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Feature Review

Addressing Research Bottlenecks to Crop Productivity

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Asymmetry of investment in crop research leads to knowledge gaps and lost opportunities to accelerate genetic gain through identifying new sources and combinations of traits and alleles. On the basis of consultation with scientists from most major seed companies, we identified several research areas with three common features: (i) relatively underrepresented in the literature; (ii) high probability of boosting productivity in a wide range of crops and environments; and (iii) could be researched in 'precompetitive' space, leveraging previous knowledge, and thereby improving models that guide crop breeding and management decisions. Areas identified included research into hormones, recombination, respiration, roots, and source–sink, which, along with new opportunities in phenomics, genomics, and bioinformatics, make it more feasible to explore crop genetic resources and improve breeding strategies.

Highlights

More symmetrical investment in crop research will create opportunities to improve crop models, combine new alleles through prebreeding, and suggest novel crop management practices.

Consensus among public and private sectors is that more investment is needed to improve understanding of hormone crosstalk, recombination rate, maintenance respiration, root structure and function, and source–sink balance.

Greater investment in these areas is expected to benefit a wide range of crops across most environments.

New opportunities in phenomics, genomics, and bioinformatics make it feasible to explore the vast untapped collections of crop genetic resources to create novel trait combinations.

Filling knowledge gaps is expected to enable a much more integrated understanding of crop yield and adaptation, improving breeding and crop management models.

Asymmetry in Crop Research

Research into crop growth and adaptation under diverse cultivation scenarios has underpinned global food security, especially since the Green Revolution, during which time the global population has more than doubled. During the same time, the global area of cultivated cereals, which account for more than 70% of total calories consumed by humans, has barely changed while yields have tripled.[i] These two statistics alone clearly support the impact of crop research on breeding and agronomy as well as effective policy decisions and the agility of farmers to adopt new technologies [1,2]. Nonetheless, the challenges that global agriculture now faces are not just to feed 10+ billion people within a generation, but to do so under a harsher and less predictable climate, and in many cases with less water and declining soil quality [1]. Clearly, research, breeding, and agronomy must be even more effective.

Crop breeding integrates effective crossing strategies combined with efficient selection of progeny [3]. To date, the most impactful breeding objectives have been to maintain resistance to the ever-evolving spectrum of pests and diseases (e.g., [4,5]), as well as an array of consumer-driven characteristics, such as storability, baking quality, and so forth (e.g., [6]). However, to improve productivity under harsher or less predictable environments will require specific knowledge gaps to be filled in the crop context. The technology now exists to apply new understanding of trait and allelic combinations to phenotype and genotype at breeding scale. Due to the large numbers involved in progeny screening (from thousands for a single cross to millions of double haploids), evaluation within environments that best represent the **target population of environments (TPE)** (see Glossary) is expedient, combined with new genomic [7], phenomic [8], and crop modeling tools [9], now at an advanced stage for commercial cereal breeding [9]. In short, breeding is a practical discipline focused on products.

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More upstream research tends to favor cutting-edge challenges, some methodological in nature. Research focusing on near- to medium-term crop productivity gains is typically not strategic enough to warrant upstream funding, while too upstream to risk funds allocated for crop breeding. As a result, the translation of knowledge from pure plant science to crop breeding has gaps [10]. Some notable exceptions include boosting photosynthesis [11], the application of tomography to capture roots images [12], and gene editing of crops [13].

Nonetheless, novelty is a significant driving force in academia, including the application of advanced technologies. As a result, knowledge of crop growth and adaptation does not grow symmetrically, creating instead islands of knowledge that are not necessarily well connected [14]. While this approach works well for pushing back specific frontiers of knowledge, crop improvement requires a more systematic understanding to achieve adaptation and yield gains of harvestable products (e.g., seeds, fruits, roots, tubers). For example, in order that improvement in a crop's photosynthetic potential will boost yield, extra **photo-assimilates** must also be distributed in a way that optimizes the development and growth of edible organs. In the case of cereals and other seed crops, this is expressed as **harvest index (HI)**. The large range in expression of HI in, for example, modern wheat cultivars, from approximately 0.4 to 0.55, and the attendant negative correlation between yield and biomass [15], attest to the apparent underutilization even of current photosynthetic capacity. Clearly, the understanding of partitioning of photo-assimilates and reproductive growth must match understanding of photosynthesis if the value of research investment is to effectively translate to food security.

There are other conundrums in crop research that point to asymmetrical knowledge. For example, the definition of HI in cereals considers only above-ground biomass. This definition is quite arbitrary, there being no scientific reason to exclude investment in below-ground biomass. The reason is a practical one, as growth analysis can be relatively easily performed on above-ground structures compared with those in the soil. Since HI is an important trait in crop improvement, this source of error is not trivial. In a study in wheat, HI differed by between 7% and 20%, depending on genotype, when considering only the above-ground biomass versus all biomass, including roots [16]. Another example of asymmetry in crop-focused academic research is the emphasis on photosynthesis over respiration, despite genetic variation in maintenance respiration associated with growth [17]. Furthermore, a number of field studies show cereal yields express a significantly stronger relationship with night temperature than with day temperature [18,19]. Because temperature affects respiration as well as other processes, such as flowering response, understanding and modeling of crop response to night as well as day temperature is a key knowledge gap. While there also needs to be renewed focus on how manipulation of photorespiration could influence crop growth and yields, the degree of asymmetry in research effort is not as great as that for respiration. Indeed, recent work has highlighted how transgenic plants engineered to use alternative photorespiratory pathways can exhibit improvements in net photosynthetic CO_2 uptake, biomass accumulation, and yield [20,21]. The importance of the environment in influencing gains arising from modifications in photorespiratory pathways is also being addressed [22].

Asymmetrical investment in crop-related research leads to additional conundrums. A literature search with the keywords 'photosynthesis' and 'drought' identifies many studies. While plant water deficit certainly inhibits gas exchange and severe stress can damage photosynthetic machinery, the primary determinants of crop yield under water deficit are access to water [23] and efficient budgeting of water [24]. Subtle cultivar-level differences in sensitivity of the photosynthetic apparatus to water deficit will have marginal impact in breeding at best; a mundane analogy would be tuning the carburetor of a motor to overcome a block in the fuel line. While other

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conundrums exist, the objective of this review is to illustrate how previous investment in crop-oriented research can be better leveraged by filling specific knowledge gaps. Since these research gaps exist for all crops to varying degrees, our premise is that addressing these could significantly boost crop improvement across a wide range of species and environments. Therefore, filling these research gaps can achieve a more systematic understanding and modeling of crop processes and how they may be improved in tandem.

Another factor that certainly influences the academic research agenda for crop species is the difficulty of working in realistic field environments, since these can only be partially controlled. Lack of control hampers rigorous research, despite the reality of most food production scenarios, where no two fields or growing seasons are ever completely the same. However, Galileo's research guideline 'measure what is measurable, and make measurable what is not so' can now be applied to a much greater degree in field environments through advances in remote sensing and geographical information services. In addition, a new generation of molecular tools permit real-time estimates of DNA translation and metabolic processes to be monitored on plant tissue taken directly from field experiments. Furthermore, **crop growth models (CGMs)** provide the mathematical framework to integrate knowledge and conduct quantitative evaluations of traits in the TPE [22,24,25] while also providing a dynamic framework to help in understanding and researching basic trait biology. As a result, unprecedented opportunities now exist to fill some of the key knowledge gaps in order to join new knowledge with previous crop research investments.

Crop Research Opportunities for Leveraging Existing Knowledge

No matter how advanced the understanding of a component of a problem, systematic improvement, whether for a genotype or a cropping system as a whole, requires broad understanding to maximize its impact. An illuminating example was work showing that zinc deficiency exacerbates drought stress due to its essential role in detoxifying reactive oxygen species, leading to foliar applications of Zn on approximately 4 million ha of wheat in Turkey alone [26]. Before that breakthrough, the investment in breeding for drought adaptation *per se* was seriously confounded and achieved marginal impact (Figure 1) [27].

Perhaps the best example of how overcoming a single bottleneck opens up many new possibilities was the introduction of semidwarf genes in cereals. Before their widespread adoption, tallness limited cereal yields due to structural failure. The source of the new allele in wheat (*Rht1*) was

Figure 1. Effect of Foliar Application of Zn (100 mg Zn m^{-2} as $ZnSO_4$ $7H_2O$) to Barley Grown on a Zn-Deficient Soil (DTPA-extractable Zn: 0.1 mg kg^{-1} soil). Effect of Zn (*green* parts of the field) was distinct within 3 weeks after Zn application. Reprinted, with permission, from [27]. Abbreviation: DTPA, diethylenetriamine pentaacetic acid.

