

Prospects for plant productivity: from the canopy to the nucleus

Population growth has been closely associated with agricultural production, since the first famine predicted by [Malthus \(1798\)](#) up to the Green Revolution of the past century. Today, we continue to face increasing demand for food and crop production ([Tilman *et al.*, 2011](#)). Considering the combined caloric or protein content of the 275 major crops used directly as human foods or as livestock and fish feeds, [Tilman *et al.* \(2011\)](#) forecast a 100% increase in global demand for crops from 2005 to 2050. Meeting this demand with the lowest impact on the environment could be achieved by sustainable intensification of existing cropland with reduced land clearing ([Tilman *et al.*, 2011](#); [Fischer and Connor, 2018](#)).

The current global yield trends of the four crops that produce two-thirds of global agricultural calories—maize, rice, wheat, and soybean—are far below what is needed to meet the projected demand. This suggests an urgent need to increase the rate of yield improvement. The current and likely future climatic variations associated with climate change maximize this challenge. Increasing average temperatures, heat waves, periods of limited water supply, excessive rain, and waterlogging have already reduced global crop production and will continue to do so in the future. Diverse and creative strategies, using multidisciplinary approaches and scales, are needed to generate a new ‘Golden Revolution’ in agriculture to meet future production and food demands ([Evans and Lawson, 2020](#)).

Crop growth and grain yield result from the interaction of plants with each other and with the surrounding environment providing cues for adaptation and resources for growth. The crop is a hierarchical system (from genes to molecules, membranes, organelles, cell, tissue, organ, plant, and to the plant community or crop) with feedbacks and compensations within each subsystem and across them ([Passioura, 2020](#)). Papers in this special issue review studies at all levels of organization, highlighting the successes, the failures, and the prospects for achieving the increment in production required in the present century.

Source and sink manipulations to improve crop grain yield

Crop photosynthesis, which is mostly determined by the area of leaves per unit ground surface area (leaf area index) and the distribution of leaves in the canopy, determines crop growth rate during the reproductive stages and, hence, productivity. Studies aiming to increase the photosynthetic rate per unit area of the leaf through the reduction of the diffusive and biochemical limitations of leaf photosynthetic CO₂ uptake are reviewed by [Araus *et al.* \(2021\)](#). They consider various mechanisms including (i) attempts to introduce C₄ metabolism into C₃ crop species (e.g. the C₄-rice project), (ii) genetic modification approaches driving increases in leaf photosynthesis, (iii) studies of the role of reactive oxygen species and their impact on photosynthesis under abiotic stress, and (iv) the overexpression of the *ZMNF-YB16* transcription factor gene enhancing drought resistance by promoting the expression of chaperones, antioxidant enzyme capacity, and photosynthesis in maize. However, attempts to increase grain yield by manipulating the biochemistry and physiology of photosynthesis at leaf level have been unsuccessful so far ([Passioura, 2020](#); [Araus *et al.*, 2021](#)). The translation of the leaf- or plant-based results to the crop level (i.e. per unit ground area) is needed to effectively determine their impact on crop growth and productivity ([Passioura, 2020](#), [Araus *et al.*, 2021](#)). In this sense, [Araus *et al.* \(2021\)](#) claim that not just leaves, but also canopy structure and non-laminar parts, matter when quantifying canopy photosynthesis.

The reproductive organ itself as a photosynthetic source in C₃ cereals (e.g. the spikes of wheat and barley), contributing to grain filling during the last phase of crop growth, is considered by [Tambussi *et al.* \(2021\)](#). Methodological approaches to measure spike photosynthesis, the existence of genetic variability, and a debate about the controversy regarding C₄ metabolism in the spike are thoroughly reviewed. The important contribution of spike photosynthesis in water-limited environments and under heat stress highlights this trait as a promising one to further increase crop productivity in the context of ongoing and future climate change ([Tambussi *et al.*, 2021](#)). As

an alternative strategy to improve photosynthesis, [Flexas et al. \(2021\)](#) discuss the effect of cell wall thickness and composition on mesophyll conductance to CO₂ diffusion and photosynthesis. They propose biotechnological strategies to manipulate cell wall properties aiming to increase photosynthesis rates.

The source activity (crop photosynthesis) also depends on the sink activity (grain number and weight). When a crop is mostly sink-limited (e.g. wheat, maize, and soybean), modification of carbon allocation is another strategy to improve productivity ([Araus et al., 2021](#)). Increasing the number of grains produced per unit area has been the main achievement of the Green Revolution in many crops. Particularly for wheat, this increment was driven by the enhancement of the number of grains produced per spike, mostly due to increased spike growth. To improve grain number and wheat productivity further, the efficiency in setting grains per unit of spike growth at anthesis (or fruiting efficiency) has been proposed as a promising trait. [Pretini et al. \(2021\)](#) comprehensively summarize the notable advances achieved during recent years in understanding the physiology and genetics of this trait. The feasibility of using this trait as an indirect selection criterion to increase grain number and crop productivity in breeding programmes, by either phenotypic or marker-assisted selection, is discussed. Interestingly, this review covers different disciplines (molecular biology, breeding, and crop physiology) at the plant- and land-based levels, bearing in mind the need for a hierarchical approach to effectively increase crop productivity.

