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Perspective

Translational Research for Climate Resilient, Higher Yielding Crops

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ABSTRACT

Investment in scientific research is generally asymmetrical: it depends on precedents, current trends in science and technology, and economic, political and social agendas. However, asymmetry occasionally leads to bottlenecks that limit delivery of valuable technologies. This review considers the case of translating plant research to crop genetic improvement. Considerable progress has been made in basic plant science in recent decades fueled largely by the revolution in genetics. Meanwhile, human population has continued to grow exponentially, the natural resource base upon which agriculture depends has diminished significantly, and the climate is becoming less conducive to agriculture in general, especially in already food insecure regions. However, although basic research has delivered promising outputs using model crop species, relatively few new ideas have been tested in a mainstream breeding context. Past successful translational research projects—including enhancing the vitamin A content of maize, increasing the ability of rice to tolerate flooding, approaches for improving the yield potential of spring wheat, and traits for increasing the climate resilience of maize and sorghum—required interdisciplinary and often international collaboration to deliver adequate proofs of concept. They were also driven by a visionary approach and the necessary time commitment from the research institutions and funding bodies involved. These attributes are prerequisite for capitalizing on basic plant research and harnessing it to food security.

KEYWORDS: breeding; physiology; development; farmers; traits; food security; nutrition

Received: 18 July 2019
Accepted: 26 August 2019
Published: 03 September 2019

Crop Breed Genet Genom. 2019;1:e190016. https://doi.org/10.20900/cbgg20190016

ABBREVIATIONS

PT, physiological trait; IWYP, International Wheat Yield Partnership; HeDWIC, Heat and Drought Wheat Improvement Consortium; HTP, high throughput phenotyping; HI, Harvest index; CT, canopy temperature; IWIN, International Wheat Improvement Network; CIMMYT, International Maize and Wheat Improvement Center; ITTA, International Institute of Tropical Agriculture; SLA, specific leaf area; QTL, quantitative trait locus; ASI, anthesis-silking interval

INTRODUCTION

In science, an idea remains a hypothesis until proven. However, in the area of crop genetic improvement, many ideas are projected from academia as solutions to challenging productivity problems, without demonstrating all the steps necessary to achieve the required genetic gains, with that task left to breeders. The explosion in fundamental plant science in recent decades has uncovered the physiological and genetic basis of many traits as well as genetic markers and assays to select for them. This has resulted in a massive pileup of ideas that have yet to be tested and translated into applied breeding programs. In the same timeframe, the world’s population has almost doubled, the natural resource base for agricultural productivity is threatened by reduced water supplies and wide-scale soil erosion, and climate is already getting generally less favorable for agriculture, especially in regions with the greatest demand for staple foods. Clearly, the need for investment in translational research is more critical than ever. Investment in scientific research generally depends on successful precedents, current trends in science and technology, as well as economic, political and social agendas. All of these are understandable factors; however, when they lead to bottlenecks that compromise the delivery of needed technologies, the situation needs to be addressed urgently.

The term “translational research” in the crop context can be defined as a systematic effort to convert basic research knowledge into practical applications. In this review, we interpret basic research to include any scientific knowledge about plants or crops that can be applied to crop improvement.

Most successful crop breeders are scientists who also become “engineers” of a cultivar delivery pipeline. In the public sector, at least, much of their efforts go into crop protection, since it is more important in terms of food and farmer security to avoid severe losses of productivity due to pest or disease than to achieve marginal yield gains. Fortunately, it tends to be easier genetically to find resistance to disease than to achieve yield gains *per se*. For example, an accelerated backcrossing program based on a known source of resistance can avert a disease epidemic, if the signs of novel virulence are detected in time [1]. However, this work is reminiscent of the legendary Sisyphus: a never-ending task, due to the constant evolution of new disease and pest races, as well as the periodic emergence of new threats (e.g., wheat blast or maize lethal necrosis); and it keeps breeders fully occupied. The task is often made harder—and more expensive—when new sources of resistance can only be found in unadapted material such as landraces or crop wild relatives [2]. As a result, the financial and logistical resources remaining for breeding programs to validate novel yield-boosting traits are often limited, especially as these traits are genetically complex, show interaction with environment, and therefore are not straightforward to measure and track between breeding generations.

This review emphasizes why translational research should be recognized and resourced as an essential link between more fundamental research and crop breeding as it adds considerable value to both. Without an adequate translational component, the societal value from today's revolution in plant sciences will remain small and often wasted. Translation often takes a long time and can thus appear unattractive to funders and scientists. However, it can be speeded up with the newer tools of marker assisted breeding, phenotyping using drones and cameras, and speed breeding, driven by modern concepts of pipeline management using digital tools and time-management criteria to ensure rapid returns on investment.

FUNDAMENTAL RESEARCH

There is no lack of literature suggesting ways to improve crop yield or increase adaptation to abiotic stress [3–11]. Many of these ideas have come from research on model species whose rapid life cycle length, convenient growth habit and other features lend them to high throughput research methods. Such research is often facilitated by the use of controlled environments so that precise treatment effects such as temperature and water levels can be assured [12] and genetic experiments can avoid being confounded by unwanted environmental variation.

In the last 15 years, for example, research on Arabidopsis and rice has revolutionized plant science, and given rise to enormous numbers of hypotheses for crops thanks to remarkable sets of tools to explore the genetic base of trait improvement. These tools allow researchers to find mutations in any gene in a directed way, find the associated phenotypes, map variation to specific genes, catalog gene sequences across the species and link gene expression to phenotypes [13]. Some discovery research is also conducted on the respective crops under field environments (e.g., Sukumaran *et al.* [14]; Molero *et al.* [15]. However, what these scholarly works lack is an adequate proof of concept in terms of plant breeding. Since most basic research is conducted in controlled environments and with model species, results cannot be readily extrapolated to crops in the field. Furthermore, breeders must select for many traits while basic researchers often work on one trait or gene, so pleitropic effects associated with novel traits always need to be verified in appropriate genetic backgrounds and environments through pre-breeding.

CROP BREEDING

Crop breeding has been evolving ever since humans first selected for favored plant types within progenitor species. The Green Revolution, in the 1960s, based on dwarfing genes and breeding genetic backgrounds to suit them, and the biotechnology revolution from the 1980s onwards, have delivered increasingly sophisticated methodologies for crop improvement. In the meantime, breeding programs have been efficiently meeting the demands of a fast-growing global population through steady genetic gains and broad-spectrum resistance to pests and diseases in most staple crops [16], with exceptionally high returns on investment documented in some (e.g., Reynolds *et al.* [17]). Many crop and policy experts suggest that this has led to complacency, however, and both public and private sectors currently struggle to achieve the investments needed to match predicted human food demand by mid-century. The situation is especially ironic, given that many breeding programs struggling for funds have already made the initial investments in modern technologies such as phenomics, genomics and informatics that are crucial to further increase genetic gains. In addition to increase the efficiency of selection for mainstream traits—yield, disease resistance, phenology, *etc.*—these technologies can be powerful tools in translational research aimed at achieving step changes in yield and adaptation to emerging stresses via the testing of hypotheses under realistic environments.

THE TRANSLATIONAL RESEARCH BOTTLENECK

In fact relatively few scientists occupy the applied research space in which proofs of concept for “yield-boosting” traits or other crop improvement hypotheses are rigorously tested in a breeding context. This is partly a result of funding constraints and partly due to the silos that typically form when different research areas are funded from different sources [18]. Translational research must ultimately demonstrate genetic gains in the field, using up to date germplasm, across an appropriate range of target environments, and ideally in genetic backgrounds that also encompass all of the collateral traits needed to make a new cultivar marketable. In other words, in the continuum from basic plant science at one end to application in crop breeding at the other, there is a bottleneck that is especially hard to fund, falling neither under one category nor the other. Scientists who conduct fundamental research often consider translational research too mundane or costly to support, are not rewarded for it and lack the resources and/or breeding experience to carry out the required work. On the other hand, breeders may view it as too risky, time-consuming and/or theoretical to divert scarce resources into. Therefore, lacking adequate proofs of concept, many proposed technologies with potential impact on crop improvement remain on the shelf, with a few exceptions in the public sector, some of which will be presented herein as case studies. In the private sector, simple economics usually drive the need for adequate proof of concept before a breeding program can take the risky investment of retooling. Again, there are exceptions, especially with hybrid maize in the United States, where profit margins are large enough to enable more research to be funded.

Funding bodies may assume that a breeding organization would routinely test promising new ideas in the interests of creating products that are more successful and gaining a bigger market share. However, the recent disappearance/reductions of “core” public funding—even for established institutes with a strong track-record of delivery—further narrows the bottleneck between basic research findings and their practical application [19].

In summary, the contention of this review is that results from upstream plant science and their application in downstream problem-solving research are too uncoupled. Better linkage of fundamental research to breeding, via well-focused, translational research, is a necessary goal to achieve global productivity targets in the face of warmer temperatures, declining water resources and increased demand from a growing population [20], and can add value to a considerable body of pre-existing basic research through boosting modern plant breeding.

The remainder of this review will describe steps for translating promising technologies—already supported by scientific data—into viable breeding methodologies. Several case studies are also outlined.

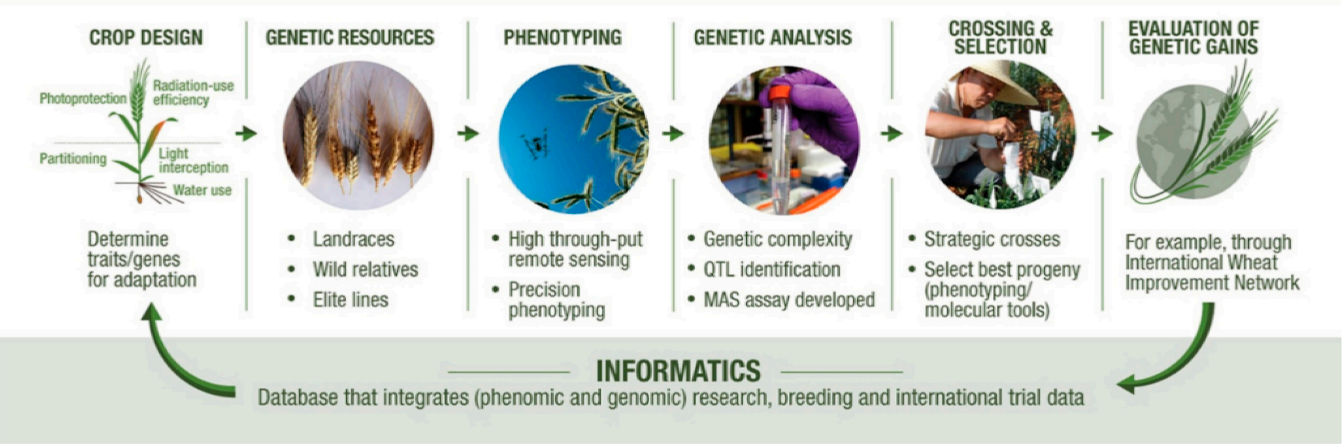

Figure 1. Main research steps involved in translating promising technologies into genetic gains. Adapted from Reynolds and Langridge [21], an open access article distributed under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

TRANSLATIONAL RESEARCH PIPELINE

A generic scheme of a translational research pipeline for quantitative traits (*i.e.*, traits controlled by many genes and their interactions), to test hypotheses about the impact of novel trait sources, trait combinations, and selection technologies in a crop improvement context, is presented in

Figure 1. The pipeline consists of a series of steps that are approximately sequential, although not all steps may be necessary.