Glossary

Carbon use efficiency (CUE): fraction of photosynthetically fixed carbon that is retained in plant biomass once carbon release by plant respiration is accounted for.
CRISPR-associated protein 9 (Cas9): CRISPR (clustered regularly interspaced short palindromic repeat) associated endonuclease widely used in gene editing.
Crop growth models (CGMs): cognitive models that represent in mathematical form the current knowledge in crop physiology that is relevant to solving a scientific or engineering problem.
DNA double-strand breaks (DSBs): lesion to DNA backbone that initiates crossover formation during meiosis.
***fancm*:** fanconia anemia complementation group M is a DEAD-box ATP-dependent DNA helicase that functions to suppress class II crossovers.
***figl1*:** fidgetin-like 1 is an ATPase family AAA domain-containing protein that functions to suppress class II crossovers.
H3K9me2: histone H3 lysine 9 dimethylation is a repressive heterochromatic histone modification.
Harvest index (HI): the proportion of total crop measurable dry mass that is harvested.
HEI10: human enhancer of invasion 10 is a ubiquitin E3 ligase that promotes class I crossovers.
Hormone crosstalk: two or more hormones affect each other in signal transduction or metabolic pathways.
Hormone interaction: the way of two or more hormones having effects on each other.
Novel trait variation (NTV): refers to genes or alleles that condition a trait of interest not commonly found in breeding populations.
Photo-assimilates: carbohydrates produced by current or previous photosynthesis (the latter when using reserves) translocated to active sinks (e.g., growing grains during the effective grain filling period).
Quantitative trait loci (QTLs): genetic loci showing a significant statistical association with inheritance of a quantitative trait.
Radiation-use efficiency (RUE): is the canopy net photosynthesis accumulated over a certain period of time (estimated as the ratio between

Norin 10, originally from the variety Daruma, developed by Gonjiro Inazuka in Japan in 1935. While it took more than 10 years to achieve its effective introgression, pleiotropic effects of the *Rht* gene also improved HI and nitrogen use efficiency [28]. This spearheaded the Green Revolution for wheat and other cereals, more than tripling yield potential and saving an estimated 1 billion lives at a time of widespread famine [28].

The aforementioned examples illustrate the value of systematic, demand-driven crop research that does not shy away from logistical challenges. Five examples of challenging research areas that, if tackled more systematically, are likely to open productivity bottlenecks are discussed herein, along with a discussion of how new knowledge can be used in breeding and to improve CGMs. An exhaustive review of these research areas cannot be presented here, nor can all of the potential bottlenecks, as these will emerge as understanding improves. Nonetheless, these areas were broadly agreed on as major knowledge bottlenecks with potential to improve crop productivity among authors and their colleagues from both public and private sectors. Furthermore, improved understanding in these areas can be expected to be complementary to each other and to existing knowledge (Figure 2).

In the opinion of authors and other colleagues, some of the 'best bets' for achieving step changes in productivity across a broad range of crops include investment in root structure and function, roles of **hormone crosstalk**, efficiency of maintenance respiration, increasing sink strength to boost carbon assimilation and yield, and engineering meiotic recombination to harness genetic diversity. To illustrate how improved understanding of more basic science would create opportunities in crop improvement, two additional areas are reviewed: exploration of genetic resources for prebreeding and Illuminating 'black boxes' in simulation modelling. Since authorship represents a range of scientific stakeholders from the public and private sectors, the topics are priorities in the 'precompetitive space' as defined by the major seed companies involved in this exercise; in other words, areas with general benefit that, if neglected, potentially hold back progress for the industry.

biomass and photosynthetic active radiation intercepted, both over the period considered).
***recq4a*:** RecQ ATP-dependent DNA helicase A that functions to suppress class II crossovers.
***recq4b*:** RecQ ATP-dependent DNA helicase B that functions to suppress class II crossovers.
***RECQ7*:** RecQ ATP-dependent DNA helicase that controls recombination in wheat.
Root system architecture (RSA): structural and dimensional aspects of root organ expression
Sink strength: refers to the intrinsic capacity of sinks to uptake and use resources, given by the number and potential size of sinks.
SPO11: SPORULATION11 is a DNA topoisomerase VI subunit A that is required to generate meiotic DSBs.
Target population of environments (TPE): a subset of crop environments encompassing the same breeding objectives.
TILLING: targeting-induced local lesions in genomes is a reverse genetic strategy used to identify nucleotide variation in specific genomic regions among individuals in a population.

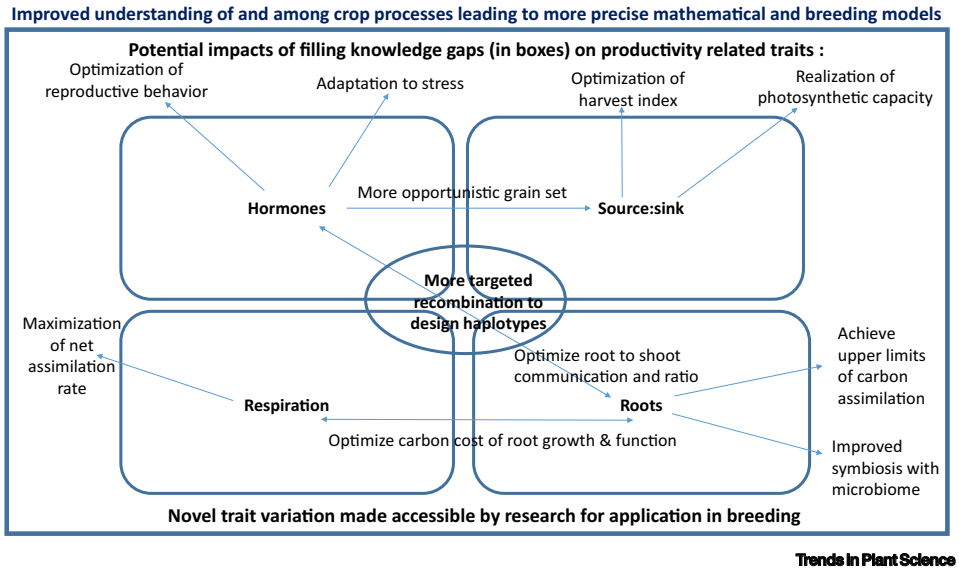


Figure 2. Current Trait Knowledge Bottlenecks and Potential Research Outcomes in Crop Productivity.

Root Structure and Function

To aid foraging, root growth and development are responsive to abiotic and biotic signals in the local soil environment [12]. This highly adaptable behavior, termed 'developmental plasticity', offers breeders opportunities to create crops with 'customized' **root system architecture (RSA)** better adapted to forage for heterogenous resources in specific soil conditions [29]. For example, nitrogen (N) in the form of nitrate (NO_3^-) is a particular challenge for root capture, as it is highly mobile and leaches into deeper soil layers. To aid N capture, breeders could exploit steeper root angle in brace and crown roots [30], elongation of lateral and seminal roots [31], and reduced root length density near the soil surface and reduced numbers of axial roots [32]. These plastic traits would serve to increase exploration of deeper soil layers where N is more abundant. In contrast, phosphate (P) is available in an inorganic form that is highly immobile and concentrated in the topsoil [33]. To aid P capture, breeders could exploit increased numbers and lengths of roots in patches of high P availability [34], shallower root angle [33], increased numbers and lengths of root hairs [35], and cluster root formation [36]. In sorghum, genetic variation in root angle [37] enables the development of genotype × management technologies. Skip row systems can benefit from genotypes expressing low angles, thereby increasing grain growth [37].

However, despite important advances in knowledge about crop roots over the past decade, major gaps remain, such as the following:

- Given the increasing impact of climate change, there is an urgent need to determine how crop RSA is controlled by abiotic stress signals, often mediated by hormones, such as aerial and soil temperature. Whilst aerial heat stress impairs wheat growth at any developmental stage, RSA traits such as greater rooting depth appear to help reduce its effects [38].
- How much carbon/biomass should crops invest in their root systems to maximize resource capture and sustainability, yet minimize its impact on yield? Surprisingly, some detailed studies on root system efficiency and CGM simulations (validated with reference to field data) predict 'less is more,' where a lower density of longer lateral roots can be as effective at foraging for mobile resources [39]. In addition to RSA, anatomical scale traits such as cortical aerenchyma can reduce root respiration by up to 50% [40], enabling crops to reinvest their C in roots or other organs.
- Despite growing recognition of the importance of the soil microbiome on crop RSA and vice versa [41] and development of a multibillion-dollar industry selling microbiome-based seed coatings for crops, major gaps exist in our knowledge of the mechanisms integrating root and biotic signaling.

Studying crop RSA directly in field soil is arguably most relevant, but it poses many practical challenges. Indirect approaches such as canopy temperature measurements [38] or determining water extraction profiles using electrical resistance tomography and electromagnetic inductance methods can be used to infer root architecture traits, but currently only at a relatively coarse resolution [42]. Invasive approaches such as soil coring and 'shovelomics' have greatly facilitated the throughput of field root phenotyping [43]. However, destructive techniques can result in loss of finer-scale features (e.g., lateral roots), and measurements give only a snapshot of root development. Nondestructive imaging techniques, such as agar plates, rhizotrons, and paper-based and hydro-/aeroponic systems, enable temporal changes to be observed throughout root development [12]. Nondestructive 3D RSA analysis is possible using transparent gels [44]. Whilst growing roots in non–soil-based systems helps decrease experimental variability by reducing the impact of resource heterogeneity or microbial populations, the results are more difficult to extrapolate to field conditions. However, controlled environment phenotyping of root traits can be connected to field breeding experiments [45]. Magnetic resonance imaging and X-ray computed tomography

have been used successfully to noninvasively study 3D growth in soil [46,47]. Nevertheless, these techniques are expensive, relatively low throughput, and not yet deployable in the field.

Understanding root responses to soil stresses is vital to develop novel crop varieties [48]. As topsoil dries, there is a vertical gradient of water availability. Roots experiencing water deficit have been observed to increase their angle to reach deeper soil profiles [49]. Water deficit in upper soil profiles also suppresses lateral root and crown root growth in different plant species [50,51]. The few but long lateral RSA ideotype is suggested to be most efficient during water stress, as resources are saved to extend the root system into deeper soil profiles. More research is indeed needed to create genotype × management technologies tuned to the TPE based on fundamental understanding of root traits [52].

