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Linking integrative plant physiology with agronomy to sustain future plant production

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Abstract

Sustainable production of high-quality food is one of today's major challenges of agriculture. To achieve this goal, a better understanding of plant physiological processes and a more integrated approach with respect to current agronomical practices are needed. In this review, various examples of cooperation between integrative plant physiology and agronomy are discussed, and this demonstrates the complexity of these interrelations. The examples are meant to stimulate discussions on how both research areas can deliver solutions to avoid looming food crises due to population growth and climate change. In the last decades, unprecedented progress has been made in the understanding of how plants grow and develop in a variety of environments and in response to biotic stresses, but appropriate management and interpretation of the resulting complex datasets remains challenging. After providing an historical overview of integrative plant physiology, we discuss possible avenues of integration, involving advances in integrative plant physiology, to sustain plant production in the current postOMICs era. Finally, recommendations are provided on how to practice the transdisciplinary mindset required, emphasising a broader approach to sustainable production of high-quality food in the future, whereby all those who are involved are made partners in knowledge generation processes through transdisciplinary cooperation.

Keywords: food production, molecular plant biology, plant physiology, agronomy, sustainability, transdisciplinarity

List of abbreviations

ABA Abscisic Acid

APSIM Agricultural Production Systems Simulator

AWD Alternate Wetting and Drying

CRISPR Clustered Regularly Interspaced Short Palindromic Repeats

FSPM Functional Structural Plant Modeling

GNSS Global Navigation Satellite System

GxE(xM) Gene-Environment-Management Interaction

NOSH Nitric Oxide and Hydrogen Sulfide

QTL Quantitative Trait Locus

RNA Ribonucleic Acid

RNS Reactive Nitrogen Species

RONSS Reactive Oxygen, Nitrogen and Sulfur Species

ROS Reactive Oxygen Species

UAS Unmanned Aerial Systems

UGV Unmanned Ground Vehicles

1. Introduction

The Food and Agriculture Organization's latest report on the state of food security and nutrition in the world is disturbing: 820 million people experience hunger, two billion people are moderately or severely food-insecure (not knowing where and when they may find their next meal), and hunger is on the rise, particularly in Africa (FAO, 2019). In this context, it is imperative to reduce hunger and improve food security and human nutrition, as stated in the United Nations' sustainability goal 2 (UN, 2015). Increased global pressures, such as climate shifts and biotic disturbances, compromise crop productivity and widen the gap between food demands and crop production (FAO, 2017). Avoiding a worldwide food crisis will thus require transformative breakthroughs in fundamental and applied plant research. This review argues that integrative plant physiology could play a critical role in providing answers to the challenging questions of future agronomy. After outlining the historical context and characteristics of integrative plant physiology, we discuss several examples that demonstrate the multifaceted links between integrative plant physiology and future agronomy. Furthermore, we stress that interdisciplinary collaborations will need the active participation of stakeholders. We conclude this review by proposing a transdisciplinary mind-set to achieve this aim.

2. Integrative Plant Physiology

2.1 Historical Background

After decades of reductionist approaches and the separate development of distinct fields of biological research, the concept of integrative biology was introduced to connect different areas of scientific knowledge (Wake, 2008). In this context, the term *integration*, although still vague and relatively unfocused, emphasizes the importance of a unifying approach to fully understand biological processes. Within this background, Ulrich Kutschera (2015) coined the term Integrative Plant Physiology when reviewing Julius Sachs' pioneering work. Sachs had developed plant physiology as a distinct field of study, advancing botany by adopting novel, quantitative, experimental approaches performed under controlled conditions. Prior to Sachs, descriptive botany dominated plant sciences, although with notable exceptions such as work by Jan Baptist van Helmont on biomass-production (1648) and Stephen Hales on transpiration (1724). Sachs' emphasis on elucidating physicochemical causes for observed plant responses ushered in the modern area of plant physiology (Kutschera, 2015; see also Kutschera and Niklas, 2018). Introducing new standards of scientific rigor, and concurrent substantial advances in instrumentation, led to remarkable advances in the millennial science of botany and generated a substantial knowledge base. Perhaps unavoidably, however, this led to a fragmentation of knowledge, expertise and understanding across a range of sub-disciplines of plant physiology, such as, but not limited to, genetic, molecular, cytological, biochemical, and organismal plant biology. These sub-disciplines often focus on only one or two among multiple possible organizational levels (gene, RNA, cells, tissues, and organs). Consequently, the unitary big-picture approach advocated by Sachs has largely disappeared, and plant molecular disciplines do, at times, operate with little cross-reference.

2.2 Relations to neighboring disciplines

Understanding the integration of physiological functions that regulate plant growth and development is of paramount importance in plant biology, particularly within the context of

climate change. In their listing of “Grand Challenges”, Mykles et al. (2010) refer to vertical integration across organizational levels and bridging e.g. genetic, molecular, cytological, biochemical, organismal and ecological plant biology. In the strictest sense, the concept of Integrative Plant Physiology refers to a holistic perspective of plant physiology that integrates not only across organizational levels, but also between organs within the plant (*via*, e.g., long-distance signaling and transport). Integrative Plant Physiology is not a novel concept (e.g. consider Julius Sachs' work), but rather a concept that has become particularly relevant in the context of rapidly expanding knowledge in the aforementioned sub-disciplines of plant physiology. Integrative Plant Physiology is also timely as it is needed to address important challenges in agronomy, such as responses to multiple co-occurring stressors, by elucidating physiological and genetic bases for complex traits such as yield, developing breeding strategies for climate adaptation, improving the understanding of plant primary and secondary metabolism for metabolic engineering, and developing strategies to manage landscape agroecology. Integrating these challenges into a coherent research strategy requires definitions of disciplinary roles and relations. Boulton (2005) stresses the importance of keeping knowledge structures explicit to avoid epistemological confusion, mismatches between scales of observation and resulting uncertainties of integrated theories. The development of trans-specialist understanding and overcoming disciplinary boundaries must also be based on co-learning among specialists based on their disciplinary histories and epistemologies (Tell et al., 2017). It is important in this process to negotiate knowledge among adjacent disciplines to maintain explicitness of knowledge structures. Simply explaining agronomic observations with plant molecular biological processes will, in most cases, be highly problematic, because they would disregard other drivers (Passioura, 2010). The latter will cause variations in production ecological states which molecular biology does not account for (Fig. 1). Integrative Plant Physiology is of high importance in this collaboration, because it provides an understanding of genetic regulatory principles underlying physiological mechanisms that need to be known for explaining observations at the plant ecological level. Translating the resulting integrated knowledge into plant production practice requires a transdisciplinary research approach which addresses relations between people, plant and land that are determined by social, political, demographic and cultural requirements for plant production.

