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Preparing for an uncertain future: molecular responses of plants facing climate change

Isabel Bäurle¹, Laurent Laplaze² and Antoine Martin³

¹ Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany

² DIADE, Univ Montpellier, IRD, CIRAD, Montpellier, France

³ IPSiM, Univ Montpellier, CNRS, INRAE, Institut Agro, Montpellier, France

Corresponding Isabel Bäurle, Laurent Laplaze and Antoine Martin

isabel.baeurle@uni-potsdam.de

laurent.laplaze@ird.fr

antoine.martin@cnrs.fr

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Keywords

Adaptation, Climate change, Drought, Elevated CO₂, Heat stress, Mitigation, Resilience

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Introductory paragraph

Climate change is mostly driven by the elevation of atmospheric CO₂ concentration. It leads to the increase in ambient temperature and temperature extremes, as well as to the reduction in water availability. Despite the apparent benefit that an elevation of CO₂ and ambient temperature might have on the production of plant biomass, climate change severely challenges the plant life cycle, and thus increasingly leads to food insecurity. Investigating the molecular mechanisms of plant adaptation to climate change is thus a pressing issue. This was the theme of the EMBO Workshop “Molecular responses of plants facing climate change” in June 2022 in Montpellier, France. Here, we summarise some key insights presented during the conference on the investigation of molecular mechanisms of plant adaptation to environmental constraints in a changing climate.

How to deal with increasing temperatures?

Ambient temperatures affect all aspects of growth and development. Morphological responses to mildly elevated temperatures include the regulation of elongation growth in the shoot and the root (Quint *et al.*, 2016). In the shoot, several thermosensors including Phytochrome B perceive temperature and coordinate with PHYTOCHROME-INTERACTING FACTOR 4 (PIF4) (Delker *et al.*, 2022; Perrella *et al.*, 2022). PIF4 then integrates with the auxin and brassinosteroid signalling pathways for a coherent growth response. Carolin Delker (University of Halle) discussed how shoot and root responses involve distinct sensing and signalling mechanisms. In nature, however, not only temperatures vary, but also light quality (shading) and water availability. Jorge Casal (University of Buenos Aires) highlighted the integration of different environmental cues at the level of photoreceptors and downstream signalling pathways to appropriately gauge complex environments (Casal and Balasubramanian, 2019; Romero-Montepaone *et al.*, 2020).

The heat stress (HS) response allows plants to acclimate to extreme temperatures through the activation of HEAT SHOCK TRANSCRIPTION FACTORS (HSFs) transcription factors

that induce the expression of chaperones (Heat Shock Proteins, HSPs) and enzymes that produce thermoprotective and ROS-scavenging metabolites (Guihur *et al.*, 2022; Ohama *et al.*, 2017). The current view is that HEAT SHOCK TRANSCRIPTION FACTOR A1 (HSFA1) isoforms are maintained in an inactive state in the cytoplasm through complexation with chaperones and rapidly move into the nucleus after HS to activate transcription, when the HSPs are recruited away to misfolded proteins (Ohama *et al.*, 2017). Phil Wigge (IGZ Großbeeren) presented data that suggest an alternative mode of regulation of at least one HSFA1 isoform by liquid-liquid-phase separation. Intrinsically disordered domains within HSFA1 trigger phase separation at elevated temperatures, similar to what has been described for EARLY FLOWERING 3 (ELF3) (Jung *et al.*, 2020). Thus, HSFA1 may directly sense temperature. Temperature-dependent alternative splicing may constitute a parallel mechanism. Sotirios Fragkostefanakis (University of Frankfurt) reported on general splicing regulators with a specific role in HS-dependent alternative splicing, thus illustrating a feedback loop to fine-tune HS response (Hu *et al.*, 2020; Rosenkranz *et al.*, 2022).

