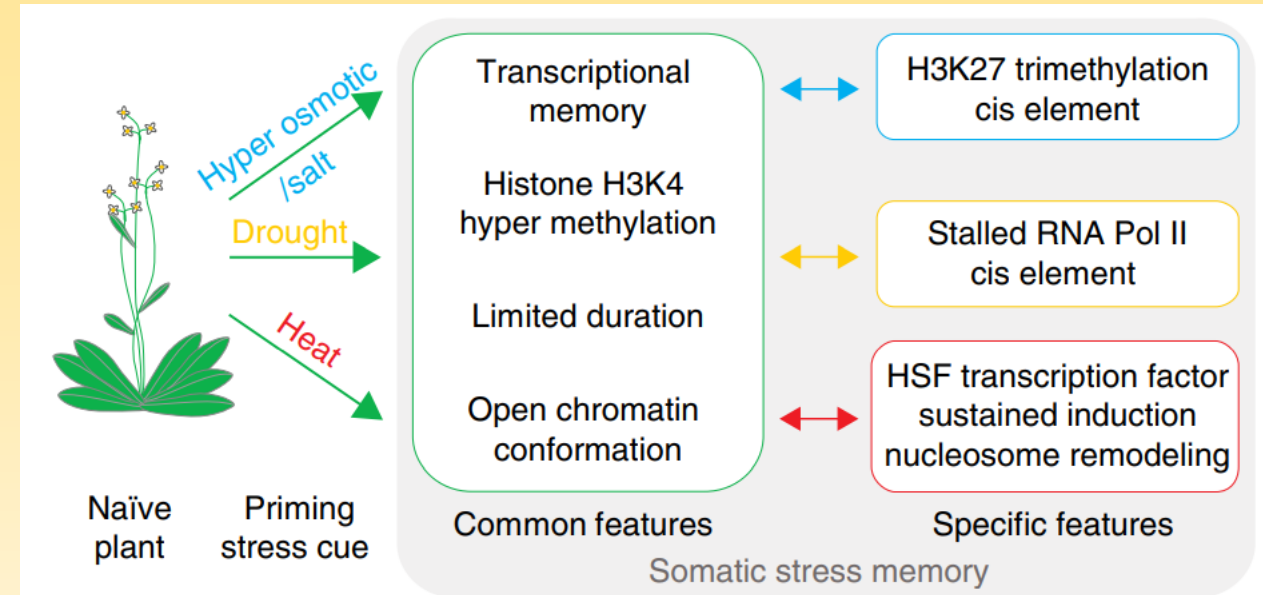
Sustained expression of genes after the stress (Charng et al. 2006, Stief et al. 2014)

Stalling of RNA polymerase II that potentiates transcription (Ding et al. 2012)

Accumulation of proteins (mitogen-activated protein kinases-MPKs, Beckers et al. 2009)

Alternative splicing (Sanyal et al. 2018, Ling et al. 2018)

**Mitotic stability of stress –induced chromatin changes  
i.e. epigenetic marks**



Lämke and Bäurle, 2017

Molecular features of somatic stress memory in response to abiotic stress cues. Somatic priming of plants by an abiotic (hyperosmotic, drought, or heat) stress cue has common features that are displayed in the central box.