There are seven main research steps involved in translating promising technologies into genetic gain:

(a) **Crop Design—Establishing the Hypothesis:** The new "idea" (trait/allele/methodology) must be complementary to a package of prerequisite traits and screens associated with a given target environment;
(b) **Genetic Resources:** novel genetic variation can be explored among genebank accessions, when candidate traits/alleles are identified, and can profit from new screening tools;
(c) **Phenotyping:** high throughput phenotyping is prerequisite for evaluating large germplasm collections and breeding generations, while precision phenotyping can identify variation for a wider range of traits among candidate parents;
(d) **Genetic Analysis:** knowing the genetic basis of traits helps refine strategic crossing and can lead to marker assisted selection. Precision phenotyping is paramount (and often expensive) to generate the data that allow marker identification;
(e) **Crossing and Selection:** making crosses involving new traits/alleles provides the experimental material for measuring genetic gains, while the effectiveness of new screening technologies can be rigorously tested through well controlled progeny selection;
(f) **Evaluation of Genetic Gains:** by testing the best performing progeny from experimental crosses in real world multi-location yield trials and not in greenhouses, the impact of new technologies is quantified across a representative range of target growing environments worldwide; and
(g) **Informatics:** large data sets collected are used to refine breeding strategies and document the scientific basis of yield gains.

Crop Design

Crop Design is usually the first step where a new "idea" or hypothesis, *i.e.*, a trait, allele or selection methodology must be evaluated for its potential complementarity to a package of prerequisite traits and screens associated with a given target environment [22]. As an example, the hypothesis that the trait canopy temperature (CT) is related to root system efficiency has been validated in different environments, e.g., in wheat [23]. In the crop design phase it was necessary to show that CT was linked with water availability in the subsoil of the target environment. Another consideration was whether the selection environment was suitable for measurement of the trait, which is a function of temperature and relative humidity [24]. It was also necessary to verify that there was sufficient genetic variation among genotypes for CT to be used as a sensitive selection system [25].

Genetic Resources

Genetic resources provide different opportunities for validation of a trait or selection methodology depending on the context. Using again the example of CT, screening genetic resources for the trait under appropriate environments enabled the identification of new and possibly better sources of rooting capacity for use in crossing programs [26]. The variation found in genetic resources can also allow us to more accurately test the primary hypothesis. Genetic resource collections also provide a platform for evaluating new selection tools and protocols. Especially in this context, it is important to keep in mind that genetic resources come in many shapes and sizes, from panels of well-adapted advanced breeding lines, to bi-parental mapping populations, to landraces and wild progenitors whose growth habits and phenology may bear little resemblance to cultivated species. Nevertheless, testing new screening approaches on well-designed genetic resources panels can simultaneously provide a rigorous proof of concept and identify promising genotypes. DNA marker data associated with the trait would complement this exercise and provide the opportunity to explore novel genetic variation around known loci.

Phenotyping

Phenotyping is an essential step to test and validate hypotheses. This can be simple, even by eye, or complex due to the transient nature of the trait or its small magnitude. High throughput phenotyping (HTP) typically uses remote sensing to measure traits that can be measured non-destructively. Because it is cheaper and/or faster, HTP is a prerequisite for evaluating large germplasm collections and breeding generations, though obviously not all traits are amenable to HTP [27]. Precision phenotyping is typically invasive or destructive, and although more expensive and slower, can identify variation for a wider range of traits among smaller panels of pre-selected candidate parents. However, phenotyping is not just about tools and quantitative assays. Populations of plants must be controlled in terms of height and phenology to avoid the risk of confounding effects [25,28]. Furthermore, for accuracy, the selection environments must simulate as much as possible the water, light and temperature profiles of the target breeding environments as well their agronomy.

Genetic Analysis

Genetic analysis of novel traits can help refine crossing strategies to ensure complementary alleles, and lead to marker assisted progeny selection. Such deterministic use of molecular markers can complement genomic selection models to improve selection efficiency, especially where trait expression is harder to select for in specific environments. Translational research involving genetic analysis provides an especially important validation step because epistasis, G × E, and trait compensation can lead to unpredictable outcomes when stacking desirable traits in different genetic backgrounds [29,30].

Table 1. Types of crosses involved in translational research to demonstrate impact of new physiological traits and new trait combinations.

Pre-breeding Objective	Maternal parent	Paternal parent	Back or top cross
Enrich expression of a previously validated physiological trait (PT) in elite genetic backgrounds	Elite line	Elite line	
Test impact of a new PT, in an elite genetic background	Trait source	Elite line	
Test impact of a new simply inherited PT, in an elite genetic background	Trait source	Elite line	Backcross with Elite line
Test impact of new strategic combinations of PTs from 2 parents	Trait source	Trait source	
Test impact of new strategic combinations of multiple PTs from 3 parents	Trait source	Trait source	Topcross with trait source
Test impact of new PT source from non-adapted background, in an elite genetic background	Trait source in exotic	Elite line	Backcross with Elite line
Enhance the frequency of favorable alleles for a complex trait via recurrent selection to develop improved trait source lines for use in breeding crosses	Elite lines for cycle 0; sub-set of selected lines for subsequent cycle	Trait source(s) for cycle 0; sub-set of selected lines for subsequent cycles	

Crossing and Selection

Crosses involving new traits/alleles provide the definitive experimental platform for quantifying genetic gain, while the effectiveness of new screening technologies can be rigorously tested through well-controlled progeny selection. However, different kinds of crosses and selection processes are applied depending largely on trait heritability and genetic backgrounds. Where a trait has a relatively simple genetic basis and is either associated with reliable molecular markers or a heritable phenotype, backcrossing into a range of elite breeding lines is the favoured and fastest approach. However, yield and many of its physiological drivers are complex, so simple backcrossing and use of markers is not generally an option. Different crossing strategies and their objectives are summarized in Table 1.

Evaluation of Genetic Gains

Evaluation of the best performing progeny from experimental crosses over a representative range of target environments enables quantification of the impact of new technologies in terms of realized productivity. Genotype by environment interactions can be estimated by spanning the relevant extremes expected in the target population of environments. Many argue that to adequately ground-truth results, farm trials should be used for such nurseries instead of experimental stations. However, as long as both are managed within a range of recognized standards and represent target agro-ecosystems, results should be comparable.

Evaluation of genetic gains in any context adds to the knowledge base and can inspire new approaches in translational research. For example, a recent comprehensive study by Voss-Fels *et al.* [31] showed that commercial breeding in favourable environments resulted in improvement in the physiology and haplotypes of winter wheat cultivars grown across a wide range of environments in Western Europe, information that can be applied directly to refine breeding strategies.

Informatics

Curation and analysis of large data sets collected in research, breeding and multi-location testing can help refine breeding strategies and document the scientific basis of yield gains, thereby providing new inputs for crop design, as well as feedback to the research community at large. Informatics is increasingly being used at all stages of the breeding process pipeline, including the barcoding of plots and trials to make automated analysis of trials easier and less error-prone.

CASE STUDIES

Case Study 1: Translational Research Platforms for Spring Wheat: The International Wheat Yield Partnership (IWYP) and Heat and Drought Wheat Improvement Consortium (HeDWIC)

In 2010 the CGIAR Research Program on Wheat (WHEAT, https://wheat.org/) formalized the need to boost both wheat yield potential as well as its adaptation to heat and drought stress. A large part of the strategy was to harness previous research conducted by labs around the world to boost genetic gains in wheat, capitalizing also on the research and pre-breeding outputs of WHEAT and the testing networks of the International Wheat Improvement Network (IWIN). Examples of the research to be validated and translated include work on cellular and canopy level photosynthesis, partitioning of assimilates among plant organs including the roots, and phenological development [32]. As a result of the concerted efforts of many stakeholders, two translational research platforms were established: the International Wheat Yield Partnership (IWYP) http://iwyp.org/ and the Heat and Drought Wheat Improvement Consortium (HeDWIC) https://www.hedwic.org/. Both platforms are located in a major wheat agro-ecosystem in northwest Mexico, and are supported by infrastructure of the International Maize and Wheat Improvement Centre (CIMMYT) (Supplementary Table S1), a large interdisciplinary team of international collaborators (see previous links), and a number of funding agencies who are acknowledged at the end of this review.

IWYP was established to both generate new hypotheses and test existing hypotheses for how yield potential can be increased in wheat. The new hypotheses are generated by international research teams focused on discovering new aspects of source and sink traits. Many new types of germplasm are being screened with new and proven technologies for specific traits and the traits are being linked to molecular markers coming from state-of-the-art genomics. The purpose of the funded research projects is to provide a number of new ideas and hypotheses to break the constraints currently limiting yield in wheat production (https://iwyp.org/funded-projects/). Each of these projects feeds its outputs into the validation and testing systems of CIMMYT and other institutions.

Even though many of the projects produce valuable new discoveries relating to important sub-traits of yield, it is not expected that all the discoveries will be reproduced in different elite germplasm, in high yielding environments or will be novel to elite germplasm. Thus the discoveries are first validated. Next, and most importantly, because single trait discoveries are unlikely to achieve major yield gains on their own, they need to be combined with other trait improvements in pre-breeding programs. The more that can be stacked, the more likely that new gains will be recognized. When such gains are realized via the wide area testing systems, then the translation of discovery to the frontiers of breeding can be considered complete [33]. Thus IWYP seeks to generate and test hypotheses through agriculturally relevant research to the point where clear conclusions can be made about the relevance of a discovery to agricultural performance in elite material in farmers' fields, thereby minimizing the investment and risk associated with adoption into mainstream breeding.

Boosting yield through improving source and sink balance

One of the main hypotheses tested through translational research at these hubs was that yield could be boosted in spring wheat environments – environments that occupy around 140 M·ha worldwide and 80 M·ha in less developed countries—by simultaneously boosting assimilate supply (source) and its partitioning to grains (sink strength). Both theory and research indicate that increases in photosynthetic rate [34] can boost radiation use efficiency, while studies of historic genetic gains indicate that both biomass and harvest index (HI) are associated with yield gains [35]. Since both source (*i.e.*, biomass and related traits) and sink (*i.e.*, HI and related traits) appear to drive yield, it has been suggested that achieving more optimal balance between source and sink is a way to increase rates of genetic gains [36–38]. When evaluating genetic resource collections, biomass is often expressed at levels considerably greater than checks, under both optimal and stressed conditions [26] and relatively large variation in expression of HI is also common even among elite cultivars.

