

In pursuit of a better world: crop improvement and the CGIAR

SUPPLEMENTARY MATERIAL to the manuscript

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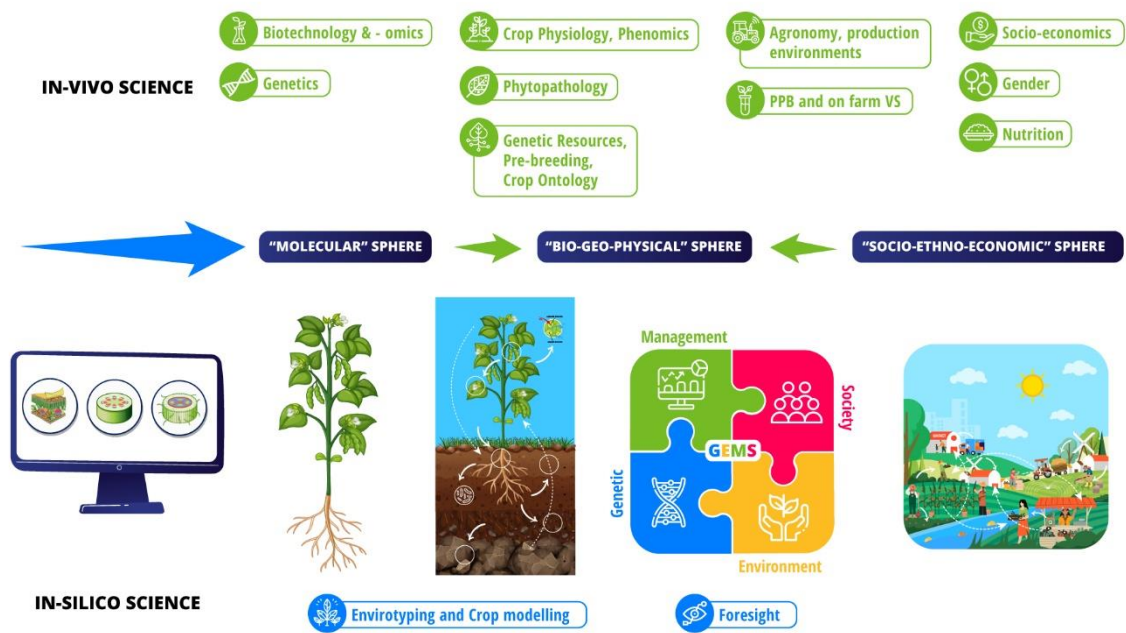
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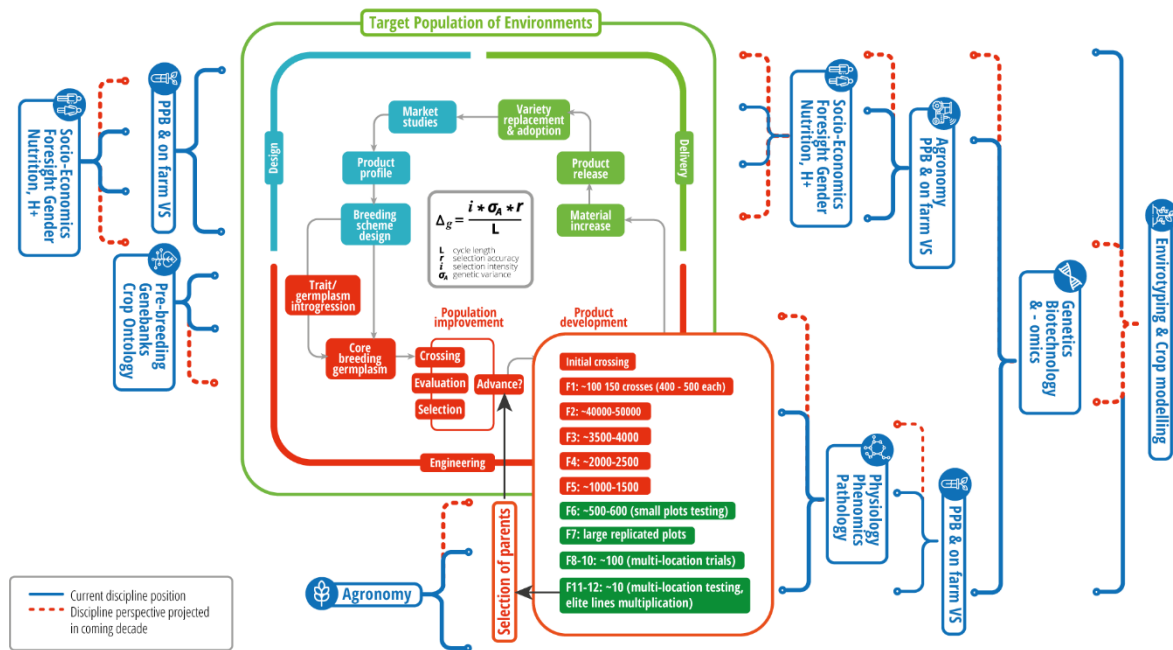
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Supplementary Figures:



Supplementary Fig. S1 The multi-disciplinary flow from molecules to socio-economic



Supplementary Fig. S2 Figure reflects the contributions of invited experts and summarizes the interdisciplinary eco-system surrounding the core crop-improvement processes. Each discipline name is labeled with the number of the respective paragraphs which contains full description of the disciplinary contribution. The span of disciplinary contribution is visualized in the current situation (span of the blue bracket) and as projected in the upcoming decade (red extended parts of the blue brackets)

Supplementary Mat. 1 Global food & nutrition security – the never-ending struggle to achieve sufficient, high quality, and sustainable agricultural production.