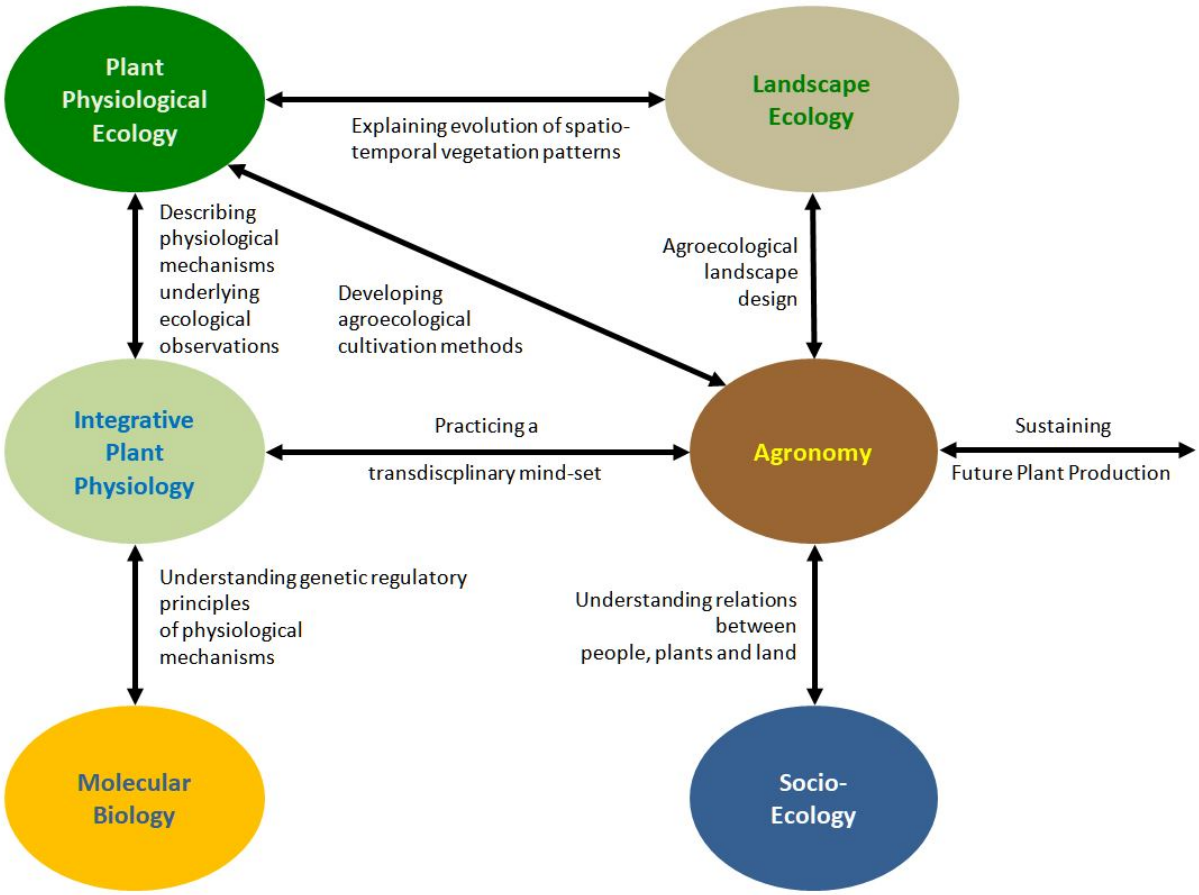


Fig. 1 Translating plant molecular and ecological theories into plant production practices requires transdisciplinary cooperation between integrative plant physiology and agronomy in specific socio-ecological contexts

2.3 Disciplinary characteristics

Plant biology has generated vast amounts of information on underlying processes that allow plant growth and development in widely different and fluctuating environments. High-throughput technologies have generated large OMICs datasets. Combined genomic, epigenetic, transcriptomic, proteomic, and metabolomic data yield novel insights into the organizational networks that underpin cellular responses to genetic or environmental change (Fukushima et al., 2009). To exploit this treasure trove of data, systems biology in particular aims to predict plant responses based on an understanding of these plant response networks (Alon 2020) using advances in computational analysis (Mochida and Shinozaki, 2011). However, despite notable advances in systems biology (Coruzzi et al., 2018; Watanabe et al., 2019), the use of OMICs approaches to interpret whole plant physiology has been questioned by some (do Amaral and Souza, 2017). In particular, the Cartesian model, positing that understanding constituent parts can lead to full understanding of complex processes, has been questioned (Souza et al., 2016). Passioura (2010) has argued that scaling up from gene expression to the whole plant needs to address tradeoffs and other interactions to generate useful new insights. Complex new organismal traits cannot necessarily be inferred from study of individual components and/or relationships between individual components and organismal responses are not always linear (Souza et al., 2016).

Alternative concepts such, as General Systems Theory developed by Bertalanffy (1968), advocate an organismal perspective that incorporates both bottom-up and top-down elements. In plant biology, these complementary elements are seen, e.g. in the control of morphogenesis, where local development is guided by a combination of molecular information within a cell and organism-wide gradients of positional information (Potters et al., 2009). The Synergetics concept proposed by Haken (2016) identifies “self-organization as a property of open and complex systems composed of parts, elements, components and units, whose network of interactions serves for the exchange of matter, energy and information among their parts and with their surroundings”. Cooperation among individual components produces functional systems, with new emerging characteristics surpassing the combination of traits of the individual traits.

On a more practical level, scaling from gene to organism across organizational levels is a formidable challenge due to variation in experimental conditions across published studies. Many studies report plant responses measured under a single set of experimental conditions that differ from those used by other researchers. Larger, coordinated experiments are needed to comprehensively identify the major environmental drivers of plant responses (see, e.g., Castagna et al., 2017). Alternatively, existing scattered and incoherent information could be unified using meta-analytic techniques and novel metaheuristic algorithms (Sabzi et al., 2018), thus generating new insights from the existing knowledge.

Studying plant responses to environmental factors is essential for testing the applicability of integrative plant physiological knowledge under real ecological conditions. Such testing at the plant level must include at least three distinct levels of complexity: (i) integration of signals generated by environmental conditions (both abiotic and biotic); (ii) integration of signals within the different parts (cells/organs) of the plant; (iii) integration of the developmental program over time (Fig. 2). Abiotic factors include, e.g. light, water availability, temperature, and the presence of pollutants. Among biotic factors, all signals deriving from viruses, bacteria, fungi, and insects must be integrated over time within the plant developmental program. Some biotic interactions with mycorrhizal fungi and bacteria enhance plant growth and yield (Finkel et al., 2017). Without carefully considering all environmental conditions, lab-based plant physiological studies will have limited relevance for plant performance in the field (Poorter et al. 2016). For instance, photosynthetic capacity and leaf structure markedly differ between plants grown under realistic, fluctuating light levels, and those subjected to a square wave pattern (Vialet-Chabrand et al., 2017). Selye (1936) and Lichtenthaler (1998) visualized the responses of plants to environmental stressors, and identified an alarm phase, a resistance phase, and an exhaustion phase. Yet, many existing studies capture only one point in time, for one dose of the environmental parameter, and for one plant species, which results in incoherent information unsuitable for scaling up.

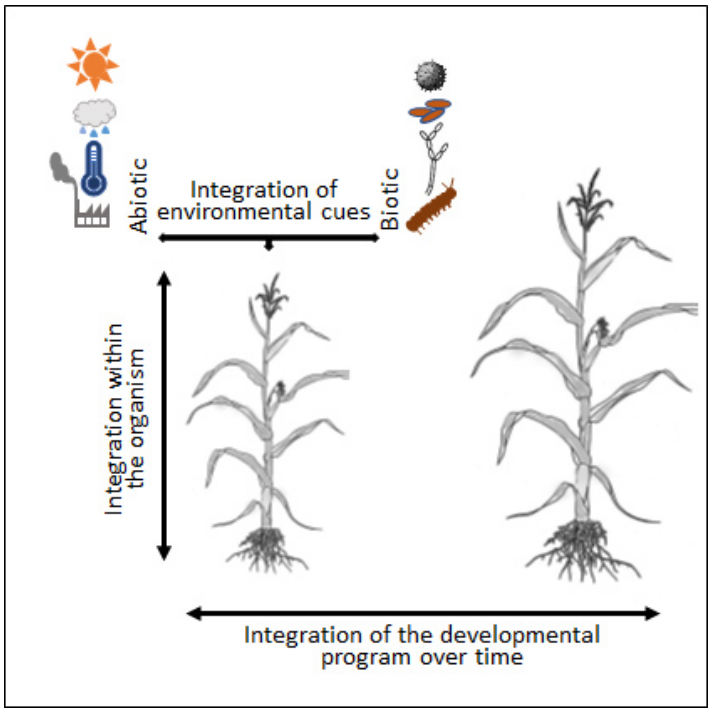


Fig 2 Schematic view of the different levels of integration occurring in plant physiological processes. See text for details.

Integrative plant physiology is defined as an interdisciplinary research area that investigates the function of the whole plant over its lifetime in complex, realistic environments. In this definition, interdisciplinarity refers to different sub-disciplines coming together within the discipline of plant physiology. By this definition, Integrative Plant Physiology is the logical partner of Agronomy, with the two disciplines working together with a common objective to sustain world food supply through transdisciplinary research. Achieving this partnership may not have to be prohibitively complex, as argued by Passioura (2010) who concluded that “the most effective research in this arena has resulted from a culture of collegiate dialogue between scientists working at different scales.”

3. Avenues of Integration

3.1 Plant structure and function

Plants exquisitely coordinate and integrate their structure and physiology. Since most plants are rooted in particular places during their post-embryonic stage of life, they employ remarkable mechanisms of adjusting growth, reproduction, and defense in response to environmental cues. Signaling networks perceive and transduce environmental cues and modulate multiple aspects of plant form and function to coordinate growth, reproduction, and defense against physical and biological stressors. These networks integrate key regulators including plant hormones, transcription factors, protein kinases and other components of the signaling pathways that perceive and relay environmental cues to changes in gene expression. One example of such relays are ubiquitous, multi-component networks based on the balance of oxidants and antioxidants (redox balance) that interact with plant hormones, transcription factors and protein kinases to modulate gene expression (for recent reviews, see Foyer and Noctor, 2009; Munné-Bosch et al., 2013; Demmig-Adams et al., 2018, 2019). These networks

orchestrate a coordinated response of different organs and ultimately of the whole plant to its environment, including long-distance signaling, not only root-shoot communication through the xylem but also maintenance of a source-sink balance between the above-ground photosynthetic structures (source of sugar) with all sugar-consuming sinks of the plant through the phloem (Adams et al., 2018).