Nonetheless, colonizing deeper soil profiles is challenging due to mechanical impedance [53]. Wheat roots growing at 90 cm are only found in macropores, suggesting their roots only grow by soil deformation in shallow uncompacted soil [54]. Interestingly, maize and soybean roots preferentially grow towards macropores using a process termed 'trematotropism' [55]. The ability to locate and grow through macropores could confer a deep rooting architecture and aid reaching water supplies. Instead, the ability to deform strong soil is assumed to be the most important trait for deep rooting [56]. Despite the potential importance of either response, the mechanisms underpinning them remain unclear. The recent identification that the plant signal ethylene controls root responses to hard soil opens up new opportunities to select compaction-resistant crop roots [57]. Some of the other impacts of hormones on root growth are presented next.

Roles of Hormone Crosstalk: Regulating Root Growth and Source-sink Relations

The role of individual hormones in determining plant growth and development is well documented. However, how hormones function interactively is still unclear. For example, an improved understanding of how hormone crosstalk regulates root growth and source–sink relationships could be applied in crop improvement.

Root Growth

Dicotyledonous taproot systems and monocotyledonous fibrous systems, comprising primary and lateral roots, are complex and heterogeneous. Multiple hormones and their synergistic or antagonistic interactions differentially regulate growth of different root types [58] (Box 1).

Ethylene–auxin crosstalk is the best-established **hormone interaction** controlling primary root growth, with high concentrations synergistically inhibiting root elongation by modulating cell proliferation in apical meristems and cell elongation in the elongation zone [58]. Manipulating auxin transport can regulate root architecture, with large root angle (facilitating nutrient scavenging) resulting from a mutation in *OsPIN2* [59], while decreased expression of the auxin transporter *OsPIN5b* enhanced root vigor and rice yield [60]. Deeper rooting (e.g., facilitated by the rice DRO1 gene [61]) should enhance water uptake, boosting yields of cereal crops growing on residual soil water.

Tissue water status determines abscisic acid (ABA) effects on root elongation, with high ABA concentrations inhibiting root elongation at high water potentials but endogenous ABA accumulation maintaining primary root elongation at low water potentials [58,62]. Thus, constitutive ABA overproduction may constrain root elongation in moist soils but facilitate it in dry soils. ABA regulates root elongation by modulating ethylene sensitivity [63] and auxin transport [64], but root ABA concentration was not correlated with genetic variation in maize root growth in dry soil [65]. Manipulating ABA enhances rice yield [66] and may affect root growth.

Box 1. Hormonal Crosstalk in Regulating Root Elongation

POLARIS (PLS), encoding a 36–amino acid peptide, modulates both auxin transport and represses ethylene signaling to allow proper root elongation in Arabidopsis [209,210] and may be the crosspoint at which ethylene and auxin interact for root growth. ABA regulates root elongation by modulating ethylene sensitivity [63] and auxin transport [64,211] (Figure I). CK and auxin crosstalk controls root elongation of Arabidopsis via an auxin repressor gene, SHY2 (SHORT HYPOCOTYL 2); cytokinin-response transcription factor, ARR1, can directly bind and activate SHY2, which represses auxin signaling that negatively regulates auxin transporters, such as PIN and PAT [212,213] (Figure I). While the specific mechanism (s) by which strigolactones (SLs) affect root growth have yet to be fully elucidated, they can positively regulate root elongation by promoting root meristematic cell division, potentially by suppressing auxin transport [214,215]. SLs may induce SHY2 expression to inhibit auxin flux [216].

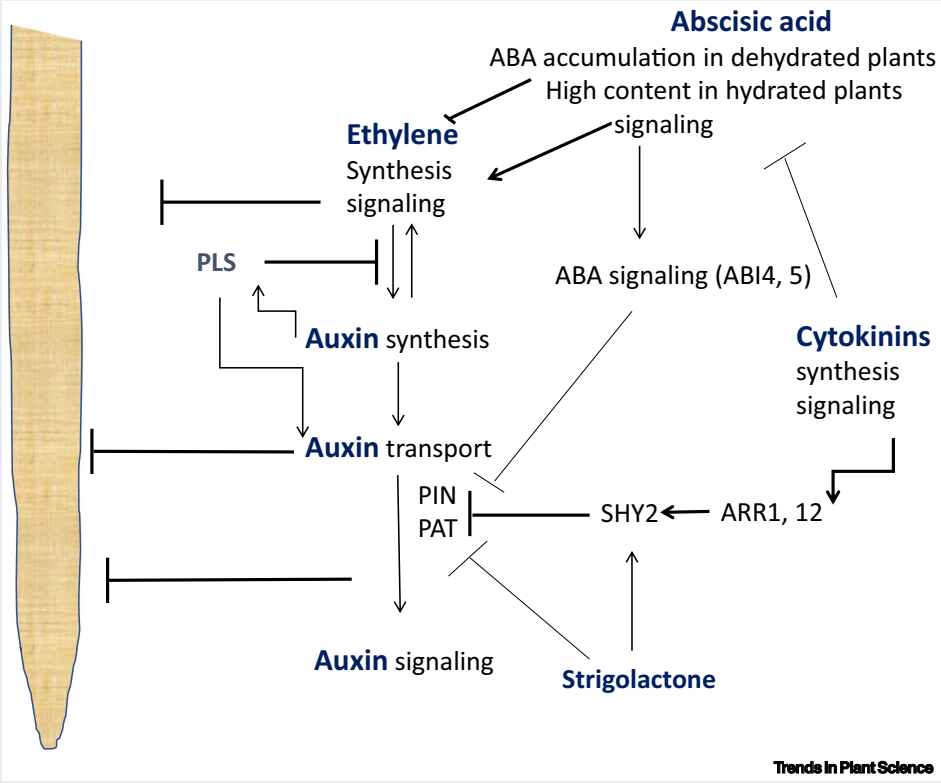


Figure I. Schematic Pathways of Hormonal Crosstalk in Regulating Root Elongation. Arrows indicate positive regulation, and stop lines indicate negative regulation. Abbreviations: ABI, abscisic acid insensitive for ABA signaling; ARR, A-type Arabidopsis response regulators for cytokinin response; PAT, polar auxin transporter; PIN, pin-formed protein as auxin efflux carrier; PLS, polaris peptide; SHY, short hypocotyl 2 as auxin repressor.

Cytokinins (CKs) inhibit Arabidopsis (*Arabidopsis thaliana*) root elongation [58] but can promote crown and lateral root elongation in cereal and grass species [67]. Nevertheless, root-specific overexpression of cytokinin oxidase-dehydrogenase (*CKX*) genes increased root growth of both Arabidopsis [68] and barley [69] without penalizing grain yield.

Hormone interactions and regulatory hubs (Box 1) interactively determine tap versus fibrous root growth. Understanding these genetic components may help identify alleles associated with favorable root phenotypes. Alternatively, applying deficit irrigation techniques with repeated drying and rewetting cycles (alternate wetting and drying in rice; alternate partial rootzone drying in furrow-irrigated crops) can stimulate root growth via hormonal mechanisms [70].

Source and Sink Strength for Grain Yields

Hormones affect grain yields by regulating source and sink capacity or strength. CKs enhance sink strength by (i) increasing the number or reproductive organs [71]; (ii) positively regulating cell-cycle genes controlling cell proliferation in developing seeds [72]; and (iii) increasing grain-filling rates, promoting assimilate supply to grains from source organs, especially in late-flowering (inferior) spikelets [73,74]. Elevating endogenous CK concentrations genetically (by overexpressing *ipt* or downregulating *CKX* genes) altered carbohydrate assimilation and supply and increased plant productivity [71,75,76]. High ethylene levels can reduce grain yields by (i) limiting source strength by accelerating leaf senescence; (ii) inhibiting grain-filling rates by restricting assimilate partitioning to developing grains resulting in low starch biosynthesis and high accumulation of soluble carbohydrates [77,78]; and (iii) reducing sink size by accelerating embryo and grain abortion [79,80]. Whereas low ABA levels correlate with poor grain filling, high levels suppress sucrose transport to, and starch synthesis in, grains [81,82]. ABA/ethylene ratio is positively related to grain filling rate by regulating starch synthesis [83].

Manipulating CK, ABA, and ethylene levels/interactions may increase grain-filling rate and yield, perhaps by affecting sugar transporters and starch synthesis that regulate source–sink relationships and sink strength during grain filling (Box 2) [84].

Future Perspectives on Hormone Crosstalk

Mechanisms of hormonal regulation of root growth have mostly been elucidated with the simple, dicot taproot system of Arabidopsis, often *in vitro* (agar). Since this environment poorly simulates the biophysical conditions crop roots are exposed to, more systematic hormone phenotyping of relevant organs and tissues at key/sensitive growth stages is necessary in field-grown plants. Similarly, targeted gene editing [80] regulating hormone–sugar crosstalk and key molecular hubs controlling hormonal interplay will facilitate genetic improvement in grain yield by optimizing source-–sink relationships, as discussed in the following text.

Increasing Sink-strength to Optimize Carbon Assimilation and Yield

Raising **sink strength** during grain filling (given by the number of sinks and their activity) to increase partitioning of assimilates to harvestable organs is of paramount importance for crop productivity. Nonetheless, research to improve photosynthetic/source capacity tends to predominate. This is at least in part based on assuming that improved **radiation-use efficiency (RUE)** benefits grain yield. However, this assumption neglects that photosynthesis is responsive to sink demand: Without adequate partitioning of assimilates to grain and other sinks, the source, or photosynthetic potential, will be underutilized (e.g., [85–89]).

Yield is the cumulative result of both source and sink strength over the course of development. Source strength is determined by both net photosynthetic rate and the rate of assimilate remobilization from source tissues [90]. Sink strength is the product of the size, number, and activity of sink organs; the latter refers to the specific uptake rate of resources. Although difficult to measure, methodologies are being proposed to estimate sink activity [91].