James Cock

JC I Choice of crops for improvement.

As the CGIAR developed and sustainable food production, nutritional level and economic well-being came on the agenda, the situation became more complicated. The expanded agenda of the CGIAR coincided with a large increase in the number of Centers and the crops they worked on. Added to the three major cereal grains of rice, wheat, and maize were more cereal grains, root and tuber crops, and grain legumes. In addition, two livestock centers were established. The livestock program of one of the centers (CIAT) morphed into a tropical pastures program. Several of the second generation of centers focused on specific ecologies rather than individual crops. The centers with an ecological focus did not initially choose specific crops for varietal improvement, but rather concentrated on specific production systems which addressed the sustainability issues within their ecologies. We use one of the “ecological centers”, ICRISAT, to show how these centers focused on crop improvement and chose their crops. The original

goal of ICRISAT was to use broad sense crop improvement research as the basis to improve food availability in drought-prone areas of the tropics. Rapidly, several “mandate crops” were chosen for genetic improvement. These crops were all staple food crops adapted to the drier areas of the tropics and were all either cereal grains or grain legumes.

The pathway to improved nutritional level across all the centers was clearly through increased production and hence availability of a wider range of foods including more nutritious grain legumes and animal proteins. Implicit, in the increased availability of nutritious food was the idea that low priced nutritious food would be available to all. For increased livestock production the role of those involved in crop improvement was largely improved pastures to feed ruminants, principally cattle. The production of ingredients for animal feed concentrates was barely mentioned with the CIAT cassava program being the exception. Soybeans, which have revolutionized the animal feed industry were briefly part of the CGIAR in INTSOY with the goal of INTSOY to foster the production of soybeans in tropical and subtropical environments of the LDCs, with particular attention to their use as a highly nutritious food crop by the urban and rural poor.

The World Vegetable Center recognizes the role that high value crops can play in the statement of its purpose: *“The World Vegetable Center conducts research, builds networks, and carries out training and promotion activities to raise awareness of the role of vegetables for improved health and global poverty alleviation”*.

What do we mean by a high value crop? High value crops return higher gross margins per hectare and per unit labor input than traditional commodities. Normally price premiums are due to either specific product differentiating characteristics, or the inherent skills or conditions needed to produce and market them, or to high barriers to entry into their production. These specific characteristics provide opportunities for producers to obtain a high value for their products and offer an alternative to traditional commodity markets for both food and non-food crops (Cock et al., 2005). The high gross margin per ha is attractive for the smallholder who has limited land, whilst the high gross margin per unit labor opens the way to more rewarding employment opportunities for those who do not possess land. Additionally, high value crops frequently offer not only more rural employment opportunities in the primary production but all along the supply chain than the staple foods.

In Colombia, for example, there was no such support for farmers when the new rice varieties arrived and consumers captured most of the benefits, with negative benefits to farmers, especially the smaller upland rice producers. This led to the conclusion that, in countries with a large semi-subsistence rural population, technology should be designed specifically for the smallholder (Scobie and Posada, 1978).

JCII Crop Improvement of high value crops.

A major difficulty of working with high value crops is related to the fact that they are high value. As we have noted they are either high value because they are difficult to produce or even though the basic product may be relatively easy to produce differentiation of the product adds

value. Product differentiation occurs when an offered product is perceived by the consumer to differ from its competition. Differentiation can be a broad classification of intrinsic physical characteristics and perceived attributes is useful for the purposes of managing the supply chain. This differentiation may be obtained by production in a specific niche or by management of the primary production and the post-harvest processing. The differentiation can be based both on perceptual differences and from actual product differences based on inherent product characteristics (Niederhauser, 2008). Credence attributes or process attributes to the process by which the products are produced such as bird friendly, but which are not reflected directly in the product characteristics.

