Theor. Exp. Plant Physiol. (2024) 36:567–582
https://doi.org/10.1007/s40626-024-00338-z

Crop physiology, the technology and the production gap

João Paulo Rodrigues Alves Delfino Barbosa · Alana Batista Cruz · Alexandre dos Santos Botelho · João Paulo Pennacchi · Gabriela Faria Santana

Received: 30 October 2023 / Accepted: 30 April 2024 / Published online: 11 June 2024

Abstract Crop physiology is a bridge between plant science and agronomy. Historically, crop physiology uses advanced technologies that rely on biochemical and biophysical plant traits to promote on-farm technological innovation that significantly contribute to increased plant production. Looking back and forward in the decadal scale, crop physiology is a prominent player in the reduction of plant production gap. The current plant production gap results from the growing world population and the stagnation of plant production. To reduce this gap, the plant production must be increased in the near future and continue to increase with population. In our opinion, there are two important concerns that aggravate this scenario and impose a great challenge to crop physiologists in the next few years. Firstly, a past decade of little crop yield gain. Second, the requirement that any increase in plant production should occur in a sustainable way, with minimal or no increases in land occupation, besides water and nutrients inputs. This great challenge is thought to be solved by transdisciplinary efforts to quickly incorporate new scientific discoveries and technological advances in practical applications in crop science. It is evident that crop physiology is the catalyst to such interaction. In this venture we let our opinion by philosophically discussing some contributions of crop physiology that, we believe, deserve to be explored as possible paths to reduce the plant production gap in the future, especially the implementation of technology to techniques used to overcome environmental factors in a systemic phenotyping approach.

Keywords Food Gap · Enviromics · Phenotyping · Phenomics · Genomics · Plant sciences · Plant-environment interaction · Modern farming

J. P. R. A. D. Barbosa (✉) · A. B. Cruz · A. dos Santos Botelho · J. P. Pennacchi · G. F. Santana
Laboratório de Ecofisiologia Vegetal, Departamento de Biologia, Instituto de Ciências Naturais - Universidade Federal de Lavras, Lavras, MG, Brazil
e-mail: jp.barbosa@ufla.br

1 Conceptual background

1.1 The production gap and the technological applications in crop science

The plant production gap is the difference between the amount of products of plant origin (food, energy and fiber) that is demanded by the human population and the amount of those products produced over time. The plant production gap challenge could be stated as: if the human population grows, the demand for products from plants also grows, also requiring plant production to increase. However, these growth rates are different as the growth rate of the population is greater than the growth rate of the plant production (Fig. 1).

The plant production gap has been a threat to the human population from the beginning of humanity

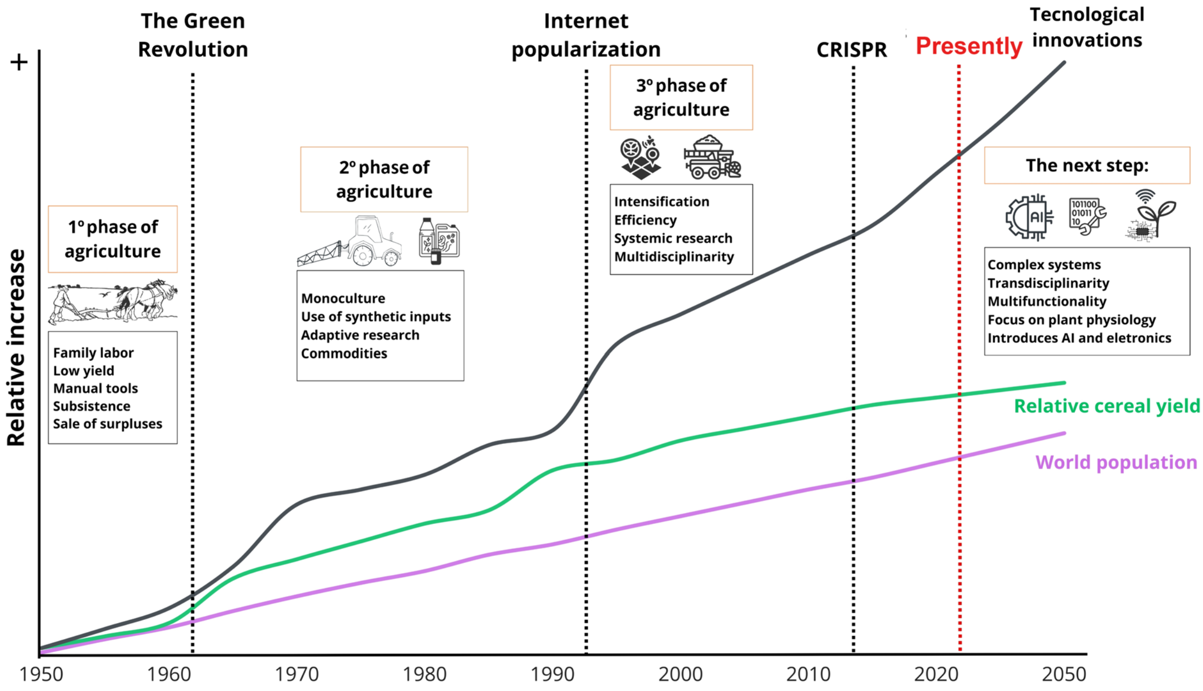

Fig. 1 Representative diagram of technological advances, crop science methods, cereal yield production, and population increase running in time

and the path to overcome it has always been thought as: plant production should grow by the opening of new croplands and/or by implementation of more advanced farming techniques. In past realities the increase in cultivation area of crop plants appeared to be the most suitable solution to close the production gap, as the speed of technology development and its applications in agriculture was very slow.

In the beginning of the 1800's, Thomas Malthus statistically proposed a theoretical model explaining the production gap (Malthus 1826), known as Malthusianism. This theory postulates that population growth is potentially exponential, while the growth of the plant production is linear, which eventually standardizes the point of the production gap.

Afterwards, the technological advances of the Green Revolution in the early 50's lead to the inauguration of Crop Science and to significant improvements in agriculture, resulting in epic shift on the increasing rate of plant production. This increment rate of the 50's was greater than population growth rate, proving Malthusianism to be wrong for not considering technology advances as a factor in the equation (reviewed in Lal 2014; Long et al. 2015). This hystorical shift in the crop production indicates that the consistent addition of technological advances to crop science can potentially overcome the plant production gap (Fig. 1).

Figure 1 provides an overall analysis of the key technological milestones since the Green Revolution on crop science. It highlights the discrepancies between technological progress and crop production over time, intertwined with population growth and the ensuing growing demand for food. Notably, especially after the widespread adoption of the internet, technological development exhibited an almost exponential growth, ushering in an era of innovations unparalleled in history. However, this recent technological "boom" did not yet proportionally reflect in agricultural productivity. Thus, translating technological advances into productivity gains is always urgent for crop science (Araus et al. 2018).

From this philosophical perspective, technology provides expressive growth in phases with cereal yields and world population, and this is probably true for other crops. Figure 1 also provides that the rate of population growth keeps ascending while the cereal yields stagnates, indicating the importance of technological breakthroughs in crop science as a path to diminish the yield gap in the near future (Aggarwal et al. 2019).

Forecasts of socio-economic-environmental scenarios for the next two decades follow the trends shown in Fig. 1 and explicitly indicate that Malthusianism is again at the door. In order to guarantee sufficient food supply, the plant production gap has to be reduced in the next few years (reviewed in Lal 2014; Tilman et al. 2011).

Looking back to our recent past, the production gap could be solved by mimicking the same strategies of the late 1950's. However, the current scenario is not the same as in the 50's, due to ongoing change in climate conditions and cropland availability, which influence not only plant behavior but also limit natural resource use. In this present scenario, the increase in plant production must occur without increasing, or rather reducing, concomitantly the use of natural resources, agricultural inputs and the opening of new croplands (Pennacchi et al. 2022).