The concept of source or sink limitation is quantitative, and the important question is to what extent source or sink limits yield realization during seed set and filling. The source–sink balance during the time of economic sink development may be defined as the difference between the amount of assimilate available and the capacity to store it. Studies show source strength is in excess in both winter and summer cereals, such as barley [92], wheat and barley [86], and maize [93]. This is consistent with the facts that (i) yield tends to be far better related to the number than to the average weight of seeds [219] and references quoted therein, (ii) seed weight tends to be insensitive or only

Box 2. Hormonal Crosstalks to Regulate Source-sink Relations and Grain Sets

Effects of individual hormones (CK, ABA, and ethylene) on source–sink relationships by controlling sink activity or sink/source size have been documented, as illustrated in Figure I. CK acts as a positive regulator for sugar transport from source to sink and starch synthesis involving enzymes, such as SuS, AGP, and SSS, in the sink tissue. ABA effects on sugar transport and starch synthesis in the sink tissue are dose dependent. Ethylene negatively affects seed sets by reducing source size by inducing leaf senescence, restricting source–sink sugar transport and starch synthesis in the sink, as well as induction of grain abortion. Grain filling may be affected by the balance of ABA and ethylene. The interaction of multiple hormones, hormone–sugar crosstalk, and key molecular hubs controlling hormonal interplay regulating source–sink relationships are still unknown. Knowledge of such information will facilitate genetic improvement in grain yield.

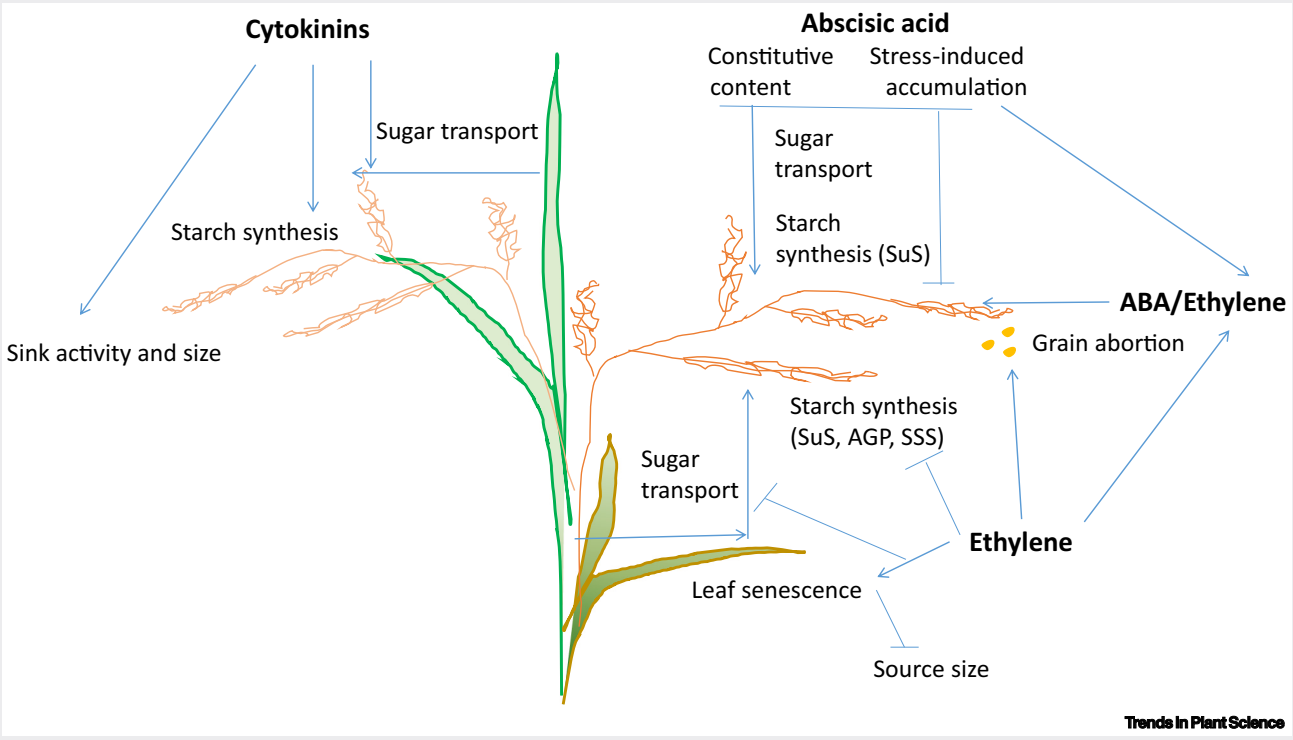


Figure I. Schematic Pathways of Hormonal Crosstalk in Regulating Source–Sink Relationships and Grain Sets. Arrows indicate positive regulation, and stop lines indicate negative regulation. Abbreviations: AGP, ADP-glucose pyrophosphorylase; SSS, soluble starch synthase; SuS, sucrose synthase.

marginally responsive to source strength per seed during seed filling [15,94,95], and (iii) photosynthesis and RUE are upregulated when sink strength is increased through breeding or treatments [85–87,96]. Sink limitation during storage organ development is not limited to grain crops but also applies to tuber and root crops such as potato or cassava [97,98].

The widespread sink limitation for yield realization during seed filling may reflect the evolutionary reward of modulating reproductive output through number rather than size [99]. This implies that stable seed size would have been adaptive [100], as size may have a marked effect upon fitness. Indeed, stabilizing selection (natural selection force in a population towards a particular value) would reduce intraspecific variability of seed size towards an optimal seed size, balancing between survival of the individuals and the number of progeny produced. As seed set precedes seed growth (even in indeterminate crops, the overlap is small), plants have tended to be conservative to ensure reaching critical seed size for survival. This would explain why breeding has consistently increased yield through increasing sink strength (seed number or potential weight) in major grain crops (e.g., in wheat [15], rice [101], and maize [102]) but not necessarily via increased leaf photosynthesis (e.g., [103]).

A solid proof of concept comes from the widespread boosts to yield of semidwarf cereals. The decrease in stem elongation increased partitioning of assimilates to the developing inflorescence, improving floret development and fertility and therefore increasing sink strength [104,105]. The resultant boost to harvest index [106–109] was likely the most important architectural change in crops for increasing yield. Improvements in harvest index have historically increased yield in major staple food crops [11], leading to broad economic gains for farmers. Complementary to improved partitioning to the growing inflorescences, plant breeders may also seek to increase seed set per unit of inflorescence [110].

Opportunities for increasing sink strength through modulating hormone crosstalk have been presented (Box 2). Another may be to regulate the concentration of trehalose-6-phosphate (T6P), a metabolite involved in signaling the sugar status of plant tissue. This aspect can be utilized to enhance the partitioning of sucrose into, for example, inflorescences. Genetic and chemical intervention approaches have been used to modify the T6P pathway and improve the performance of three food security crops: wheat (*Triticum aestivum*), maize (*Zea mays*), and rice (*Oryza sativa*) [111].

An alternative way to improve sucrose supply towards the economic sinks is via an increase in sucrose phloem loading [112–114]. The loading mechanism is conserved across most crops [97,114]. Increased sucrose transport capacity improved productivity in model crops [115,116] as well as in oilseed rape and wheat (Dr Claus Frohberg, personal communication, 2020). Since many crops still seem to have sink limitation during seed filling, with implications for realizing not only current but also improved photosynthetic potential, breeders will need to keep improving sink strength. Priority traits to optimize source–sink balance are presented in Box 3.