A translational research project within IWYP provided proof of concept that strategic crosses seeking to better balance source and sink could increase yields over either parent. Some of the best sources of aboveground biomass were identified in exotic germplasm [26], including landraces and products of interspecific hybridization, *i.e.*, synthetic wheat [39]. Favorable sources of sink related traits including HI, kernel number per m^2, thousand kernel weight, and grains per spike were identified among elite breeding lines. Crosses were designed to achieve complementation of source with sink traits, in the sense that at least one parent was selected for favorable expression of biomass (source) and the other for favorable expression of sink-related traits. Segregating progenies were selected for favorable agronomic type, including phenology, height, and disease resistance. In later generations, other performance traits that would indicate a good source-sink balance—such as cool canopy temperature, HI and yield in the selection environments—were measured to aid in choosing the best performing lines in target environments.

In this project, approximately 20–30 of the best-yielding progeny identified in the selection environment in Mexico, along with elite checks, were included in four international nurseries: the 2nd and 3rd Wheat Yield Collaboration Yield trial (WYCYT) and the 2nd and 4th Stress Adaptive Trait Yield Nursery (SATYN), targeted at temperate irrigated and hot-irrigated environments, respectively. Yield trials were grown at 50 sites in 13 countries that are part of a wider dissemination and evaluation network (Figure 2)[33]. Trials identified a number of new lines showing yield gains in comparison to parents and checks [40]. While HI was similar to checks, biomass was higher in many of the new higher yielding lines, indicating the potential to further boost yield through new rounds of crossing with locally adapted material. Subsequent international nurseries have shown further gains, averaging 7% over the best elite check [41] using this approach.

In summary, results from translational research seeking to test the hypotheses that optimizing source-sink balance can boost yield, and that selecting among genetic resources (like landraces and products of wide crossing) can provide new and better sources of important traits like biomass and kernel size, has led to positive outcomes. The IWYP and HeDWIC translational research hubs continue to test other promising candidate traits (https://iwyp.org/iwyp-research-breeding-hub/; https://www.hedwic.org/resources.html). It should be noted that such research projects lie outside the scope of most wheat breeding programs today because they are high risk, a deviation from focusing on only high yielding, adapted parental germplasm, and require both investment in phenotyping of large numbers of plants, and often special scientific expertise.

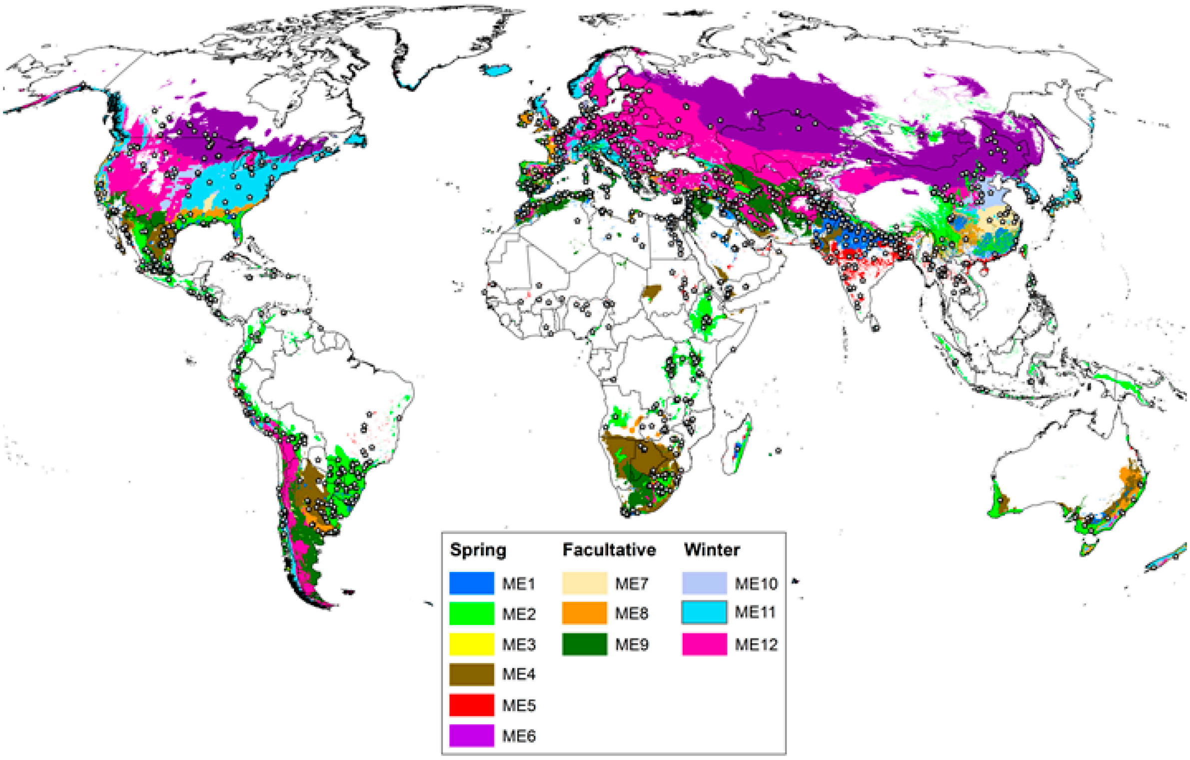

Figure 2. Mega-environments (MEs) and >700 testing sites of the International Wheat Improvement Network. Breeding is directed towards 12 different mega-environments (see box), representing a range of temperature, moisture, and disease profiles, based on up-to-date GIS and economic information (From Reynolds and Pinto [42]).

Case Study 2: Translation of Discovery through Delivery to Australian Breeders

Early vigor and water-use efficiency

In many parts of the world, water used by fall sown cereals (whether spring or winter wheat) is made available through in-crop season rainfall. In wheat, as much as 50% of this water is lost through evaporation that reduces water-use efficiency, thereby reducing total biomass and yield [43]. Barley and triticale have much smaller evaporation losses from the soil suggesting these cereals have unique adaptation mechanisms allowing them to better capture rainfall events. Wheat is very conservative in its early growth and is particularly slow in seedling emergence and leaf area development when compared with barley, triticale and oats [43].

Comparative crop research has shown that barley has more vigorous early growth owing to: (1) more rapid seedling emergence; (2) a larger embryo; and (3) a higher specific leaf area (SLA)[44]. Differences in the sizes of the first and second leaves to emerge integrate genetic variation in embryo size and SLA [45,46], and can be used to rapidly screen genotypic diversity to increase early vigor [47]. Further, gene action for early growth is additive and highly heritable, suggesting capacity for early generation testing and rapid recycling of elite alleles in a breeding program targeting greater leaf area development [48].

In this project, the scientists conducted a global survey to assess early vigor across more than 5,000 wheat varieties, breeding lines and landraces with the aim to identify genetically unrelated sources of early vigor for use in breeding. This was the crop design and hypothesis phase. After standardizing for differences in seed size, the scientists compared varieties to confirm the conservative growth of wheat compared with barley [45]. They also identified 28 high vigor genotypes from India, China, Israel, Canada, Mexico and elsewhere and assembled them into a large S1 recurrent selection program. Each cycle comprised growing 6000 F_2 progenies from 60 biparental crosses. Elite progenies were retained and tested to identify the 120 widest-leafed S0:1 families for crossing and development of the next cycle of selection. This was repeated six times over a period of 15 years [49]. Thirty families were retained from each selection cycle and, when the authors compared them in four sowings, they found the varieties had established a near 40% increase in leaf area as a result of selection for greater leaf width (Figure 3).

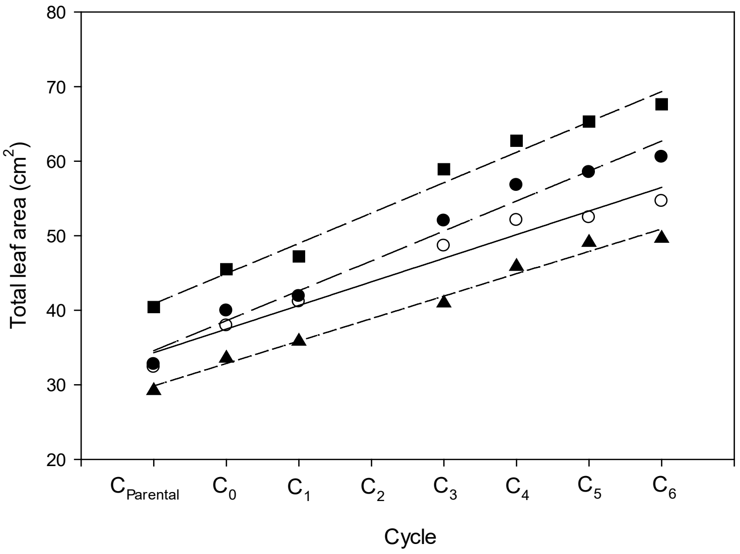

Figure 3. Relationship between cycle number and mean total leaf area measured in four environments: Sow 1 (○; r^2 = 0.93**); Sow 2 (■; r^2 = 0.94**); Sow 3 (●; r^2 = 0.93**); and Sow 4 (▲; r^2 = 0.95**) (Note that cycle 2 lines were accidently discarded during long-term seed storage).

Need for new dwarfing genes

The study authors then selected elite recurrent selection-derived progenies to deliver high vigor into commercial wheat varieties. The first high vigor × commercial variety populations lacked the early vigor of the high vigor parental germplasm owing to the suppressive effects of the *Rht1* (syn. *Rht-B1b*) and *Rht2* (syn. *Rht-D1b*) dwarfing genes on cell size [50]. There therefore had to be another discovery phase. Dwarfing genes needed to be identified that would reduce plant height without compromising cell size and consequently early vigor. Using unique genetic resource stocks arising from mutagenesis activities across the world [51], they were able to identity a number of dwarfing genes, which they assessed to confirm their neutral effects on cell size and early vigor.

In assessments across multiple studies the *Rht8, Rht12, Rht13* and *Rht18* dwarfing genes appeared the most useful in providing good agronomic performance while maintaining greater early vigor [52]. These genes allowed for good expression of early vigor and also allowed for selection of greater coleoptile length [52] and increase early leaf area development. Backcross- and top cross-derived populations were then initiated in collaboration with commercial breeders to incorporate both new dwarfing and high early vigor genes into commercially-relevant genetic backgrounds.