Exploring the roots for new strategies to improve crop performance

The plant scientific community is actively searching for new strategies to generate genetically improved, stress-resilient crops, as climate change is inevitably increasing the exposure of crops to stressful conditions. Genes whose expression is induced by stressful conditions, in particular transcription factors, have been largely used to obtain genetically modified crops, with the hope of improving the performance of plants under stress ([Wang et al., 2016](#)). Although this strategy worked well in many cases, especially in model plants, this success is not always paralleled in crops, where the transgenes often impair plants' fitness and grain yield. Among the examples of successful approaches, we can point out a technology developed within the Argentinean plant science community, whereby sunflower HD-Zip transcription factors improve crop performance under different types of stresses ([González et al., 2020](#)). HD-Zip transcription factors, especially those of subfamily I, appear to be promising candidates for molecular breeding, as they orchestrate stress responses without a significant impact on plant fitness ([Perotti et al., 2017](#)).

In this special issue, [Perotti et al. \(2021\)](#) explore a new frontier in HD-Zip transcription factor biology—their effect on

root development and plasticity during plant development and stress. Roots are the main interface for water and nutrient acquisition and also physically anchor the plant to the ground. Owing to the lack of measurable genetic or physiological knowledge, plant-breeding programmes have largely focused on optimizing the aerial part of crops, ignoring the roots. The optimization of both the below- and above-ground components of plants is now becoming a priority in the search for alternative strategies to improve future crops. A large proportion of the plant biomass lies in the roots, which adjust their growth according to the proximity of neighbouring plants. This is an essential feature for crop plants, as normally seeds are sown at a high density, and their root systems will face competition for water and nutrients. Recently, a model was produced to predict the spatial distribution of the roots of individual plants according to the density of neighbouring plants ([Cabal et al., 2020](#)). This study could pave a theoretical path to improve farming strategies to maximize nutrient and water uptake by roots, and ultimately crop grain yield.

Plant roots achieve such a spatial organization by sensing the presence of not only nutrients and water but also compounds released by neighbouring plants ([Herz et al., 2018](#)). In a process known as allelopathy, some plant species release chemical compounds that inhibit the germination or growth, or interfere with the development, of neighbouring plants and the microbial soil community ([Macias et al., 2020](#)). The manipulation of these compounds for biotechnological purposes is also becoming a point of interest as a natural alternative to weed management, especially in the context of poor public perception of the strategies currently used to deal with this problem ([Macias et al., 2019](#)). Rice plants release momilactones, which efficiently inhibit the growth of neighbouring plants, and have become a model to study this process and how it could be manipulated for crop improvement ([Serra et al., 2021](#)). In this issue, [Serra et al. \(2021\)](#) explore this natural plant warfare mechanism by focusing on the mode of action of momilactones, their biosynthesis, and their relevance for weed management.

Plants can also use chemical compounds to positively interact with the soil biosphere ([Cipollini et al., 2012](#)). Among these compounds are organic acids, which are present in exudates from the roots that are stimulated by many environmental stresses, and which have beneficial effects for the plant and its neighbours ([Panchal et al., 2021](#)). The manipulation of the biosynthesis of these compounds or release pathways with the aim of improving crop performance is one of the current developing strategies in molecular breeding. For example, transgenic tobacco plants that show over-secretion of citric acid increase the dissolution of insoluble phosphate in the soil, thus improving phosphate uptake and plant performance in deficient soils ([López-Bucio et al., 2000](#)). In this issue, organic acids and other signalling metabolites, such as nucleotide sugars, are reviewed in the context of plant stress responses and development ([Panchal et al., 2021](#), [Figueroa et al., 2021](#)).

Signal transduction and epigenetic alterations in response to stressful conditions

Plants can sense light and temperature in a very similar way by using phytochrome B (PhyB) as a photoreceptor and thermoreceptor (Legris *et al.*, 2016). Modulating the PhyB response is an interesting strategy to improve plant performance in a time of global warming (Wies *et al.*, 2019). PhyB can decode information obtained from light and temperature and, in response, reprogramme plant development and physiology to maximise carbon balance and to adapt to the environmental conditions (Casal and Questa, 2018). In this special issue, the signalling cascade triggered by PhyB, and the concomitant plant response, are reviewed in depth by Hernando *et al.* (2021). The biotechnological manipulation of receptors with the aim of improving plant performance is challenging given the pleiotropic effects that an alteration in any receptor could produce. An alternative strategy could include the manipulation of the signalling cascade downstream of the stress perception. This strategy is potentially more flexible and could be fine-tuned and directed to a specific outcome. Expanding our knowledge of the signalling cascades triggered by stressful conditions in plants is imperative. Both Martínez Pacheco *et al.*, (2021) and Welchen *et al.* (2021) discuss the signalling hubs controlled by the Target of Rapamycin (TOR) signalling network and consider the role of mitochondria in stress-response signalling.