The current production gap challenge is therefore different from the past and comprises the need to increase plant production, meeting the requirements for social, economical and environmental sustainability in adverse climatic conditions or in inapt areas (i.e.: increased temperature, abnormal rainfall, soil salinity and increased concentration of greenhouse gases). In other words: crop scientists have to develop technological applications to allow plants to produce more, with less agricultural inputs and with great resilience under adverse environments.

1.2 Crop physiology and the production gap

Crop science, as an embracing topic, aggregates diverse related research areas, such as crop physiology. This is a branch of plant science closely related with agronomy and majorly compromised with the explanation of the physiological basis of plant production and crop yield. Crop physiology is an interface between agronomy and plant physiology: agronomy provides the questions and plant physiology provides the tools, the methods and the scientific understanding to elucidate the mechanisms that drive plant production. Crop physiology serves as an important bridge between scientific discoveries and technological innovation on one side, to on-farm technological application on the other side.

Along its history, crop physiology has developed its own practical tools and methods, which explain its botanical-theoretical background linked to its practice-agronomic problems. The combination of available analytical tools with great intellectual and scientific efforts enables the deepening of the understanding of physiological mechanisms defining plant production, opening space for new agricultural techniques and directing biotechnological programs for trait-based crop breeding.

The first noteworthy contributions of crop physiology are from the 60's and 70's, when crop physiologists demanded and developed commercially available field-worthy instruments. The development and availability of instruments and methods on crop physiology in the 60's and 70's was only possible due to the post-war advances in engineering, electronics and chemistry technologies added to plant sciences. Some examples are the advent of high-throughput sensors for real-time monitoring plant traits and environmental conditions such as PAM chlorophyll fluorescence-meters, portable infrared gas-analyzers (IRGA's), a diversity of low-cost chemical reagents, sensors and laboratory equipment, and the incorporation of computational resources to statistics and modeling.

The development of measuring devices allowed non-destructive *in situ* analysis of key physiological traits and environmental characteristics, such as photosynthesis and transpiration responses to temperature and to the air vapor pressure deficit. The field-worthy instruments have also broken the time and space limitations of experimentation, expanding laboratory techniques with maintained accuracy, helping crop physiologists to unveil crop plants metabolism, development and production, not only under controlled conditions but also in face of real environmental conditions (reviewed in Beyschalg and Riel 2007). These methodological advancements were important to elucidate environmental controls and to quantify the determinism of a number of biochemical and biophysical traits to plant production interaction with environmental variability. In our opinion, this is the beginning of a tentative high-throughput quantification of the plant-environment interaction.

From the 70's to date, crop physiology has explored the mechanisms of plant production at even finer levels of details. Those achievements of the late 80's and early 90's can be attributed to the "omics" era (reviewed in Van Emon 2016) which has the advent of transgenic plants, and the validation of the mechanisms pointed out in the crop physiology researches of the early 60's. As examples, crop physiology researches lead to breakthrough discoveries on how physiological processes respond to higher atmospheric CO_2 concentrations, depletion in soil fertility and water availability, soil salinization, air pollution, heavy metals contamination, amongst others (reviewed in Barbosa et al. 2012). In other words, the research aims in the 90's was still the understanding of the plant-environment interactions, but the method was directed by a mechanistic-reductionism principle (reviewed and philosophically contextualized in Lüttge 2023).

In the last two decades the evolution in data science, robotics, computational resources capacity and sensor automation led to important advances in genomics and the arising of phenotyping platforms, opening a new phenomics era. However, this super capacity to generate and process environmental, genomic and phenomic data is lacking in an effective output of information prompted to increase plant production. In fact, we are now attempting that the interaction among the parts is more important than the isolated parts (reviewed in Souza et al. 2016) and so crop scientists are developing methods and practical tools to account for the differential response of the interactions of genotypes (G) across environments (E) producing phenotypes (P), which is currently known as enviromics (reviewed in Resende et al. 2021). Regarding this urgent need to understand the genotype by environment interaction (G.E), our opinion is that crop physiology has, again and undoubtedly, an important task on transforming scientific discoveries to technological applications and practical innovations to increase plant production outputs on crop lands. We will further discuss, in depth, this path of contribution of crop physiology to reduce the plant production gap in a topic of systemic phenotyping.

From the 50's to date it is worth mentioning that significant biotechnological and scientific outputs from crop physiology resulted in a consecutive increase in plant production, particularly because of all the efforts to unveil plant-environment interactions and its determinism to plant production. So, it is evident that throughout the history of crop science, crop physiology was always an significant catalyst to the efforts to reduce the production gap by bridging science knowledge to on-farm technological applications. This has been possible because crop physiologists develop and use plant science methodological tools to investigate plant-environment interaction in a trait-based approach and then translate experimental data into theoretical knowledge ready to be applied to new agricultural techniques.

1.3 Current contribution of crop physiology to close the production gap

Crop physiology has been contributing throughout history to increase crop yield, reducing the production gap in many ways, and its contribution as a catalyst to technological advances in crop science is widely recognized. The recent advances in molecular biology and plant genetics offer a new opportunity to further drive these efforts.

Metabolic engineering emerges as a promising tool in this context, allowing for increased nutrient uptake (such as nitrogen and phosphorus), the production of specific metabolic compounds, and enhanced tolerance to biotic and abiotic stresses (Dasgupta et al. 2020). Despite the challenge of modulating metabolic pathways due to the complexity of the pathways and their crosstalk, and the high demand of time and financial resources, important achievements have been made by crop physiologists using molecular biology techniques (Feng et al. 2007; Brooks et al. 2023).

Considering the complexity and challenges associated with modulating metabolic pathways from the laboratory to the field, it is imperative that crop physiologists take part in the practical interaction between the knowledge of crop physiology and of metabolic engineering. Any biotechnological effort aimed at optimizing the benefits derived from the application of metabolic engineering in agriculture depends on the integrative capacity of the crop physiology to regard science and on-farm practices simultaneously.

Many positive outputs from this interaction are now evident. For example, Wei et al. (2022) explored the use of transcription factors to regulate physiological traits such as photosynthesis, nitrogen assimilation, and flowering in rice plants. Specifically, they investigated the role of the gene *Dehydration-Responsive Element-Binding Protein 1C* (*OsDREB1C*), which is induced by both light and nitrogen scarcity. Overexpression of the *OsDREB1C* (*OsDREB1C*-OE) resulted in increased photosynthetic capacity and nitrogen use efficiency due to higher nitrogen absorption, as well as enhanced efficiency in photoassimilates partitioning to rice grains, increasing rice grain yield and the harvest index.

Some important contributions of crop physiology are in the path of crop breeding using biotechnological tools to bioengineering major C3 grass crops, such as rice and wheat, aiming to increase their carbon budget facing nitrogen deficiency and water scarcity (Furbank et al. 2019; Chen et al. 2023). Efforts in this bioengineering path were directed to the modeling of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), which has an affinity for atmospheric carbon dioxide (CO_2) and oxygen (O_2). Its oxygenase activity is recognized to lead to considerable losses in carbon incorporation through photorespiration. Therefore, reducing affinity to oxygen and enhancing the carboxylase activity could be a promising strategy to improve photosynthesis efficiency and, consequently, increase plant production by incrementing the carbon gain.

However, this strategy is expensive and time consuming as it deals with the high complexity of the structural, metabolic, and molecular standpoints (Whitney et al. 2015; Conlan et al. 2019; Iqbal et al. 2021). Thus, more practical, rapid, and cost-effective efforts should be directed towards developing studies to increase the concentration of CO_2 around Rubisco, which will significantly reduce photorespiration and potentialize positive carbon budget on C3 crops (McGrath and Long 2014).