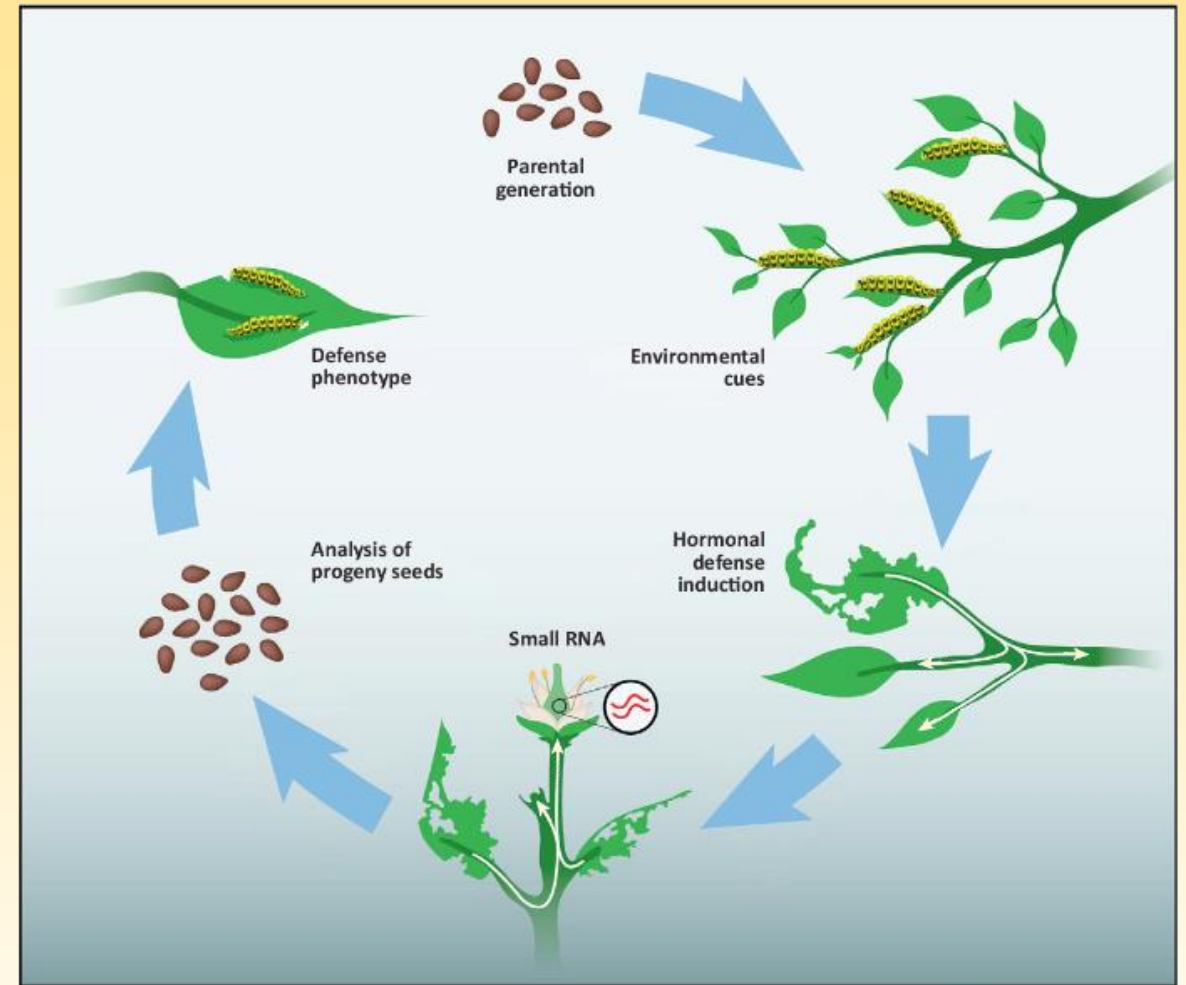
# Inter/Trans-generational memory

Seed provisioning (maternal effects) whereby different levels of resources are stored on the seed (mRNA, hormones, proteins, lipids...) (Pecinka and Mittlesen Scheid, 2012, Pecinka et al. 2013)

Transmission of structural variation in the genome

**Inheritance of the chromatin states (or epialleles) by meiosis**

Alvarez-Venegas et al. 2019



TRENDS in Ecology & Evolution

A schematic of the steps involved in the life cycle of transgenerational in induction, small RNA, analysis of progeny seeds, and the defense phenotype (Holeski et al. 2012)

Intergenerational stress memory: when only the first stress-free generation has a detectable memory effect

Transgenerational stress memory: when memory is detectable after at least two stress-free generations

# What is the contribution of epigenetic regulations to heat stress memory What is the extent of their use for thermo priming?

PCP  
PLANT & CELL PHYSIOLOGY

## Epigenetic Memory for Stress Response and Adaptation in Plants

Tetsu Kinoshita<sup>1\*</sup> and Motoaki Seki<sup>1,2,3</sup>

<sup>1</sup>Kihara Institute for Biological Research, Yokohama City University, 641-12 Maioka, Totsuka, Yokohama, Kanagawa, 244-0813 Japan

<sup>2</sup>Plant Genomic Network Research Team, RIKEN Center for Sustainable Resource Science, 1-7-22 Suehiro, Tsurumi, Yokohama, Kanagawa, 230-0045 Japan

<sup>3</sup>CREST, JST, 4-1-8 Honcho, Kawaguchi, Saitama, 332-0012 Japan

Mini Review

frontiers in  
PLANT SCIENCE

REVIEW ARTICLE  
published: 23 August 2013  
doi: 10.3389/fpls.2013.00315



## Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance

Kamila L. Bokszczanin<sup>1\*</sup>, Solanaceae Pollen Thermotolerance Initial Training Network (SPOT-ITN) Consortium\* and Sotirios Fragkostefanakis<sup>2\*</sup>