Efficiency of Maintenance Respiration

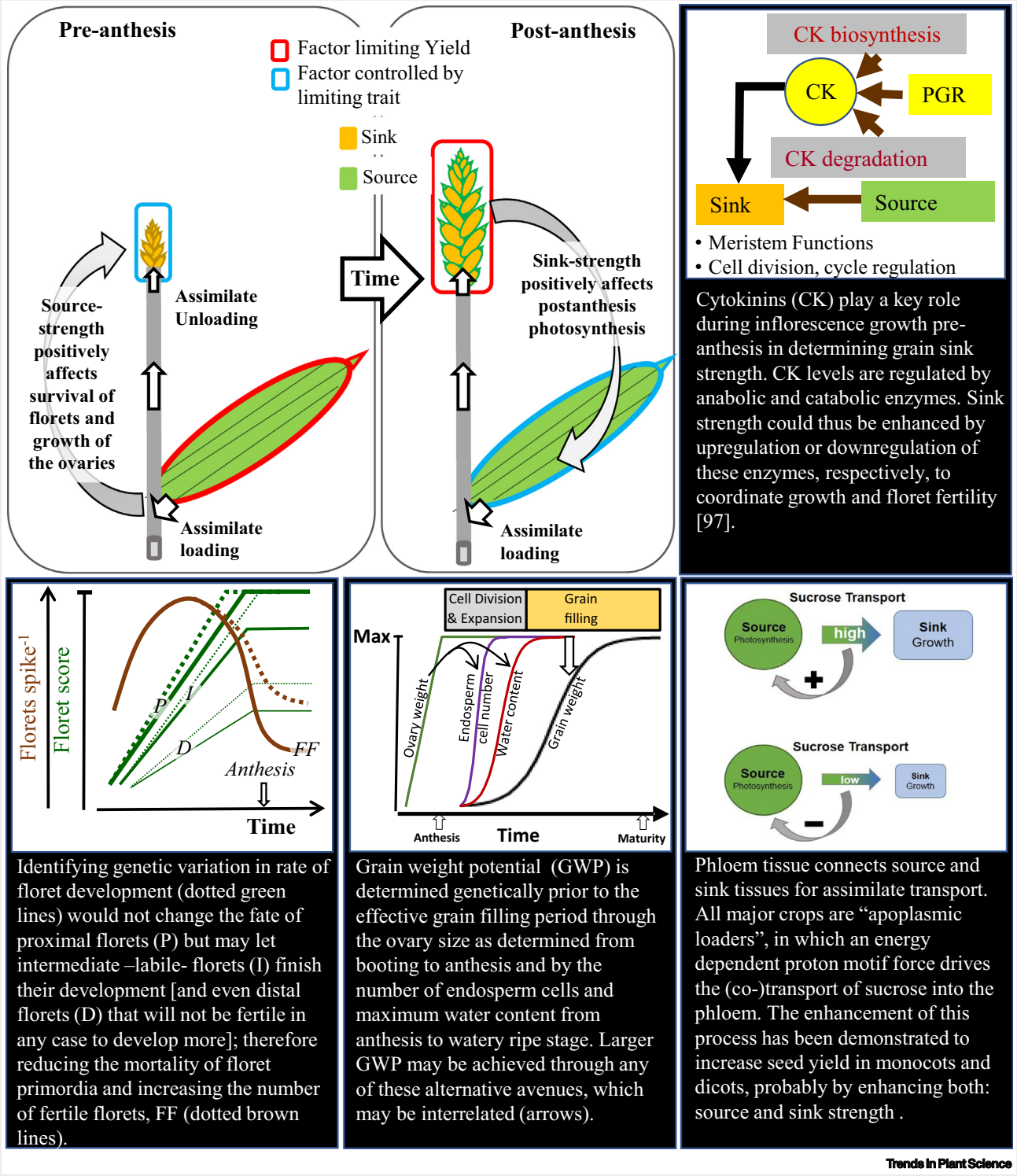
While the role of photosynthesis in crops is reasonably well documented and has led to development of screening protocols with potential for routine application in field research such as chlorophyll fluorescence [117], the same cannot be said for respiration. This bottleneck in understanding is profoundly troublesome, since many field data sets show that crop yields are significantly more influenced by night than day temperature [18,19], which could relate to effects on respiration and/or crop development.

A key approach to improving crop yields is through research targeting improvements in the efficiency with which intercepted radiation is converted into biomass [11], a trait that remains well below the theoretical maximum in elite crops (currently near 0.024, with potential to increase to 0.046–0.051 [118–120]). Along with efforts to improve photosynthesis [11], increases in biomass

Box 3. Priority Candidate Traits to Further Raise Sink-strength

In wheat, yield is mostly sink limited during the effective period of grain filling (i.e., photosynthetic capacity exceeds the demands of the growing grains). Consequently, photosynthesis of leaves and spikes is down-regulated by lack of sink strength. Sink strength is set by the number of grains and their potential size, which are determined immediately before anthesis and depend on source availability (as resource allocation to inflorescences affects survival of developing florets and growth of ovaries). The concept that yield is limited by both source and sink strength therefore becomes clear when integrated over time (Figure I). While studies and funding have mainly focused on improving photosynthesis, sink strength remains a critical research bottleneck. Increasing photosynthesis (e.g., during the stem-elongation phase; Figure I) will improve yield through increasing sink strength (with the proviso that the partitioning towards the juvenile inflorescences is maintained). Traits that would improve yield with current levels of photosynthesis include the following:

- Increasing seeds set per unit inflorescence dry matter through hormonal regulation (see also previous section ‘Roles of Hormone Crosstalk: Regulating Root Growth and Source–Sink Relationships’)
- Improving floret survival through accelerating rates of floret development
- Setting larger grain weight potential
- Enhancing phloem loading



Cytokinins (CK) play a key role during inflorescence growth pre-anthesis in determining grain sink strength. CK levels are regulated by anabolic and catabolic enzymes. Sink strength could thus be enhanced by upregulation or downregulation of these enzymes, respectively, to coordinate growth and floret fertility [97].

Identifying genetic variation in rate of floret development (dotted green lines) would not change the fate of proximal florets (P) but may let intermediate –labile- florets (I) finish their development [and even distal florets (D) that will not be fertile in any case to develop more]; therefore reducing the mortality of floret primordia and increasing the number of fertile florets, FF (dotted brown lines).

Grain weight potential (GWP) is determined genetically prior to the effective grain filling period through the ovary size as determined from booting to anthesis and by the number of endosperm cells and maximum water content from anthesis to watery ripe stage. Larger GWP may be achieved through any of these alternative avenues, which may be interrelated (arrows).

Phloem tissue connects source and sink tissues for assimilate transport. All major crops are “apoplasmic loaders”, in which an energy dependent proton motif force drives the (co-)transport of sucrose into the phloem. The enhancement of this process has been demonstrated to increase seed yield in monocots and dicots, probably by enhancing both: source and sink strength .

Figure I. Schematic Diagram Illustrating that in Preanthesis of Cereals, Source Strength Determines the Sink Strength during Postanthesis, which in Turn may Affect Source Activity during Grain Filling (top left), and Four Candidate Traits to Further Raise Sink Strength.

accumulation could also be achieved through research targeting variability in rates of respiration (Box 4). Each day, 20–70% of the CO_2 taken up by photosynthesis is released back into the atmosphere by respiration in shoots and roots [121,122]. Noting that approximately half of daily whole-plant respiration takes place in above-ground tissues [121], that growth and maintenance account for similar levels of respiratory CO_2 release [123], and that the respiration rate of mature leaves is largely a reflection of the energy needs of maintenance processes, there is an opportunity to improve the **carbon use efficiency (CUE)** of crops through screening for variability in rates of respiration in mature, fully expanded leaves (along with concomitant measurements of photosynthesis). Support for such an approach comes from past observations of a negative relationship between the rate of leaf respiration and growth and/or yield (e.g., maize [124], ryegrass [125], and canola [126,127]).

Box 4. Respiration and Carbon Use Efficiency

One way to increase biomass accumulation and yields of key cereal crops is through reducing the respiratory CO_2 release relative to the amount of CO_2 fixed through photosynthesis (Figure IA). Respiration uses sugars produced by photosynthesis to produce the carbon skeletons, reducing equivalents (NADH and $FADH_2$) and ATP needed for maintenance of mature tissues and drive the biosynthetic processes that underpin growth and yield. Coupled to these processes is the uptake of O_2 and release of CO_2 by mitochondria, with the balance between respiration and photosynthetic CO_2 uptake determining the CUE of plants (Figure IB). The greater the CUE, the greater the availability of carbon to be invested in new biomass and ultimately yield. While increases in CUE could be and are being achieved through improvements in the efficiency of photosynthesis [11], they can also be achieved through decreasing associated rates of respiratory CO_2 release (Figure IC). Key to any strategy targeting respiration as part of a novel approach to improving crop yields will be ensuring that reduced rates of respiration are linked to improvements in (i) the efficiency of chemical energy production by respiration (i.e., increasing the amount of ATP produced per unit of CO_2 released and O_2 taken up) and/or (ii) increases in the efficiency of respiratory energy use. Factors that influence the efficiency of energy production include the fraction of mitochondrial electron transport occurring via nonphosphorylating pathways (e.g., NAD(P)H dehydrogenase bypasses of complex I and the alternative oxidase) and the extent of proton leakiness through the inner mitochondrial membrane (e.g., protein movement through mitochondrial uncoupling proteins) [131]. A number of strategies are available to improve the efficiency of energy use, including reducing unnecessary turnover of proteins [202] and membranes, replacing energetically inefficient metabolic routes/reactions with efficient ones, suppressing futile cycles, and reducing the ATP costs associated with ion transport [123]. The fact that CUE values are markedly higher in inherently fast-growing grasses than in their inherently slow-growing counterparts [217] points to opportunities to screen for variability in CUE as part of novel screens to improve crop yields.

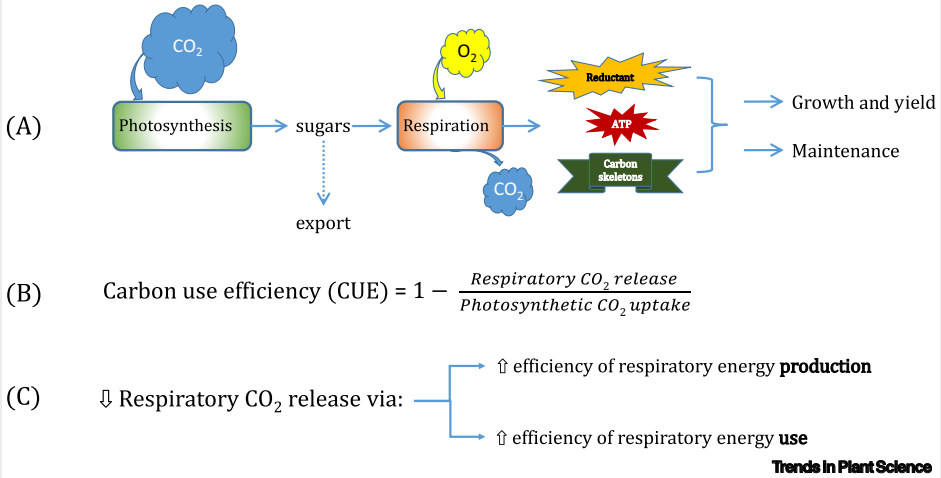


Figure I. Schematics. (A) Photosynthesis and respiration links showing how the production of reductant (NADH and FADH2), ATP, and carbon skeletons is used to support growth and maintenance processes. (B) Variations in the rate of respiratory CO_2 release per unit of photosynthesis influence the efficiency with which fixed carbon can be allocated to growth. (C) Changes in efficiency of energy production (e.g., via changes in engagement of nonphosphorylating pathways of electron transport) and/or the efficiency with which respiratory energy is used (e.g., through reduced ATP requirements to support protein turnover) can influence rates of respiratory CO_2 release, and through it, the efficiency of the respiratory system.