An alternative strategy to increase the production of C3 crops is focused on the transformation to a more C4-like plant. In dry environments, characterized by high temperatures and intense solar radiation, the C4 metabolism delivers greater efficiency in water, nitrogen, and solar radiation utilization to carbon capture in relation to C3. This is due to reduced photorespiration and improved of water-use efficiency (Ghannoum et al. 2010; Schuler et al. 2016). Unlike the C3 metabolism, C4 uses the enzyme phosphoenolpyruvate carboxylase (PEPcase) as the receptor for inorganic carbon in mesophyll cells. This enzyme has the advantage of not exhibiting dual affinity for CO_2 and O_2. The C4 metabolism requires specialized anatomy, known as Kranz anatomy, which ensures high CO_2 concentrations around Rubisco, confined to bundle sheath cells (Sage 2002; Sage et al. 2014).

The C3 to C4 transformation path has been tried with two basic strategies. First, the strategy of the carboxysomes from cyanobacteria. The cyanobacteria metabolism present a reduced photorespiration due to a mechanism that concentrates CO_2 around Rubisco using the carboxysome organelles, which are microcompartments containing the carbonic anhydrase and Rubisco enzymes (Nguyen et al. 2023). The expression of carboxysomes in the parenchyma cells of leaves of C3 crops is a promising path to be followed for constructing a CO_2 concentration mechanism in C3 plants, thus enhancing their photosynthetic efficiency and, consequently, their yield. Positive results have been observed in transformed *Nicotiana tabacum* (tobacco) plants, where carboxysomes derived from cyanobacteria were expressed, as reported by Long et al. (2018) and Ni et al. (2022).

The second strategy is transferring a complete C4 cycle to a C3 plant. This path requires an abrupt structural and biochemical change than the carboxysome strategy. As with Rubisco bioengineering, this approach is time demanding and expensive since it deals with the complexity of leaf anatomy, biochemistry, and genetic engineering. As an alternative, species with an intermediate C3-C4 metabolism are of interest, as in the C2 cycle, during the decarboxylation stage, photorespiratory glycine needs to migrate from mesophyll cells to the sheath tissue, where there is increased interaction between mitochondria and chloroplasts, allowing for the re-assimilation of CO_2 near Rubisco (Sage et al. 2012; Schlüter & Weber 2016; Kubis & Bar-Even 2019). That is to say that the main goal to the improvement of C3 assimilation is to introduce more C4-like traits than to completely transform C3 plants into C4 plants.

Photosynthesis can be affected by high-temperature conditions, causing damage to electron transport. In this context, the inhibition of Rubisco activity in high-temperature environments results in decreased Rubisco activation and consequently, reduced CO_2 assimilation. In a study conducted by Feng et al. (2007), genetic engineering techniques were employed to increase the activity of an essential enzyme in the regenerative phase of the Calvin cycle, sedoheptulose-1,7-bisphosphatase (SBPase). The researchers observed that the increased accumulation of SBPase in chloroplasts contributed to better heat stress tolerance in young rice seedlings. Additionally, transgenic plants demonstrates higher CO_2

assimilation efficiency under high-temperature conditions compared to wild plants, indicating that the overexpression of SBPase increases the thermotolerance of Rubisco activase.

These examples clearly illustrate how the manipulation of key genes associated with key physiological traits to plant production can result in significant improvements in crop yield and quality. Therefore, in our opinion it is evident that the interdisciplinarity between crop physiology and metabolic engineering is currently on the right path to contributing to the reduction of the production gap. This kind of interaction among sciences and disciplines has an important potential to enlarge the understanding of the physiological processes defining crop production, and also facilitates the practical application of trait-based plant breeding. However, it is important to highlight that these approaches face significant challenges, including the complexity of the metabolic pathways and the unforeseen outcomes of genetic modifications.

A great number of paths and strategies are being developed by plant scientists, which can be summarized in traditional and molecular (genetic transformation) plant breeding and bioengineering paths. He we will discuss examples of what has been done by plant scientists to increase plant production by altering biochemical and biophysical traits. The technological advances of the next decades will certainly serve as tools to reduce the time and cost needed for genetic transformation and bioengineering. The crop physiologists will have to use these genomic technologies, filling important gaps in the current physiological understanding of plant production.

2 Is the current production deficit attributable to deficiencies in crop physiology?

Gains in plant production from the Green Revolution appears to be slowing down or even stagnating over time, even with the massive advances in technology of the past two decades as (also supported by Lal 2014; Long et al. 2015; Zenda et al. 2023). That is to say that the current available technology is not yet resulting in an increase in plant production. This scenario is different from what was observed in the 60's-70's and again in the 80's-90's, when the rise in technology availability reflected directly in the increase in cereal yield (Fig. 1).

In our opinion, any proportional increase between technology and plant production is related, more directly or indirectly, to the catalyst role of crop physiology in aggregating technological advances to crop sciences, through breeding programs and management research, leading to an increase in plant production. So, the question arises: Is the present plant production gap caused by a lack of crop physiology? We would like to present our opinion and go further philosophically discussing this issue considering the two possible answers to the question: no or yes.

Considering the first possible answer: no. In this case there is no lack of crop physiology causing the production gap. So, crop physiology is still present and effectively catalyzing the addition of technology to crop science, but this technological amendment has had little impact on increasing plant production. In fact, there is some evidence supporting that the increase in technology is unproportional to the increase in plant production due to the reach of biological limits, or saturation of morphophysiological traits, that are particularly determinant to plant production (as reviewed by Long et al. 2015; and Zang et al. 2023).

Nevertheless, this must refer much more to the limit that can be achieved by classical breeding with specific management packages rather than to the biological limit of crops. But, if this is the case, some traits that can be listed at the physiological limit on these crop varieties are the optimization of light interception, water use efficiency, light use efficiency, resistance to pests and diseases, and the enhancement of phenotypic plasticity directed towards adaptation to different climatic conditions. On the other hand, as we discussed in Sect. 1.3, there are several examples showing that photosynthesis, growth and yield can be substantially increased through metabolic engineering. The discussion of Sect. 1.3 indicates that there are many physiological processes that are far from the saturation point, as evidenced by the higher growth or yield of some transgenic plants.

In fact, the difference between the yield potential of modern genetic resources and the actual yield achieved, at the farm level, highlights the great possibility of increasing plant production through management. Genetic advances can truly lead crop potential production closer to its biological limits, although this is not true for the real harvests, at the field (Foulkes et al. 2022). In this scope, it is crucial to better understand the interactions of genetics x environment x management (G.C.N), aiming to shorten the gap between real and potential production (Cooper et al. 2021). In summary, there is an urgent need to enlarge the understanding of the G.E interaction in delivering the production as a phenotype. We already mentioned this issue in Sect. 1.2 and we will discuss this topic further in this manuscript.

Regarding the second possible answer, yes. In this case there is a lack of crop physiology that inhibits the effective implementation of technology on crop science, limiting the plant production increment. If this is the case, there is an urgent need to get crop science to be more prone to crop physiology in order to catalyze the implementation of available technology to on-farm practices, resulting in higher plant production.

In addition to the biotechnological and bioengineering technologies discussed in Sect. 1.3 , it is evident that the integration of current telecommunication, electronics and computational technology to crop science positively resulted in agronomical advances. We can point out some good examples such as digital agriculture, precision agriculture and bioinformatics application into modern farming. However, it is evident that the implementation of those technological applications did not result in a proportional increase of plant production, as it did in the past. This way, modern farming comprises the most promising technologies for crop management improvement, but needs further practical applications to be more assertive in real-time operation, which is a reflection of the lack of physiologically-based science and technology applied in agriculture (Ziberman et al. 2016).