<sup>1</sup> GenXPro GmbH, Frankfurt am Main, Germany

Lämke and Bäurle *Genome Biology* (2017) 18:124  
DOI 10.1186/s13059-017-1263-6

Genome Biology

REVIEW

Open Access

## Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants

Jörn Lämke and Isabel Bäurle\*



Insight

## Harnessing epigenome modifications for better crops

James Giovannoni

US Department of Agriculture Robert W. Holley Center and Boyce Thompson Institute, Tower Road, Cornell University campus, Ithaca, NY 14853, USA  
james.giovannoni@ars.usda.gov; or jgg33@cornell.edu

Review

Focus: Molecular Memory

## Epigenetic memory in plants

Mayumi Iwasaki\* & Jerzy Paszkowski\*\*

THE  
EMBO  
JOURNAL

Research

New  
Phytologist

## Epigenetic variation creates potential for evolution of plant phenotypic plasticity

Yuan-Ye Zhang<sup>1</sup>, Markus Fischer<sup>1</sup>, Vincent Colot<sup>2</sup> and Oliver Bossdorf<sup>1</sup>

<sup>1</sup>Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013, Bern, Switzerland; <sup>2</sup>Institut de Biologie de l'Ecole Normale Supérieure, Centre National de la Recherche Scientifique Unité Mixte de Recherche 8197, Institut National de la Santé et de la Recherche Médicale Unité 1024, Paris F-75005, France

# Epigenetic marks involved in stress memory (Lamke and Baurle, 2017)

Stress cue	Maximal duration of memory (as analyzed)	Plant-level effect	Chromatin marks associated with priming
Somatic stress memory			
Desiccation	5–7 d	Yes	H3K4me3, paused RNA Pol II
Desiccation	4 d	ND	H3K4me3
Hyperosmotic	10 d	Yes	H3K27me3
Salt	10 d	Yes	H3K4me3
Heat, cold, or salt	10 d	Yes	H3K14ac, H3K4me2, H3K4me3
Heat	3 d	Yes	H3K4me2, H3K4me3
Heat	3 d	Yes	Histone occupancy
Systemic acquired resistance	4–6 d	Yes	H3K4me2, H3K4me3
Defense priming	ND	Yes	Histone occupancy, H3K4me3
Inter-/transgenerational stress memory			
Hyperosmotic	Inter-generational	Yes	DNA methylation
Iron deficiency	Inter-generational	Yes	
Various	Inter-generational	Yes	
Bacterial infection, chemical stressors	Inter-generational	Yes	DNA methylation
Bacterial infection	Inter-generational	Yes	H3K27me3, DNA methylation
Caterpillar herbivory	Trans-generational	Yes	DNA methylation

*d* days, *ND* not determined

Lamke and Baurle, 2017

**Memory genes** : Heat inducible genes that show sustained activation after a priming stress and/or enhance induction upon recurring heat stress)

# Evidence of priming mediated-improved thermotolerance: during the crop cycle

Species	Priming treatment Following HS	Effect on primed plants (vs. Unprimed) under HT	Gene expression and/or Epigenetic marks	reference
Wheat	Before anthesis 32/28°C (d/n) for 2d	Improved photosynthesis and antioxidant	up-regulated expressions of	Wang et al. 2011, 13
winter wheat				et al. 2016
Oilseed rap				et al. 2021

These priming protocols raise the question of how to apply such pre-acclimation treatment on crops grown in the field ?

They are mostly dedicated to decipher plant high-temperature responsive processes under repeated stresses for further breeding perspectives (acquired thermotolerance)

- Grafting of primed plants (tree species, Kapazoglou et al. 2021)
- Clonal propagation of primed plants (tissues)

Pea



The Plant Journal (2018) 96, 22–38

doi: 10.1111/tpj.14058

Ma

## Maintenance of grafting-induced epigenetic variations in the asexual progeny of *Brassica oleracea* and *B. juncea* chimera

Tall

Ningning Yu<sup>1</sup>, Liwen Cao<sup>1</sup>, Lu Yuan<sup>1</sup>, Xiao Zhi<sup>1</sup>, Yiqian Chen<sup>1</sup>, Susheng Gan<sup>2</sup>  and Liping Chen<sup>1,\*</sup> 


<sup>1</sup>Department of Horticulture, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China, and