If a widely available technology that can be extensively used becomes available, then it is difficult to differentiate the product which tends to become a commodity. Hence, the traditional CGIAR approach to crop improvement of technology that is applicable in large broadly defined recommendation domains or agroecological zones is not suitable for high value differentiated products. Nevertheless, in a pre-proposal to the CGIAR in 2007 for a challenge program on high value crops, the approach for cultivar development was to be through “traditional plant breeding and selection methods” (AVDRC, 2007). If the breeding were to be carried out within the CGIAR centers, specific crops would have to be selected. This presents major problems, first how would priorities be set, and second success would likely lead to commoditization of the selected crops which would cease to be high value crops! When I was attempting to set up the Tropical Fruits Program in CIAT the first question I was always asked was “Which fruits we were going to choose?”. The approach we adopted was not to choose any specific fruit. We reasoned that the choice of the high value crop was for our partners in national or local agencies: the role of an international center was to support them in their efforts (Cock and Voss, 2004). We suggest that, *while development of individual crops requires very crop-specific research, there are several overriding problems that are being addressed more generically. The activities of broad-based support given by CIAT are directed to three principal areas: Generic research to open new opportunities in a number of crops; defining what crops can be grown where; and establishment of rural agro-enterprises.* This generic research would cover a wide range of expertise and that the CGIAR should provide a platform which researchers and R&D personnel from both the public and private sector could develop high value crops.

JC III The conundrum of addressing rural poverty while providing the urban population with low cost food.

Bàge (2003) indicated that several important investors in agricultural research wished to ascertain how agricultural research has responded to the needs of the rural poor in developing countries. Lipton (2003) clearly identified the difficulty of developing a coherent strategy when he asked the question; “*How can the direct poverty impact of agricultural research (on-farm employment and real wages) be pro-poor as well as the indirect, food- buying impact (on food prices)?*” He then went on to suggest that, assuming a land constraint, there are two “tightrope conditions” that must be met to have a favorable impact on both farmers and the rural population and food prices. First labor productivity must increase, but land productivity must increase faster. Second, as new production technology is adopted and food prices fall, this price

fall must be slower than the rise in total factor productivity in food farming if both food sellers and food buyers are to gain. Lipton (2003) then goes on to say that we were lucky that these two tightropes were walked in the green revolution. As mentioned above, it was more than luck with policies to maintain prices and subsidized inputs the tight ropes were walked in Asia. However, in Colombia without the policies implemented in Asia, rice farmers lost their balance and fell off the tightrope whilst the main benefits went to the urban consumers (Scobie and Posado, 1978). I suggest that it is not healthy for the CGIAR to depend on a strategy that depends on either luck or major policy decisions to ensure the improved wellbeing of the rural population while at the same time guaranteeing a well fed population at large.

JC IV Higher farm incomes as an objective.

An early recognition of specific strategies to increase incomes of the rural poor was adopted by cassava researchers at CIAT and IITA in a program supported by the IDRC of Canada. *The[se] research programs are oriented not just to producing new germ plasm per se but to producing germ plasm which can be utilized to produce higher farm incomes through the sale of a readily marketable commodity* (Nestel and Cock, 1976). This was probably the first program in the CGIAR system that was explicitly directed towards improved well-being of the farmers, which was to be achieved through a value chain approach which identified potential new markets for cassava products and how farmers could profitably enter into them (Lynam and Byerlee, 2017).

Later in the early 1990s, Edward Schuh, the Head of Agriculture and World Development at the World Bank, argued that the scope of the CGIAR System could productively be expanded noting that cash crops could generate income and employment for the rapidly growing agricultural labor force around the world which would directly impact on rural poverty (Kramer 2016). At the start of the new millenium, Thomas Lumpkin, then Director General of the World Vegetable Centre (AVDRC) made a concerted effort to get higher value horticultural crops more prominently represented in the CGIAR centers. He presented a report to the CGIAR directed at priorities for the poor titled: *“Increasing income through fruit and vegetable production opportunities and challenges”* (Lumpkin et al., 2005). At about the same time, CIAT established a tropical fruits program as *“Tropical fruits offer a magnificent opportunity to increase incomes of the rural poor with the added benefit of providing a healthy, productive and pleasant living environment.”* (Cock and Voss, 2005). Furthermore, AVDRC in 2007 presented, on behalf of itself and various partners both from within and outside the CGIAR, a pre-proposal on High Value Crops to be considered as a challenge program by the CGIAR. The purpose of this challenge program was specifically to address opportunities to increase incomes and improve livelihoods of the poor through diversification into a range of high value agricultural crops and products (copy available from the authors). This proposal apparently did not prosper, and the CIAT tropical fruit program was closed a few years later and the World Vegetable Centre continued to receive little attention from the CGIAR. Over the years Bioversity International had promoted research on NUS (neglected and underutilized species), which are frequently also high value crops, stressing their potential role in increasing farm incomes and providing more nutritious foods and suggesting that more research should be

devoted to them. Despite these cogent petitions for work on high value crops that are not traditional staples to increase rural incomes, and also to provide more nutritious food, they have not been put on the CGIAR agenda.

JC V Is the CGIAR seriously concerned about rural happiness?

The document celebrating the 40 years of the CGIAR mentions happiness only in the introductory statements with reference to the mandate of achieving the goals “*children for happiness*” and “*food for all and forever.*” Similarly, in this same document whilst wellbeing is mentioned several times in the objectives of the CGIAR, the only other mention refers to “*the well-being of staff and their families*” with staff being those of one of the centers (CGIAR 2012). The publication attractively titled “*Efforts that Brought Happiness*” produced by ICRISAT, apparently to demonstrate how it has contributed to happiness, fails to mention happiness in the rest of the document (Khanwalkar and Wani, 2013)!