In a practical perspective, when plants are established in the field, the genetic potential is already set and cannot be improved or altered. Also, farmers have very limited control over the climatic environment, mainly in rainfed, open fields. Thus, agricultural management remains as the factor that farmers can interfere to enhance the genetic capacity of plants to achieve their potential production under a certain climate variability.

Considering those arguments, our opinion is that the plant production gap is caused by a technological lack, which we believe is a consequence of a formation issue of the present generation of crop scientists, that is particularly very poor in plant physiology. We call this problem as "a lack of crop physiology". The crop physiology lack might be a consequence of current academic and scientific formation that is, in general, poor in plant physiology and even more poor in field practices on plant physiology. The current formation of crop physiologists is multidisciplinary, but has yet to achieve transdisciplinarity, a potential subsequent phase.

While multidisciplinarity applies knowledge from one area to another, transdisciplinarity seeks the fusion of scientific findings and its technological applications, fostering new viewpoints and pushing the boundaries of scientific knowledge and technological innovation (Barbosa et al. 2012). In our opinion, crop physiology could be the integrative discipline to promote transdisciplinarity in the formation processes of any professional working with agriculture and crop plants. The goal of transdisciplinarity is not merely to combine techniques and methods from different areas but to generate innovative perspectives and paradigms with practical implications. It is evident that crop physiologists may make the most important contribution to this challenge due their scientific background and skills. To overcome challenges in plant productivity, it is crucial to not just merge scientific findings and brand new technologies, but deeply integrate distinct disciplines, advocating for the holistic view that crop physiology carries in its essence and that, in our opinion, is lacking in the current formation of plant biologists and agronomists.

Thus, it is imperative to improve the formation process of the next generation of crop scientists to not only promote research and technological development but to ensure that innovations are tangible, enlightening, and readily integrable, aiming to align scientific progress with sustainable plant production. We are convinced that crop physiology has the transdisciplinarity requirements to align scientific progress with sustainable plant production, emerging as a catalyst for this much-needed transdisciplinarity to happen in the crop sciences formation in the near future. In other words, in our opinion crop science needs to be the most physiologically-based science!

Considering those arguments, we consider that there is a great parcel of the available scientific knowledge and technology of plant physiology to be incorporated into crop science through crop physiology. The recent discoveries in the field of plant phenomics have a great potential to shift up plant production in the next decades as it was observed in the the 60's-70's and again in the 80's-90's, but this necessary increment in plant production will only be achieved if the scientific and technological hub is crop physiology. There is urgent to bring a sustainable increment of the crop production by supporting more efficient agricultural management and boosting plant production without increasing the requirement of on field resources. However, this ideal scenario will only be achieved with a change in the formation processes with the recognition of the importance of the crop physiology as catalyst to the addition of science and technology to on-farm plant production practices.

3 How can advancements in crop physiology contribute to mitigating the near-future production gap?

Considering the discussion to this point, we understand that: i) there are currently significant advances in genomics that can potentially contribute to the immediate reduction of the production gap; ii) there are available technological packages and resources ready for applications in crop monitoring and management that potentially enhance the production in crop lands. From these perspectives, we present the Systemic Phenotyping as a path that, in our opinion, should be taken as a standing point to integrate across the advances in genomics, management and scientific formation to reach significant and sustainable increments in crop production.

3.1 The systemic phenotyping as a conceptual standing point for a trait-based optimization of the plant production

Crop physiologists have been enlarging the understanding of how biochemical and biophysical traits at fine organizational levels are related to plant production. These physiological traits are intrinsically influenced by the interactions of plants with their physical, chemical and biotic environments, culminating in the expression of the phenotype. Within this consideration, the production of a plant could be approached as an integrative, emergent phenotypic trait. In a systemic conceptualization, production is a phenotypic trait that emerges from morphophysiological traits of lower hierarchical levels, in time or space (Barbosa et al. 2012; Souza et al. 2016; Pennacchi et al. 2021; Cooper et al. 2021).

Within this perspective, crop physiologists that are researching the phenomics aiming the increase in plant production must consider that the plant production (PP) itself is the phenotype, and any variation on the genotype (G), or/and environment (E), has the potential to cause a variation on the production. From this perspective, a gain in crop yield must be based on a systemic view of the multiple-traits varying according to the genotype, environment and genotype-environment interaction (G.E), which can be called the enviromics (reviewed in Resende et al. 2021). Again, it is important to highlight that the interaction variable G.E is as much important as the isolated variables G and E, being a variable to the equation itself. To systematize this approach, the starting-point is the classical phenotype formalism (Eq. 1), which statement is that the phenotype (P) can be defined as a systemic resultant of the genotype (G), of the environment (E) and of the genotype-environment interaction (G.E) (Xu, 2016; Pennacchi et al. 2021; Resende et al. 2021).

$$P = G + E + G.E \quad (1)$$

To include the management technology variable to the Eq. 1, we can consider that the variable E can be decomposed in two components: the climatic component and the management, that is the "production nexus" component. The climatic component (C) corresponds to the site and seasonal characteristics of rainfall, temperature, frosts, wind speed and other conditions imposed by climate determinants on the cropland and that is difficult or too expensive to manage. The management or "production nexus" component (N) is the technological input package that is available to manage soil fertility, irrigation, crop protection, among others. It is the summarization of the technological level applied to agricultural management to improve the environment to the genotype requirements and to deliver the genetic potential of the crop. Within this consideration, the Eq. 1 can be rewrite from Pennacchi et al. (2021) and Cooper et. (2021) as Eq. 2:

$$PP = G + C + N + G.C.N \quad (2)$$

were plant production (PP) is dependent on the plant genotype (G), the climatic conditions (C), the "production nexus" (N) and the interaction among genotype, climate and management (G.C.N).

The optimization of the variable PP can be carried out considering that G is defined by biophysical and biochemical traits at smaller hierarchical levels, which assume homeostasis values depending on variations in C and N, defining traits at higher hierarchical levels. Thus, the systemic phenotyping processes will only be effective in increasing on-farm PP in the near future if crop physiologists are able to attribute variations in PP to variations in biophysical and biochemical traits in different phenological phases, integrating the spatial and temporal dimensionalities of the envieronment and management technology through the G.C.N variable. That is to say that the development of the methods, tools and formalism to an effective quantitative enviromics is a priority for crop physiologists.

The most sensible scientific strategy to increase plant production using a trait-based approach appears to be the modulation of plants to climatic uncertainties (affecting the variable C) by plant breeding (modulating the variable G aiming resilience) or by resource amendment through crop management (altering the variable N). In this regard, crop physiology can contribute to elucidate some important plant traits defining plant production (especially related to the G.C.N variable), contributing to the selection of genotypes in traditional breeding programs, supporting biotechnological efforts to plant breeding using molecular tools and also validating the research of new bioproducts, biostimulants and management techniques (Wallace et al. 2018).

However, there is an urgent need for a further deepening in the understanding of plant response to the environment, especially under stress conditions, in order to reduce the exposure of the most vulnerable crop systems to adverse events resulting from global climate change. Due to this urgency, paths and strategies that increase plant production by altering the management seem to be less expensive and more effective in the short run, deserving attention and foment by scientific stakeholders.

Considering Eq. 2 and what we discussed so far, crop physiology contributes scientifically and technologically on the variables G and N and in their interaction (G.C.N). We already discussed how crop physiology has been contributing to engineer plant traits and to innovate on management practices. Even if crop physiology has little to no potential to impact in the variable C, it has a strong potential and also has all the scientific tools to investigate the G.C.N interaction and quantitatively determine its importance to increase PP.

The proposal of using a systemic approach in phenotyping efforts is quite challenging, but it is of great technological relevance and scientific contribution to agriculture as it could be a pioneering application to reduce the gap between the technological potential of phenotyping and the productive potential of crops. This is to show that any plant physiology research based in Eq. 2 is of important scientific contribution. Also, tools to quantitatively investigate the G.C.N effects over PP have to be developed and exhaustively explored by the present and next generation of crop physiologists.