Successfully incorporating plant physiology at the agronomic level requires transformation of conceptual knowledge about plant structure and function into quantitative relationships via tools such as Functional-Structural Plant Modeling FSPM (Godin and Sinoquet, 2005; Vos et al., 2010; Buck-Sorlin, 2013; DeJong et al., 2011; Sarlikioti et al., 2011; Garin et al., 2014; Sievänen et al., 2014; Evers and Bastiaans, 2016; Vries et al., 2018). Plants flexibly respond to variations in the physical environment, soil nutrient availability, and various stresses, mainly by plastically changing their architecture (adding new organs by branching or shedding old ones by abscission). Contemporary crop models applied in agronomy (for a comprehensive list of crop models see Di Paola et al. [2015]) do not characterize plant structure and thus do not fully capture this plastic response of a plant stand. FSPM is a paradigm that takes process-based modeling a step further by explicitly considering not only static plant architecture (as a snapshot of plant morphology at a certain developmental stage) but incorporating patterns of organ formation by defining organs/botanical entities as modules, which allows a fully object-oriented approach to programming.

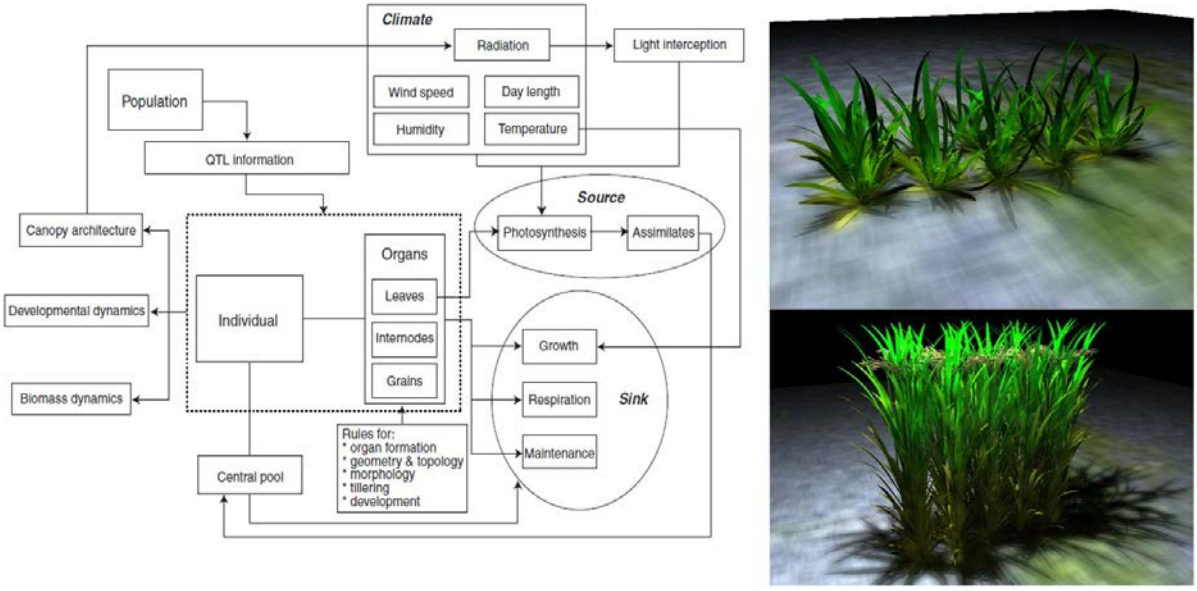


Fig. 3 Illustration of a multi-scaled functional structural plant model (FSPM) of rice, including a micrometeorological model, as well as source and sink activities that are connected via the central assimilate pool and by a framework of morphogenetic rules that establish the structure (left). Virtual rice plants at an early (top right) and late (bottom right) stage of development. Taken from Xu et al. (2011).

Multi-scaled 3D models as illustrated in Fig. 3 are increasingly used to characterize plant structure and function. In this example, a rice 3D model combines data from quantitative genetics, morphology, and crop physiology in a comprehensive genotype-phenotype modeling framework, i.e. the reconstruction of rice morphology from growth rules, QTL-genotype modifying model parameters, and interaction with a simulated light environment. This framework also allows some basic “virtual breeding”. However, this explicitness comes at a cost: fitting numerous model parameters can become daunting, and considering a three-

dimensional light environment can slow down simulation speed considerably. On the other hand, increasing availability of new high throughput phenotyping workflows and development of artificial neural network techniques to automate object segregation from images promises to widen the bottlenecks of FSPM with respect to phenotyping and parameterization.

There is an ongoing debate among the different modeling schools of whether crop models for optimizing plant production are best developed using FSPMs or whether classical crop models should be refined by implementing more physiological functions. It is, however, clear, that the complex interactions among carbon, nutrient, and water relations, coupled with responses to other aspects of the abiotic (e.g., water deficit, light, temperature, salinity) and biotic (e.g., competition with weeds, pathogen infection, herbivory) environment, need to be further investigated before the following questions can be answered:

- Can and should these interactions be captured in models that must be both scientifically valid and applicable in agronomic engineering?
- Can models give predictive answers to physiological problems that have not yet been investigated experimentally?
- Can models integrate qualitative and quantitative knowledge from different plant science fields into a single framework?

While initial experiments can be conducted under controlled conditions, findings will need to be tested under field conditions and using a systems approach that simultaneously addresses dynamic physical and chemical interactions among soils, plants, and the atmosphere. The resulting insights may help design improved crop models that incorporate physiological functions and can be applied to optimize plant-production systems in the face of climate change.

3.2 Integrating responses to concurrent multiple stressors

Under field conditions, plants can be exposed to multiple stressors, which often cause non-additive, synergistic responses, and these interactive effects on yield can be genotype-dependent (Rossini et al., 2016). The impact of multiple stressors, and their interactions with others, is difficult to predict. For example, heat and drought often occur together and negate the expected benefits of elevated atmospheric CO_2 concentrations in soybean (Gray et al., 2016). Elevated CO_2 ameliorates the impact of drought stress on rice yield, by allowing 1-2 days more growth when the soil is allowed to dry at panicle initiation and/or anthesis (Baker et al., 1997). Elevated CO_2 or high-temperature exposure during the reproductive stages increase or decrease rice yields, respectively, while the interactive effect is inconsistent Boote et al., 2005). Moreover, plant responses to stressors depends on developmental stage, with certain phases being particularly sensitive (e.g., increased vulnerability to heat stress during reproduction). Furthermore, stress can affect the timing of developmental transitions (Boote et al., 2013; Feng et al., 2019). How plants integrate responses to multiple stressors, and how this integration can be used to make crops more climate resilient remains poorly understood.

Under field conditions, plants are often exposed to concurrent abiotic and biotic stresses. Reactive oxygen species (ROS) have been proposed to integrate stress responses, with ROS homeostasis conferring cross tolerance against abiotic and biotic stressors (Perez and Brown, 2014; Hossain et al., 2015; Carmody et al., 2016; Raja et al., 2016; Qi et al., 2018). How ROS formation and scavenging is adjusted to avoid oxidative damage, and stimulates stress-protection mechanisms, remains a challenging question. Reactive oxygen and nitrogen species

(RONS) have been proposed to integrate stress responses, with RONS homeostasis conferring cross tolerance against abiotic and biotic stressors (del Rio, 2015). Numerous studies identified reactive oxygen species (ROS) and reactive nitrogen species (RNS) as signal transducers during cross talks of cellular and biological plant processes (Molassiotis and Fotopoulos, 2011). Priming of seeds or seedlings with UV may increase multiple stress tolerance by triggering formation of ROS (Thomas and Puthur, 2017; Bigot et al., 2018). Similarly, priming of plants with chemicals that affect ROS homeostasis or other stress-signaling pathways holds promise for improving stress tolerance (Savvides et al., 2014). Such approaches are becoming more commonplace, with intensive industry interest in developing new biostimulants.

Considering the increasing incidence of climate-related stress, it is important to simulate stress responses in crop models for more targeted intervention and to select the best genotypes. Integration of Genotype *x* Environment *x* Management (GxE(xM)) interactions into crop models does, however, remain challenging (Boote et al., 2013; Chenu et al., 2017). Considering the lack of mechanistic understanding of the response to multiple stressors on the physiology of plants, process-based crop models may not adequately predict yield in future multi-stress environments or extreme and/or highly variable climates. On the other hand, statistical models on their own may not provide specific information on adaptation measures. Recently, a hybrid model incorporating outputs from the process-based APSIM model into a Random Forest machine-learning model was shown to improve wheat yield projections in Australia (Feng et al., 2019). In particular, artificial intelligence was proposed to enhance the ability of process-based models to predict impacts of extreme climatic events on future crop production (Huntingfort et al., 2019).

3.3 Priming for improved plant stress response

Different methodologies have been employed to enhance plant abiotic stress tolerance; some are particularly time-consuming (e.g. conventional breeding) and others are currently unacceptable in many countries (e.g. genetic modification; Hu and Xiong, 2014). Close examination of plant-to-plant communication in nature has revealed an attractive, alternative solution, i.e. the strategy of priming. Priming occurs when prior exposure to a mild biotic or abiotic stress factor makes a plant more resistant to future exposure. This response is analogous to the concept of vaccination, where administration of inactivated antigenic material stimulates adaptive disease immunity and, ultimately, defeats pathogen infection. Although the process of priming has long been known, it has only recently been suggested to improve crop tolerance to multiple environmental stressors under field conditions, as a form of cross-protection (Savvides et al., 2016).