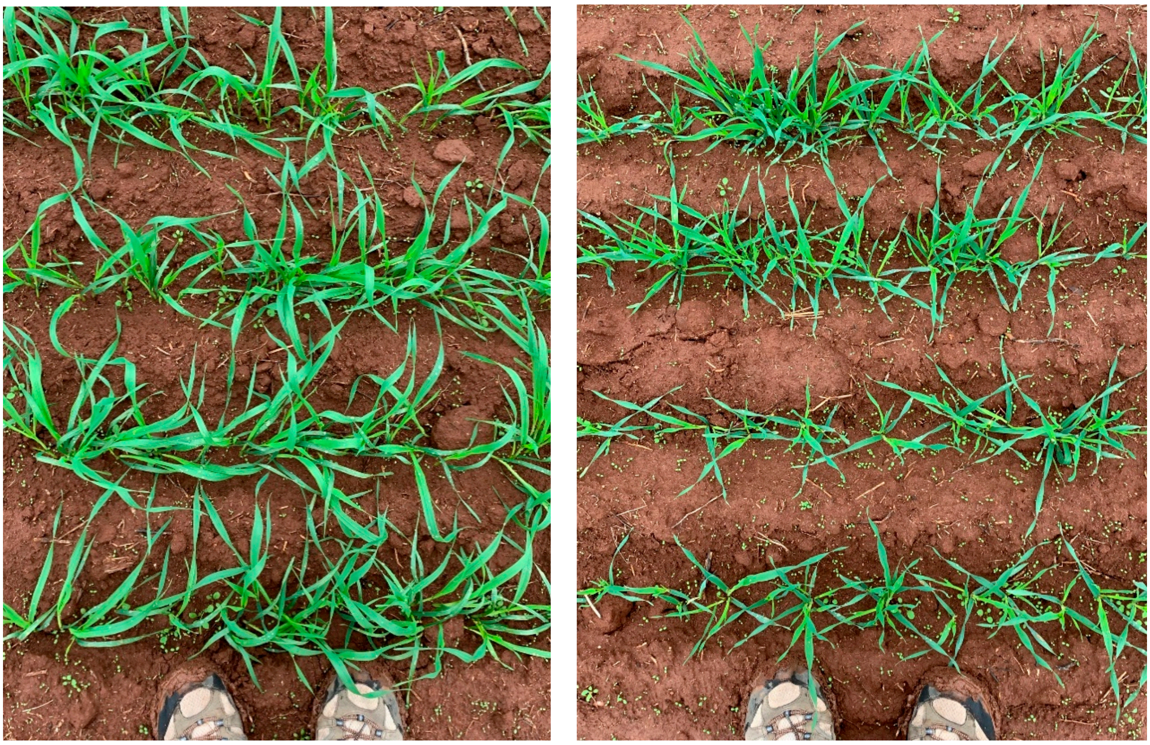

Figure 4. High early vigor wheat germplasm containing a new dwarfing gene (**left**) sown side-by-side with barley variety Fathom (**right**) in the field in Australia. Seeding rate was the same (100 kg/ha) for both plots.

The capacity to integrate across multi-stage selection activities (*i.e.*, combine selection for greater early leaf area and then alternative dwarfing genes) in delivering new high early vigor wheats is shown in Figure 4 where a high vigor, dwarf wheat breeding line is shown together with a high vigor barley variety sown in the same experiment. The figure highlights the increased early growth in wheat and its capacity to shade the soil and reduce soil-water loss through soil evaporation. The greater early ground cover of the new wheat is also important in achieving greater crop-weed competitiveness [53,54].

Delivery

These activities undertaken over 20 years of genetic and physiological research have identified: (1) the need for transformational change in early wheat growth, (2) the translational learnings from barley to the drivers of early vigor, (3) the need to look widely for new high early vigor genetics, (4) the need to use unique population-based breeding methods to accumulate multiple alleles for a polygenic trait together in developing parental germplasm, and (5) the importance of changing dwarfing genes to maximize early vigor expression.

The new high vigor wheats have had a high uptake into commercial breeding programs (e.g., Figure 5). Critical in this uptake have been: (1) close and ongoing communication between researchers and the breeding companies, (2) a clear value proposition in the importance of greater early vigor for improving productivity in rainfed farming systems, (3) the development of breeder-friendly populations in elite commercial genetic backgrounds, and (4) identification of efficient high-throughput selection methods (phenotyping and/or diagnostic markers).

Figure 5. Dr. Daniel Mullan, a commercial wheat breeder with Intergrain Wheat Breeding company in Australia, highlighting advanced high early vigor wheat breeding lines at the Intergrain wheat breeding nursery at Lake Grace in WA, Australia.

Case Study 3: Translation: from Casual Observation to Predicting Stress Tolerance and Stability: Anthesis Silking Interval (ASI) and Maize

Maize is the cereal with largest annual global production at 1096 M tons annually. Average yields are low, however, in drought-prone and infertile environments such as Africa (2.0 t/ha compared to western Europe at 8.9 t/ha and North America at 10.9 t/ha [55]). This outcrossing species is historically vulnerable to stress at pollination. Maize breeders working in rainfed summer nurseries in the Corn Belt region of the Midwestern United States often noted that drought stressed plants suffered a large delay in silk emergence and were often barren [56]. Silk delay was also observed at high plant density [57]. Anthesis date is little affected by stress, so ultimately the delay was expressed relative to anthesis date and termed the anthesis-silking interval (ASI) [58] a strong relationship between grain yield (GY) and ASI in tropical maize. The genetic correlation between GY under severe stress at flowering and ASI reached as much as -0.60, with GY showing a dependence on ASI of the general form $GY = \exp^{(a + b \times ASI)}$ (Figure 6A).

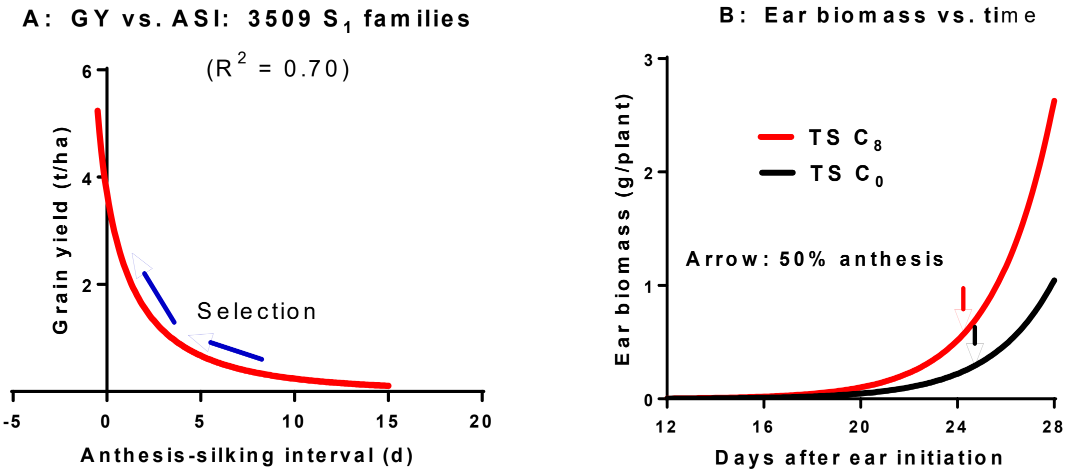

Figure 6. (**A**) General relationship between grain yield (GY) and ASI in 3509 S_1 families of tropical maize evaluated under a range of water deficits, Mexico. Selection arrows show the direction of changes towards higher GY and lower ASI [59]. (**B**) Ear biomass *vs* days from ear initiation in selection cycles of Tuxpeño Sequía (TS) evaluated under a range of plant densities [60].

An indicator of partitioning

ASI is a visual indicator of ear growth rate and hence useful for estimating partitioning to the ear under a wide array of stresses that reduce plant growth rate at flowering in maize. These stresses include drought, high plant density and low soil nitrogen (N)[61]. Reducing plant height by selection also decreases ASI and increases HI, resulting in grain-efficient density-tolerant cultivars [62]. In the study, contrasting selections—developed under managed drought stress and evaluated under a range of densities—showed increased ear growth rate (Figure 6B) and increases in GY and HI under flowering stress. Short ASI selections showed greater biomass at pollination, with an increased rate of kernel set, and hence increased GY. (Although in extreme cases, pollen shortage may contribute to loss of GY, reduced kernel set mainly reflects a failure of spikelets to reach the biomass threshold needed for successful pollination.) In addition, as the study indicates, kernel set in the Corn Belt region of the U.S. has been positively linked to assimilate flux reaching the ear during silking, hence the importance of low ASI [63].

If stress occurs outside of the flowering period (10 days before to 14 days after anthesis), selections with long vs. short ASI generally do not differ in performance. The adaptive value of long ASI in unimproved landraces is unclear. It may serve to prevent self-pollination, since inbred offspring lack fitness and would be more susceptible to stress [61].

ASI use in maize breeding programs

ASI generally forms part of a selection index—along with GY, barrenness and stay-green scores—as the broad-sense heritability of ASI is moderate and similar to that for GY (0.51 *vs* 0.43) [59,64]. During the validation phase of the project to validate ASI, recurrent selection schemes using an index that included ASI were carried out over 2–9 cycles in six tropical populations under managed drought stress, with average GY gains per cycle of 164 kg/ha, 0.04 ears per plant, and −0.86 d for ASI under drought and similar gains evident under low N [65,66].

Scientists have been using managed stress environments as a phenotyping tool to expose variation for GY, ASI and leaf senescence extensively since 1995 in donor-funded breeding initiatives in sub-Saharan Africa. Currently there are two research projects supported by the Bill & Melinda Gates Foundation and USAID operating in 13 countries in the region: Stress Tolerant Maize for Africa (STMA) and the TELA Maize Project (TELA). These and their predecessors released new stress tolerant cultivars that were planted in 2018 on 3.5 M·ha in 10 sub-Saharan African countries (https://stma.cimmyt.org, 2019).

In temperate maize multi-location testing, high plant densities have resulted in a steady improvement in ASI over the past 70 years, although a 2002 study indicated that elite hybrids still show a strong association between GY and ASI under severe drought stress. [67,68]. As genomic selection has become mainstream in commercial breeding programs, ASI observed under managed stress conditions has been incorporated in the genomic prediction models of drought tolerance along with the primary trait of grain yield [69].

Future trends

As leading breeding programs focus on yield stability and ASI, susceptibility to stress at flowering is diminishing in maize, and in the future ASI should account for a smaller portion of the variability in GY under mid-season drought or high plant density. Already ASI is part of basket of traits being used for genomic selection in doubled haploid lines in both temperate and tropical maize improvement for stressed or marginal production conditions [69–71]. ASI has been incorporated in a proprietary version of the crop model APSIM used to inform breeders of appropriate breeding strategies for stressed environments [72]. In addition, as relatively unimproved genotypes are tapped as sources of resistance to pests or stresses, selection for little or no silk delay under stress will play a role in ensuring that their progenies are stable in GY and high in harvest index. The trait that began as a casual observation in drought-stricken breeding nurseries has been successfully translated into mainline selection criteria and models that predict stress tolerant, stable and efficient maize cultivars for the future.

Case Study 4: Science from Bacteria, Algae, Plants, Gerbils and Pigs Translated into Nutritious Maize for Humans

Millions of people, especially children and pregnant women, suffer from vitamin A deficiency (VAD), resulting in blindness or compromised immune system and associated morbidity and mortality [73]. Liver, fish, sweet potato, spinach, carrot and mango are good dietary sources, whereas most staple food crops, including maize, have little vitamin A or its precursor provitamin A (proVA) carotenoids. Breeding micronutrient-enriched staple crop varieties, such as proVA-enriched maize, is an attractive public health intervention because large populations in low- and middle-income countries rely on inexpensive staple foods and cannot always access nutritious, balanced diets.