3.2 The practical application of the enviromics to a systemic phenotyping

Plant physiologists have been studying and detailing plant-environment interactions and the importance of abiotic and biotic stresses on defining PP for a long time. There are a number of such studies in a multitude of time–space scales and a lot of knowledge has been delivered about plant physiological responses to biotic and abiotic stresses, such as: water scarcity, nutrient deficiency, heat, increase in CO_2, proliferation of pests and diseases. The output consensus of this experimentation is that: in adverse environments there is a disruption of plant homeostasis by impairing physiological traits such as photosynthesis and antioxidant defenses, drastically impacting plant growth. Such decreasing pattern directly affects carbon budget, biomass production and allocation and, consequently plant production (Barbosa et al. 2012; Lal 2021; Zenda et al. 2023).

For this reason, climate changes have become of major concern among crop scientists since they treat food production by the increase of adverse environmental conditions. Thus, scientists from different fields are seeking to go even more deeper in the understanding of the plant-environment relation, and many researches and scientists are interested in technological applications for remote monitoring of plants and their environment in real time and at fine scales, aiming for management practices improvement to reduce the negative impacts of environmental stresses over plant production (Lal 2021; Resende et al. 2021; Ninomiya 2022).

Within such concern, high-throughput phenotyping tools and methods have evolved greatly in the past years and has brought great advances in the monitoring of plant traits, allowing investigation on the variations of the phenotype in higher frequency. Even so, the outputs of the high-throughput phenotyping efforts did not result in proportional practical increase of plant production. So, the next frontier for improving crop management to its best, may be the practical application of the enviromics to a systemic phenotyping. In other words, there is a recognition that the genotype-environment interaction is of great importance to define and monitor the phenotype.

In the last 3 years, a number of studies are adopting enviromics as the environment-dependent part of reaction norm models for genetic performance with the goal of exploiting patterns of G.C.N. The objective of any of these research efforts to study and discretize the G.C.N variable must be, however, to strategically potentialize trait-based self-regulation of the genomic in relation to the variables that may impact it (i.e. C and N) using available technological applications to modem farming.

Currently modern farming management is based on the interpretation of visual or sensor-acquired data, from which farmers infer about plant physiological status. The most common indicators for management are: soil and plant water status, leaf color and area, plant growth rate and phenological development. The biggest limitation for management decisions is based on the lack of precise and real-time information about plant homeostatic status. In this sense, a trait-based integrative information system could boost plant production. Although the idea of a trait-based self-regulation of plant production to the environmental conditions may be seen as a very idealistic and futurist solution, this may be a feasible and fruitful solution to reduce the problem of the technological lack previously discussed.

A number of studies demonstrate that crop plants respond to natural stimuli through gradients or electrical potentials (as revised by Sareen and Maes 2019). Plants exhibit various movements, from climbing habits to prey capture, as seen in carnivorous species of the *Dionaea* genus, and reactions to touch, as in sensitive plants of the *Mimosa* genus. They also adjust the position of their leaves to optimize light interception, responding to hormonal and/or environmental *stimuli*, as described by Hamann et al. (2015) and Sareen (2017). Because of this, the enviromics monitoring and quantification on the field is possible due to the very nature of plants. They are already equipped with intrinsic devices with self-adjusting signaling networks to monitor the surrounding environment, so we just need to capture and translate the plant signals to get the G.C.N variability.

In response to environmental stresses, the majority of the crop plants produce high levels of reactive oxygen species (ROS), an influx of calcium ions (Ca^{2+}), and protein phosphorylation. This systemic response ultimately leads to yield losses if we consider that PP is a result of the physiological homeostasis, which in turn is dependent on the environment. This stress scenario clearly indicates the crucial need to integrate the crop physiology with monitoring innovations in order to facilitate the understanding of plant performance in the field. As already discussed, the use of available technological applications on plants can potentially enable a better knowledge about their physiological status according to the surrounding environment.

In our opinion, the most feasible alternative is to develop crop plants capable of, quantitatively, returning a continuous, or even discrete, variable regarding their interaction with the environment. This is a visionary objective that could be pursued by a transdisciplinary effort led by genetic engineering and bioelectronics technology enhancing the genotypic resource and returning higher plant production on-farm level. In other words, crop physiologists have to develop enviromics to be a quantitative variable, so that Eq. 2 should be a fine-scaled dynamic estimation model of the phenotype. The inputs are real-time, process level, high-throughput plant traits, environmental variability, management practice effect and the enviromics, outputting instant variations of the production as an emergent phenotype. This model will optimize management and the use of agricultural inputs, with precision, to achieve high and sustainable plant production.

In other words, if G expresses the productive potential and C can be monitored, then G.E can be optimized using N to reach the best genetic potential to the G.C.N. This level of precision agriculture has to be achieved in the next few years to close the production gap. So, what are the possible alternatives to have this most desirable model?

The use of natural electrical and ultrasonic signals emitted by the plants may be a path to quantify the plant physiological-environmental interaction (Mudrilov et al. 2021; Itzhak et al. 2023). However, it is not difficult to think about the integration of natural and artificial systems inside a plant, bringing plant-environment sensing and agricultural management to a higher level of efficiency (Vurro et al. 2023).

Currently, the use of technological resources has become a reality in diverse areas of science, ranging from the development of artificial intelligence to mechanical robotic devices controlled by organic commands (Warwick 2003), not to mention smartphones with their multiple accessible functionalities with a simple touch, face id or voice command. Technologies have become more accessible and plays a fundamental role in simplifying and enhancing our day by day lives in the last decades and must increase in the near future. So, why not apply these innovations that are already available for improving plant production?

The use of high-technology, such as artificial intelligence, could probably create a pathway for crop plants to be programmed to self-adjust to the environment conditions through precision management (Zhao et al. 2022; Sareen and Maes 2019). Alternatively, the use of artificial intelligence could improve the monitoring of plant physiological status optimizing the decision making at the farm-level. This may be a huge step forward in crop management and plant breeding. Anyway, this technology could optimize plant production in relation to resource availability increasing water and nitrogen use efficiency.

For example, connecting the plant with nanosensors to quantitatively determine the G.C.E together with artificial intelligence tools could help farmers to know and better analyze the causes and effects of environmental issues and use management practices to protect the plants against the loss of homeostasis under stressful conditions (Yin et al. 2021). However, this approach can be limiting, underscoring the increasing importance of technologies such as chips, electrodes, and biosensors in contemporary agriculture. The use of these devices in plants, as reviewed in Lo Presti et al. (2023), plays a crucial role in providing a more precise and detailed insight into the actual inputs to quench the input needs of plants, transforming the way we understand and interact with crop plants.

The strategy of using plant embedded sensors for real-time and organ specific monitoring of the environmental conditions through the use of bioelectronic sensors (i.e. mechatronic devices that convert biotic signals and processes into electronic signals) and dynamic modulation of plant physiological processes is undoubtedly of outstanding potential to reduce the production gap (Dufil et al. 2022).

Another value would be real-time trait monitoring. This would allow a detailed knowledge about the functioning of the plant and its reaction to environmental changes and could potentialize the use of resources on farm management (Sareen and Maes 2019; Saharan et al. 2022; Zhang et al. 2022). Such technology will also allow the study of plants from inside out, based on inner electrical responses. It could improve our understanding of the fast physiological responses as the electrical pathways regulating gas exchange in multi-environmental situations (Sareen 2017; Sareen and Maes 2019).