Priming can be achieved by pre-exposing plants to mildly stressful conditions, applying microorganisms (biological priming; Balestrini et al., 2018) or chemical compounds (chemical priming; Savvides et al., 2016) acting as signal transducers that activate plant defense systems. Increasing attention is being paid to chemical priming, with either natural or synthetic compounds, due to the vast range of molecules with the potential to act as priming agents. Numerous reports exist, with examples including amino acids such as proline (Islam et al. 2009), hormones such as salicylic acid (Yang et al., 2015), melatonin (Arnao and Hernández-Ruiz, 2019; Wang et al. 2018), as well as synthetic compounds such as nitric oxide and hydrogen sulfide (NOSH) chimeras (Antoniou et al., 2020) and even fungicides applied at low concentrations (Filippou et al., 2016). Reactive oxygen, nitrogen and sulfur species (RONSS) are of particular interest, because they represent key molecules involved in cellular signaling processes and transcript regulation during stress, and play a critical role in

plant acclimation to a multitude of stress factors (Antoniou et al., 2016). Furthermore, recent reports propose employing advanced nanomaterials (such as nanoparticles and polymers) as growth-promoting and stress-protecting compounds (Shang et al., 2019), although these will need to be employed with caution due to their limitations (Zulfiqar et al., 2019). Plant priming can be considered an example of integrative plant physiology, as it highlights the potential of inter-disciplinary approaches by combining synthetic biology, material science, environmental management and plant physiology towards developing sustainable agricultural technologies.

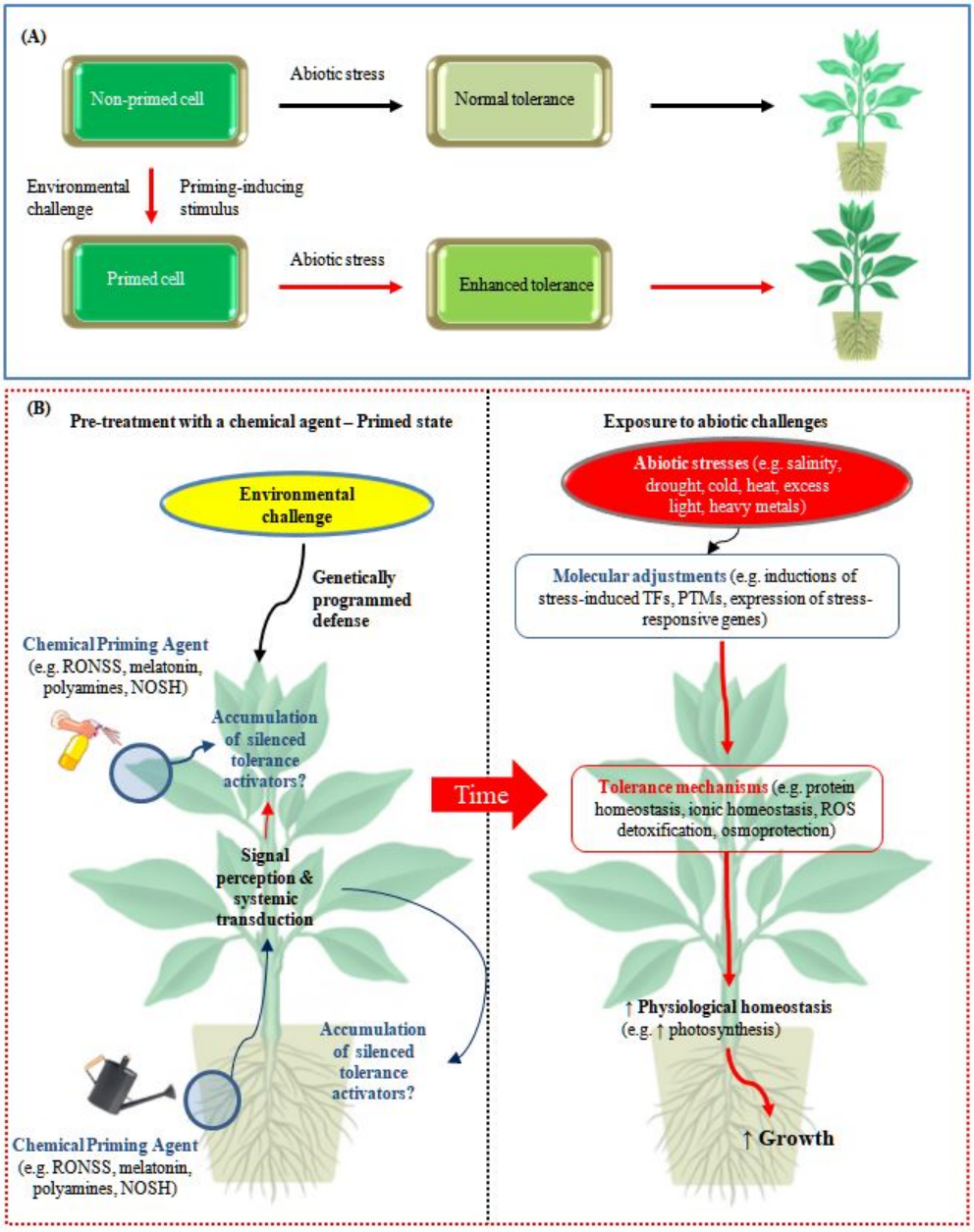


Fig. 4 (A) Pre-treatment with a priming-inducing stimulus (e.g., chemical priming agent) and/or environmental stimulus results in enhanced cell tolerance and reduces plant growth inhibition. (B) Chemical priming technologies turn on signaling pathways, potentially resulting in systemic accumulation of dormancy-tolerance signals; upon stress exposure, primed plants show enhanced tolerance-related responses (e.g. ROS-detoxification, osmoprotection), or ion balance that are, at least partly regulated by different molecular mechanisms (e.g. transcriptional regulation, post-translational modifications); enhanced plant

tolerance improves physiological equilibrium and plant growth. Figure adapted from Savvides et al. (2016).

Growth protocols are needed that simultaneously optimize crop yield and nutritional quality. Priming of antioxidant production by strategic, mild exposures to environmental stressors can enhance crop nutritional quality without curbing yield under field conditions, as successfully demonstrated for increasing the concentration of various phytochemicals, and improving flavor of grape berries, without decreasing yield (Acevedo-Opazo et al., 2010; Teixeira et al., 2013).

Production of antioxidant vitamins and essential antioxidant micronutrients for the human consumer by leafy crops is challenging, since leaves produce antioxidants particularly when absorbed light is in excess of the excitation energy that can be used for photosynthesis and growth (Cohu et al., 2014; Stewart et al., 2020). When plant growth is fast under favorable conditions, foliar levels of antioxidants involved in removing excess excitation energy are lower; when growth is slower under harsher conditions, foliar antioxidant levels rise. For example, the growth light intensity needed to saturate plant yield is lower than that needed to produce high levels of zeaxanthin, an essential human micronutrient that protects the human eye against damage by intense light as well as protecting membrane function in other organs (Cohu et al., 2014). The same is true for vitamin E (tocopherol), a lipophilic antioxidant that generally accumulates in leaves under stressful conditions to protect chloroplasts from oxidative damage when growth is limited (Muñoz and Munné-Bosch, 2019). Since such biostimulants are potent gene regulators acting at low concentrations in a highly context-specific manner, more work is needed to exclude any unintended effects on human health (Demmig-Adams et al., 2019; Tran and Demmig-Adams, 2007).

3.4 Integrating responses to sequential multiple stressors – a case of water-saving irrigation

Irrigation science is a sub-discipline in which a significant disparity can be encountered between farmer practice (water is applied when it is available, often with little consideration for plant requirements) and physiological principles that aim to apply enough irrigation at the times it is needed. Plant physiological measurements of leaf / stem water potential, canopy temperature and stem diameter have all been utilized in irrigation scheduling (Jones, 2004; Fernández and Cuevas, 2010), but limitations of cost, labor and technical expertise restrict their routine use by farmers. Nevertheless, scientist-farmer collaborations can help commercial enterprises to make significant water savings by using an understanding of actual crop water requirements to change farmer decision-making (see, e.g., La Rosa et al., 2016). Such knowledge exchange may ultimately prove more effective in guiding farmer practice than developing high-tech precision irrigation systems that use plant physiological knowledge to intentionally alter product quality.