In addition to the effect of human greenhouse gas emission on global warming, it also produces a decline of the protective ozone layer, resulting in greater exposure to UV radiation. Although plants can tolerate UV radiation, and exposure to natural UV radiation even appears to improve recovery from desiccation in some desert plants (Ekwealor *et al.*, 2021), this radiation normally has harmful effects resulting from DNA damage (Strzalka *et al.*, 2020). Plants deploy an arsenal of tools to protect themselves from UV radiation; these range from specialized pigments to transcriptional reprogramming, enhanced DNA damage repair mechanisms, and post-transcriptional regulation (Re *et al.*, 2020; Qian *et al.*, 2020; Tanaka *et al.*, 2002). UV-B is the main waveband reaching the Earth's surface that causes deleterious effects on DNA integrity. In this special issue, Casati and Gomez (2021) evaluate the effects of UV-B on chromatin dynamics and DNA damage and how this process impacts plant fitness.

It is interesting to observe that many epigenetic pathways, for example, the mechanisms involved in transposon silencing, are also important for DNA damage repair under UV-B exposure (Casati and Gomez, 2021). Direct epigenetic modifications over DNA or histones have been shown to influence plant metabolism and stress tolerance (Lamke and Baurle, 2017). Understanding the molecular mechanisms behind the response to UV-B and the molecular basis of epigenetic adaptation of plants to a hostile environment is essential to develop optimal strategies for molecular breeding in the future.

Interestingly, epigenetic-triggered adaptation can be inherited transgenerationally, allowing the offspring to better adapt to the hostile environment (Ganguly *et al.*, 2017). Transposable elements (TEs) play critical roles in such epigenetic adaptation programmes. TEs are commonly activated during stressful conditions, with various outcomes destined to increase the chances that the offspring will survive extreme conditions (Dubin *et al.*, 2018). The mobilization of TEs after stress-induced activation can lead to neofunctionalization of genes, the creation of new stress-inducible regulatory elements, and even modification of the 3D structure of the chromatin, providing new regulatory features (Ariel and Manavella 2021; Dubin *et al.*, 2018; Gagliardi *et al.*, 2019). TE activation also triggers a burst in the production of non-coding RNAs (ncRNAs), which impacts plant fitness (Nuthikattu *et al.*, 2013). Among these ncRNAs, small RNAs not only trigger DNA methylation, gene silencing, and gene transcription reprogramming but also represent one of the main components of inheritable epigenetic responses to stressful conditions (Ariel and Manavella, 2021). Interestingly, both long ncRNAs and small ncRNAs, produced in response to stress, can interact with the chromatin and reshape the epigenetic landscape—a level of regulation that, along with improved physiological performance, can be transmitted to new generations.

In a time of climate change, the stress-induced activation of TEs is not trivial and leads us to explore the epigenetic pathway as a source of crop improvement. Extreme temperatures activate epigenetic programmes such as TE activation but also affect the dynamics of RNAs secondary structure, which in turn affect their functions. An example is the role of the mRNA secondary structure in maize during anthocyanin biosynthesis (Wang and Wessler, 2001). In Arabidopsis, an *in vivo* genome-wide study revealed that the mRNA secondary structures of stress-inducible genes tend to be dynamic (Ding *et al.*, 2014). In this regard, environmental changes triggered by temperature are more likely to affect ncRNAs, as they rely on secondary structures to achieve their functions. Understanding the structure–function relationship of the RNA secondary structure is critical for future crop improvement by precision engineering using gene editing. In this issue, Zhu *et al.* (2021) provide an updated overview of our current tools designed to study RNA structure and functions. Nowadays, the understanding of the epigenetic pathways has gained particular importance with the development of CRISPR/Cas9-based editing tools that allow alteration of the crop epigenome and stress resistance without changing the DNA sequence (Khan *et al.*, 2018; Puchta, 2016).

Concluding remarks

Food demand has been increasing over the past centuries and will continue to rise in the near future. Crop production has improved accordingly in the past, either by increasing the area of land under cropping or by increasing the productivity of

agricultural land. There is wide consensus that future increases in crop production should be achieved by sustainable intensification and without clearing new land. Scientific knowledge is being generated faster than ever before, but we are still failing to translate this knowledge into improved crop productivity (Passioura, 2020). Multidisciplinary, hierarchical approaches should be implemented to generate the Golden Revolution in agriculture, proposed by Evans and Lawson (2020), that is necessary to meet future demands. Within this spirit, it is critical to keep alive scientific meetings where interdisciplinarity, rather than specificity, is the premise. The biannual meeting of the Argentinean Society of Plant Physiology, which inspired this special issue, is an excellent example of a scientific event where molecular biologists, ecophysiologicals, and plant breeders come together to discuss new ideas and strategies to improve crop productivity.

Keywords: Climate change, crop epigenetic manipulation, crop productivity, photosynthesis, plant–plant interactions, stress-resilient crops

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