In a recent study, Roy and De (2022) discussed an application for real-time information directly from the plants through electrodes implanted in the leaves. Zheng et al. (2015) developed a sensor coupled to maize leaves, thereby establishing a more precise relationship between relative water content and leaf electrical conductivity. This result represents a significant step toward more efficient and sustainable agriculture, where the plants themselves can signal the need of water in contrast with the current irrigation management focused on measuring soil electrical conductivity, as mentioned by Li et al. (2006) and listed by Yin et al. (2021).

When there is a reduction in water supply in the soil, there is an increase in the concentration of abscisic acid (ABA) and reactive oxygen species (ROS). ABA triggers signaling for the stomata closure in the leaves to preserve leaf water status (Apel and Hirt 2004; Baxter et al. 2013; Waadt et al. 2014). However, this mechanism comes at a cost, as reduced stomatal opening also limits CO_2 assimilation, resulting in reduced plant production. Recent advances in biotechnology have allowed the development of biosensors, as reviewed by Elli et al. (2022), enabling real-time detection of water shortage on the plant system, providing more accurate information, and expediting decision-making in response to abiotic stresses.

In two studies performed with tomato (*Solanum lycopersicum*) and with the use of biosensors, variations in solute concentration in the plant sap were demonstrated (Coppedé et al. 2017; Janni et al. 2019). In another study, Jones et al. (2014) developed a sensor for ABA concentrations. These findings indicate that sensors and biosensors are an effective, direct, rapid, and ecologically sustainable tool for detecting water stress in plants, minimizing yield losses. Zhao et al. (2022) have suggested incorporating a synthetic polymer into plants, capable of adjusting the folding angle of leaves in response to temperature and exposure to ultraviolet light. Sareen (2017) developed phototropic robots that, without causing stress to the plants, were able to shape their growth trajectories. This combination allows for direct and real-time observation of plant responses to internal and external *stimuli*, as well as the management of plant traits.

The interaction of plant physiology with mechatronic technology is a catalyst standing point enabling the understanding of plant-enviroment interactions, monitoring of plant internal processes and using that information to improve precision agriculture technologies in a contemporary and innovative way (Sareen 2017). Thus, the use of technology once again enable crop physiologists to explore the boundaries of developing more resilient and resource-efficient crops, contributing to the accomplishment of more effective agricultural solutions throught breeding, bioengineering and management, especially in the face of climate change.

As mentioned, the plant production gains achieved by crop physiology from the Green Revolution have already reached a plateau. However, in the face of increasing food demand and climate change, crop physiologists are challenged to respond innovatively in the coming years. The ability to monitor the plant-environment interaction in real-time in the field, with the assistance of a computer, while another device provides information about weather conditions, and then integrating this data to control or even anticipate plant responses, is revolutionary (Hamann et al. 2015).

In the past, agricultural management decisions were made based on the average behavior of big land areas inside the farm. In the [resent time, this scale is narrowing down to a trait scale and differential applications of resources are more and more precise, based on remote sensing. Despite the great advantages, there is still room for improvements in the plant-environment interaction monitoring, which will lead to higher resource-use efficiency and increase of plant production. If plants can communicate their detailed physiological-traits, we could use artificial intelligence to adjust crop management, in real-time, on very fine scales, potentializing genetic resources and decreasing the plant production gap.

4 Concluding remarks

The current production gap arises from Malthusianism forecasts due to climate change and other environmental and social constraints to plant production. In addition, there is a stagnation on crop yield gains and the need for sustainable management practices. The task of producing more with less resources and maintaining the same area is great! It is a great challenge for all crop scientists and agricultural stakeholders with scientific formation and technology background on the Green Revolution. This challenge must be overcome by transdisciplinary efforts and it is evident that a central piece on this venture is crop physiology, since it is the branch of plant physiology that integrates and aggregates, systematically, information from molecular to canopy level, putting it in favor of agriculture.

From this perspective, it is clear that the current plant production gap will only be closed by an overwhelming technological breakthrough in plant science. In the long run, bioengineering and plant phenomics are the paths to be followed. In the short run, the plant-environment interactions have to be accessed by incorporating plant physiology to management practices in modern agriculture. In this short-term path, strategies that can combine the implementation of bioinformatics, modern sensors, the Internet of Things (IoT) and Artificial Intelligence (AI) algorithms pave the way for a new phase in understanding and working with the concept of enviromics to increase plant production efficiency in agriculture (i.e.increase production with lower resource input). However, this technological advance in crop physiology suggests an urgent re-evaluation of our educational methods, encouraging the training of professionals with a broad, systemic, and integrated perspective of plant production.

The present generation of crop physiologists must keep up with new technologies, while the future generation should learn from the outset to connect diverse fields of knowledge and must be transdisciplinary. For this to be achieved, it is essential to rethink how education and formation is delivered and absorbed by the ongoing crop physiologists in the universities and research centers. This shift in crop physiology has the potential to bridge the gap between technological advances and practical progress in agriculture, especially when looking at the imbalance between crop yield and the rising demand for food and other plant resources.

Furthermore, the agriculture of the future will not just focus on producing more but on the use of resources in the most efficient way. Given the constraints of our available resources, it is crucial to use them responsibly. The practical application of enviromics in a systematic phenotyping approach, by providing real-time information on the crop needs to maximize plant production, prove to be an invaluable tool for a more rational resource use. So, this is a priority goal for crop physiology. With the development of proper tools and methods to measure and quantitatively formalize the plant-environmental interactions as a valiable in the production equation, we envision a more efficient agriculture, emphasizing the sustainability triad: environmentally correct, financially feasible, and socially fair. This aims not only meet the world's demand for plant products but also the demand to produce in a way that respects and safeguards our environment, merging technological innovation with a commitment to sustainability.

Acknowledgements The authors acknowledge the financial support from the Brazilian Coordination of Superior Level Staff Improvement—CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) – Finance Code 001; The Brazilian National Council for Scientific and Technological Development—CNPq (Conselho Nacional Desenvolvimento Científico e Tecnológico), the Research Supporting Foundation of Minas Gerais State—FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais—APQ- 02653-18). JPRADB acknowledges the CNPq for a research fellowship (#312488/2022-0). We also thank Prof. Alysson Paolinelli (*in memorian*) for his invaluable contribution to the increment of plant production in tropical conditions as an agronomist, professor, scientist, stakeholder and policy maker.

Funding Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Finance Code 001 - Alana Batista Cruz and-João Paulo Pennacchi. Conselho Nacional de Desenvolvimento Científico e Tecnológico, PQ 312488/2022-0 - João Paulo Rodrigues Alves Delfino Barbosa. Fundação de Amparo à Pesquisa do Estado de Minas Gerais, APQ- 02653-18, João Paulo Rodrigues Alves Delfino Barbosa.

Data availability This is a perspective paper and data availability statement is not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest. Author João Paulo Rodrigues Alves Delfino Barbosa is Guest Editor for Theoretical and Experimental Plant Physiology and the peer-review process for this article was independently handled by another member of the journal editorial board.

