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SPECIAL ISSUE EDITORIAL

Plant responses and adaptations to a changing climate

Global emissions of CO_2 and other greenhouse gases have increased steadily since the pre-industrial era (Pedersen et al., 2021) leading to global temperature increases of >1 °C with most of this increase occurring within the last 50 years (IPCC, 2021). The observed increase in global warming compared to historical averages (1850–1900) is unprecedented and has not been observed in the past 125 000 years. Greater heating will be accompanied by increases in extreme precipitation, tropical storms, and flooding events across all seasons, but more likely to occur in the autumn and winter months in wetter regions of the globe (Hirabayashi et al., 2021; IPCC, 2021; Tabari, 2021). Warming will also lead to increases in global sea level rise of up to 0.55 m or more by 2100 due to the melting of mountain and polar glaciers (IPCC, 2021; Vousdoukas et al., 2018). Coastal flooding events will be compounded by extreme meteorological tides, storm surge, and precipitation, which are predicted to increase by more than 25% by 2100 (Bevacqua et al., 2020). Flooding, which results in either submergence or waterlogging, is responsible for more crop production losses than any other abiotic stress besides drought (Kaur et al., 2020).

In addition to the threats posed by extreme precipitation events and sea level rise, global climate changes will also lead to frequent and extreme heatwaves and droughts, which will drive changes in soil moisture, particularly in many regions across North, Central, and South America, the Mediterranean basin, northern and southern Africa, Australia, and western and southern Asia (IPCC, 2021; Naumann et al., 2018). About 50% of the Earth's land surface is characterized as arid, semi-arid, or dry subhumid (Zika and Erb, 2009). For these drying areas, the duration and magnitude of drought is predicted to double for 30% of the global land mass resulting in a five-fold increase in water demand deficits during the 21st century (Naumann et al., 2018). In addition to the global expansion of dry lands, soil drying and the resulting leaf:air vapor pressure deficits will reduce terrestrial net primary production, reduce terrestrial carbon sinks, and reshape the geographical redistribution of plants (Zhao and Running, 2009). Rare, 1-in-100-year droughts, will become more common, occurring every 2–5 years for many parts of Africa, Australia, southern Europe, southern and central United States, central America, the Caribbean, northwest China, and regions of South America.

IMPACTS ON AGRICULTURE

Increased soil drying brought about by global climate change will threaten global food security and curtail biomass feedstock production for biofuels. Multi-ensemble modeling of the global impact of climate change for 1981–2010, compared with pre-industrial climactic conditions, demonstrates that global mean yields of wheat (*Triticum aestivum*), maize (*Zea mays*), and soybean (*Glycine max*) have declined by 1.8, 4.1, and 4.5%, respectively, even when CO_2 fertilization effects and modernized agronomic practices are taken into account (Iizumi et al., 2018). Indeed, the physiological responses of plants to elevated CO_2 in the 21st century are not likely to offset the negative consequences of surface drying (Dai et al., 2018). A meta-analysis of multiple published simulations of crop yields predicts aggregate production losses for wheat, rice (*Oryza sativa*), and maize in both temperate and tropical regions by 2 °C warming with even greater crop losses in the second half of the 21st century (Challinor et al., 2014). Yield loss risks under drought conditions arising from global warming are predicted by ensemble modeling to increase by 9–19% for major crops including wheat, maize, rice, and soybean by the end of the 21st century (Leng and Hall, 2019). In addition to rain-fed crop production, which depends upon ambient precipitation patterns, irrigated crops depend upon the availability of groundwater resources. Irrigated agriculture uses 20% of total cultivated land area, but contributes to 40% of global crop production, and accounts for approximately 70% of global water withdrawals (FAO, 2017). However, overreliance on ground water resources has led to alarming rates of aquifer depletion (Famiglietti and Rodell, 2013; Voss et al., 2013). Anthropogenic climate change has led to reduced and earlier annual snow pack melt (Bormann et al., 2018), which drives even greater ground water depletion (Cuthber et al., 2019). In addition to these biophysical impacts of global climate change, increased losses in agricultural production are anticipated due to the changing geographical range of pathogens (Bebber, 2015) and the impacts of, for example, increased temperature on plant–pathogen interaction (Desaint et al., 2021). Furthermore, sea level rise will submerge large coastal regions currently used for crop production, further limiting agricultural production potential (Wang et al., 2018).

As the global climate crisis worsens, critical gains in agricultural production on the order of 60% will be necessary to meet the global food demands of a growing human population estimated to increase to more than 9 billion by 2050 (United Nations, 2019). Agriculture and land-use changes from agricultural expansion contribute up to 25% of greenhouse gas emissions, which poses additional challenges to maintaining a balance between terrestrial carbon sequestration strategies and attempts to meet current and future food demands (Crippa et al., 2021; Searchinger et al., 2018). Thus, a clear and present need exists to develop novel strategies to produce more climate-resilient crops. This special issue encompasses a range of topics that outline potentially useful strategies to fortify the climate resilience of crops to ensure a reliable supply of food, feed, fiber, and biofuels for humankind in the not-so-distant future.