The fact that respiration is temperature sensitive and warming nights are leading to lower yields of rice [128] and wheat [129] is also consistent with a respiration–yield link, although other factors may also be at play (e.g., vpd [130], hastened crop development).

Box 4 outlines the components via which decreases in the rate of respiratory CO_2 release can contribute to increases in CUE. So long as any decrease in respiration rate is coupled to increases in the efficiency of respiratory energy production and/or efficiency of respiratory energy use, there is scope to achieve increased rates of biomass accumulation during growth (and thus yield) through screening for lines with reduced rates of leaf respiration in mature leaves, a proposition supported by the few studies available [124–127]. Despite this, relatively little attention has been given to screening for variability in leaf respiration rates in crops or how it is linked to differences in crop performance. This is partly due to the small number of research groups specialize in plant respiration, but also to the low throughput capacity of commonly used methods such as portable infrared gas analyzers (to measure respiratory CO_2 release) and Clark-type electrodes (to measure respiratory O_2 release). The inability to screen large numbers has meant that researchers could not exploit potential genetic variation in crop respiration. Further, while there is strong evidence that rates of leaf respiration are influenced by the environment (e.g., growth irradiance and temperature, soil moisture, and nutrient availability [131–133]) in a duration-dependent manner, the lack of high-throughput methods for measuring leaf respiration has meant that the contribution of the environment to variations in leaf respiration of field-grown crops has not been established.

The development of high-throughput, fluorophore-based measurements of respiratory O_2 consumption in plant tissues [134–138] represents a game-changer for studies assessing the potential of variability in leaf respiration to influence crop growth and yields. Using an automated gas-phase method, changes in the partial pressure of O_2 through time are measured using a robotic system that quantifies the fluorescent emission from fluorophores that are in contact with air in closed vessels containing plant material [137]. This method has been used to characterize leaf respiration rates in a wide range of plant species, both under controlled environments and in field conditions [134–138]. This approach has also enabled exploration of hyperspectral reflectance as a predictor of leaf respiratory O_2 uptake in nearly 1400 samples of wheat [136]. There is thus great potential for large screens of leaf respiration to be possible, either directly through use of the fluorophore approach or through noninvasive, repeated measurements made using hyperspectral reflectance (either at the leaf level or in the future, using aerial or satellite platforms). The ability to screen variability in genetically diverse germplasm and breeding populations will enable characterization of the genetic architecture of the trait and use of germplasm with reduced rates of leaf respiration in breeding.

Engineering Meiotic Recombination to Harness Genetic Diversity

Meiosis is a highly conserved cell division in plants, animals, and fungi that generates haploid gametes required for sexual reproduction. During meiosis, homologous chromosomes become physically associated and undergo reciprocal recombination (crossover), which can create new combinations of genetic variation. Crop breeders rely on meiosis to create lines with novel trait combinations, where recombination is a vital tool [139]. However, breeders currently have little to no influence on the recombination process, and furthermore, the levels and patterns of crossovers along chromosomes can limit genetic improvement of varieties.

The major limitations facing breeders in terms of recombination are (i) there are relatively few crossovers per chromosome per meiosis (typically one or two), and (ii) large regions of crop chromosomes, usually flanking the centromere, can be potently suppressed for recombination [139]. This combination of factors means that breeders need to generate very large populations of

plants to recover the desired recombinants; yet, some critical crossovers are simply never achieved. As recombination similarly underpins genetic research into diverse traits, these limitations also slow down the identification of specific variants that cause phenotypes of interest. For example, enhanced recombination will help separate tightly linked **quantitative trait loci (QTLs)** with opposing effects that would otherwise be impossible to detect. A major challenge is using new insights into molecular control of meiotic recombination to develop technologies that allow precision control of recombination in plant genomes [139]. It is also important to consider that plant species vary enormously in genome size and ploidy, meaning that solutions from one genome may not translate easily to another.

Increasing global crossover numbers per meiosis has the potential to allow breeders and scientists to achieve recombinants of choice in smaller populations, which could significantly reduce time and costs (Box 5). Notwithstanding the importance of maintaining favorable haplotypes, modelling work indicates that elevated recombination can lead to substantial increases in genetic gain during recurrent selection [140]. Work in diverse eukaryotes has shown that despite there being few crossovers, there are many more initiation events with the potential to yield a crossover. For example, in most plants, it is estimated there are between 100 and 1000 meiotic **DNA double-strand breaks (DSBs)** per meiosis, of which approximately 10–20% are typically repaired as crossovers [141,142]. This means that there is a huge potential to increase crossovers, even without considering increasing DSB numbers. For example, manipulation of the two major crossover pathways in plants has already resulted in significant increases of recombination. In the ***recq4a recq4b***, ***figl1***, and ***fancm*** mutants, class II crossovers mediate the recombination increase [143–145], while overexpression of the class I pathway protein **HEI10** is also sufficient to globally increase recombination [146,147]. Furthermore, combination of *recq4a recq4b* and *HEI10* leads to an additive crossover increase in Arabidopsis [147]. Research into these pathways may lead to more efficient molecular approaches in crops, although the *figl1* mutation causes sterility in rice, pea, and tomato [145]. Importantly, genetic mapping in wheat has revealed a novel helicase gene, ***RECQ7***, that controls meiotic recombination [148]. These loci could potentially be combined with stress treatments (e.g., elevated temperature or chemicals) to increase global crossover frequency [149,150].

Unlocking recombination cold spots will have a significant impact on breeding (Box 5). Typically, large plant chromosomes show a pronounced bias of crossover frequency towards the subtelomeres, with recombination suppression in the centromere-proximal regions [151,152]. Despite this, useful genetic variation can be found in the recombination-suppressed parts of crop genomes, which as a consequence may cause linkage drag during selection and thereby limit crop improvement [139]. As deleterious mutations tend to accumulate in low-recombination regions [153], unlocking crossovers here would also allow breeders to purge unfavorable alleles. Many plant genomes show elevated levels of repeats and silencing epigenetic marks, including DNA methylation, in the regions surrounding the centromeres. Indeed, DNA methylation and **H3K9me2** mutants in Arabidopsis have been observed to increase centromere-proximal crossover frequency [154]. Hence, disrupting these epigenetic marks in crop genomes may be one solution to unlock recombination. Indeed, virus-induced gene silencing of *MET1* and *DDM1* in wheat caused a redistribution of crossovers along the chromosomes [155]. However, it is also important to note that structural polymorphism (e.g., insertion-deletions, inversions, and translocations) also suppress crossovers [156], which are more likely to occur in repetitive genome regions and in wide crosses.

Targeted meiotic recombination is the ultimate technology to precisely direct crossovers to loci of choice in plant genomes, thus eliminating the need for numerous backcrosses to remove linkage

Box 5. Strategies to Control Meiotic Recombination and Accelerate Crop Breeding

We consider a hypothetical crop with five chromosomes and two parental backgrounds (P_1 = *red*; P_2 = *blue*) (Figure I). In this situation, the breeder wishes to introgress a centromere-proximal target locus in P_1, located on the first chromosome, into an otherwise P_2 genetic background. We show the genotype of representative gametes produced from different generations during a hypothetical introgression experiment (Figure I). The parents are crossed to generate a P_1/P_2 F_1 hybrid, followed by repeated backcrossing to the P_2 parent (e.g., BC_1 = backcross 1). In the wild-type context, the desired introgression is not achieved until the BC_6 generation. We next show three contexts where the introgression has been accelerated by (i) unlocking centromere-proximal crossovers, such as by using DNA methylation mutants [154]; (ii) promoting genome-wide hyper-recombination, such as via *HEI10* or *recq4a recq4b* [145,147]; or (iii) locus-specific targeting of meiotic recombination [158] (Figure I). When a target locus is closely located to an unfavorable allele, linkage drag may not be overcome even with repeated backcrosses. In such cases, a targeted recombination approach may be the solution. Note also that the hypothetical crop represented here is a diploid species with five chromosomes (Figure I). The situation becomes more complicated when considering allo- and autopolyploid species. For example, bread wheat is an allohexaploid where meiotic stability requires the *Ph1* locus that includes the ZIP4 crossover recombination gene [218].