References

Aggarwal P, Vyas S, Thornton P, Campbell BM, Kropff M (2019) Importance of considering technology growth in impact assessments of climate change on agriculture. Glob Food Sec 23:41–48. https://doi.org/10.1016/j.gfs.2019.04.002

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399. https://doi.org/10.1146/annurev.arplant.55.031903.141701

Araus JL, Kefauver SC, Zaman-Allah M, Olsen MS, Cairns JE (2018) Translating high-throughput phenotyping into genetic gain. Trends Plant Sci 23:451–466. https://doi.org/10.1016/j.tplants.2018.02.001

Barbosa JPRAD, Rambal S, Soares AM, Mouillot F, Nogueira JMP, Martins GA (2012) Plant physiological ecology and the global changes. Ciênc Agrotec 36:253–269. https://doi.org/10.1590/S1413-70542012000300001

Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signalling. J Exp Bot 65:1229–1240. https://doi.org/10.1093/jxb/ert375

Beyschlag & W, Ryel RJ, (2007) Plant physiological ecology: an essential link for integrating across disciplines and scales in plant ecology. Flora 202:608–623. https://doi.org/10.1016/j.flora.2007.05.001

Brooks EG, Elorriaga E, Liu Y, Duduit JR, Yuan G, Tsai CJ, Tuskan GA, Ranney TG, Yang X, Liu W (2023) Plant promoters and terminators for high-precision bioengineering. BioDesign Res 5:0013. https://doi.org/10.34133/bdr.0013

Chen T, Hojka M, Davey P, Sun Y, Dykes GF, Zhou F, Lawson T, Nixon PJ, Lin Y, Liu L-N (2023) Engineering α-carboxysomes into plant chloroplasts to support autotrophic photosynthesis. Nat Commun 14:2118. https://doi.org/10.1038/s41467-023-37490-0

Conlan B, Birch R, Kelso C, Holland S, De Souza AP, Long SP, Beck JL, Whitney SM (2019) BSD2 is a Rubisco-specific assembly chaperone, forms intermediary hetero-oligomeric complexes, and is nonlimiting to growth in tobacco. Plant Cell Environ 42:1287–1301. https://doi.org/10.1111/pce.13473

Cooper M, Voss-Fels KP, Messina CD, Tang T, Hammer GL (2021) Tackling G × E × M interactions to close on-farm yield-gaps: creating novel pathways for crop improvement by predicting contributions of genetics and management to crop productivity. Theor Appl Genet 134:1625–1644. https://doi.org/10.1007/s00122-021-03812-3

Coppedè N, Janni M, Bettelli M, Maida CL, Gentile F, Villani M, Ruotolo R, Iannotta S, Marmiroli N, Marmiroli M, Zappettini A (2017) An in vivo biosensing, biomimetic electrochemical transistor with applications in plant science and precision farming. Sci Rep 7:16195. https://doi.org/10.1038/s41598-017-16217-4

Dasgupta A, Chowdhury N, De RK (2020) Metabolic pathway engineering: perspectives and applications. Comput Methods Programs Biomed 192:105436. https://doi.org/10.1016/j.cmpb.2020.105436

Dufil G, Bernacka-Wojcik I, Armada-Moreira A, Stavrinidou E (2022) Plant bioelectronics and biohybrids: the growing contribution of organic electronic and carbon-based Materials. Chem Rev 122:4847–4883. https://doi.org/10.1021/acs.chemrev.1c00525

Elli G, Hamed S, Petrelli M, Ibba P, Ciocca M, Lugli P, Petti L (2022) Field-effect transistor-based biosensors for environmental and agricultural monitoring. Sensors 22:4178. https://doi.org/10.3390/s22114178

Feng L, Wang K, Li Y, Tan Y, Kong J, Li H, Li Y, Zhu Y (2007) Overexpression of SBPase enhances photosynthesis against high temperature stress in transgenic rice plants. Plant Cell Rep 26:1635–1646. https://doi.org/10.1007/s00299-006-0299-y

Foulkes MJ, Molero G, Griffiths S, Slafer GA, Reynolds MP (2022) Yield Potential. In: Reynolds MP, Braun HJ (eds) Wheat Improvement. Springer, Cham., pp 379–396. https://doi.org/10.1007/978-3-030-90673-3_21

Furbank RT, Jimenez-Berni JA, George-Jaeggli B, Potgieter AB, Deery DM (2019) Field crop phenomics: enabling breeding for radiation use efficiency and biomass in cereal crops. New Phytol 223:1714–1727. https://doi.org/10.1111/nph.15817

Ghannoum O, Evans JR, Von Caemmerer S (2010) Chapter & nitrogen and water use efficiency of C4 plants. In: Raghavendra AS, Sage RF (eds) C4 photosynthesis and related CO_2 concentrating mechanisms, advances in photosynthesis and respiration. Springer, Netherlands, pp 129–146. https://doi.org/10.1007/978-90-481-9407-0_8

Hamann H, Wahby M, Schmickl T, Zahadat P, Hofstadler D, Stoy K, Risi S, Faina A, Veenstra F, Kernbach S, Kuksin I, Kernbach O, Ayres P, Wojtaszek P (2015) Flora robotica - mixed societies of symbiotic robot-plant biohybrids. IEEE Symposium Series on Computational Intelligence Presented at the IEEE Symposium Series on Computational Intelligence (SSCI). IEEE, Cape Town, South Africa, pp 1102–1109. https://doi.org/10.1109/SSCI.2015.158

Khait I, Lewin-Epstein O, Sharon R et al (2023) Sounds emitted by plants under stress are airborne and informative. Cell 186(7):1328–1336. https://doi.org/10.1016/j.cell.2023.03.009

Iqbal WA, Miller IG, Moore RL, Hope IJ, Cowan-Turner D, Kapralov MV (2021) Rubisco substitutions predicted to enhance crop performance through carbon uptake modelling. J Exp Bot 72:6066–6075. https://doi.org/10.1093/jxb/erab278

Janni M, Coppede N, Bettelli M, Briglia N, Petrozza A, Summerer S, Vurro F, Danzi D, Cellini F, Marmiroli N, Pignone D, Iannotta S, Zappettini A (2019) In Vivo phenotyping for the early detection of drought stress in tomato. Plant Phenomics. https://doi.org/10.34133/2019/6168209

Jones AM, Danielson JÅ, ManojKumar SN, Lanquar V, Grossmann G, Frommer WB (2014) Abscisic Acid Dynamics in Roots Detected with Genetically Encoded FRET Sensors. Elife 3:e01741. https://doi.org/10.7554/eLife.01741

Kubis A, Bar-Even A (2019) Synthetic biology approaches for improving photosynthesis. J Exp Bot 70:1425–1433. https://doi.org/10.1093/jxb/erz029

Lal R (2014) Climate strategic soil management. Challenges 5:43–74. https://doi.org/10.3390/challe5010043

Li M, Wang M, Wang Q (2006) Development and performance test of a portable soil ec detector. Appl Eng Agric 22:301–307. https://doi.org/10.13031/2013.20276

Lo Presti D, Di Tocco J, Massaroni C, Cimini S, De Gara L, Singh S, Raucci A, Manganiello G, Woo SL, Schena E, Cinti S (2023) Current understanding, challenges and perspective on portable systems applied to plant monitoring and precision agriculture. Biosens and Bioelectron 222:115005. https://doi.org/10.1016/j.bios.2022.115005

Long BM, Hee WY, Sharwood RE, Rae BD, Kaines S, Lim Y-L, Nguyen ND, Massey B, Bala S, Von Caemmerer S, Badger MR, Price GD (2018) Carboxysome encapsulation of the CO_2-fixing enzyme Rubisco in tobacco chloroplasts. Nat Commun 9:3570. https://doi.org/10.1038/s41467-018-06044-0

Long SP, Marshall-Colon A, Zhu XG (2015) Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell 161:56–66. https://doi.org/10.1016/j.cell.2015.03.019

Lüttge U (2023) Two contrasting principles, reductionist and systemic: fundamentally separated or dynamically interacting? Theor Exp Plant Physiol. https://doi.org/10.1007/s40626-023-00279-z

Malthus, T. 1826. An essay on the principle of population. 6th edition. London: John Murray. http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=A545.1&viewtype=text

McGrath JM, Long SP (2014) Can the cyanobacterial carbon-concentrating mechanism increase photosynthesis in crop species? A theoretical analysis. Plant Physiol 164:2247–2261. https://doi.org/10.1104/pp.113.232611

Mudrilov M, Ladeynova M, Grinberg M, Balalaeva I, Vodeneev V (2021) Electrical signaling of plants under abiotic stressors: transmission of stimulus-specific information. Int J Mol Sci 22:10715. https://doi.org/10.3390/ijms221910715