A moderate HS event can prime a plant and lead to a more efficient response upon recurrent stress after a stress-free interval lasting several days. This so-called HS memory shows complex regulation, including epigenetic modifications, protein stability and stable metabolites (Balazadeh, 2022; Oberkofler *et al.*, 2021). Isabel Bäurle (University of Potsdam) discussed epigenetic changes involving hyper-methylation of histone H3 lysine 4 (H3K4) and showed how locus-specific epigenetic editing of H3K4me3 impairs the memory (Oberkofler and Baurle, 2022; Oberkofler *et al.*, 2021). Specialized HSF complexes govern these epigenetic modifications (Friedrich *et al.*, 2021). In contrast, the autophagy cellular degradation machinery negatively impacts HS memory by degrading HSPs and other thermoprotective proteins, as Salma Balazadeh (University of Leiden) discussed (Balazadeh, 2022; Thirumalaikumar *et al.*, 2021). In a parallel pathway the metalloprotease FtsH6 degrades HSP21, thus modulating HS memory (Sedaghatmehr *et al.*, 2016). Improving HS memory provides an interesting avenue to increase tolerance to HS without affecting growth in stress-free conditions. Improvement of HS tolerance may also stem from clever

manipulation of the soil microbiome. Heribert Hirt (King Abdullah University of Science and Technology) presented data showing that desert root endophytes induce thermotolerance by boosting HS memory (Shekhawat *et al.*, 2021).

How to deal with water stress?

Root traits can be targeted to improve water capture in crops (Lynch, 2022) and tolerance to water stress based on a good characterization of the stress pattern and soil characteristics of the target area. Several mechanisms that optimise root development in response to changing soil water content (in time and space) are prime candidates. Xerobranching, the local inhibition of root branching when the root tip loses contact with wet soil (as in air gaps or dry soil regions), is an abscisic acid (ABA)-dependent adaptive process described in cereals and *Arabidopsis* (Orman-Ligeza *et al.*, 2018). Malcolm Bennett (University of Nottingham) described how a xerobranching water stress stimulus on a root tip leads to release of ABA from the phloem that induces plasmodesmata closure in root outer tissues, which prevents the movement of auxin from the epidermis to the pericycle required for lateral root formation (Mehra *et al.*, 2022). This model explains how hydraulics controls root architecture via co-transport of phytohormones. Hydropatterning is another mechanism that regulates the radial positioning of lateral roots, root hairs, or aerenchyma depending on differences in water availability across the circumferential axis of the root to optimise root architecture to local water content (Bao *et al.*, 2014). This adaptive response is ABA-independent but dependent on sumoylation of AUXIN RESPONSE FACTOR 7 (ARF7), a key regulator of auxin response during lateral root formation (Orosa-Puente *et al.*, 2018). José Dinneny (Stanford University) reported that maize varieties are highly diverse for hydropatterning and that hydropatterning was a good predictor of root system depth, a trait associated with better water stress tolerance.

Integrating root architecture and anatomical and physiological properties of tissues is important to understand water dynamics in the root system (Maurel and Nacry, 2020).