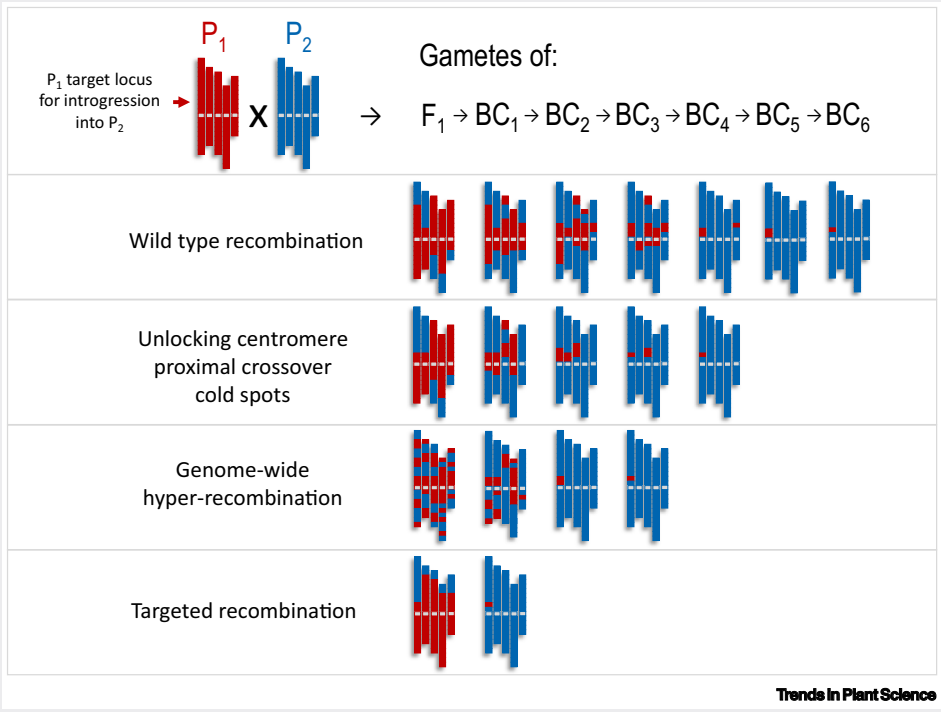


Figure I. Introgression of a Target Locus in Wild-Type Versus Recombination-Engineered Backgrounds in a Hypothetical Crop Species to Accelerate Research and use of Improved Traits.

drag (Box 5). This has been successfully achieved in budding yeast, where tethering of **SPO11**, the protein that initiates meiotic DSB formation, is sufficient to create new recombination hotspots [157]. As the meiotic DSB machinery, including SPO11, is highly conserved across eukaryotes, tethering recombination factors is an attractive approach to be developed for plants. Further work will be required to determine which factor, or combination of factors, is sufficient to generate recombination hotspots at loci of choice in plant genomes. An alternative and related approach is to induce targeted recombination in somatic cells before forming the germline cells, such as via **CRISPR-associated protein 9 (Cas9)**, which has been successful in tomato [158].

Solving the research bottlenecks described in other parts of this publication to model and create new combinations of traits and alleles will be achieved faster and cheaper if we can control

recombination. Prebreeding will be the crucible that provides proof of concept for such models, as discussed subsequently.

Leveraging Improved Understanding to Achieve Productivity Gains

Science breakthroughs coming from the topics discussed and their integration (Figure 2) can be translated into specific crop improvement technologies. These include improved CGMs that help prioritize research targets and their potential for scale-out based on simulations [24,159–161], and genetic improvement involving the identification of novel trait sources and their evaluation in a realistic breeding context, accompanied by improved crop husbandry.

Exploration of Genetic Resources for Pre-breeding

When lack of variation within extant breeding gene pools limits the potential to make genetic gain, useful variation can often be found in progenitor varieties, landraces, or crop wild relatives. The process of 'prebreeding' links trait discovery with variety development and involves identifying and introducing **novel trait variation (NTV)** from unadapted gene pools into elite breeding populations.

With an estimated 7 million diverse accessions of crop genetic resources available in over 1750 national and international *ex situ* collections worldwide and significantly more managed *in situ*, these underutilized resources represent significant opportunities to exploit almost any trait, and especially those which have been hitherto overlooked [162,163]. Defining precompetitive traits of interest to public and/or private sector breeders for a particular crop and TPE is the first step in a prebreeding program.

Historically, resistance to pests and diseases, fertility traits (i.e., cytoplasmic male sterility), and abiotic stress tolerance have been targets of successful prebreeding efforts [164,165], and there is increasing interest in prebreeding to introduce trait combinations targeted to specific TPEs. Methods to increase genome-wide and local levels of recombination (discussed previously) are of great interest for accelerating the introgression process.

Reverse genetics approaches are valuable in cases where a major gene governing a trait of interest has been well characterized; variants can be generated via **TILLING** [166] or introduced via genome editing [167] directly in breeding lines. This avoids linkage drag and shortcuts the backcrossing process, which typically requires 3–5 years, enabling evaluation of NTV to proceed rapidly in the context of the larger breeding program. Successful genome editing has been reported in banana, tomato, potato, rice, wheat, maize, soybean, and several fruit crops [13,168–171], as well as *de novo* domestication [170] from wild crop relatives.

If the genetic architecture of a desired trait is complex but robust screening methods are available, backcrossing with unadapted sources may be effective [172–174]. Where trait inheritance is complex and precision phenotyping methods are not well developed, recurrent selection aided by predictive modeling and genomic selection (GS) is the most expedient way to integrate NTV into elite breeding material. This is time consuming and exploratory in nature; it requires the development of a training population, phenotyping for performance across years and environments, predictive modeling, and multiple generations of recombination and selection guided by GS, as discussed previously [173–175].

Among the traits most neglected in breeding (due to phenotyping challenges) but with high potential payoff in terms of climate resilience is RSA. The rest of this section discusses opportunities to improve RSA, considering outputs from research in genomics and phenomics and how they may be used to explore genetic diversity.

Adaptive RSA, to withstand both drought and heat stress in the field, respectively, has been identified in wheat and other crops, indicating some common genetic basis [176]. The *DEEPER ROOTING 1* (*DRO1)* gene [49,177] is a regulator of root growth angle. *DRO1* orthologs exist in both monocot and dicot plant species [178], and experiments in rice, wheat [178], and *Arabidopsis* and *Prunus* [179] suggest functional similarity with influence on root system architecture. It has not yet been determined whether orthologues of *DRO1* underlie some of the major QTLs identified for rooting depth in maize [180], wheat [181], sorghum [182], barley [183], chickpea [184], and other crops. In addition to impacting root system architecture and drought tolerance, the *DRO1* gene contributes to higher harvest index, nitrogen uptake, and flux of cytokinin from root to shoot during grain filling in paddy rice [49,185]. *DRO1* carries a highly conserved EAR motif (ethylene-responsive element binding factor-associated amphiphilic repression motif; [186]) that serves as an important repressor of gene expression in response to abiotic stress, helping to limit cell damage [187].

Thus, variation in *DRO1* represents an interesting target for breeders because it regulates both morphological and physiological responses to drought and has no demonstrated cost to plants under nonstress conditions. Natural variation at the *DRO1* locus can be explored in diverse germplasm resources based on sequence data to identify potential donor lines carrying alleles of interest [187]. Subsequently, marker-assisted selection or genome editing may be used to introduce rooting depth variation into elite breeding backgrounds as part of the prebreeding pipeline, followed by evaluation of the prebred lines for their response to drought tolerance in a TPE. Crop and breeding simulations in maize support this hypothesis [188].

Enhanced use of forward genetics approaches is also of critical importance. Tools that allow routine, noninvasive imaging of root systems *in situ*, including X-ray computed tomography and magnetic resonance imaging [189,190], represent an opportunity to discover as yet uncharacterized NTV associated with root system architecture. This ‘phenotyping first’ strategy makes no assumptions about the gene(s) involved and would revolutionize the study of root biology under field conditions. It could also accelerate breeding efforts to explicitly select for root parameters of interest and would be applicable in a wide array of species, including root and tuber crops [161,162].

Canopy temperature is coupled to root water uptake via evaporative cooling from stomata [191], and their degree of coupling can be manipulated experimentally through modifying water regimes and atmospheric demand. Thus, canopy temperature offers a valuable screening tool for characterizing diverse donors and prebreeding materials in terms of relative access to water, including those carrying known variants of target genes such as *DRO1*, *ERECTA* (*ER*) (a gene that exerts stomatal control over transpiration efficiency [192]), and/or *Photosystem II Subunit S* (*PsbS*) (a gene that regulates stomatal opening in response to light with demonstrated impact on water use efficiency in tobacco [193]), with demonstrated impacts on both drought tolerance and yield in bread wheat and maize [194,195].

Collectively, these approaches can accelerate prebreeding efforts for enhanced climate resilience by (i) using crop and breeding simulation to identity trait combinations of interest [188], (ii) using targeted genotypic and phenotypic screening methodologies, and (iii) using genomic strategies to efficiently integrate NTV into elite breeding material. In concert with the development of predictions of potential trait targets to accelerate genetic gain for yield, such as those emphasized in the previous text, there is a need to advance predictive modeling capabilities to prioritize among the many opportunities for combinations of experimental evaluation strategies and ultimately to inject into breeding programs.

Illuminating 'Black Boxes' in Simulation Modelling

Improved soybean varieties [196] and drought-tolerant maize, now grown in more than 81 000 km^2 in the USA, resulted from understanding how stomatal conductance responds to vapor pressure deficit [197] and designing breeding strategies [9,188] to exploit water conservation during vegetative growth to improve plant water status at flowering [24] and kernel set [198]. This is an example of targeted breeding to rebalance source–sink interactions (Box 3) to increase yield while recognizing water availability in the TPE. Despite incomplete knowledge, using a CGM based on demand/supply concepts, sink strength based on number and growth rate of sink organs ([113]; Box 3), and competition among organs, it was possible to understand and model the emergence of phenotypes [160,198] to inform breeding [9,188].

Other black boxes are worth illuminating. Mass allocation among organs remains largely a descriptive exercise, while it has played a critical role in the long-term yield improvement in various crops [45,108–110,199]. In an iterative manner, maize breeders improved sink strength, agronomists increased plant population, and roots systems adapted to crowding and with enhanced efficiency [45,200]. This interplay of processes operating at different scales and organs is not captured in any modeling framework, with root/shoot resource allocation being one of the least-known process in modeling. Emergent behavior due to competition among individuals in a crop setting is largely absent in CGMs. Developing views of hormonal crosstalk in regulating root elongation, source–sink relationships and grain set (Box 1 and 2) can help interpret how increased grain set in maize, for example, may have resulted in root systems adapting to crowding, responding to the environment [46,50,51], and enhancing efficiency [45,200].