UNDERSTANDING DROUGHT AND OTHER ABIOTIC STRESSES

Drought is by far one of the most prevalent abiotic stress conditions to limit crop yield worldwide. In the coming years, drought periods are projected to increase in intensity and duration, due to climate change, inflicting a higher than ever yield penalty on agricultural production. In their review article, Berrío et al. (2022) discuss several strategies to enhance drought resilience in crops focusing on 'growth-centered' and 'drought resilience without growth penalty' strategies. They highlight several different molecular players that were successfully used to engineer drought tolerance in plants, as well as discuss the role of hormones such as abscisic acid, brassinosteroids, cytokinins, ethylene, and strigolactones. In addition, they discuss future perspectives for the development of new strategies to improve drought tolerance under field conditions.

In their encompassing review, Kuromori et al. (2022) address plant responses to drought at the single-cell and whole-plant levels. They discuss recent advancements in our understanding of how drought is sensed in leaves and roots, and how different parts of the plant use long-distance signaling to coordinate responses to drought at the whole-plant level. Focusing on abscisic acid and peptide signaling they also highlight selected mechanisms for plant adaptation and resistance to drought and underscore the importance of phenotyping for measuring plant adaptation to drought conditions for the purpose of breeding.

Environmental stress conditions, such as drought, heat, or cold stresses, disrupt cellular homeostasis and result in the accumulation of reactive oxygen species (ROS). Unopposed, ROS can cause oxidative stress that will damage many processes in plants and reduce yield. In their article, Kerchev and Van Breusegem (2022) review the decade-long research effort to improve oxidative stress resilience in crops by boosting their antioxidant machinery. They highlight the pros and cons of different strategies and propose new avenues for future research and development in this important subject.

The review by Rivero et al. (2022) addresses the critical challenge that environmental stress conditions do not occur in isolation and that predictions of plant responses to multiple stresses is often not possible from our current understanding of responses to a single stress. Addressing combined abiotic stress as well as interactions between abiotic and biotic stress conditions, the authors outline our knowledge of the different physiological outcomes of stress combinations, as well as underlying molecular mechanisms – identifying integrators of combined stress responses as well as highlighting the complexity of this challenge. They end with recommendations of key technologies required – involving genetics, synthetic biology, and engineering – and a call to arms for collaboration across stresses and disciplines.

Also focusing on drought and the different molecular mechanisms involved in drought tolerance and drought recovery, Tang and Bassham (2022) address the important process of autophagy and its role in inducing drought tolerance. Autophagy is a subcellular degradation and recycling process that functions during plant development and responses to different stresses. As discussed in their article, autophagy can selectively degrade important proteins such as aquaporins to adjust water permeability, remove damaged proteins to reduce toxicity, and degrade components of hormone signaling pathways to modulate stress responses. In addition, during recovery, autophagy helps reset the cell status. The authors conclude that manipulating autophagy is a promising approach to enhance drought resilience in crops.

CLIMATE-RESILIENT FOOD PRODUCTION SYSTEMS

The review by Zsögön et al. (2022) discusses increasing climate resilience in the food system by diversification of the crops – in terms of both crop species and varieties of a crop – used in global agriculture. The authors outline the impact of climate change on agriculture, including combinations of stress discussed in more depth elsewhere in this special issue, and highlight key aspects of the crop domestication process and crop adaptations to specific environments beyond their center of origin. They ask what we can learn from domestication to apply in the design of new crops for future climatic conditions, be that through classical or new breeding technologies, and capturing of genetic diversity that may have been lost through domestication and artificial selection?

In addition to diversifying our crop portfolio and altering the structure of crop canopies, altering root architecture has long been viewed as a critically important means of improving the climate resilience of crops. Lynch (2022) reviews the role of different root anatomical phenotypes as a means to improve water and nitrogen capture while also sequestering CO_2 in the soil. The metabolic costs, constraints, and benefits of root growth angles, number of axial roots, rooting depth, and lateral branching are explored. The strengths and weaknesses of various root ideotypes are evaluated in the context of low- and high-input soil agroecosystems and various biotic and abiotic stressors, with the goal of defining the optimal fitness of root phenotypes using *in-silico* modeling tools across a range of scales and environments.