Nguyen ND, Pulsford SB, Hee WY, Rae BD, Rourke LM, Price GD, Long BM (2023) Towards engineering a hybrid carboxysome. Photosynth Res 156:265–277. https://doi.org/10.1007/s11120-023-01009-x

Ni T, Sun Y, Burn W, Al-Hazeem MMJ, Zhu Y, Yu X, Liu L-N, Zhang P (2022) Structure and assembly of cargo Rubisco in two native α-carboxysomes. Nat Commun 13:4299. https://doi.org/10.1038/s41467-022-32004-w

Ninomiya S (2022) High-throughput field crop phenotyping: current status and challenges. Breed Sci 72:3–18. https://doi.org/10.1270/jsbbs.21069
Pennacchi JP, Virlet N, Barbosa JPRAD, Parry MAJ, Feuerhelm D, Hawkesford M, Carmo-Silva E (2022) A predictive model of wheat grain yield based on canopy reflectance indices and theoretical definition of yield potential. Theor Exp Plant Physiol 34:537–550. https://doi.org/10.1007/s40626-022-00263-z
Pennacchi JP, Lira JMS, Rodrigues M, Garcia FHS, Mendonça AMDC, Barbosa JPRAD (2021) A systemic approach to the quantification of the phenotypic plasticity of plant physiological traits: the multivariate plasticity index. J Exp Bot 72(5):1864–1878. https://doi.org/10.1093/jxb/eraa545
Resende RT, Piepho HP, Rosa GJM et al (2021) Enviromics in breeding: applications and perspectives on envirotypic-assisted selection. Theor Appl Genet 134:95–112. https://doi.org/10.1007/s00122-020-03684-z
Roy SK, De D (2022) Genetic algorithm based internet of precision agricultural things (IopaT) for agriculture 4.0. Internet Things 18:100201. https://doi.org/10.1016/j.iot.2020.100201
Sage RF (2002) Variation in the kcat of Rubisco in C3 and C4 plants and some implications for photosynthetic performance at high and low temperature. J Exp Bot 53:609–620. https://doi.org/10.1093/jexbot/53.369.609
Sage RF, Khoshravesh R, Sage TL (2014) From proto-Kranz to C4 Kranz: building the bridge to C4 photosynthesis. J Exp Bot 65:3341–3356. https://doi.org/10.1093/jxb/eru180
Sage RF, Sage TL, Kocacinar F (2012) Photorespiration and the evolution of C4 photosynthesis. Annu Rev Plant Biol 63:19–47. https://doi.org/10.1146/annurev-arplant-042811-105511
Saharan BS, Brar B, Duhan JS, Kumar R, Marwaha S, Rajput VD, Minkina T (2022) Molecular and physiological mechanisms to mitigate abiotic stress conditions in plants. Life 12:1634. https://doi.org/10.3390/life12101634
Sareen H, Maes P (2019) Cyborg botany: exploring in-planta cybernetic systems for interaction. Extended Abstracts of the 2019 CHI Conference on Human Factors in Computing Systems. Presented at the CHI 19: CHI Conference on Human Factors in Computing Systems, ACM, Glasgow Scotland Uk, pp 1–6. https://doi.org/10.1145/3290607.3313091
Sareen H (2017) Cyborg botany: augmented plants as sensors, displays and actuators. Dissertation, Massachusetts Institute of Technology
Schlüter U, Weber APM (2016) The road to C 4 photosynthesis: evolution of a complex trait via intermediary states. Plant Cell Physiol 57:881–889. https://doi.org/10.1093/pcp/pcw009
Souza GM, Prado CHBA, Ribeiro RV, Barbosa JPRAD, Gonçalves AN, Habermann G (2016) Toward a systemic plant physiology. Theor Exp Plant Physiol 28:341–346. https://doi.org/10.1007/s40626-016-0071-9
Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci USA 108:20260–20264. https://doi.org/10.1073/pnas.1116437108
Van Emon JM (2016) The omics revolution in agricultural research. J Agric Food Chem 64:36–44. https://doi.org/10.1021/acs.jafc.5b04515
Vurro F, Manfredi R, Bettelli M, Bocci G, Cologni AL, Cornali S, Reggiani R, Marchetti E, Coppedè N, Caselli S, Zappettini A, Janni M (2023) In vivo sensing to monitor tomato plants in field conditions and optimize crop water management. Precision Agric 24:2479–2499. https://doi.org/10.1007/s11119-023-10049-1
Waadt R, Hitomi K, Nishimura N, Hitomi C, Adams SR, Getzoff ED, Schroeder JI (2014) FRET-based reporters for the direct visualization of abscisic acid concentration changes and distribution in Arabidopsis. Elife 3:e01739. https://doi.org/10.7554/eLife.01739
Warwick K (2003) Cyborg morals, cyborg values, cyborg ethics. Ethics Inf Technol 5:131–137. https://doi.org/10.1023/B:ETIN.0000006870.65865.cf
Wei S, Li X, Lu Z, Zhang H, Ye X, Zhou Y, Li J, Yan Y, Pei H, Duan F, Wang D, Chen S, Wang P, Zhang C, Shang L, Zhou Y, Yan P, Zhao M, Huang J, Bock R, Qian Q, Zhou W (2022) A transcriptional regulator that boosts grain yields and shortens the growth duration of rice. Science 377:eabi8455. https://doi.org/10.1126/science.abi8455
Whitney SM, Birch R, Kelso C, Beck JL, Kapralov MV (2015) Improving recombinant rubisco biogenesis, plant photosynthesis and growth by coexpressing its ancillary RAF1 chaperone. Proc Natl Acad Sci USA 112:3564–3569. https://doi.org/10.1073/pnas.1420536112
Wallace JG, Rodgers-Melnick E, Buckler ES (2018) On the Road to Breeding 4.0: unraveling the good, the bad, and the boring of crop quantitative genomics. Annu Rev Genet 52:421–444. https://doi.org/10.1146/annurev-genet-120116-024846
Xu Y, Zhang X, Li H, Zheng H, Zhang J, Olsen MS, Varshney RK, Prasanna BM, Qian Q (2022) Smart breeding driven by big data, artificial intelligence, and integrated genomic-enviromic prediction. Mol Plant 15:1664–1695. https://doi.org/10.1016/j.molp.2022.09.001
Yin H, Cao Y, Marelli B, Zeng X, Mason AJ, Cao C (2021) Soil sensors and plant wearables for smart and precision agriculture. Advanced Mater 33:2007764. https://doi.org/10.1002/adma.202007764
Zenda T, Wang N, Yan X, Dong A, Yang Q, Zhong Y, Duan H (2023) Opportunities and avenues for achieving crop climate resilience. Environ Exp Bot 213:105414. https://doi.org/10.1016/j.envexpbot.2023.105414
Zhang H, Zhu J, Gong Z, Zhu J-K (2022) Abiotic stress responses in plants. Nat Rev Genet 23:104–119. https://doi.org/10.1038/s41576-021-00413-0
Zhao J, Ma Y, Steinmetz NF, Bae J (2022) Toward plant cyborgs: hydrogels incorporated onto plant tissues enable programmable shape control. ACS Macro Lett 11:961–966. https://doi.org/10.1021/acsmacrolett.2c00282
Zheng L, Wang Z, Sun H, Zhang M, Li M (2015) Real-time evaluation of corn leaf water content based on the electrical property of leaf. Comput Electron Agric 112:102–109. https://doi.org/10.1016/j.compag.2014.11.007
Zilberman A, Ben Asher J, Kopeika NS (2016) Remote sensing in precision farming: real-time monitoring of water and fertilizer requirements of agricultural crops. In: Neale CMU, Maltese A (eds) Presented at the SPIE Remote

Sensing. Edinburgh, United Kingdom, p 99981R. https://doi.org/10.1117/12.2242724