Crop improvement efforts in the CGIAR are largely directed towards adapting specific crops to the likely new climate they will face if they are still grown in the same place. However, it is becoming clear that it may neither be possible nor desirable to adapt many crops to the new circumstances. Cropping patterns may change entirely with new crops more suitable for the novel conditions entering some areas to displace others. How can the CGIAR breeders manage this situation? First, they must recognize the reality that farmers are likely to change crops as climate change takes hold. An interesting observation from Indonesia is farmers' reaction to a delay in the onset of the rains in parts of Java. Farmers know that a late start to the rainy season is normally associated with the ENSO phenomenon and rains will not only start later but they will also be less intense. Consequently, many farmers switch from rice to maize when the rains are delayed (Naylor et al., 2007): this clearly indicates that faced with major changes in weather patterns, farmers will indeed change crops. This adaptation to changing climate, rather than weather, is already happening in the Andean zone with organizations developing potatoes for the higher altitude paramos of the Andes (Palacios Nuñez, 2014).

JC VI Giving farmers what they need.

Much of the CGIAR effort is directed to reducing yield gaps and increasing potential yields, with often little attention to farmers preferences. In much Colombia and Ecuador the Andean Blackberry (*Rubus glaucus*) is extremely popular and is greatly appreciated for making fruit juices. Traditionally, harvesting the blackberries was not popular as the plants are thorny. However, a thornless mutation was discovered and even though it yields no more than the thorny varieties it is now widely adopted because it makes growers lives easier and more pleasant. Several years ago, in Colombia, a high total sugar production with remarkably high sucrose sugarcane clone was developed. Although it was pushed by researchers from the local sugarcane research center, where one of us worked at the time, it was never widely grown because it was difficult to manage and the price premium paid to farmers for the high sucrose content was unattractive.

In the race to increase productivity per unit land area breeders select cultivars that respond to high levels of fertilizer application. However, when farmers have limited resources, spending money on fertilizer and foregoing weed control is not a sensible strategy. Fertilizer applications with poor weed control likely leads to a great crop of weeds! Hence, strategies to improve crop yields in a stepwise fashion normally emphasize weed control in the early steps followed by fertilizer at a later stage (see for example Fremont et al., 2009). Crop improvement programs should recognize that farmers may adopt technology in a stepwise fashion according to their resource availability. Thus, for example it could well be more important to incorporate herbicide resistance in fertilizer responsive varieties to facilitate weed control and liberate resources for the purchase of fertilizers. The NERICA rice varieties for West Africa have been specifically developed for weed competitiveness (Wopereis et al., 2008) and have been widely adopted.

These examples suggest to us that more attention should be paid in crop improvement to producing cultivars which farmers prefer. Furthermore, farmers are probably more interested in increasing their labor productivity than land productivity. If technology improves both that is fine, but if land productivity is increased with no commensurate increase in labor productivity farmers are unlikely to find it attractive: simply put this means more work for nothing in return. Hence, the current excessive emphasis on increasing yield at whatever cost may not be a recipe for successful adoption of genetically improved materials and increased overall production of food products. We feel that breeders should work more closely with both agronomists and social scientists to ensure that they produce varieties that farmers appreciate rather than those that the breeders themselves believe growers will accept.

JC VII Additional information on high value crops.

There appear to be two major types of high value crops. Firstly, there are those like Brazil nuts (*Bertholletia excelsa*), which are, for some reason or other, difficult to produce. The product *per se* has a high value and the skilled producer who can overcome the difficulties of producing the crop can obtain large profits without having to differentiate the product in terms of quality. Secondly there are those crops where the high value is obtained by differentiating the quality of the final product, as for example in gourmet coffees. Of these two types of high value crops the supply chains of the former function similarly to those of traditional commodities, with smaller volumes, whilst the latter tend to be characterized by higher degrees of two-way information coordination between producers and consumers.

When high value crops are mentioned for the developed countries, they are frequently associated with export crops. The expansion of markets and the liberalization of trade policies are providing new opportunities for rural people to escape poverty through production and exchange of non-staple crops (Lumpkin, 2005). However, we should consider the wisdom of C. K. Prahalad, "*If we stop thinking of the poor as victims or as a burden and think of them as resilient and creative entrepreneurs and value-conscious consumers, a whole new world of opportunity will open up.*" Rambutan (*Nephelium lappaceum*) in Honduras shows that this is a reality. The Fundación Hondureña de Investigación Agrícola began promoting rambutan for export to the United States of America around the turn of the last century. Initially demand

locally, first in Honduras and later in the neighboring countries was so great that it was only in 2018 that the first major exports were made to the USA (AHPERAMBUTAN, 2006; Procomer, 2018). Hence, crop improvement of high value crops can be aimed at both local and export markets.