Relatively simple agronomic changes in irrigation practices that are easily implemented offer opportunities for *in planta* integration of different physiological processes to save water, while maintaining yield and increasing product quality. Alternate wetting and drying (AWD) of rice intentionally imposes sequential multiple stressors by allowing soil water status to fluctuate between inundation (paddy rice) and a mild-to-moderate level of soil drying. Farmer adoption is encouraged by installing perforated plastic pipes in the soil to estimate water table height, with safe AWD requiring re-flooding when the water table drops to 15-20 cm below soil surface (Bouman et al., 2007). Although a comprehensive meta-analysis of 56 independent studies demonstrated that AWD substantially decreased water use (by 25%)

while maintaining rice yields compared to continuous flooding, the yield response in a given trial (Carrijo et al., 2017) depends on integration of various environmental cues during crop phenology (Fig. 2) and co-ordination of root and shoot growth responses. More severe soil drying (Ψ_{soil} < -20 kPa) during AWD thus substantially limited rice yields in alkaline soils (pH > 7), possibly because ammonia volatilization under these soil conditions significantly decreased crop nitrogen uptake (Carrijo et al., 2017). Likewise, imposing AWD for the entire cropping season significantly decreased yield, in contrast to imposing AWD only during the vegetative or reproductive growth stages (Carrijo et al., 2017). Co-ordination of root and shoot growth (presumably mediated by long-distance exchange of photoassimilates and phytohormones) may be critical to allow the plant to allocate resources according to the most limiting resource.

Any specific irrigation technique has potential trade-offs (e.g. yield *versus* quality) and integrating knowledge from diverse sub-disciplines may be necessary to ensure viable agronomic packages that do not compromise productivity. For example, flooding of rice constrains weed growth and weed control is an inherent challenge with AWD. However, combining deep fertilizer placement with AWD restricts root growth of the weed *Echincochloa crus-galli*, making it less competitive with rice (Weerarathne et al. 2015). Contributions from both irrigation and weed sciences thus demonstrate that rice integrates abiotic and biotic environmental cues, and allows development of an integrated package to sustain productivity. Moreover, restricting the phenological period of AWD implementation from the heading stage substantially increases 2-acetyl-1-pyrroline biosynthesis and grain quality of aromatic rice, and is based on a significant OMICs data set on metabolomics and gene expression (Bao et al., 2018). Water-saving irrigation can thus be implemented without compromising quality.

While AWD can increase rice yields under some circumstances (Norton et al., 2017; Thakur et al., 2018), these gains appear difficult to reproduce without an integrated understanding of plant physiological responses. While conventional analysis partitions grain yield into number of spikes, seed number and 1000 grain weight, trade-offs among these variables imply fine-regulation of tillering, seed set and grain filling rate (perhaps mediated by hormones altering source-sink relations) in response to prevailing acute stresses experienced by the plant at specific phenological phases.

Whereas AWD can alter leaf angle, thereby affecting light penetration into canopy and photosynthesis (Price et al., 2013) as well as tiller dynamics and leading to a greater fraction of productive tillers (Howell et al., 2015; Norton et al., 2017), the role of hormones in remobilizing stem carbohydrates to the grain has also been studied (Yang and Zhang, 2010). Early-flowering superior spikelets showed no treatment differences in grain filling-rates or the activities of enzymes involved in converting sucrose to starch, but higher ABA concentrations in the grains of AWD-treated plants were highly correlated with enzyme activities and increased grain-filling rate in later-flowering inferior spikelets (Zhang et al., 2012). Future work should aim to understand phytohormonal regulation of other plant physiological responses (e.g., leaf growth and photosynthesis) in vegetative plants (e.g., see Pérez-Pérez et al. [2020] and Puertolas et al. [2020]; in this issue), and how constitutive variation in phytohormone levels (using rice transformed with hormone biosynthesis/metabolism genes) affects grain-filling rates. Such understanding may be able to direct plant breeding efforts in selecting specific alleles that allow favorable agronomic responses to specific crop management techniques such as AWD.

3.5 Plant breeding

Traditional breeding methods have made important contributions to crop productivity and sustainability over the past 50 years (Voss-Fels et al., 2019), but are unable to keep pace with the rapidly rising food demand (Fischer and Edmeades, 2010). Contemporary breeding methods implementing marker-assisted or genomic selection, at various stages of breeding, or CRISPR-based genome editing for rapid transfer of desirable genetic variants (Chen et al., 2019; Taylor, 2019; Wolter et al., 2019; Zhang et al., 2019), accelerate breeding progress, and offer more flexible opportunities for selecting specific traits. However, overcoming the genotype-phenotype gap (Gjuvsland et al., 2013) is an increasing challenge as molecular biology provides ever more information. Even though breeding progress is generally rapid for simple traits (e.g., plant height, monogenic disease resistances, environmentally-stable grain quality traits), the physiological and genetic basis of complex traits (such as yield, abiotic stress tolerance or nutrient-use efficiency) and their environmental interactions is not yet understood well enough to enable efficient and effective selection for traits with low heritability. An increased focus on integrative plant physiological research may help overcome this bottleneck.

In the past, physiological models were not suitable to incorporate GxE (xM) interactions into systems models, due to a lack of high-quality physiological data about relevant developmental processes and systems across the entire cropping cycle under realistic field conditions. Due to this limitation, models are frequently based on either (i) high-resolution data across various processes throughout the lifecycle of a single genotype (e.g., cultivar), (ii) medium-resolution data across fewer processes on a selection of representative cultivars, or (iii) very-low-resolution data on large populations of genotypes. Option (i) provides excellent insight for modeling at a physiological process level, but no information on the general relevance of the model across cultivars. Option (iii) can provide deep insight into G*x*E interactions, but no information on the impact of genetic variation for key processes or G*x*E interactions. Compromising on the resolution of physiological data (with respect to temporal density or variety of measurements), the genetic resolution (number of genotypes), or on the resolution of environmental or management factors (number of environments) inevitably weakens the relevance of models. Thus far, this situation has represented the *status quo* because optimizing all aspects at once was not technically feasible.

Recent technical advances are providing exciting new opportunities to overcome these previous limitations. Generation of standardized, high-resolution genotype data in large populations (including regulatory data that can help explain gene-gene interactions and metabolic systems in an environmental context) is no longer a major financial bottleneck (Voss-Fels and Snowdon, 2016). For selected crops, high-throughput controlled-environment phenotyping systems can intensively analyze large populations for specific characters (e.g., early biomass development, root morphology, leaf architecture, heat or drought stress responses) or trait-calibrated physiological parameters (reflectance, temperature, water loss) at a single-plant or pot level. Large-container phenotyping systems (Hohmann et al., 2016) can provide considerable detail on physiological and architectural responses of plants growing in a field-like situation, throughout the entire vegetation period and under well-characterized environmental conditions.

Finally, field-based phenotyping systems using cameras and sensors carried on drones or tractors can provide high-resolution physiological and developmental data throughout the growing season in association with corresponding environmental data (Araus and Cairns, 2014). In the future, increased resolution and reduced cost of satellite imaging may further increase the availability of detailed data on crop development and performance. This growing accessibility and resolution of phenotype data for broad genotype collections provides deeper

insight into how cultivar differences impact performance under different conditions. Phenotyping methods informed by a physiological framework that dissects and models complex traits in relation to highly resolved genotypes can help incorporate G*x*E*(x*M) data into performance models. Models based on such comprehensive data allow cultivar-specific management decisions based on more accurate predictions of genotype performance in given environmental scenarios.

3.6 Breeding for climatestress – learning from wild species

Current crops were bred to be high-yielding in systems that minimize exposure to stress which makes current management practices unsustainable. Breeding crops for improved climate adaptation is a necessity in the face of climate change with increased occurrences of, e.g., heat and drought, and the need to exploit marginal lands for crop production. Ancestral lines or relatives of elite crops are generally more stress-tolerant, but have lower yields than the elite cultivars. Current attention is focusing on wild crop relatives, not just as models to study stress responses, but also as sources for introgressing alleles that confer tolerance into elite germplasm (Mickelbart et al., 2015; Prohens et al., 2017; Mammadov et al., 2018) or for improved exploitation limiting resources. Successful examples include, e.g., introgression of disease-resistance traits from wild crop relatives, such as light blight resistance into potato or stem rust resistance into wheat (Dempewolf et al., 2017).

Genetic analyses have shown substantial gene flow during and after domestication between crops and their wild relatives, indicating wild introgression of alleles with potentially beneficial effects (Janzen et al., 2017; Wang et al., 2019; Wolfe et al., 2019). Recent successful attempts to increase abiotic and biotic stress resistance by creating introgression lines from crosses of crops with wild relatives include disease resistance in pigeon pea (Sharma et al., 2019), or drought tolerance in peanut (Dutra et al., 2018) and sunflower (Hussain et al., 2019). Such pre-breeding approaches are useful to re-capture genetic diversity that may have been lost in the gene pool of elite cultivars.