Basic research studying bacteria, algae and model plant species elucidated the biochemical pathway by which plants synthesize carotenoids [74,75]. This understanding enabled the search for natural or mutation-induced allelic diversity for enzymes affecting the production, accumulation, and degradation of proVA carotenoids in maize. *Harjes et al.* [76] reported alleles of lycopene epsilon cyclase (LycE) in maize that increase the production of carotenoids along the “beta” relative to the “alpha” branch of the pathway, thus favoring accumulation of beta-carotene and beta-cryptoxanthin, the carotenoids with largest proVA activity. Two years later, Yan *et al.* [77] reported the discovery of maize allelic variants for beta-carotene hydroxylase (CrtRB1) that slow the conversion of beta-carotene to beta-cryptoxanthin, thereby favoring accumulation of the most effective precursor of vitamin A, beta-carotene. The use of molecular-marker-assisted selection (MAS) for favorable alleles of LycE or CrtRB1 to breed proVA-enriched maize varieties thus became an attractive possibility.

The search for maize germplasm with higher concentrations of proVA carotenoids identified three temperate inbreds [76] that were subsequently used to form pre-breeding populations in Illinois, USA [78]. These lines and three narrow-based pre-breeding populations were shared with breeders at CIMMYT and International Institute of Tropical Agriculture (IITA). In parallel, ten orange and flint-grained Argentinian landraces from CIMMYT’s germplasm bank were found to carry the favorable CrtRB1 allele identified by Yan *et al.* [77], albeit at low frequency [79,80]. In practice, the temperate inbred lines and pre-breeding populations were used extensively in crosses with elite CIMMYT and IITA lines, whereas the Argentinian landraces were never used due to anticipated costs of breeding to overcome their poor agronomic performance and linkage drag.

The translational breakthrough was Babu *et al.*'s [81] validation in 26 tropical maize crosses of consistent favorable effects of alleles and their associated molecular markers for LycE and CrtRB1, as originally discovered by Harjes *et al.* [76] and Yan *et al.* [77]. The subsequent application of MAS for the favorable CrtRB1 allele, using DNA extracted from seed of numerous segregating breeding crosses prior to planting—planting only the MAS-selected seeds—resulted in rapid increases in the concentrations of proVA carotenoids in pre-breeding lines [82]. ProVA concentrations in CIMMYT breeding lines increased from less than 2 to 8 $\mu g \cdot g^{-1}$ in the first cycle of breeding, and have now reached 20 or more $\mu g \cdot g^{-1}$ in best lines of second and third cycles of breeding [83]. These achievements should be compared to the breeding target of 15 $\mu g \cdot g^{-1}$, which is estimated to provide 50 percent of the daily proVA requirement for children and women, assuming common daily intakes of maize [84]. Although mainstream proVA breeding at CIMMYT no longer uses MAS for LycE or CrtRB1 (because the germplasm has achieved desired concentrations of proVA, and these favorable alleles are likely fixed), other proVA maize breeding programs continue to use these markers, e.g., Zunjare *et al.* [85].

Translating nutrition science into proVA maize breeding goals was crucial to this story. Gerbil, piglet and chicken models established that proVA carotenoids in maize in the diets of these animals is bioavailable and bioefficacious (e.g., Davis *et al.* [86]; Heying *et al.* [87,88]). Robust evidence of the value of proVA maize for alleviating human VAD, however, came from long-term, community-based, placebo-controlled trials with children in three Zambian villages [89].

The impact of proVA-enriched maize on the health of maize-consuming, VAD populations will depend on many factors, but varieties are currently grown and consumed in Zambia [84], and more than 40 varieties have been released for cultivation in eight countries in sub-Saharan Africa and Brazil [90]. In the meantime, proVA maize translational research is taking new and exciting directions as evidence from mycology, toxicology and human cancer research led to preliminary findings that enhanced proVA concentrations in maize grain reduce colonization and aflatoxin production by *Aspergillus flavus* [83]. If these results are validated, the impacts of proVA-enriched maize could grow to include health benefits for millions of children suffering stunting or underweight, and adults developing liver and other cancers from consumption of aflatoxin-contaminated maize. Such evidence of enhanced impact potential of proVA maize might stimulate investments to translate additional basic science, such as the role of CCD1 in degrading and thereby reducing the amounts of proVA carotenoids in grain [91], into practical tools used by breeding programs.

Case Study 5: Translation of SUB1 Alleles into Elite Rice for Flooding Tolerance

This example, while scientifically simpler than many others, records how after a desirable genetic trait is recognized it can take a long time to incorporate the trait improvement optimally into elite germplasm breeding programs. The development of flooding tolerant rice based on a specific SUB 1A allele took over 50 years at the International Rice Research Institute in the Philippines (1960–2010) together with expert molecular analyses by others. The translation program to achieve efficient incorporation into elite high yielding cultivars also took detailed research using molecular marker technologies that were not available at the time when trait introgression started [92].

Fast flooding affects over 22 million hectares worldwide of lowland rainfed rice, some 18% of the global supply [93]. In Bangladesh and India alone an estimated 10 million hectares suffer from the threat of additional flooding each Monsoon season. Traditionally, landraces that can endure 10 days or more of complete submergence are cultivated on susceptible flood plains. These land races retain viability under water and resume growth upon de-submergence. However, these submergence tolerant landraces are very low yielding, producing only 25–30% of the yield of advanced semi-dwarf varieties which usually died within 7 days of complete flooding because of their sensitivity to the anaerobic conditions of complete submergence.

Rice breeders in the 1960s [94] recognized the need to introduce higher yielding submergence tolerant varieties. By the early 1950s landraces with unusual flooding and submergence tolerance had been recognized, and during the 1970s were systematically screened. Several important accessions with resilience to complete submergence were found: FR13A from Orissa, India and Kurkaruppan, Goda Heenati and Thavalu from Sri Lanka. Their 10-day old seedlings survived 7 days of complete submergence. This knowledge led to the initiation of backcrossing into advanced breeding lines to see if the trait could be readily transferred. Work began in the 1980s [95]. However, submergence tolerance from FR13A was not successfully introduced into productive short-to-intermediate stature lines by backcrossing until the mid-1990s [96].

The genetic control of submergence tolerance was not revealed until the mid-1990s. Previously it appeared to be a typical quantitative trait [95]. Then several independent studies found that up to 70% of the phenotypic variation in tolerance was due to a major chromosome 9 QTL (termed SUB 1) with other minor QTLs accounting for less than 30% of the phenotypic variation [97]. SUB1 was further mapped to a 0.16-cM region on chromosome 9 using F_2 progeny mapping, before being further limited to a 0.075 cM locus (150 kb; Xu *et al.* [98]). Further fine mapping of SUB1 showed it to encode two or three ethylene-responsive DNA binding proteins. All *Oryza sativa* accessions carry SUB1B and SUB1C sequences at this locus but an additional SUB1A allele (SUB1A) is present in some lines.

This probably arose from a duplication of the SUB1B gene. Variant SUB1A-1 is found only in lines tolerant to flooding such as FR13A, whereas the SUB1A-2 allele is characteristic of accessions which are sensitive to flooding. The protein products of both alleles are identical with the exception of Ser_{186} in the flood tolerant allele and Pro_{186} in the flood intolerant allele [92]. Allele SUB1A-1 is much more highly expressed in leaves in response to flooding than the allele SUB1A-2 and is clearly responsible for the resilient flooding tolerance. Single nucleotide polymorphisms were identified within SUB1A and SUB1C regions that could be used as molecular markers in breeding [99]. A small genomic region containing SUB1A-1 has been introgressed into modern high yielding varieties such as Swarna and BR11 [99] using marker assisted back crossing. The importance of flooding tolerance has meant that most lowland high yielding varieties now carry the SUB1A-1 allele and are tolerant to the stress [92,98,100].

Submergence causes death by many metabolic disturbances. Notably, it inhibits photosynthesis and respiration. SUB 1A-1 promotes better maintenance of soluble carbohydrate, chlorophyll and oxygen levels in a submergence-dependent manner as revealed by microarray and metabolite studies [92]. Ethylene is a key hormone induced by flooding and induces expression of SUB1A. Ethylene normally induces gibberellic acid that promotes seedling elongation. The induction of SUB 1A expression by ethylene during submergence disrupts this strategy to aid survival.

The translation of the submergence trait from landraces into elite varieties is an excellent example of the impact of translational research, which resulted in very important gains for rice agriculture. It is also noteworthy that vital discoveries were necessary along the way to define the genetic changes required for introduction via marker assisted backcrossing.

Case Study 6: Translational Research in Sorghum

The Australian sorghum industry exemplifies an efficient delivery pathway to move public-sector pre-breeding germplasm into private sector breeding programs. A key element of this approach is the simultaneous evaluation of various target traits in conjunction with selelction for grain yield across the target population of environments for the crop. This has reduced bottlenecks between upstream research (encompassing both gene-to-phenotype and phenotype-to-gene approaches) and practical breeding outcomes for grain-growers.

A study that examined wheat and sorghum yields over the past 30–40 years in Australia showed that sorghum yields were 2.1% per year [101]: almost twice that for wheat (1.2% per year). While yield trends for sorghum and wheat were similar in wet environments, in dry environments relative yield trends for sorghum were 3.6 times those for wheat. The effects of yield advances could not be clearly apportioned to either agronomic practices or varieties. However, both crops would have benefited from the same agronomy changes (e.g., controlled traffic, minimum tillage), suggesting that genetics are likely important. While the impact of CO_2 fertilization on yield increases was probably not significant in this study, there may have been a slight benefit under water-limited conditions for the C4 sorghum crop. The extra work necessary to retain high grain quality and disease resistance in wheat may also have been a factor in its moderately slower progress. [101].

The higher rate of genetic gain in dry than wet environments can be partly attributed to the transfer of pre-breeding germplasm with the stay-green drought adaptation trait to the private sector (~50% genetic contribution of pre-breeding genetics to all hybrids) over a long period of time from the mid-1970s onwards [102]. Concurrent selection for yield, as well as for drought-adaptation and insect resistance traits, has helped the uptake of these traits by private breeding companies. In addition, considerable effort has been put into developing intellectual property systems conducive to uptake of germplasm by companies [102].

The stay-green trait is a good example of a translational “phenotype-to-gene” approach in the Australian public sector sorghum pre-breeding program that enhances the delivery of drought-adapted germplasm to private sector breeding companies and, ultimately, to grain growers. Stay-green plants are characterized by the maintainence of relatively more green leaves during grain filling under end-of season drought. Stay-green was first observed as a drought adaptation phenotype more than 35 years ago by sorghum breeders in the U.S. led by Darrell Rosenow and in Australia, under Bob Henzell. Initially, breeders selected for the trait by a visual rating late in the grain-filling period. Currently, breeders use drones with various spectral indices to screen thousands of lines for stay-green in the field. Since the stay-green phenotype is an emergent consequence of causal mechanisms before anthesis that regulate water supply (e.g., root architecture) and demand (e.g., canopy development), components of the trait, such as tillering and root angle, are now being screened directly in the pre-breeding program.