JC VIII The importance of labor productivity. Note: This section is largely taken from Labour Productivity: The forgotten yield gap. Cock J.H. & S.Prager. In preparation.

Although poverty manifests itself in many ways, surely one of the surest ways out of poverty is well rewarded employment, whether self-employed or working for someone else. However, moving out of poverty is more than just having a job. As Ulysses J. (Jerry) Grant the director general of CIAT noted in a conference in 1972 when challenged that mechanization would reduce employment: “*Is it not true that development is related to the type of work people do?*” and then went on to question whether we should expect people to do certain types of manual labor (Lynam and Byerlee, 2107). Additionally, agricultural labor productivity is currently alarmingly low in most of the developing world, particularly on the smallest farms where many of the options to increase labor productivity are not easily applied. As farmers can only profitably offer jobs if the marginal rate of return is greater than the marginal cost of employment, an essential ingredient of any serious program aimed at rural poverty is increased labor productivity. An ancillary benefit of increased labor productivity is that it is normally associated with less drudgery and more pleasant working conditions. Additionally, increased labor productivity frequently increases local, rural off farm employment opportunities. The question then becomes as to how can labor productivity be increased? Simplistically there are two options: to produce physically more with less work or to produce higher value products. As discussed in the main document and in supplementary information JC IV, the former option should be taken care of if serious attention is paid to high value crops. For the staple crops the CGIAR system has consistently concentrated on simply producing more per unit land area and has largely ignored increasing labor productivity. Some have assumed that labor productivity increases in step with increased yield, but there is little evidence to support this intuitive claim (Craig and Pardey, 1997). I remember a hive of activity in the early days of IRRI in the large workshops in Los Baños with the development of labor-saving machinery and later on a smaller scale at CIAT and IITA developing and testing cassava harvesters and processing equipment and mechanized rice puddling. However, development of labor-saving technology has largely fallen off the CGIAR agenda. Thus, in spite of the well-known high cost of manual weed control and massive uptake of specific herbicide resistant cultivars in many crops, they have not been a feature of the CGIAR’s crop improvement agenda even though their potential to increase labor productivity is immense (Pachico et al., 2002). Cassava was genetically transformed to be herbicide resistant in the mid 1990s but resistant cultivars have not been produced (Chavarriaga et al., 2016).

JC IX An example of how selecting for a trait may not lead to the hoped-for result.

Recently in cassava much effort has been placed on increasing the inherent rate of photosynthesis (see for example De Souza et al., 2017). Sonnewald et al. 2020 aim to increase

the source of carbohydrates for starch through modification of the metabolic pathways of photosynthesis, sucrose synthesis and phloem loading using molecular tools. However, it is well known that cassava photosynthesis is normally limited by stomatal conductance mediated by leaf to air vapor pressure deficit rather than the inherent rate of photosynthesis (see for example El Sharkawy and Cock). Thus, Vongcharoen et al., concluded that " ... *the main determinant of net photosynthesis in the rainy and cool seasons was photosynthetically active radiation, whereas in the hot season vapour pressure deficit was the major factor*". The question then becomes as to whether research on the basic metabolism of photosynthesis will pay off more than looking at stomatal control by VPD. It has been suggested that for those conditions where drought is not a problem yields of cassava could be increased more simply by breeding for less sensitive stomata than through fancy metabolic changes to photosynthesis (Cock and Connor, 2021 in press).

JC X. Crop monitoring for selection and release.

A novel approach which is gaining momentum is to move away from identification of representative sites and scaling out from them towards use of the principles of precision agriculture. Precision agriculture is based on the principles of: (a) capture of data at an appropriate scale and frequency (b) analysis and interpretation of that information; and (c) implementation of a management response based on the analysis (National Research Council, 1997). These same principles have been used to determine which cultivars of sugarcane are well adapted to particular environmental conditions and how they respond to management. The system monitors weather, soil type, cultivars grown, cane yield and quality and several of the major management practices such as data of planting and harvest and use of ripeners of every sugarcane field in the major growing areas of Colombia. The data is then analysed and used by growers to determine, inter alia, which is the most suitable variety for their fields (Cock et al. 2011). As new varieties come available some early adopters try them and share their information so that other farmers can gain from their experience. Effectively every cane field becomes an experiment providing information on varietal performance under a range of management and environmental conditions. In Australia a similar scheme was set up for rice (Lacy 2011). More recently within the CGIAR system the same approach has been used with small farmers to draw insights in the whole G X E X M continuum (Jimenez et al., 2016; Jimenez et al., 2019). In oil palm similar methodology based on commercial field data has been used to determine nutrient response under varying weather conditions (Cock et al., 2016) and could be This approach may be the epitome of on farm research. This approach jointly should be jointly targeting, and thus move away from the idea of context (field) specific solutions.