More targeted marker-assisted breeding approaches can be used to introgress specific genetic loci with known function. This approach requires an understanding of the genetic basis of desirable traits, which can be advanced by mapping of quantitative trait loci (QTL), e.g., in crosses between cultivated crops and their wild relatives (Hartmann et al., 2014; Li et al., 2019) or through genome-wide association mapping (Rothan et al., 2019). Based on knowledge gained from wild crop relatives, targeted insertion or modification of genes through gene-editing technologies such as CRISPR can also increase the adaptability of elite germplasm to climate change (Rothan et al., 2019). However, the policy and regulation landscape, especially in the European Union, may currently hamper introduction of gene-edited crops (Schulman et al., 2020).

3.7 Climate-smart plant production

Future plant production systems must be adaptable to climate change. Understanding integrated plant physiological responses to climate-change related perturbations of the physical environment is an important prerequisite. How plants maintain productivity under more extreme environmental conditions, but also under increasing variability of conditions over the course of the growing season, both need to be better understood. This challenge has led to calls to develop “climate-resilient crops for improving global food security and safety” (Dhankher and Foyer, 2018).

As an example of the guidance that can be provided by integrative plant physiology, concomitant characterization of plant photosynthetic capacity and leaf vascular anatomy identified foliar anatomical features that help maintain high photosynthetic productivity under extreme temperatures. These features included foliar sugar-transporting infrastructure (Adams et al., 2014, 2016, 2018) as well as traits protecting the integrity of the leaf's water-transport system against injury (Glime et al. [2020], in this issue). Of particular interest to develop climate-resilient crops are trait combinations that offer simultaneous protection against both heat/drought-induced and freeze-thaw-induced injury to plant water transport (Glime et al. [2020], in this issue). Leaves achieve a multitude of trait combinations to match a wide range of climates by independently adjusting xylem traits at the level of single water conduits, individual veins and their composition, and the total length of veins and volume of water conduits at the leaf level. A better understanding of such trait combinations will support the development of crops customized for specific environmental contexts.

Understanding plant physiological responses is essential to unravel crop responses to climate change. However, climatic changes may also affect essential ecosystem services that could compromise crop yield. Farming with alternative pollinators (Christmann and Aw-Hassan, 2012) has been proposed as a strategy to increase surrounding biodiversity of wild pollinators and increase crop productivity. Modifying adjacent natural habitats not only attracts and protects pollinators, but also attracts predators and increases system biodiversity, thus increasing system resilience (Richards, 2001; Tschumi et al., 2015). Knowledge on the combined physiological responses of multi-species assemblages is required to design effective wildflower strips that provide enhanced pollination services to future cropping systems.

Globalization has brought increased numbers of invasive species that affect global biodiversity, and most countries have a limited capacity to act against invasions (Early et al., 2016). In addition, agricultural practices themselves also affect non-native weed richness in crop fields (Ikegami et al., 2019). Invasive plant species may exert different impacts on crop cultivars by competing for resources or pollinators through secondary plant defense compounds, such as root exudates of *Ambrossia artemisiifolia* that inhibit tomato, lettuce, and winter wheat growth (Vidotto et al., 2013). The impact of invasive species depends on interactions among environmental conditions, soil type, community assemblages, and crop management strategies, and thus requires an understanding of crop physiological responses, the invader and the surrounding community.

3.8 Remote sensing, artificial intelligence and robotics

High-resolution methods of near- and remote sensing are promising alternatives for deducing spatio-temporal dynamics in plant physiological behavior from hyperspectral, thermal, and optical measurements of plant canopy signals. It may be possible to integrate canopy information from the soil-plant-atmosphere continuum with routine environmental monitoring networks, biophysical modeling, and artificial intelligence. The resulting outputs and real-time information about physical, chemical, and physiological states of plant production systems would considerably improve decision making beyond traditional heuristic agronomic management approaches.

Assimilating spatio-temporal variation into plant modeling requires integration of vast amounts of data (Fig. 5). Advances in high-throughput sequencing technologies, mass spectrometry, improved sensor technology and high-throughput phenotyping platforms have facilitated massive data acquisition through sensor-to-plant and plant-to-sensor approaches (Argueso et al., 2019). Moreover, plant phenotypic plasticity, including memory or acclimation processes

and non-linear responses can generate complex physiological data sets on plant responses to the environment (Fenollosa and Munné-Bosch, 2019). Physiological and transcriptional memory in guard cells during repetitive drying stress , for example, determines physiological-hydraulic adaptation to fluctuating soil water supply conditions (Virlouvet and Fromm, 2015). Crop water demand modeling under fluctuating soil water availability requires temporal definition of plant physiological responses by considering plant memory from an integrative point of view. However, integrating genetic diversity and GxE(xM) interactions into crop models remains challenging (Boote et al., 2013; Chenu et al., 2017). Highly-replicated phenotyping across time and space may result in large datasets that accomplish the seven V from Big Data, i.e. high volume, high acquisition velocity, data variety, variability, diverse veracity, visualization and value (Ma et al., 2014). The greatest challenge is not acquiring massive amounts of data, but analyzing these to create understanding (Tardieu et al., 2017). Complex algorithms that consider spatio-temporal variability using zone segmentation in a multivariate climate space have allowed better predictions of crop yield (Leroux et al., 2018). To improve crop-yield predictions in the context of climate change, integrative plant physiology needs to assimilate data science to truly merge spatio-temporal and variability dynamics of crop production as well as design and test strategies of mitigation and adaptation to environmental pressures.

While regression analysis can infer crop yield under conditions with specific limiting environmental variables, multivariate analyses are better suited to accounting for a larger fraction of crop-yield variability. In addition, machine-learning algorithms (such as multivariate regression, decision trees, Bayesian models and artificial neural networks) are beginning to be used to predict crop yields (Fig 5). Machine-learning algorithms can make predictions without being explicitly programmed to perform the task, instead relying on pattern recognition from a data subset optimized over a remaining random subset (Liakos et al., 2018). Such algorithms include different data structures, such as images, gene or environmental information. Today, crop yield datasets can be mined with different approaches including supervised, unsupervised and reinforced machine learning algorithms (Fig 5). Their predictions of crop yield may outperform classical approaches (Marko et al., 2017).

Relationships between meteorological variables and rice-yield variability were evaluated using conditional inference forests (Delerce et al., 2016), and partial least-squares regression predicted leaf photosynthetic capacity (Heckmann at al., 2017). Pre-harvest remote sensing images were used to predict soybean yield using convolutional and recurrent neural networks. Convolutional neural networks were used to predict crop yields from satellite images, which outperformed other machine-learning methods (Russello, 2018), and are thus proposed as key tools to link plant physiology to crop yield for gaining a holistic understanding of plant physiology responses (Yamamoto, 2019). Despite the huge potential of machine-learning algorithms, model construction requires more than simply running a default algorithm (see Khaki and Wang, 2019), and depends on experts who understand the agricultural system’s requirements, plant physiology responses, as well as the mathematics behind the algorithms. Such expertise is needed to reduce uncertainty and stochasticity in crop- production models for climate-smart crop production solutions.

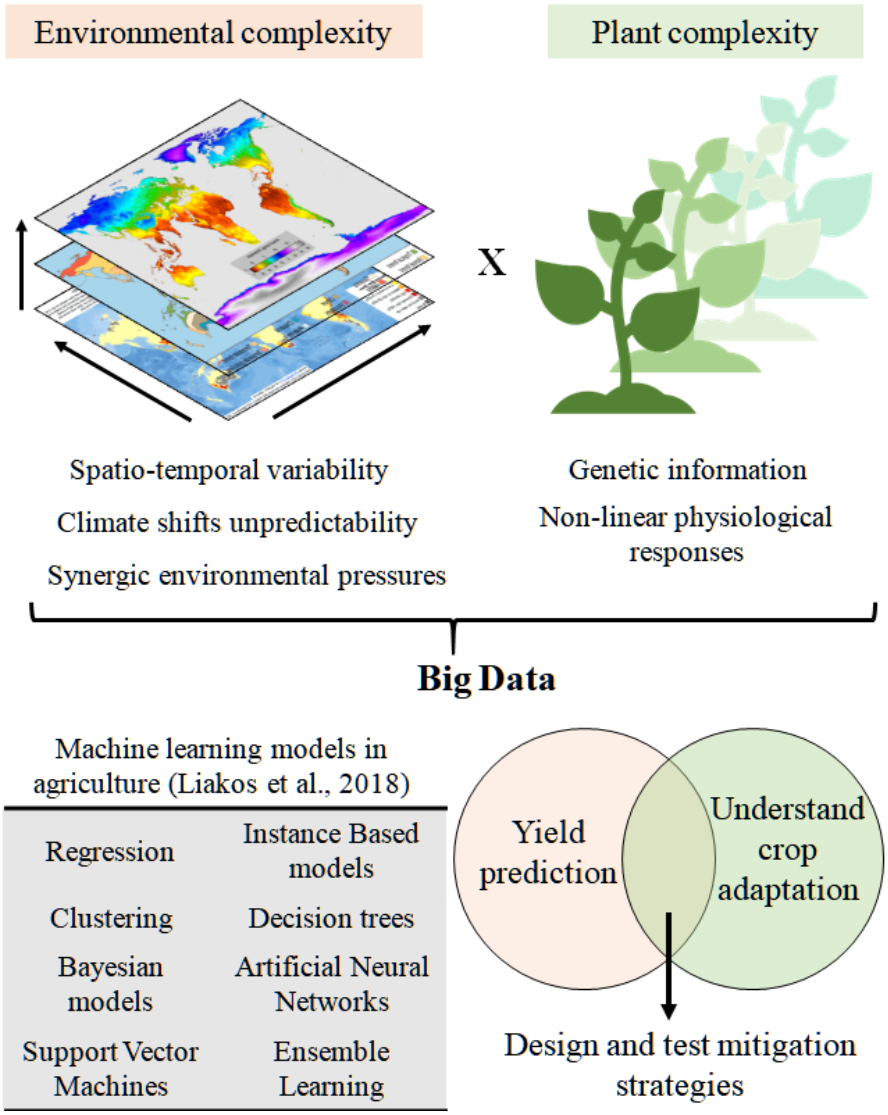


Fig. 5 Big data and machine learning for climate-smart production. List of machine learning models from Liakos et al. (2018).