AIR POLLUTION

In addition to climate-driven stresses brought about by greenhouse gas emissions, anthropogenic air pollutants such as ozone (O_3) can result in major oxidative stress, reduced rates of photosynthesis, accelerated senescence, and decreased crop yields. In their review of the negative impacts that rising O_3 levels have on crop performance, Montes et al. summarize the results gained from years of studies conducted at Free Air Concentration Enrichment (O_3-FACE) facilities (Montes et al., 2022). The authors detail the major observations gathered from O_3-FACE facilities throughout the globe in the Northern Hemisphere and the different responses of C_3 photosynthesis (e.g., chickpea [*Cicer arietinum*], soybean, rice, snapbean [*Phaseolus vulgaris*], wheat, and various woody crops) compared with C_4 photosynthesis (e.g., maize, sorghum [*Sorghum bicolor*], sugarcane [*Saccharum officinarum*], and switchgrass [*Panicum virgatum*]) crops. Several O_3-FACE studies have also revealed large genetic variations in the sensitivity to O_3 exposure, which provide opportunities to potentially reduce crop damage and reductions in crop yield brought about by O_3 in the future. Furthermore, the authors discuss the interactions of O_3 pollution with other climate change stressors including drought and heat and the potentially ameliorating effects of elevated atmospheric [CO_2].

PLANT IMMUNE RESPONSES

Climate change is altering the diversity and spatial distribution of many different pathogens, as well as the disease outcome from pathogen infection of crops, impacting agricultural production. As a wider range of pathosystems is investigated, and the identification of molecular mechanisms underlying multigenic quantitative resistance increases, Delplace et al. (2022) argue for the plant defense response to be seen as a complex network of interactions with a spectrum of disease outcomes. They demonstrate the networked nature of pathogen detection at the cell surface and intracellularly and the key role dynamic protein complexes play in both detection and signal transduction. The review highlights network properties with relevance to biological function in host immunity, as well as the need to examine immunity within fluctuating environmental conditions and the value of large-scale data (with increasing cellular and temporal resolution) and network integration to enable prediction of immunity under a changing climate.

The reviews contained in this special issue not only provide new insights into the major challenges presented by the global climate crisis, but also illuminate our mechanistic understanding of the ways in which plants respond and adapt to a wide range of environmental stresses including anthropogenic, abiotic and biotic stressors, and combinatorial stresses to plants, soils, and associated microbiomes (Zandalinas et al., 2021). Such novel information will provide researchers with the knowledge they will need to formulate creative strategies for the development and testing of the climate-resilient crops essential for our immediate future to sustain and enhance global food security and plant biodiversity.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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REFERENCES

Bebber, D.P. (2015) Range-expanding pests and pathogens in a warming world. *Annual Review of Phytopathology*, **53**, 335–356.

Berrío, R.T., Nelissen, H., Inzé, D. & Dubois, M. (2022) Increasing yield on dry fields: molecular pathways with growing potential. *The Plant Journal*, **109**, 323–341.

Bevacqua, E., Vousdoukas, M.I., Zappa, G., Hodges, K., Shepherd, T.G., Maraun, D. *et al.* (2020) More meteorological events that drive compound coastal flooding are projected under climate change. *Communications Earth & Environment*, **1**, 47.

Bormann, K.J., Brown, R.D., Derksen, C. & Painter, T.H. (2018) Estimating snow-cover trends from space. *Nature Climate Change*, **8**, 924.

Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R. & Chhetri, N. (2014) A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, **4**, 287–291.

Crippa, M., Solazzo, E., Guizzardi, D., Monforti-Ferrario, F., Tubiello, F.N. & Leip, A.J.N.F. (2021) Food systems are responsible for a third of global anthropogenic GHG emissions. *Nature Food*, **2**, 198–209.

Cuthber, M.O., Gleeson, T., Moosdorf, N., Befus, K.M., Schneider, A., Hartmann, J. *et al.* (2019) Global patterns and dynamics of climate–groundwater interactions. *Nature Climate Change*, **9**, 137.

Dai, A., Zhao, T. & Chen, J. (2018) Climate change and drought: a precipitation and evaporation perspective. *Current Climate Change Reports*, **4**, 301–312.

Delplace, F., Huard-Chauveau, C., Berthomé, R. & Roby, D. (2022) Network organization of the plant immune system: from pathogen perception to robust defense induction. *The Plant Journal*, **109**, 447–470.

Desaint, H., Aoun, N., Deslandes, L., Vailleau, F., Roux, F. & Berthomé, R. (2021) Fight hard or die trying: when plants face pathogens under heat stress. *New Phytologist*, **229**, 712–734.

Famiglietti, J.S. & Rodell, M. (2013) Water in the balance. *Science*, **340**, 1300–1301.

FAO. (2017) Coping with water scarcity in agriculture: a global framework for actions in a changing climate: Food and Agriculture Organization of the United Nations. Rome. http://www.fao.org/3/a-i5604e.pdf [Accessed 24th December 2021].