Supplementary Mat. 2 Biotechnology & -omics

Noel Thomas Ellis, Julie Hofer, Paul Chavarriaga, Sandra Valdes

Future approaches to obtaining useful genetic variation in CI programs include generating it *de novo* by mutagenesis or transgenesis. Mutant populations have the great advantage that the

variation can be organized into an accessible array of stocks as typified by (but not restricted to) TiLLING populations (Colbert et al., 2001) and related methods. Transgenesis is currently more popular than mutagenesis, but has the disadvantage that you need to know from the outset which genes to work with and their mechanism of action in relation to the trait of interest. This is a very focused and restrictive approach in marked contrast to open and genome-wide mutagenesis. Furthermore, we still have the regulatory framework, which makes transgenesis an expensive option. Huge numbers of crop plant individuals exist at a given time. For rice, with current global production of about 500 Mt and a thousand seed weight of 30g, this means about 10^{16} seeds exist per year. For lentil, with a global production of 6 Mt and thousand seed weight around 50g, two orders of magnitude fewer seeds exist per year. We know that the spontaneous mutation rate of DNA is ca. 10^{-9} per base pair per year, so for either of these crops, in any year we can expect that there exist many independent individuals that carry a single base change at any given nucleotide in the genome. Chemical or physical mutagenesis simply increases the frequency of these events so that mutations can be found in a manageable number of plants. For this reason, it is clear why mutagenesis is not subject to the same type of regulation as transgenesis. Mutagenesis can, in principle, provide any single base mutation in any crop, which can then be deployed in a variety. Such activities may become a future component of CI programmes.

While mutagenesis is a very powerful approach, it is limited to finding variation in genes already in existence in a given species. If, for example, we want to produce human vaccines in plants, then mutagenesis is not a viable approach, but this can be achieved by transgenesis. Likewise for insect toxins and herbicide resistances. Such variants have been useful in agriculture and should not be ignored, but they are specifically tailored and should not be seen as a substitute for the random variation, which may be accessed in natural populations, or by mutagenesis.

Today the importance of genome editing for the advancement of world agriculture is undeniable, not only because the technology won the Nobel Prize/2020 (Jennifer Doudna and Emmanuelle Charpentier), but also because it allows recreating traits in varieties of high consumption for human and animals, or even for industrial uses. In some cases, breeders would not even have considered introducing these traits into their programs due to the difficulty of introgression into elite varieties. For example, knockout mutations useful for evolution and adaptation of crops to the environment are abundant (Grey et al., 2020), although, for some, the ease of their introduction into elite varieties by conventional breeding may be an obstacle. This paradigm is changing with the use of gene editing and rice is a good example: it was recently demonstrated that the use of CRISPR-Cas9 to mutate specific regions of rice genes produced mega-varieties resistant to multiple strains of *Xanthomonas oryzae* pv. *oryzae* (Xoo), the causal agent of bacterial blight (Oliva et al., 2019). Resistance was incorporated for up to five strains of Xoo in indica and japonica mega cultivars. Such an achievement has been possible only through gene editing.

However, rice may be considered today a "model plant" for gene editing, research on more complex crops such as maize, cassava, beans and cocoa and others, is focused to modify complex agronomic traits such i.e. starch quality in cassava or grain number in rice. The

nutritional quality of crops for human consumption is another trait subject of improvement by gene editing. Thus, avoiding the absorption and/or accumulation of heavy metals such as cadmium (Cd) and arsenic is being researched in cocoa and rice. The genes involved are unique and are identified in both crops. Proofs of concept in rice did shown that knocking them out prevents the absorption of Cd by the root and therefore its accumulation in the grain (Tang et al., 2017), without affecting yield.

Several CGIAR Centers have genetically edited crops (GEds) as tools for breeding, i.e., CIMMYT, IRRI, IITA & CIAT, indicating that conventional and molecular breeders are clear about the power of gene editing to modify characteristics in their crops. Therefore, there should not be barriers for using the technology in breeding. However, the barrier might be the consumer itself, but also breeders and decision makers. Consumers still do not yet perceive the benefits of GEds, with exceptions such as Calyno™ soybean oil, high in oleic acid, already grown in the USA. Opponents of GEds' want to classify them as GMOs or transgenic, which would make them unattainable for improvement within the CGIAR due to excessive regulation and cost implied in their release. Fortunately, regulators in several countries understood that the GEd technology must be more democratic, and be available to countries for their own developments, not only to serve the interests of the mega-seed industry. Scientists who use genome editing for CI helped achieve this milestone thanks to a more effective and assertive communication with consumers and regulators.

The regulation in ten American countries, plus Australia, Japan, Israel and Russia, allows the cultivation of genetically edited varieties that do not contain transgenes, considering them as conventional varieties. Colombia's agricultural authorities have declared two gene-edited crops as conventional cultivars: Waxy corn, not yet planted in the country, and the Xoo-resistant rice mentioned above. The latter was the product of a collaborative effort of seven institutions (Oliva et al., 2019). Two of them are International Centers, IRRI and CIAT, thus demonstrating that the technology is available to the Centers. Of course, for its commercialization, agreements must be signed with the owners of the technology, as CIMMYT has already done and CIAT will soon do so.