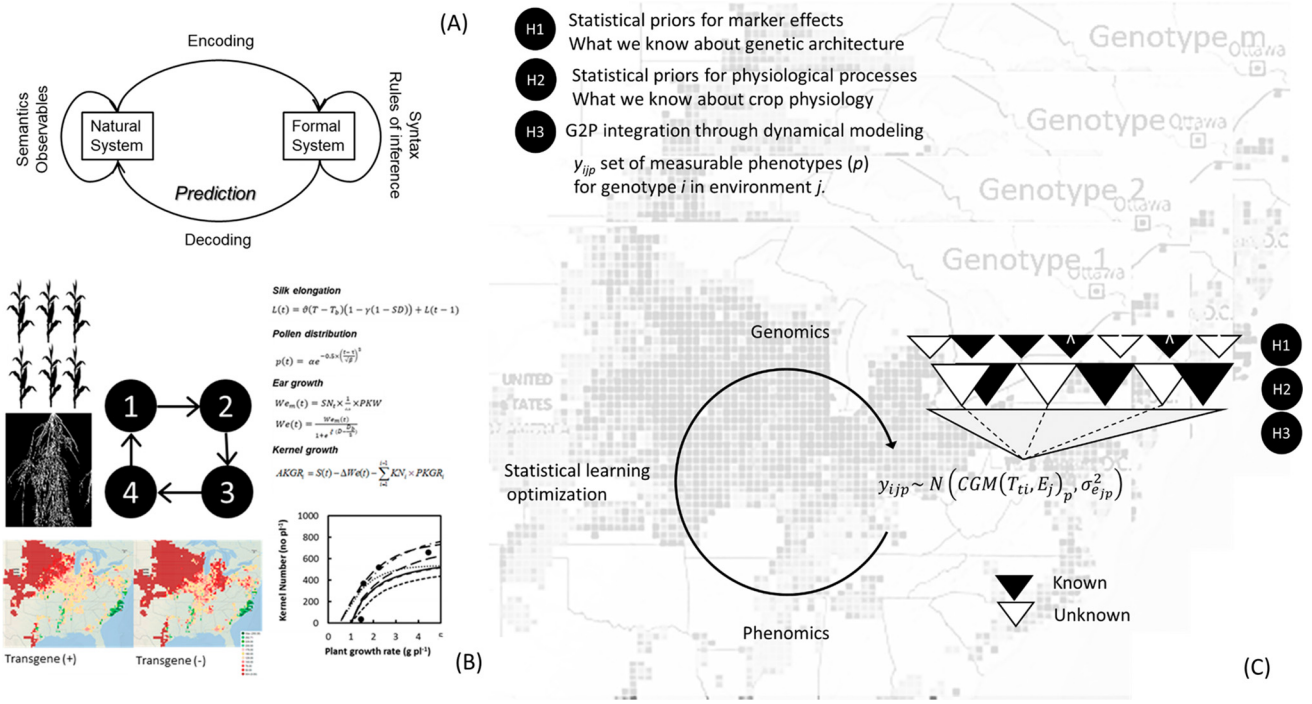


Figure 3. Illuminating Black Boxes Could Improve Functionality and Predictive Skill Through Iterative Model Building (A), which is Illustrated in (B), from Model Improvement (1) to Spatial Assessment of the Trait (4). Hierarchical Bayesian dynamic modeling provides a transparent framework for knowledge and data assimilation to define the opacity of modeling boxes. Illuminating black boxes could be conducive to improve functionality and predictive skill. (C) Prediction for various genotypes using Messina *et al*. [204] model and georeferenced environmental databases shown as background.

Advances in hormonal crosstalk networks (Box 1 and 2) offer an optimistic perspective to deal with such complexity and make informed selections based on root plasticity traits, and mass allocation once we encode this knowledge in crop models (Figure 3B). Combining high-throughput phenotyping, improved analytical techniques, and CGMs, new knowledge will lead to a better use of existing crop genetic resources and enable breeders to deal quantitatively with the complex regulatory networks from hormones, to organs, to communities of plants.

Most CGMs use the concept of RUE [201] due in part to our limited understanding of regulation of maintenance respiration (*m*) and partitioning [152,164] . Models based on RUE implicitly assume that ~20% of seasonal photosynthesis is used in maintenance respiration (Ng and Loomis, 1984, cited in [202]). Advancing our understanding of the physiological and genetic determinants of *m* and homeostasis to temperature [164] will enable the use of models to identify opportunities for the improvement of use efficiency, thereby increasing crop yields (Box 4).

Crop growth and development models in combination with georeferenced databases allow prediction of performance of untested genotypes/traits across the broad TPE (Figure 3B). They also provide an avenue to structure dialogue between fundamental and translational research on trait relevance and the identification of bottlenecks for crop productivity [25,203]. Bayesian approaches further enabled integration of the quantitative genetics framework that underpins genetic gain in breeding with the physiological knowledge captured in CGMs (Figure 3C) [52,204]. In gene-to-phenotype modeling, prior knowledge and beliefs translate into definitions of statistical priors for physiological traits, thus enabling modeling important breeding concepts such as trait breeding values and genotypic value of individuals (Figure 3C). The posterior distributions provide assessments of how much we really know, given our available data, and enable scientists to define the opacity of the black boxes by estimating the uncertainty in the parameters. This Bayesian dynamic modeling framework provides the means to assimilate data collected within different stages of the breeding program [204] (Figure 3). It includes the flexibility to use phenomic data [205] collected in time and derived from remote sensing and images of tissues, organs, and plants [9,43,44,189] to estimate the rates $\frac{dy}{dt}$ of processes that give rise to the observed trait phenotypes (*y*). Increasing biological reality for processes described here and resulting from future research will inexorably expand the domain of application of CGMs, but, more important, it will increase the capability of CGMs for *ex ante* analyses and design approaches to tackle bottlenecks in crop improvement. Today, it is possible to use a CGM [198] to conduct a retrospective analysis of yield response to water deficit in gene-edited maize [80,206] but not prospective analyses on the manipulation of genes controlling hormone synthesis and their crosstalk effects on yield. The integration of crosstalk hormonal networks (Box 1 and 2) within the Bayesian hierarchical framework (Figure 3) will fundamentally change the paradigm from descriptive to prescriptive crop modeling. Further understanding of these networks will improve the genetic models we can embed within CGMs (Figure 3C), yield prediction, our capability to explore opportunities for network optimization within the TPE, and design genotype × management technologies for cropping systems [52,207].

Concluding Remarks and Future Perspectives

While other areas of crop science (e.g., carbon assimilation of nonleaf tissue and whole canopies, the genetics of wide adaptation), if adequately resourced, could also fill important knowledge gaps (and merit review), the examples presented here provide a basis for targeted investigation, combining breakthrough technologies with proven ones. While the review tends to focus on opportunities for genetic improvement through crop breeding, increased knowledge integration within a modelling capability will create opportunities to improve crop adaptation through better-targeted use of external inputs and design of genotype × management technologies

Outstanding Questions

To what extent can current (and future) photosynthetic potential be fully realized by optimizing source–sink balance with respect to seeds and other edible crop organs across crops and environments?

How can we better understand and control hormone crosstalk in crops, such as in terms of stress response and optimizing?

Is there scope for including genetic variation in maintenance respiration in crops when designing crosses and selecting progeny, especially under warmer climates?

What crop root characteristics should be selected for different environments, and how can we accelerate throughput of selection, either by representing or by actually conducting root measurements in realistic field conditions?

To what extent will filling these knowledge gaps provide new opportunities for generating more synergy among traits in strategic crossing to increase the complementarity of alleles coming from different parental sources?

To what extent will filling these knowledge gaps provide opportunities for more improved crop management in terms of (i) planting systems, (ii) precision application of inputs, and (iii) use of exogenous application of plant growth regulators, either to better condition crops to known stresses or to ameliorate the effects of unpredictable stresses, for example?

How will filling such knowledge gaps help improve leverage of extant knowledge?

What other significant knowledge gaps exist that should be investigated?

To what extent will the precision of mathematical crop models be improved by replacing such knowledge gaps or 'black boxes' with new data based on research?

How can this new knowledge be used to explore novel trait sources and diversity from the vast collections of largely untapped genetic resources in collections worldwide?

[52]. Apart from modified planting and tillage systems and precision applications of water and fertilizer, these could potentially include exogenous application of plant growth regulators to boost or protect growth at key phases of crop development, for acclimation to anticipated stresses, and to ameliorate the negative impact of unpredictable climate shocks.

Can the public and private sectors agree to pool resources to investigate these issues, in precompetitive space, to raise the 'knowledge bar' for the benefit of all stakeholders?

Maximizing the impact of crop research requires a continuous cross-stakeholder interaction to share knowhow obtained from discovery research in formats tailored to stakeholder use requirements [208]. Consensus among public and private crop scientists represents, if nothing else, a useful platform to begin discussing some of the obvious asymmetries in crop research that currently hold back genetic gains and yield gaps in a wide range of crops and environments. This aligns with society's expectations that the academic, crop improvement, and farmer communities ensure future food security in a generally less predictable if not harsher climate and would lead to a more stable foundation for crop science to embrace increasingly realistic research scenarios (see Outstanding Questions).

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Declaration of Interests

The authors have no interests to declare.

Resources

[i]https://ourworldindata.org/crop-yields

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