Stay-green is a drought adaptation mechanism that improves grain yield and lodging resistance in sorghum and other cereals. Consequently, many physiological [103–109] and genetic studies [110–112] have been undertaken to better understand this trait. Genotypes containing the stay-green trait exhibit less branching (tillering) and smaller upper leaves, leading to decreased green leaf area at flowering [108,109]. Decreasing transpirational leaf area saves soil water before flowering for use after flowering when the grain is filling. Higher water uptake after flowering in stay-green lines leads to increased nitrogen uptake, biomass production, grain number and yield. Notably, stay-green genotypes do not yield significantly less under well-watered conditions.

In addition, an important link has been established between canopy development before flowering and the impact on crop water use patterns and grain yield after flowering under end-of-season drought [108]. Stay-green QTL also impact the anatomy of leaves and the growth of roots [109]. There are many ways by which Stg QTLs can modify canopy development, resulting in considerable plasticity. It is likely that the physiological mechanisms underlying stay-green in sorghum will also operate with similar functionality in other major cereals such as maize, wheat, and rice [109].

While studies of near-isogenic lines have provided clear understanding of the physiological mechanisms underlying stay-green, including yield benefits under drought, the best evidence of its impact in multiple genetic backgrounds and environments comes from a study investigating the relationship between stay-green and yield using data from breeding trials that sampled over 1600 hybrid combinations and more than 20 environments with mean yields varying from 2.3 to 10.5 $t{\cdot}ha^{-1}$ [112]. Most associations in this study were positive, specifically for environments yielding below 6 $t{\cdot}ha^{-1}$. Post-flowering drought is a major constraint to sorghum production worldwide and in Australia, limiting yields to 1.2 and 2.5 $t{\cdot}ha^{-1}$, respectively. The results in how that selecting for stay-green in elite sorghum hybrids should be beneficial in a wide range of environments, particularly when water is limiting..

Long-term selection for stay-green and grain yield has indirectly improved component traits and associated water capture and efficiency traits (e.g., root angle, transpiration efficiency). Evidence indicates that elite pre-breeding germplasm is extreme for both traits [102]. For example, there is evidence of an association between narrow root angle, yield and stay-green in hybrids grown in Australian environments [113]. Narrow root angle is associated with increased water extraction in deep soils, while wide root angle may be useful in skip-row systems on shallow soils. Some germplasm from the Australian public sector sorghum pre-breeding program has extreme root angle phenotypes, suggesting indirect selection for the trait. Furthermore, diversity of root phenotypes in experimental hybrids is much greater than the commercial range [102].

TRANSLATIONAL RESEARCH AND INTELLECTUAL PROPERTY RIGHTS

It is often said that intellectual property rights (IPRs) inhibit translational research. It is the case that all such projects should be scrutinised by experts to avoid contravening, knowingly or unknowingly, laws associated with patented germplasm, genes or technologies but very few projects in fact need be discarded because of IPRs. This is because (i) globally, little germplasm and few genes/markers or technologies are patented or unavailable for research and exploitation, (ii) dialog with holders of relevant IPRs often result in opportunities to test hypotheses because they could result in the outcomes being nearer to market, *i.e.*, more valuable, and (iii) there are often ways around the IPRs, e.g., by using different germplasm or variant genes, when the IPRs are fully understood.

Sometimes the existence of patented elements becomes a driver for the investment in translational research because of the promise of additional financial rewards. It is worth noting that the founding principles of awarding IPRs was to provide inventors the chance to get the translational work done before a competitor has the same chance. Therefore IPRs are not necessarily at odds with greatly increasing the volumes of translational research, providing detailed awareness exists.

CONCLUSIONS

While crop breeding and research into the complex traits that drive yield gains have existed in relative isolation for decades, often based around different species and growing environments, translational research pipelines based on application-relevant criteria can break down these silos through collaboration aimed at:

1. Identifying “best-bet” traits likely to boost yield when introgressed into elite germplasm based on conceptual or simulation models.
2. Accessing a wide range of both exotic and current breeding material to identify novel and better sources of trait expression and their genetic bases.
3. Testing hypotheses by making crosses using sources of traits proposed by research (Table 1), bringing them into elite germplasm and field testing progeny across a range of target environments (Figure 2).
4. Gaining a practical understanding of trait and allelic interactions through genetic and physiological dissection of successful progeny and their parents and comprehensive analysis of multi-location yield trials.

When such translational research efforts are associated with mature breeding and pre-breeding programs, added value is generated from pre-existing knowledge networks, germplasm and infrastructure (Supplementary Table S1), and the possibility to deploy multiple research activities involving different ideas and technologies on common panels of breeder-relevant germplasm. This focused approach can achieve a more comprehensive understanding of the relative contributions and interactions among novel traits and genes contributing to yield, while ensuring that conclusions are based on up to date breeding material and pertinent environments. Additional benefits include more efficient use of research resources and opportunities for closer interactions between disciplinary scientists and practicing breeders.

The relatively poor linkages between discovery research teams around the world and plant breeding teams delivering on the frontiers of variety production are a serious impediment to improving genetic gains in crop production. The extraordinary advances in understanding the genetic basis of important traits in academia are vital but even more vital is the translation of these into crop production. Without this translation, much of the societal value of the discovery research is lost. Thus establishing systems for generating and testing new hypotheses in agriculturally relevant systems must become a priority to achieve new gains from research.

That given, it is worth keeping in mind two of the main drivers common to the successful examples of translational research presented here. First, solutions require interdisciplinary and typically international collaboration (due to the transnational nature of agriculture) to adequately frame the problem and develop technologies that convince established breeding programs to retool. Second, a visionary approach is needed from both scientists and funding bodies that recognizes the time and commitment required to translate a piece of research into an improved cultivar. These attributes are prerequisite to capitalize on basic plant research so it can positively impact food security.

SUPPLEMENTARY MATERIALS

The following supplementary materials are available online at https://doi.org/10.20900/cbgg20190016, Supplementary Table S1: Resources supporting IWYP and HeDWIC Hubs.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

ACKNOWLEDGMENTS

Authors would like to acknowledge the following funding organizations for their commitment to translational research.

The International Wheat Yield Partnership (IWYP) is supported by the Biotechnology and Biological Sciences Research Council (BBSRC) in the UK; the U. S. Agency for International Development (USAID) in the USA; and the Syngenta Foundation for Sustainable Agriculture (SFSA) in Switzerland.

The Heat and Drought Wheat Improvement Consortium (HeDWIC) is supported by the Sustainable Modernization of Traditional Agriculture (MasAgro) Project by the Ministry of Agriculture and Rural Development (SADER) of the Government of Mexico; previous projects that underpinned HeDWIC were supported by Australia's Grains Research and Development Corporation (GRDC).

The Queensland Government's Department of Agriculture and Fisheries in collaboration with The Grains Research and Development Corporation (GRDC) have provided long-term investment for the public sector sorghum pre-breeding program in Australia, including research on the stay-green trait. More recently, this translational research has been led by the Queensland Alliance for Agriculture and Food Innovation (QAAFI) within The University of Queensland.

ASI validation work and ASI translation and extension components with support from the United Nations Development Programme (UNDP) and the Bill and Melinda Gates Foundation, respectively.

Financial support for the maize proVA work was partially provided by HarvestPlus (www.HarvestPlus.org), a global alliance of agriculture and nutrition research institutions working to increase the micronutrient density of staple food crops through biofortification. The CGIAR Research Program MAIZE (CRP-MAIZE) also supported this research.

CRPWHEAT: The following countries and organizations are Window 1 funders of CGIAR: Australia, the Bill & Melinda Gates Foundation, Belgium, Canada, France, India, Japan, Netherlands, New Zealand, Norway, Sweden, Switzerland, the United Kingdom, and the World Bank. Funding agencies of Australia, the United Kingdom (DFID) and USA (USAID) contribute vital Window 2 funding.

CRPMAIZE receives support from the Governments of Australia, Belgium, Canada, China, France, India, Japan, Korea, Mexico, Netherlands, New Zealand, Norway, Sweden, Switzerland, United Kingdom, United States, and the World Bank. The views expressed do not necessarily reflect those of these funders.

We appreciate Fatima Escalante's help with editing the manuscript.

REFERENCES

1. Singh RP, Hodson DP, Huerta-Espino J, Jin Y, Bhavani S, Njau P, et al. The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production. Annu Rev Phytopathol. 2011;49:465-81.
2. Smale M, Reynolds MP, Warburton M, Skovmand B, Trethowan R, Singh RP, et al. Dimensions of diversity in modern spring bread wheat in developing countries from 1965. Crop Sci. 2002;42(6):1766-79.
3. Araus JL, Slafer GA, Royo C, Serret MD. Breeding for Yield Potential and Stress Adaptation in Cereals. Crit Rev Plant Sci. 2008;27(6):377-412.
4. Fischer RA, Edmeades GO. Breeding and cereal yield progress. Crop Sci. 2010;50(Sup 1):S85-98.
5. Govindaraj M, Pattanashetti SK, Patne N, Kanatti AA. Breeding Cultivars for Heat Stress Tolerance in Staple Food Crops. In: Çiftçi YO, editor. Next Generation Plant Breeding. London (UK): IntechOpen; 2018. p. 45-74.
6. Jha UC, Bohra A, Singh NP. Heat stress in crop plants: its nature, impacts and integrated breeding strategies to improve heat tolerance. Plant Breed. 2014;133(6):679-701.
7. Kumar S, Gupta P, Kumar J, Pratap A. Phenotyping Crop Plants for Drought and Heat-Related Traits. In: Kumar J, Pratap A, Kumar S, editors. Phenomics in Crop Plants: Trends, Options and Limitations. New Delhi (India): Springer; 2015. p. 89-100.
8. Lamaoui M, Jemo M, Datla R, Bekkaoui F. Heat and Drought Stresses in Crops and Approaches for Their Mitigation. Front Chem. 2018;6:26.
9. Mathan J, Bhattacharya J, Ranjan A. Enhancing crop yield by optimizing plant developmental features. Development. 2016;143:3283-94.
10. Sreeman SM, Vijayaraghavareddy P, Sreevathsa R, Rajendrareddy S, Arakesh S, Bharti P, et al. Introgression of Physiological Traits for a Comprehensive Improvement of Drought Adaptation in Crop Plants. Front Chem. 2018;6:92.