Supplementary Mat. 3 The Essential and Enduring Role of Genetics in Crop Improvement

Noel Ellis, Julie Hoffer, Enghwa Ng

Genetics and the Breeders' Equation

Genetics is often misconstrued either as breeding or genomics. It is neither, but it is an important analytical tool necessary for the core function of a crop improvement (CI) programme to perform its core functions, breeding per se together with the conservation and use of germplasm resources (see above and below).

Past and current status

The CI projects have to effectively iterate between a limited time and space resources to optimize the overall breeding strategy efficiently. In this process, an effective surrogate for a target trait can be very helpful and that is where the role of genetics in CI process is indispensable. If prior genetic analysis can define allelic variation that determines a desirable trait, then that can be used instead of some potentially destructive and lengthy alternative test (for example the genetic determinants of disease resistance). The use of genetic markers for traits can save the expenses and efforts linked to large phenotyping trials. Indeed, selection can also be accelerated by markers permitting the identification of heterozygotes. This allows the breeder to skip a generation in a breeding programme because there is no need to wait to manipulate recessive alleles. Still, many of the molecular markers published to date are not suitable for use in breeding programs. In order to effectively deploy markers for improved selection intensity and accuracy, markers need to pass through robust production validation (common in private sector programs), a step which is often non-existent in most public breeding programs.

Identifying useful variation in germplasm collections has been a mainstay of activity in the CGIAR. This variation has a number of great advantages. First, it is accessible: it actually exists. Secondly, this variation has survived in real plants, therefore it is robust as these variants have survived in the face of natural selection (vonWettberg et al., 2018). Currently there are some challenges: first, the availability of germplasm for breeding is not as straightforward as once it was. The International Treaty on Plant Genetic Resources intended to make sure that the benefits of natural variation were equitably shared, but in practice many countries have put up barriers to the free movement of this material. Secondly, the useful variation is buried in many diverse genetic backgrounds under the cover of genetic linkages, poly-genic interactions or interactions with environment, where it is not necessarily obvious or accessible. When discovered, it requires elaborate action, using knowledge of genetics, crossing, or genome manipulations to transfer it into genotypes which can be exploited efficiently in breeding for particular context. These diverse backgrounds; i.e. not only alleles but also allelic combinations, all need to be maintained, which is a larger and more complex task than maintaining allelic variation, because a huge number of accessions represent combinations of variants (useful and otherwise).

Variability is of little interest for CI programmes if it is not heritable. We need to realise that genetic variation can be heritable but unseen. The classic example was the cross between two white-flowered sweet pea lines which generated a purple-flowered F1 and many different flower colours in the F2. (Bateson, Saunders and Punnet, 1905, Edwards 2012). This can be ascribed to genetic heterogeneity, whereby alleles at different loci confer a particular phenotype (in this case the white-flowered phenotype). The appearance of colour in the progeny plants is due to recessive inheritance of white alleles. In this case *ccRR* is white-flowered, *CCrr* is also white-flowered, but their F1 progeny (*CcRr*) has a dominant allele for each and has coloured flowers. The important point is that there is no phenotypic difference between the two white-flowered types, but there is a genetic difference (think what that means for σ_g/σ_p !). In addition,

combining these genetic differences releases hitherto hidden genetic variation in the F1 and subsequent generations.

A problem with quantitative genetics approaches is that they would not distinguish between the two white-flowered types because there is no phenotypic difference. Genetic heterogeneity is not restricted to flower colour, it can apply to all kinds of recessive alleles. Essentially this is why Hartl (1997) pointed out that quantitative variation can be derived from Mendelian genetics but not vice versa ‘The point the reader needs to drive home is that, whereas continuous variation can be inferred from Mendelian heredity, Mendelian heredity cannot be inferred from continuous variation.’ Looking at the breeders’ equation from a quantitative viewpoint thus misses an important contribution to available genetic variation.

Currently, genome-wide marker-traits association studies (GWAS) are popular uses of efficient sequencing methods and diverse germplasm. When this is coupled to replicated trials of diverse inbred lines, the power for correlating genetic and phenotypic variation is high, essentially because alleles in the sampled population behave independently. Two problems exist; one is due to genetic heterogeneity, as discussed above. This leads to conflicting associations between genotype and phenotype, for the excellent reason that there is indeed such a conflict. What was considered a single phenotype is in fact conditioned by different genes. The second is that population structure may lead to particular alleles being restricted to genetically distinct subgroups, thus creating associations due to population history rather than due to a causal relationship between phenotype and genotype. These problems are well known and are easily overcome because the predictions of GWAS are testable in many different types of genetic analysis, such as mutagenesis or linkage mapping.

Once the markers associated with target traits are identified (e.g. by GWAS) and rigorously validated, the desired variation can be used for improvement of elite germplasm. In this regard, marker assisted back-crossing (MABC) has been extensively used by many public programs in the frequently-called “molecular breeding pipeline”. MABC is a breeding tool which might bring in the key traits if used carefully but this method should not be considered in a mainstream breeding pipeline. Unless the donor parents in MABC are not derived from an elite background, this method can even create unintended consequences. It is important to note that MABC does not drive the long term genetic gain in breeding programs unless in light of modern breeding strategy which focuses on continuous elite population improvement, rapid recycling of elite materials and systematic extraction of high performing progenies.