Hirabayashi, Y., Tanoue, M., Sasaki, O., Zhou, X. & Yamazaki, D. (2021) Global exposure to flooding from the new CMIP6 climate model projections. *Scientific Reports*, **11**, 3740.

Iizumi, T., Shiogama, H., Imada, Y., Hanasaki, N., Takikawa, H. & Nishimori, M. (2018) Crop production losses associated with anthropogenic climate change for 1981–2010 compared with preindustrial levels. *International Journal of Climatology*, **38**, 5405–5417.

IPCC. (2021) Climate Change 2021: The Physical Science Basis. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, C., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R. & Zhou, B. (Eds) *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press, pp. In press.

Kaur, G., Singh, G., Motavalli, P.P., Nelson, K.A., Orlowski, J.M. & Golden, B.R. (2020) Impacts and management strategies for crop production in waterlogged or flooded soils: a review. *Agronomy Journal*, **112**, 1475–1501.

Kerchev, P.I. & Van Breusegem, F. (2022) Improving oxidative stress resilience in plants. *The Plant Journal*, **109**, 359–372.

Kuromori, T., Fujita, M., Takahashi, F., Yamaguchi-Shinozaki, K. & Shinozaki, K. (2022) Inter-tissue and inter-organ signaling in drought stress response and phenotyping of drought tolerance. *The Plant Journal*, **109**, 342–358.

Leng, G. & Hall, J. (2019) Crop yield sensitivity of global major agricultural countries to droughts and the projected changes in the future. *Science of the Total Environment*, **654**, 811–821.

Lynch, J.P. (2022) Engineering root architecture to address global challenges. *The Plant Journal*, **109**, 415–431.

Montes, C.M., Demler, H.J., Li, S., Martin, D.G. & Ainsworth, E.A. (2022) Approaches to investigate crop responses to ozone pollution: from O_3-FACE to satellite-enabled modeling. *The Plant Journal*, **109**, 432–446.

Naumann, G., Alfieri, L., Wyser, K., Mentaschi, L., Betts, R.A., Carrao, H. *et al.* (2018) Global changes in drought conditions under different levels of warming. *Geophysical Research Letters*, **45**, 3285–3296.

Pedersen, J.S.T., Santos, F.D., van Vuuren, D., Gupta, J., Coelho, R.E., Aparício, B.A. *et al.* (2021) An assessment of the performance of scenarios against historical global emissions for IPCC reports. *Global Environmental Change*, **66**, 102199.

Rivero, R.M., Mittler, R., Blumwald, E. & Zandalinas, S.I. (2022) Developing climate-resilient crops: improving plant tolerance to stress combination. *The Plant Journal*, **109**, 373–389.

Searchinger, T.D., Wirsenius, S., Beringer, T. & Dumas, P. (2018) Assessing the efficiency of changes in land use for mitigating climate change. *Nature*, **564**, 249–253.

Tabari, H. (2021) Extreme value analysis dilemma for climate change impact assessment on global flood and extreme precipitation. *Journal of Hydrology*, **593**, 125932.

Tang, J. & Bassham, D.C. (2022) Autophagy during drought: function, regulation, and potential application. *The Plant Journal*, **109**, 390–401.

United Nations. (2019) *World population prospects 2019: Highlights*. New York, NY: United Nations Department for Economic and Social Affairs.

Voss, K.A., Famiglietti, J.S., Lo, M., Linage, C., Rodell, M. & Swenson, S.C. (2013) Groundwater depletion in the Middle East from GRACE with implications for transboundary water management in the Tigris-Euphrates-Western Iran region. *Water Resources Research*, **49**, 904–914.

Vousdoukas, M.I., Mentaschi, L., Voukouvalas, E., Verlaan, M., Jevrejeva, S., Jackson, L.P. *et al.* (2018) Global probabilistic projections of extreme sea levels show intensification of coastal flood hazard. *Nature Communications*, **9**, 2360.

Wang, J., Vanga, S.K., Saxena, R., Orsat, V. & Raghavan, V. (2018) Effect of climate change on the yield of cereal crops: a review. *Climate*, **6**, 41.

Zandalinas, S.I., Fritschi, F.B. & Mittler, R. (2021) Global warming, climate change, and environmental pollution: Recipe for a multifactorial stress combination disaster. *Trends in Plant Science*, **26**, 588–599.

Zhao, M. & Running, S.W. (2009) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940–943.

Zika, M. & Erb, K.H. (2009) The global loss of net primary production resulting from human-induced soil degradation in drylands. *Ecological Economics*, **69**, 310–318.

Zsögön, A., Peres, L.E.P., Xiao, Y., Yan, J. & Fernie, A.R. (2022) Enhancing crop diversity for food security in the face of climate uncertainty. *The Plant Journal*, **109**, 402–414.