<sup>2</sup>Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA

American Journal of Botany

ON THE NATURE OF THINGS: ESSAYS  
New Ideas and Directions in Botany

**Epigenetic variation for agronomic improvement: an opportunity for vegetatively propagated crops**

Mathieu Latutrie<sup>1,2,3,\*</sup>, Delphine Gourcilleau<sup>2,\*</sup>, and Benoit Pujol<sup>1,2,3</sup> 



# Evidence of priming mediated- improved thermotolerance :Inter/Trans-generational memory

Species Priming treatment Effect on primed plants (vs. Unprimed) Gene expression and/or references

Most studies on Arabidopsis, or on other stress (pathogen attacks, salt stress...)

Arab



ARTICLE  
DOI: [10.1038/s41467-018-02839-3](https://doi.org/10.1038/s41467-018-02839-3) OPEN

A naturally occurring epiallele associates with leaf senescence and local climate adaptation in *Arabidopsis* accessions

Li He<sup>1,2</sup>, Wenwu Wu<sup>1,4</sup>, Gaurav Zinta<sup>1</sup>, Lan Yang<sup>1</sup>, Dong Wang<sup>1</sup>, Renyi Liu<sup>1</sup>, Huiming Zhang<sup>1</sup>, Zhimin Zheng<sup>1</sup>,  
Rahul Sharma<sup>1,5</sup>, and Shuang Li<sup>1,2,3</sup>

Transgenerational memory heat stress effect i.e. does heat

Plant Cell Rep (2017) 36:203–217  
DOI 10.1007/s00299-016-2072-1 

ORIGINAL ARTICLE

**Epiallelic changes in known stress-responsive genes under extreme drought conditions in *Brassica juncea* (L.) Czern.**

Rahul Sharma

Whe

Rice

Epigenetics 8:8, 864–872; August 2013; © 2013 Landes Bioscience

**Epigenetic marks in an adaptive water stress-responsive gene in tomato roots under normal and drought conditions**

Rodrigo M González<sup>1,†</sup>, Martiniano M Ricardi<sup>1,†</sup> and Norberto D Iusem<sup>1,2,\*</sup>

**Epigenetic QTL Mapping in *Brassica napus***

Yan Long,<sup>\*,1</sup> Wei Xia,<sup>\*,1</sup> Ruiyuan Li,<sup>\*</sup> Jing Wang,<sup>\*</sup> Mingqin Shao,<sup>\*</sup> Ji Feng,<sup>\*</sup> Graham J. King,<sup>†</sup> and Jinling Meng<sup>\*,2</sup>

<sup>\*</sup>National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China and <sup>†</sup>Southern Cross Plant Science, Southern Cross University, Lismore, NSW 2480, Australia

# Acclimation to heat stress to maintain or even to improve crop performances under recurrent stresses at the cycle level and over generations

Heat stress is often studied by subjecting plants to **prolonged increases in temperatures**.

However, heat stress responses under a prolonged stress might differ from the ones triggered by **repeated stresses**.

Repeated stresses can lead to a primed state that further help the crops facing subsequent stresses. For breeders, these stressing sequences can be used as **priming protocols** for thermotolerance acquisition.

- **Identification of priming protocols** for intra and inter/trans-generational memory  
-> features of the priming protocols to target the specific processes that control the traits of interest
- **The identification of underlying priming mechanisms can harness priming based crop improvement**  
-> **potential of epibreeding**: identification of EpiQTLs/Epialleles in breeding programs

# Conclusions- Take Home Messages

Three fold lever of action for crop acclimation to heat stress: from the farming system down to the genes and the regulation of gene expression.

-> **agricultural practices** to adapt crops to high temperatures

**Thanks for your attention**

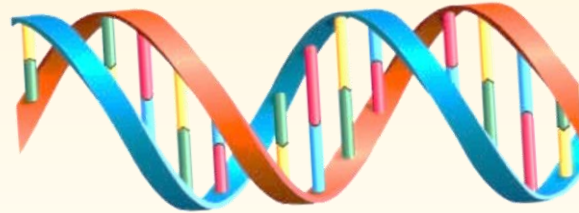
and adapt crops to high temperatures using strategies

-> **crop genetic improvement**: available genetic resources, development of tools for high throughput genetic variability screening, legislation concerning the breeding techniques

-> **stress memory and priming**: inheritance, features of the priming protocols, potential of epibreeding



**Agricultural practices**



**Crop Genetic Improvement**



**Stress memory  
And priming**