11. Tuberosa R. Phenotyping for drought tolerance of crops in the genomics era. Front Physiol. 2012;3:347.
12. Poorter H, Fiorani F, Pieruschka R, Wojciechowski T, Van Der Putten WH, Kleyer M, et al. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytol. 2016;212(4):838-55. doi: 10.1111/nph.14243
13. Hu H, Scheben A, Edwards D. Advances in Integrating Genomics and Bioinformatics in the Plant Breeding Pipeline. Agriculture. 2018;8(6):75.
14. Sukumaran S, Lopes M, Dreisigacker S, Reynolds M. Genetic analysis of multi-environmental spring wheat trials identifies genomic regions for locus-specific trade-offs for grain weight and grain number. Theor Appl Genet. 2018;131(4):985-98.
15. Molero G, Joynson R, Pinera-Chavez FJ, Gardiner L, Rivera-Amado C, Hall A, et al. Elucidating the genetic basis of biomass accumulation and radiation use efficiency in spring wheat and its role in yield potential. Plant Biotechnol J. 2019;17(7):1276-88.
16. Fischer RA, Byerlee D, Edmeades G. Crop yields and global food security. Canberra (Australia): Australian Centre for International Agricultural Research (ACIAR); 2014.
17. Reynolds MP, Braun HJ, Cavalieri AJ, Chapotin S, Davies WJ, Ellul P, et al. Improving global integration of crop research. Science. 2017;357(6349):359-60.
18. Borrell A, Reynolds M. Integrating islands of knowledge for greater synergy and efficiency in crop research. Food Energy Secur. 2017;6(1):26-32.
19. Leeuwis C, Klerkx L, Schut M. Reforming the research policy and impact culture in the CGIAR: Integrating science and systemic capacity development. Glob Food Sec. 2018;16:17-21.
20. Ray DK, Mueller ND, West PC, Foley JA. Yield Trends Are Insufficient to Double Global Crop Production by 2050. PLoS One. 2013;8(6):e66428.
21. Reynolds M, Langridge P. Physiological breeding. Curr Opin Plant Biol. 2016;31:162-71. doi: 10.1016/j.pbi.2016.04.005
22. Donald CM. The breeding of crop ideotypes. Euphytica. 1968;17:385-403.
23. Pinto RS, Reynolds MP. Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. Theor Appl Genet. 2015;128(4):575-85.
24. Amani I, Fischer RA, Reynolds MP. Canopy Temperature Depression Association with Yield of Irrigated Spring Wheat Cultivars in a Hot Climate. J Agron Crop Sci. 1996;176(2):119-29.
25. Pinto RS, Reynolds MP, Mathews KL, McIntyre CL, Olivares-Villegas J-J, Chapman SC. Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. Theor Appl Genet. 2010 Oct;121(6):1001-21.
26. Reynolds MP, Tattaris M, Cossani M, Ellis M, Yamaguchi-Shinozaki K, Saint-Pierre C. Exploring Genetic Resources to Increase Adaptation of Wheat to Climate Change. In: Ogihara Y, Takumi S, Handa H, editors. Advances in Wheat Genetics: From Genome to Field. Tokyo (Japan): Springer; 2015. p. 355-68.

27. Araus JL, Kefauver SC, Zaman-Allah M, Olsen MS, Cairns JE. Translating High-Throughput Phenotyping into Genetic Gain. Trends Plant Sci. 2018;23(5):451-66.
28. Lopes MS, Dreisigacker S, Peña RJ, Sukumaran S, Reynolds MP. Genetic characterization of the wheat association mapping initiative (WAMI) panel for dissection of complex traits in spring wheat. Theor Appl Genet. 2015;128(3):453-64.
29. Wade MJ, Winther RG, Agrawal AF, Goodnight CJ. Alternative definitions of epistasis: dependence and interaction. Trends Ecol Evol. 2001;16(9):498-504.
30. Phillips PC. Epistasis—the essential role of gene interactions in the structure and evolution of genetic systems. Nat Rev Genet. 2008;9(11):855-67.
31. Voss-Fels KP, Stahl A, Wittkop B, Lichthardt C, Nagler S, Rose T, et al. Breeding improves wheat productivity under contrasting agrochemical input levels. Nat Plants. 2019;5:706-14.
32. Reynolds M, Foulkes J, Furbank R, Griffiths S, King J, Murchie E, et al. Achieving yield gains in wheat. Plant Cell Environ. 2012;35(10):1799-823.
33. FeedtheFuture. High yielding genetically diverse wheat lines based on physiological traits delivered to public & private breeders globally. Available from: https://feedthefuture.globalinnovationexchange.org/innovation/international-nurseries-containing-wheat-lines-with-outstanding-expression-of-yield-potential-related-traits-and-adaptation-made-available-and-distributed-to-breeders-and-researchers-worldwide. Accessed 2019 Aug 21.
34. Taylor SH, Long SP. Slow induction of photosynthesis on shade to sun transitions in wheat may cost at least 21% of productivity. Philos Trans R Soc B Biol Sci. 2017;372(1730):20160543.
35. Aisawi KAB, Reynolds MP, Singh RP, Foulkes MJ. The physiological basis of the genetic progress in yield potential of CIMMYT spring wheat cultivars from 1966 to 2009. Crop Sci. 2015;55(4):1749-64.
36. Slafer GA, Savin R. Source-sink relationships and grain mass at different positions within the spike in wheat. Field Crops Res. 1994;37(1):39-49.
37. Reynolds MP, Pellegrineschi A, Skovmand B. Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. Ann Appl Biol. 2005;146(1):39-49.
38. Slafer GA, Elia M, Savin R, García GA, Terrile II, Ferrante A, et al. Fruiting efficiency: An alternative trait to further rise wheat yield. Food Energy Secur. 2015;4(2):92-109.
39. Trethowan RM, Mujeeb-Kazi A. Novel germplasm resources for improving environmental stress tolerance of hexaploid wheat. Crop Sci. 2008;48(4):1255-65.
40. Reynolds MP, Pask AJD, Hoppitt WJE, Sonder K, Sukumaran S, Molero G, et al. Strategic crossing of biomass and harvest index—source and sink—achieves genetic gains in wheat. Euphytica. 2017;213(11):23.
41. CIMMYT International Nurseries. 4th Wheat Yield Consortium Yield Trial. Available from: http://hdl.handle.net/11529/10548294. Accessed 2019 Aug 31.

42. Reynolds MP, Pinto F. Tools and application of phenotyping in wheat. In: Friedt F, Orden W, editors. Advances in breeding techniques for cereal crops. Cambridge (UK): Burleigh Dodds Science Publishing; 2019. p. 460.
43. López-Castañeda C, Richards RA. Variation in temperate cereals in rainfed environments III. Water use and water-use efficiency. Field Crops Res. 1994;39(2-3):85-98.
44. López-Castañeda C, Richards RA, Farquhar GD, Williamson RE. Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. Crop Sci. 1996;36(5):1257-66.
45. Richards RA, Lukacs Z. Seedling vigour in wheat-sources of variation for genetic and agronomic improvement. Aust J Agric Res. 2002;53(1):41-50.
46. Rebetzke GJ, Botwright TL, Moore CS, Richards RA, Condon AG. Genotypic variation in specific leaf area for genetic improvement of early vigour in wheat. Field Crops Res. 2004;88(2-3):179-89.
47. Rebetzke GJ, Richards RA. Genetic improvement of early vigour in wheat. Aust J Agric Res. 1999;50(3):291-301.
48. Rebetzke GJ, Lopez-Casteneda C, Botwright-Acuna T, Condon AG, Richards RA. Inheritance of coleoptile tiller appearance and size in wheat. Aust J Agric Res. 2008;59(9):863-73.
49. Zhang L, Condon AG, Richards RA, Rebetzke GJ. Recurrent selection for wider seedling leaves increases early leaf area development in wheat (*Triticum aestivum* L.). J Exp Bot. 2015;66(5):1215-26.
50. Botwright TL, Rebetzke GJ, Condon AG, Richards RA. Influence of the gibberellin-sensitive Rht8 dwarfing gene on leaf epidermal cell dimensions and early vigour in wheat (*Triticum aestivum* L.). Ann Bot. 2005;95(4):631-9.
51. Konzak CF. Genetic analysis, genetic improvement and evaluation of induced semi-dwarf mutants in wheat. In: Semi-dwarf cereal mutants and their use in cross-breeding III. Vienna (Austria): International Atomic Energy Agency; 1988. p. 77-94.
52. Rebetzke GJ, Ellis MH, Bonnett DG, Mickelson B, Condon AG, Richards RA. Height reduction and agronomic performance for selected gibberellin-responsive dwarfing genes in bread wheat (*Triticum aestivum* L.). Field Crops Res. 2012;126:87-96.
53. Coleman RK, Gill GS, Rebetzke GJ. Identification of quantitative trait loci (QTL) for traits conferring weed competitiveness in wheat (*Triticum aestivum* L.). Aust J Agric Res. 2001;52(12):1235-46.
54. Zerner RK, Gill GS, Rebetzke GJ. Stability of wheat cultivars in weed competitive ability in differing environments in southern Australia. Crop Pasture Sci. 2016;67(7):695-702.
55. FAOSTAT. Available from: http://www.fao.org. Accessed 2019 Aug 31.
56. Tatum LA. Breeding for drought and heat tolerance. In: Heckendorn W, Gregory J, editors. Proceedings of 9th Annual Hybrid Corn Industry Research Conference. Chicago (US): American Seed Trade Association; 1954. p. 22-8.
57. Dungan GH, Lang AL, Pendleton JW. Corn plant population in relation to soil productivity. Adv Agron. 1959;10:435-73.