Recent advances in robotics and automation offer new opportunities for plant sensing, vegetation classification, phenotyping, and executing field management. Novel robotic vision techniques are currently developed to facilitate automated navigation in agricultural fields, improve perception of plant environments and performing field management tasks such as weeding (Lehnert et al., 2020). Challenges associated with accurate steering through crop stands can be met by equipping robots with real-time differential Global Navigation Satellite Systems (GNSS), path tracking and motion controllers and applying advanced adaptive nonlinear modeling approaches for controlling movement (Kayacan et al., 2018). Stereo-vision and laser-scanning methods offer fascinating new opportunities for detecting and classifying plant architecture features such as branching angles, stem lengths, three-dimensional leaf shapes and their distribution within canopies (Guo and Xu, 2016; Paulus et al., 2013; Wahabzada et al., 2015; Lottes et al., 2018). Such knowledge is crucially important for interpreting physiology-related vegetation signals such as sun-induced fluorescence from diverse vegetation types using airborne hyperspectral measurements and applying radiative transfer modeling (Bandopadhyay et al., 2019; Schickling et al., 2016). Using appropriate sensors, unmanned aerial systems (UAS) are increasingly used for carrying out such operations and determining phenotype characteristics (Roth et al., 2018). Pretto et al. (2019)

developed an exciting solution for improving precision-management of crop stands through coupling UAS with unmanned ground vehicles (UGV). UGS infer spatial information about crop density, nitrogen status and weed infestation from processing signals of appropriate sensors directed towards large areas, transmit this information into UGVs for comparison against their own perceptions of plant stands and environments, negotiate both types of information through dedicated algorithms and decide on automated management actions on this basis. On the other hand, human capabilities of perception, thinking and action, unmatched by autonomous robots, can be utilized in human-robot interactions to carry out farming operations which are unhealthy to manual operators such as spraying (Bechar and Vigneault, 2015; Berenstein and Edan, 2017). The advantage of such systems is that sensing, precision management, artificial and human intelligence are fused to minimize negative impacts of agrochemicals on the environment, such as robots that perform weeding operations without applying selective herbicides (van Evert et al., 2011; Wu et al. 2020). Figure 6 shows an unmanned robot that fuses optical and ultrasonic information from dedicated sensors for identifying weeds that are laser-burned at early stages of development (methods described in Pretto et al., 2019 and Wu et al. 2020). The underlying vegetation classification can allow micro-scale management of highly diverse plant communities, thus making monocultures and their vulnerabilities (Na et al., 2019) obsolete and opening new options for agroecological design of cropping systems.



Fig. 6 Robot scanning an agricultural field with various sensors, classifying species, detecting weeds and targeting them for burning with a laser (left). Crop and weeds as seen from a robot (top right). Laser-burning a weed (bottom right). Pictures courtesy of CRC Phenorob, University of Bonn (www.phenorob.de).

3.9 Landscape agroecology

Agricultural land-use typically follows a pattern from pre-settlement natural vegetation to frontier clearing, subsistence agriculture, small-scale farms, and, finally, to intensive

agriculture (Foley, 2005). Today, crop and pasture lands cover about 40% of the earth's land area (FAO, 2019). Options for further expansion of land are limited and human influences on global biogeochemical cycles are unprecedented (Evans, 1998; Murphy 2007; Waters 2016). Massive use of chemicals and fossil-fuel-based energy in industrial crop farming cause major environmental problems at local and global scales (Malézieux et al., 2012). Agroecology mitigates such negative impacts by applying plant-ecological concepts and principles to design and manage agricultural systems (Altieri, 1995).

Varying species composition, spacing, density, spatial patterns, timing and sequencing provides multiple options for agroecological plant production design (Woijtkowski, 2019). Such options will leverage the realization that each plant grows in the context of other plants (Tixier, 2020), and that plant physiological principles can be applied to generate synergistic effects to optimize resource use by minimizing plant-to-plant competition, and improve stress adaptation to climate-change-related perturbations of the physical environment. Malézieux et al. (2009) discuss several options for improving resource uses, yield stability and product quality through mixed cropping design. Using nature as a design principle has a large potential for improving the sustainability and resilience of cropping systems as demonstrated by Malézieux et al. (2012), Li et al. (2014), Lambers and Olivera (2020), Mitchell et al. (2008) and Funashabi (2016). Knowledge on multispecies physiological responses will be required to design effective wildflower strips that benefit cropping systems and boost soil microbial biodiversity, increase early growth and performance after short-term cover crop rotation (Peralta et al., 2018; Tschumi et al., 2016). A global long-term agroecological network, similar as the Long-Term Ecological Research (Willig and Walker, 2016), needs to be established to monitor and test these and other approaches in different environments to gain insights into their spatio-temporal dynamics, as well as understanding their ecological and social consequences. Applying the various technical options described in the previous section has a huge potential for attaining this goal.

Scaling agroecological principles to the landscape level requires consideration of reciprocal interactions between patterns and processes, heterogeneity, scaling, critical thresholds, and boundaries and flows (Turner and Gardner, 2015). Solutions will need to be context-specific since interactions between physical, climatic, chemical and biological landscape characteristics are highly site-specific and influenced by local cultures. Furthermore, extrapolating these characteristics into the future will be challenging, because landscapes might change in unpredictable ways. Past landscapes no longer exist, and present ones will likely change dramatically (Wiens, 2013).

In the past, agroecological research focused primarily on solving scientific and technical problems while disregarding feedbacks between plant production-systems and social communities. Repeated failures in applying technical solutions recently motivated agroecologists to develop participatory and transdisciplinary research approaches (Mendez et al., 2019). The application of evolutionary ecology models and concepts to the study of human behavioral diversity (Winterhalder and Smith, 2000) is a research area in its infancy that may provide highly relevant information about human-landscape interactions. Human dependency on plants can be traced back at least 50000 years and encompassed thousands of plant species (Murphy, 2007). In contrast, global crop production today is based primarily on cultivating just five species, i.e., rice, wheat, maize, millet and sorghum (Beck et al., 2016), all of which were selected for their economic characteristics while disregarding social and environmental consequences (IAASTD, 2009). To become successful, future agronomy should adopt plant-physiological and ecological principles as well as consider social perceptions and consequences of the methods they propose. Comparing historical and today's

interrelations among people, plants and land will reveal general behavioral-response patterns that might inform the design of future agroecological landscapes.

Repeated food crises and global change have generated a renewed interest in applying a variety of cultivation options (Wojtkowski, 2019) to create forms of agriculture that are more ecologically and biologically diverse as well as more resilient, sustainable and socially just (Altieri 2012; Snapp and Pound 2017). Whether such goals can be achieved in the context of current approaches to development is debatable (Mugwanya, 2019), with land-use development strategies failing when planners are insensitive or directly inimical to local people, or when ideas are shaped by naive and idealized visions of apolitical conservation (Anderson and Grove, 1999). These and other examples demonstrate that implementing concepts developed by integrative plant physiology and agronomy is not a trivial task, and requires consideration of the multi-facetted nature of people-land relations. A transdisciplinary concept is proposed in the following section to tackle these challenges.

4. Practicing a Transdisciplinary Mindset

Examples of interactions between integrative plant physiology and agronomy discussed in the previous sections demonstrate the complexity of interrelations that remain to be synthesized into a coherent research framework. Examples were chosen based on the authors' expertise to stimulate discussions on how the two research areas may contribute to avert looming food crises (Evans, 1998; Murphy, 2007; Oreskes and Conway, 2014). Collaboration between integrative plant physiology and agronomy will also require an exercise in metacognition – thinking about thinking. Past concepts of technology adoption (Sumberg, 2016) need to be broadened to include all stakeholders in knowledge generation through transdisciplinary cooperation.