Christophe Maurel (Institute for Plant Sciences of Montpellier) showed that different maize root types have different hydraulic properties and response to water stress exploiting HydroRoot, a model for root hydraulics (Boursiac *et al.*, 2022), and split root experiments. He further reported genetic diversity in maize for root hydraulics. How root hydraulics relates to plant response to water stress still needs to be evaluated. Optimising water acquisition by roots will increase water depletion in the soil and will ultimately have limited impact when available soil water is limited. Another complementary strategy is to improve water use efficiency, i.e., the amount of carbon fixed per unit water consumed. Transpiration is regulated by stomata opening, a process that appeared in the earliest land plants (Clark *et al.*, 2022). Optimising stomatal movement in response to environmental signals could improve plant water use efficiency and drought tolerance. Regulation of stomatal closure by ABA and CO₂ is mediated by a complex signalling pathway involving several kinases (MPKs, OST1, HT1) and the GHR1 receptor-like pseudokinase that was described by Hannes Kollist (University of Tartu) (Horak *et al.*, 2016; Sierla *et al.*, 2018). Stomata integrate environmental signals to optimise gas exchange and water loss. These signalling pathways ultimately lead to the coordinated regulation of different ion transporters localised at the plasma or vacuolar membrane of guard cells (Cubero-Font and De Angeli, 2021) as well as aquaporins of the PLASMA MEMBRANE INTRINSIC PROTEIN (PIP) subfamily (Ding *et al.*, 2022). The ability of the plant to restrict its transpiration when the evaporative demand is very high, and therefore when the water cost of carbon fixation is elevated is a key trait for water use efficiency (Burridge *et al.*, 2022). Pablo Affortit (IRD) presented data showing a link between transpiration efficiency and transpiration restriction under high vapor pressure deficit on the one hand and plant hydraulics and root traits (in particular the root/shoot ratio) on the other hand in African rice (Affortit *et al.*, 2022) thus linking transpiration regulation to root water uptake. Interestingly, during drought stress, the photosynthetic apparatus is protected by a feedback control by photorespiration (Leverne and Krieger-Liszky, 2021) and Anja Krieger-Liszky presented evidence that signals deriving from the plastoquinone pool could regulate root growth. Altogether, this suggests mechanisms that integrate water stress perception in

the photosynthetic tissues with root development and water uptake. Further work is needed to decipher the regulation of transpiration by plant hydraulics and photosynthesis.

The elevation of CO₂ in the atmosphere: benefits, costs and opportunities

Elevated CO₂ concentration (eCO₂) promotes the production of biomass, as the current CO₂ concentration is a limiting factor for photosynthesis of C3 plants (Ainsworth and Long, 2021). As mentioned by Christine Foyer (University of Birmingham), this is a favourable circumstance in a world showing a growing population. However, this CO₂ fertilisation effect is less than expected due to the acclimation of photosynthesis to eCO₂. Boosting photosynthesis of C3 plants, and understanding the mechanisms behind eCO₂ acclimation in a CO₂-enriched world is therefore a main objective for plant scientists (Simkin *et al.*, 2019). Different routes to improve photosynthesis were discussed during this workshop. One example was presented by Alejandro Perdomo (Lancaster University), who showed that the transcriptional regulation of Rubisco activase can be a way to improve Rubisco efficiency, and thus to increase carbon fixation and yield (Perdomo *et al.*, 2017). Florian Busch (University of Birmingham) discussed the different limitations of CO₂ assimilation, and highlighted that the most relevant targets for improving photosynthesis vary depending on the environment. Together with Arnold Bloom (UC Davis), they stressed the importance of photorespiration, and challenged the view that this metabolic pathway would be a cost for plants compared to the improvement of photosynthesis (Busch *et al.*, 2018; Shi and Bloom, 2021).

However, the increase in carbon uptake and biomass production will not occur independently of other major metabolic pathways. This seems especially true considering that photosynthesis might not be the main limiting parameter for growth and yield, in opposition to nutrient and especially to nitrogen limitation (Sinclair *et al.*, 2019). This is reminiscent of an unexpected negative effect of eCO₂ on plants. Indeed, the growth under eCO₂ leads to a decline in the mineral composition of C3 plants, which might create a serious threat for food

and nutritional security at the end of this century (Gojon *et al.*, 2022). Different approaches to identify the genetic and molecular mechanisms behind the negative effect of eCO₂ on plant nutrient content have been presented. The use of natural genetic variation or the inference of gene networks under simulated future climate notably led to the identification of genes involved in the response of plants to eCO₂ (Cassan, Martin *et al.*, unpublished). Arnold Bloom presented data showing yield and protein content of several wheat lines over 35 years of cultivation in California. During this period CO₂ increased in the atmosphere, while yield decreased but not protein content, suggesting that plants sacrificed yield to maintain organic N (Bloom and Plant, 2021). This also suggests that fast adaptive mechanisms to the changing atmosphere might happen, and remain to be identified.