58. DuPlessis DP, Dijkhuis FJ. The influence of time lag between pollen shedding and silking on the yield of maize. South Afr J Agric Sci. 1967;10:667-74.
59. Bolaños J, Edmeades GO. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. Field Crops Res. 1996;48(1):65-80.
60. Edmeades GO, Bolaños J, Hernandez M, Bello S. Causes for silk delay in lowland tropical maize population. Crop Sci. 1993;33(5):1029-35.
61. Edmeades GO, Bolaños J, Elings A, Ribaut JM, Bänziger M. The role and regulation of the anthesis-silking interval in maize. In: Westgate ME, Boote KJ, editors. Physiology and modeling kernel set in maize, CSSA Special Publication 29, 2000. Madison (US): CSSA; Madison (US): ASA; 2000. p. 43-73.
62. Johnson EC, Fischer KS, Edmeades GO, Palmer AFE. Recurrent selection for reduced plant height in lowland tropical maize. Crop Sci. 1986;26(2):253-60.
63. Schussler JR, Westgate ME. Assimilate flux determines kernel set at low water potential in maize. Crop Sci. 1995;35(4):1074-80.
64. Bänziger M, Lafitte HR. Efficiency of secondary traits for improving maize for low-nitrogen target environments. Crop Sci. 1997;37(4):1110-7.
65. Edmeades GO, Trevisan W, Prasanna BM, Campos H. Tropical maize (*Zea mays* L.). In: Campos H, Caligari PDS, editors. Genetic improvement of tropical crops. Cham (Switzerland): Springer; 2017. p. 57-109.
66. Bolanos J, Edmeades GO. Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. Field Crops Res. 1993;31:253-68.
67. Campos H, Cooper M, Habben J, Edmeades GO, Schussler JR. Improving drought tolerance in maize: a view from industry. Field Crops Res. 2004;90(1): 19-34.
68. Barker TC, Campos H, Cooper M, Dolan D, Edmeades G, Habben J. Improving drought tolerance in maize. In: Janick J, editor. Plant Breeding Reviews, Volume 25. Hoboken (US): John Wiley & Sons, Inc.; 2005. p. 173-253.
69. Cooper M, Gho C, Leafgren R, Tang T, Messina C. Breeding drought-tolerant maize hybrids for the US corn-belt: discovery to product. J Exp Bot. 2014;65(21):6191-204.
70. Semagn K, Beyene Y, Babu R, Nair S, Gowda M, Das B, et al. Quantitative trait loci mapping and molecular breeding for developing stress resilient maize for sub-Saharan Africa. Crop Sci. 2015;55(4):1449-59.
71. Beyene Y, Semagn K, Mugo S, Tarekegne A, Babu R, Meisel B, et al. Genetic gains in grain yield through genomic selection in eight bi-parental maize populations under drought stress. Crop Sci. 2015;55(1):154-63.
72. Messina CD, Podlich D, Dong Z, Samples M, Cooper M. Yield-trait performance landscapes: from theory to application in breeding maize for drought tolerance. J Exp Bot. 2011;62(3):855-68.
73. World Health Organization. Global prevalence of vitamin A deficiency in populations at risk 1995–2005. WHO global database on vitamin A deficiency. Geneva (Switzerland): WHO; 2009. p. 55. Available from: https://apps.who.int/iris/bitstream/handle/10665/44110/9789241598019_eng.pdf. Accessed 2019 Aug 31.

74. Hirschberg JM, Cohen M, Harker T, Lotan VM, Pecker I. Molecular genetics of the carotenoid biosynthesis pathway in plants and algae. Pure Appl Chem. 1997;69(10):2151-8.
75. DellaPenna D, Pogson B. Vitamin synthesis in plants: tocopherols and carotenoids. Annu Rev Plant Biol. 2006;57:711-38.
76. Harjes C, Rocherford T, Bai L, Brutnell T, Bermudez-Kandiannis C, Sowinski S, et al. Natural genetic variation in lycopene epsilon cyclase tapped for maize biofortification. Science. 2008;319(5861):330-3.
77. Yan J, Bermudez-Kandianis CB, Harjes CE, Bai L, Kim E, Yang X, et al. Rare genetic variation at *Zea mays crtRB1* increases β-carotene in maize grain. Nat Genet. 2010;42:322-7.
78. Rocheford TR. (Agronomy Department, Purdue University, West Lafayette, Indiana, USA). Personal communication. 2019 Aug 28.
79. Palacios N. (Global Maize Program, CIMMYT, Texcoco, Mexico). Unpublished data. 2010.
80. Palacios N. (Global Maize Program, CIMMYT, Texcoco, Mexico). Personal communication. 2019 Jun 27.
81. Babu R, Palacios Rojas N, Gao S, Yan J, Pixley K. Validation of the effects of molecular marker polymorphisms in LcyE and CrtRB1 on provitamin A concentrations for 26 tropical maize populations. Theor Appl Genet. 2013;126(2):389-99.
82. Pixley K, Palacios Rojas N, Babu R, Mutale R, Surles R, Simpungwe E. Biofortification of maize with provitamin A carotenoids. In: Tanumihardjo SA, editor. Carotenoids in Human Health, Nutrition and Health. New York (US): Springer Science and Business Media; 2013. p. 271-92.
83. Suwarno WB, Hannok P, Palacios-Rojas N, Windham G, Crossa J, Pixley KV. Provitamin A carotenoids in grain reduce aflatoxin contamination of maize while combating vitamin A deficiency. Front Plant Sci. 2019;10:30.
84. Simpungwe E, Dhliwayo T, Palenberg M, Taleon V, Birol E, Oparinde A, et al. Orange maize in Zambia: Crop development and delivery experience. Afr J Food Agric Nutr Dev. 2017;17(2):11973-99.
85. Zunjare RU, Hossain F, Muthusamy V, Baveja A, Chauhan HS, Bhat JS, et al. Development of biofortified maize hybrids through marker- assisted stacking of β-carotene hydroxylase, lycopene-ε-cyclase and opaque2 genes. Front Plant Sci. 2018;9:178.
86. Davis C, Jing H, Howe JA, Rocheford T, Tanumihardjo SA. β-cryptoxanthin from supplements or carotenoid-enhanced maize maintains liver vitamin A in Mongolian gerbils (*Meriones unguiculatus*) better than or equal to β-carotene supplements. Br J Nutr. 2008;100(4):786-93.
87. Heying EK, Grahn M, Pixley KV, Rocheford T, Tanumihardjo SA. High-provitamin A carotenoid (orange) maize increases hepatic vitamin A reserves of offspring in a vitamin A-depleted sow-piglet model during lactation. J Nutr. 2013;143(7):1141-6.

88. Heying EK, Tanumihardjo JP, Vasic V, Cook M, Palacios-Rojas N, Tanumihardjo SA. Biofortified orange maize enhances β-cryptoxanthin concentrations in egg yolks of laying hens better than tangerine peel fortificant. J Agric Food Chem. 2014;62(49):11892-900.
89. Gannon B, Kaliwile C, Arscott SA, Schmaelzle S, Chileshe J, Kalungwana N, et al. Biofortified orange maize is as efficacious as a vitamin A supplement in Zambian children even in the presence of high liver reserves of vitamin A: a community-based, randomized placebo-controlled trial. Am J Clin Nutr. 2014;100(6):1541-50.
90. Listman GM, Guzman C, Palacios-Rojas N, Pfeiffer WH, SanVicente F, Govindan V. Improving nutrition through biofortification: preharvest and postharvest technologies. Cereal Foods World. 2019;64(3):1-7.
91. Kandianis CB, Stevens R, Liu W, Palacios N, Montgomery K, Pixley K, et al. Genetic architecture controlling variation in grain carotenoid composition and concentrations in two maize populations. Theor Appl Genet. 2013;126(11):2879-95.
92. Bailey-Serres J, Fukao T, Ronald P, Ismail A, Heuer S, Mackill D. Submergence Tolerant Rice: SUB1's Journey from Landrace to Modern Cultivar. Rice. 2010;3(2-3):138-47.
93. Khush GS. Terminology of rice growing environments. Manila (Philippines): International Rice Research Institute; 1984. p. 5-10.
94. Mackill DJ, Coffman WR, Garrity DP. Rainfed lowland rice improvement. Manila (Philippines): International Rice Research Institute; 1996. p. 242.
95. Mohanty HK, Khush GS. Diallel analysis of submergence tolerance in rice, *Oryza sativa* L. Theor Appl Genet. 1985;70(5):467-73.
96. Mishra SB, Senadhira D, Manigbas NL. Genetics of submergence tolerance in rice (*Oryza sativa* L.). Field Crops Res. 1996;46(1-3):177-81.
97. Siangliw M, Toojinda T, Tragoonrung S, Vanavichit A. Thai jasmine rice carrying QTLch9 (SubQTL) is submergence tolerant. Ann Bot. 2003;91(2): 255-61.
98. Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, et al. Sub1A is an ethylene responsive-factor-like gene that confers submergence tolerance to rice. Nature. 2006;442:705-8.
99. Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S, et al. Development of submergence tolerant rice cultivars: the Sub1 locus and beyond. Ann Bot. 2009;103(2):151-60.
100. MacKill DJ. Breeding for resistance to abiotic stresses in rice: the value of quantitative trait loci. In: Lamkey KR, Lee M, editors. Plant Breeding: The Arnel R Hallauer International Symposium. Ames (US): Blackwell Publishing; 2006. p. 201-12.
101. Potgieter AB, Lobell DB, Hammer GL, Jordan DR, Davis P, Brider J. Yield trends under varying environmental conditions for sorghum and wheat across Australia. Agric For Meteorol. 2016;228-9:276-85.
102. Jordan D. (Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, Warwick, Australia). Personal communication. 2019 Jul 8.

103. Borrell AK, Hammer GL, Douglas ACL. Does maintaining green leaf area in sorghum improve yield under drought? I. Leaf growth and senescence. Crop Sci. 2000;40(4):1026-37.
104. Borrell AK, Hammer GL, Henzell RG. Does maintaining green leaf area in sorghum improve yield under drought? II. Dry matter production and yield. Crop Sci. 2000;40(4):1037-48.
105. Vadez V, Deshpande SP, Kholova J, Hammer GL, Borrell AK, Talwar HS, et al. Stay-green quantitative trait loci's effects on water extraction, transpiration efficiency and seed yield depend on recipient parent background. Funct Plant Biol. 2011;38(7):553-66.
106. van Oosterom EJ, Borrell AK, Deifel KS, Hammer GL. Does Increased Leaf Appearance Rate Enhance Adaptation to Post-anthesis Drought Stress in Sorghum? Crop Sci. 2011;51(6):2728-40.
107. George-Jaeggli B, Mortlock MY, Borrell AK. Bigger is not always better: reducing leaf area helps stay-green sorghum use soil water more slowly. Environ Exp Bot. 2017;138:119-29.
108. Borrell AK, van Oosterom EJ, Mullet JE, George-Jaeggli B, Jordan DR, Klein PE, et al. Stay-green alleles individually enhance grain yield in sorghum under drought by modifying canopy development and water uptake patterns. New Phytol. 2014;203(3):817-30.
109. Borrell AK, Mullet JE, George-Jaeggli B, van Oosterom EJ, Hammer GL, Klein PE, et al. Drought adaptation of stay-green in sorghum associated with canopy development, leaf anatomy, root growth and water uptake. J Exp Bot. 2014;65(21):6251-63.
110. Tao YZ, Henzell RG, Jordan DR, Butler DG, Kelly AM, McIntyre CL. Identification of genomic regions associated with stay green in sorghum by testing RILs in multiple environments. Theor Appl Genet. 2000;100(8):1225-32.
111. Harris K, Subudhi PK, Borrell A, Jordan D, Rosenow D, Nguyen H, et al. Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. J Exp Bot. 2007;58(2):327-38.
112. Jordan DR, Hunt CH, Cruickshank AW, Borrell AK, Henzell RG. The relationship between the stay-green trait and grain yield in elite sorghum hybrids grown in a range of environments. Crop Sci. 2012;52(3):1153-61.
113. Mace ES, Singh V, Van Oosterom EJ, Hammer GL, Hunt CH, Jordan DR. QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. Theor Appl Genet. 2012;124(1):97-109.

How to cite this article:
Reynolds M, Borrell A, Braun H, Edmeades G, Flavell R, Gwyn J, et al. Translational Research for Climate Resilient, Higher Yielding Crops. Crop Breed Genet Genom. 2019;1:e190016. https://doi.org/10.20900/cbgg20190016