Approaches for improving transdisciplinary cooperation, establishing societal relevance, and transforming science into decision making (Klein, 2014), include a philosophical framework for open and critical transdisciplinary inquiry of Russel (2010) that is based on Habermas' theory of "knowledge and human interests" (Habermas, 1972). It posits that the structure and dynamics of systems cannot be conclusively determined with the scientific method, because these systems are open systems, subject to socio-cultural influences and exist independently of human understanding, which is shaped by beliefs, values, and interests. This realization leads to a call for a pluralistic approach in which concepts of inquiry are subjected to continuous negotiation and revision as well as use of ethical considerations in the selection of what is included or excluded in transdisciplinary inquiry.

In order to base transdisciplinary research on the above commitments (Russel, 2010), integrative plant physiology and agronomy should actively engage with relevant stakeholders, thus transitioning from a "science for society" towards "science with society" approach (Scholz and Staufacher, 2009). Such collaboration involves science-policy dialogue, public-private partnerships, developing science-based solutions together with agricultural extension services, environmental protection agencies, public administration or environmental legislation. While elaboration of these topics is beyond the scope of the present review, here we use the example of small farmers (Fig. 7), who represent the majority of farmers worldwide (Altieri, 2012), are exposed to rapid changes in developments in their societies, and are in states of transitions between traditional and modern farming.

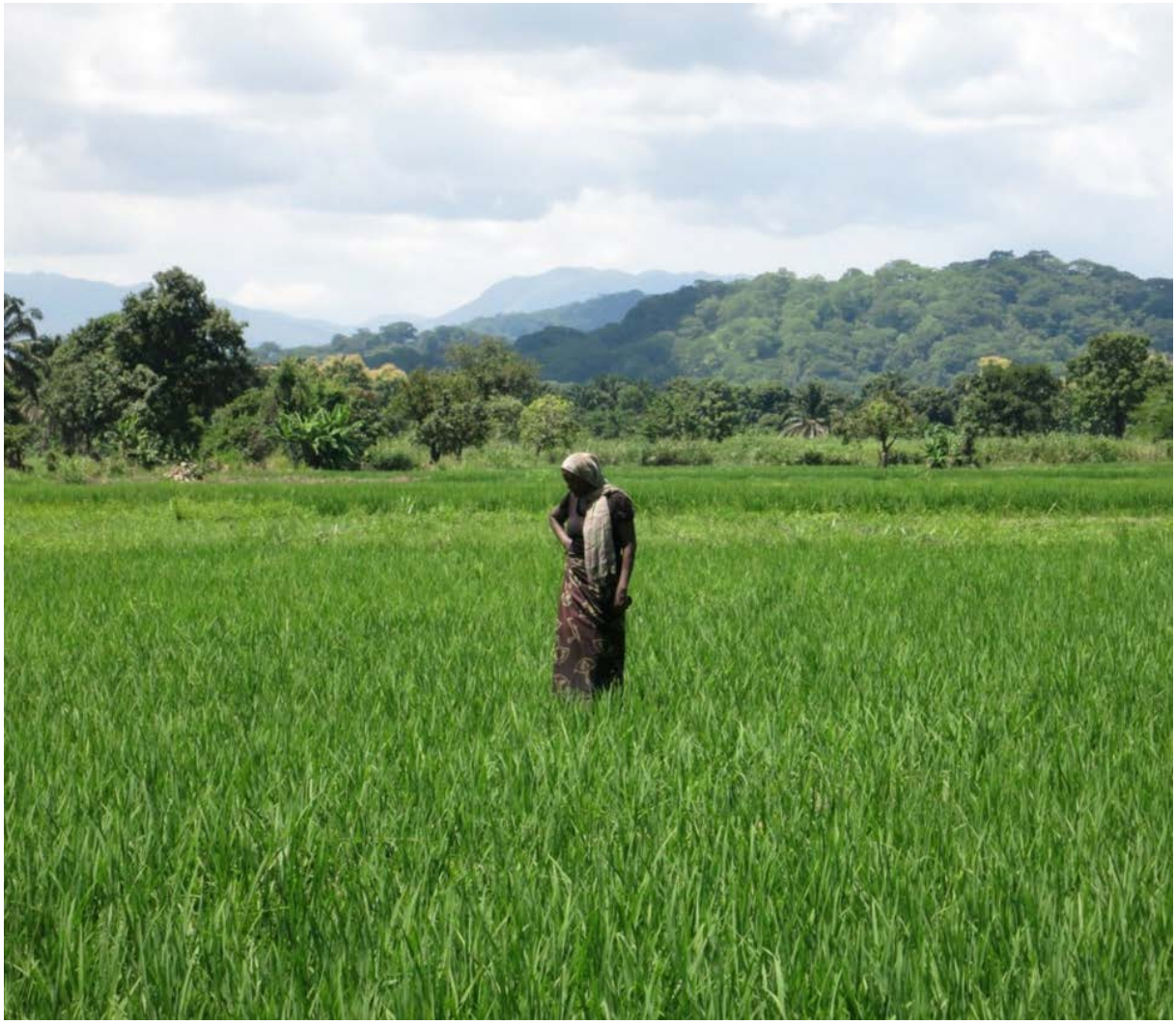


Fig. 7 Tanzanian rice farmer contemplating about the future of her farm plot. Understanding the integration of molecular biological processes at the plant level and transforming this knowledge into agronomic practices has a great potential to make plant production in rural areas such as shown above more sustainable. Transdisciplinary exchange among farmers, agronomists and plant physiologists should be promoted to overcome knowledge boundaries and make solutions socially and ecologically viable. Picture courtesy of CRC Future Rural Africa, University of Bonn (www.crc228.de).

Small farmers have developed an astonishing variety of plant-cultivation methods that evolved from continuous adaptation to environmental constraints in many places over long times since the Neolithic revolution (Bellwood, 2007; Murphy, 2007). These farmers' mode of investigation is holistic, locally-valid, contextual and value-laden (Herman, 2016), thereby leading to highly nuanced, practical agroecological knowledge in social contexts based on long-term trial-and-error. However, the current rate of global change compromises continuation with this approach that requires long times. Integrating these farmers' traditional methods of investigation into transdisciplinary research conducted by agronomy and integrated plant physiology has a great potential to overcome this dilemma. For example, small farmers adapt to drought stress by considering a change of crop types, varieties and adjusting management within the range of environmental, technological and social options available to them. This process can be accelerated by utilizing plant physiological knowledge about genetic, biochemical and organismal regulatory principles of plant adaptation to drought stress. Translating this knowledge into stress management practices requires careful

selection of technology options. Alternatively, high-tech solutions such as robotics, precision agriculture and efficient computation are inaccessible to small farmers, but may not be irrelevant to them. Improved understanding about the spatio-temporal complexity of crop physiological dynamics, gained by applying advanced technology, could very well be utilized to design field management practices that fit local ecological, environmental and socio-cultural contexts. Successful implementation will require involving local communities, government institutions, and policy makers. Transdisciplinary research need to be based on joint knowledge-generation processes to ensure societal relevancy of the proposed technology options. Ethical issues need to be considered, such as equal access to sufficient food to sustain a healthy and productive life and eradication of hunger (Pinstrup-Andersen and Pandya-Lorch, 1998; UN, 2017). Balancing the right for food against the need for environmental protection will require close communication among all stakeholders to resolve these and other ethical concerns *via* carefully negotiated knowledge.

This example elucidates a vision for how each participant's knowledge about agronomic systems can become relevant by integration with the knowledge of other participants and consideration of socio-cultural influences. To overcome obstacles in integration (Campbell, 2005), it is important to keep knowledge structures explicit (Boulton et al., 2005). A knowledge-exchange network of pluralistic nature is envisioned that considers social consequences of technologies for local socio-cultural settings. Evaluating societal consequences of transdisciplinary research is required to achieve this aim (Holzer et al., 2019). Such integration and evaluation will not only improve the quality of transdisciplinary research, but also increase the societal value of joint integrated plant physiological and agronomic research.

Conclusions

The OMICs era has led to an explosion of fragmented, highly specialized knowledge about plants. Advances in analyzing methods, artificial intelligence, and computer science offer unprecedented new opportunities for establishing causal relations between different levels of plant system organization and developing complex plant physiological theories on this basis. Integrative plant physiology applies these methods to characterize plant function in complex, realistic environments. The resulting insights into complex plant responses to the environment can be utilized by various means to improve the adaptive capacities of plant production systems to population growth and climate change. Strengthening linkages between integrative plant physiology and agronomy has a large potential to reach this aim, as demonstrated by the examples discussed in this review. Implementation in practice requires development and application of dedicated trandisciplinary research approaches to make solutions socially relevant and ecologically sustainable. Whether the research framework we propose becomes successful depends on how open we are in overcoming our knowledge boundaries.

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