Plants are also an extraordinary sink of carbon. The increase of CO₂ in the atmosphere may lead to an augmentation in plant biomass, making plants a natural trap for atmospheric CO₂ (Lynch, 2022) (Box 2). This was the subject of the keynote given by Joanne Chory (The Salk Institute), who presented data showing how root systems can be improved to capture and store carbon stably in the ground, contributing to the mitigation of climate change.

Overall conclusion

The complex nature of a changing climate requires plants to be systemically more efficient in dealing with the constraints that have been discussed here individually. A more integrated view and approach is required, as a plant that is more efficient in dealing with temperature extremes may at the same time be more vulnerable at elevated ambient temperature, drought stress or CO₂-rich environment. This complexity calls for multi-partner initiatives that have the expertise and the means to tackle systemic aspects, ideally not in model plants, but directly in crop species.

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Conflict of interest

No conflict of interest declared

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Box 1. The main factors of climate change influencing plant growth, development and physiology.

CO₂ concentration, temperature, and water availability are climate change-associated factors that are critical for plant growth and development. Climate change threatens both biodiversity and agriculture, with far-reaching implications for food security. Climate change is expected to reduce yield and to impact the quality of production, imposing major constraints on the higher demand of plant-based resources imposed by the growing population (Nelson, 2010). Thus, considerable research in the field focuses on understanding the physiological processes and underlying molecular mechanisms through which plants can adapt to these changes (Ahuja *et al.*, 2010; Nicotra *et al.*, 2010).

Text included in the Box 1 illustration:

Heat: Climate change will increase not only average temperatures, but also the frequency and extremity of heat waves. Thus, plants will have to face and adapt to increasing ambient temperatures as well as extremely high temperatures. With global yields of major crops predicted to decrease between 3 % and 7 % for every 1°C increase in temperature (Zhao *et al.*, 2017), the generation of more heat resilient plants is a pivotal target of breeding efforts to adapt agriculture to future climate.

Drought: Water is a key input for agriculture and the main factor limiting plant production worldwide. Climate change will lead to hotter and drier climates thus increasing the evaporative demand. At the same time, increasing competition from industries and cities for water together with reduced and more unpredictable rainfall reduces water availability for agriculture. This calls for a multiscale integrative approach combining the use of more water-efficient crops combined with water-efficient agronomical practices and water management strategies at the farm and landscape level.

Elevated CO₂: Climate change is driven by the elevation of green-house gases in the atmosphere, and mostly by that of CO₂. The concentration of CO₂ in the atmosphere has increased from 340 ppm in 1980 to 420 ppm in 2022, and projections predict concentrations

ranging from 750 to 1000 ppm depending on the scenarios at the end of the century (IPCC, 2021). This will lead to major consequences for the physiology of plants. On the one hand, elevated CO₂ is expected to increase the production of green biomass, which is a benefit for agriculture. On the other hand, the growth under elevated CO₂ significantly reduces plant nutritional quality, which might negatively impact the risk of starvation and nutrient deficiencies.

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Box 2. Some future challenges for plant science in the context of climate change

Despite the progress already made, many challenges lie ahead: in many cases it is still an open question whether the mechanisms identified in one developmental stage are transferable to other developmental stages within one species. Moreover, whether the mechanisms outlined above and unraveled mostly in model plants are conserved in crop species remains an important question to investigate. Devising better adapted crops will require a good understanding of the stress pattern faced by crops in the target environments, a process that will benefit from the recent advances in crop modelling (Burridge *et al.*, 2022). The emission of greenhouse gases (notably nitrous oxide coming indirectly from N fertilizers, and methane from livestock), the use of fossil fuels (including for the production of N fertilizers) and intensive irrigation make agriculture a major contributor to climate change. Conversely, plant growth has been proposed as a solution to mitigate greenhouse gas emissions and the associated climate change effects. Indeed, by their ability to fix C and produce biomass, plants are an ideal tool to capture and to sequester atmospheric CO₂ either as biomass or in soils. The worldwide distribution of crops makes them an excellent system to deploy a C-sequestration plan at a large scale. However, we still need to identify the best root traits to mobilise to achieve this goal and how this will impact the carbon dynamics in the soil in realistic (field) conditions. In addition, the development of root systems capable of taking up nutrients and water more efficiently from the soil is a way to reduce the use of N fertilizers and water, thereby considerably reducing the impact of agriculture on climate. Therefore, the comprehension of the mechanisms driving root system development, N and water use efficiency under climate change is a major challenge to produce climate-resilient crops. Much remains to be understood in order to develop and use such climate-resilient plants in the near future (Dhankher and Foyer, 2018; Rivero *et al.*, 2022).

Ultimately, developing strategies to adapt agriculture to and mitigate the effects of climate change is a challenge that will require a truly interdisciplinary effort. While plant breeding will be a key component, sustainable solutions are unlikely to arise just from one discipline and

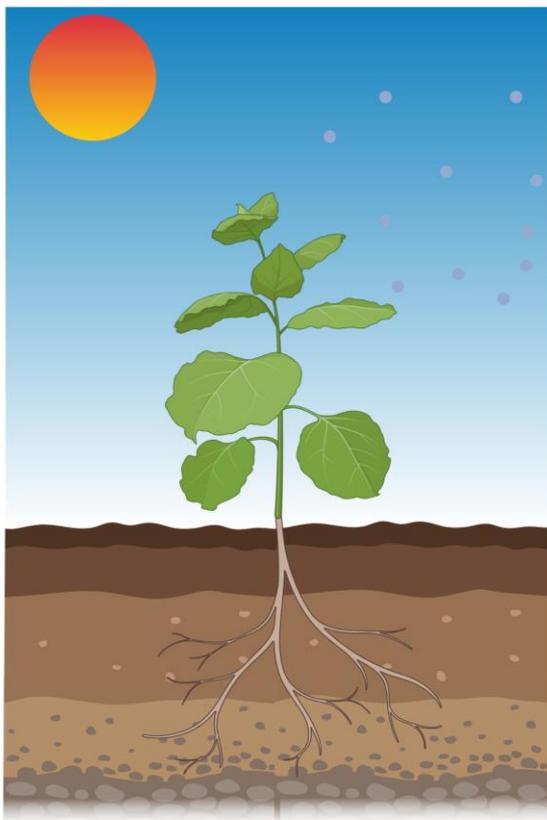
will depend on system thinking. Plant biologists need to team up with other scientists such as soil scientists, agronomists, hydrologists, economists to address these pressing issues.

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Figure 1

Heat:

Climate change will increase not only average temperatures, but also the frequency and extremity of heat waves. Thus, plants will have to face and adapt to increasing ambient temperatures as well as extremely high temperatures. With global yields of major crops predicted to decrease between 3 % and 7 % for every 1°C increase in temperature (Zhao *et al.*, 2017), the generation of more heat resilient plants is a pivotal target of breeding efforts to adapt agriculture to future climate.

**Elevated CO₂:**

Climate change is driven by the elevation of green-house gases in the atmosphere, and mostly by that of CO₂. The concentration of CO₂ in the atmosphere has increased from 340 ppm in 1980 to 420 ppm in 2022, and projections predict concentrations ranging from 750 to 1000 ppm depending on the scenarios at the end of the century (IPCC, 2021). This will lead to major consequences for the physiology of plants. On the one hand, elevated CO₂ is expected to increase the production of green biomass, which is a benefit for agriculture. On the other hand, the growth under elevated CO₂ significantly reduces plant nutritional quality, which might negatively impact the risk of starvation and nutrient deficiencies.

Drought:

Water is a key input for agriculture and the main factor limiting plant production worldwide. Climate change will lead to hotter and drier climates thus increasing the evaporative demand. At the same time, increasing competition from industries and cities for water together with reduced and more unpredictable rainfall reduces water availability for agriculture. This calls for a multiscale integrative approach combining the use of more water-efficient crops combined with water-efficient agronomical practices and water management strategies at the farm and landscape level.

Accepted