Perspectives

Current and future breeding in CI programmes include genomic-led approaches such as Genomic Selection (GS). GS is essentially serial correlation analyses whereby scores for a given trait are assigned to genotypes in a small experiment, but at a large scale genotyping is used as the basis of selection, the success of which is in turn assessed in a new cycle of small scale experimentation. This has huge logistical benefits, but suffers from the problem of genetic heterogeneity as discussed in above and of course relies on the assumption that all the

interesting variation is phenotypically displayed and traits phenotyped in a representative, homogeneous environments and that different traits do not give incompatible estimates of 'breeding value'. It is perhaps not surprising that this approach was first realized in animal breeding where the individuals are highly valued and breeds have a constrained range of genetic variation with minimum environmental influence, in marked contrast with many crop species.

GS is a fashionable approach of interest for many public breeding programs but its utility and effectiveness has largely remained in the proof of concept stage. Upto certain extent, this can be considered a bandwagon which can literally ruin small breeding programs in an attempt to replicate the successful private sector initiatives (e.g. Technow et al., 2015, Millet et al., 2018, Bernardo et al., 2016). Effective GS strategy draws on well-integrated cross functional teams to be able to deliver breeding outputs in the most cost-effective manner. Well designed GS pipelines also rely heavily on a robust breeding database to support timely decision making, ideally, such a system should be automated and operating at a large enough scale to defray the sunk cost. This is in addition to the well curated historic data to build appropriate models to accurately predict future performance. At the current stage of GS implementation in most public programs, it is wise to consider using GS methods to enrich the elite breeding pool rather than using GS as a selection tool to advance and release progeny as the genotyping and bioinformatic costs will far exceed the potential gain and selection accuracy.

Practical support the CI teams

There are many genetics tools available and these can considerably contribute to the effectiveness of the CI program. The cost of genotyping decreased exponentially in the last decade and the turnover for genotyping services can be as low as 0.1 USD/marker/line with throughput of 1000s lines evaluated per day. Still, many smaller programs keep struggling with the low return on investment while trying to set up in-house molecular facilities. Efficient use of molecular tools, i.e. production genotyping is usually best outsourced to service vendors as it would minimize sunk costs in setting up in house facilities. Also, given the usual project funding modality, it can be challenging for many smaller programs to have sustainable resources to maintain and keep up the facilities updated with the latest tools and technologies.

The increased accessibility of molecular tools opens CI-teams more rapid dissection of the relationship between phenotype and genotype. Understanding this relationship is crucial because genotype is what is manipulated in breeding and the genotype is distributed as crop varieties with predicted properties for the farmer, yet is the phenotype (yield, quality) that is of economic importance. The phenotypic expression of the released variety (breeding output) is the consequence of interactions between the genetic information in a given environment and therefore points out to the limitations of pure genomic approaches to accelerate selections of genotypes suited to particular environmental context (especially the complex ones). To address this particular constraint, the single most important tool is to incorporate diverse disciplines and collaboration.

Formula 1. Breeders' Equation(s)

$$\text{Eq.1: } R = h^2 S = i h^2 \sigma_p; (h = \sigma_g / \sigma_p)$$

$$\text{Eq.2: } \Delta G = (\sigma_g i r) / L$$

Equation 1 presents the breeders' equation from the point of view of the gain in the trait of interest (Heywood 2005), while equation 2 presents this in terms of genetic rather than phenotypic improvement (Cobb et al., 2019). R is the magnitude of improvement, h^2 is the additive genetic variance divided by the phenotypic variance, σ_g is the standard deviation of the genetic component of the variation, σ_p is the standard deviation of the phenotypic variation, S is the selection differential (or the difference between the trait value among the selected individuals and that of the population as a whole), i is the selection intensity. ΔG is the genetic gain, r is the selection accuracy and L is the number of generations.

Breeding is about heritable phenotypic improvement, so either way, these equations simply state that improvement from breeding depends on three things. The first is that there must be some variation in the characteristic of interest (σ_p); the more variation that is available, the more progress can be made. The second is basically how hard you work: how strict (or intense: i) is the selection the breeder makes (this can include how many cycles of breeding are involved (L is the number of years per cycle)). The third is that this variation has to be heritable (h) - if it isn't then the breeder will get nowhere. Thus the "breeders' equation" quantifies, directly or indirectly, the progress which can be made as a function of phenotypic variability, heritability of that variation and the intensity and duration of the selection process. The second form of equation 1 nicely separates two factors over which the breeder has some control - the selection intensity and the range of variation within the breeder's lines - from the one factor outside the breeder's control: the heritability of the trait. Note that the heritability is squared, which means that it is the factor to which R is most sensitive. This alone should emphasise the importance of genetics, but as we will see, genetics also impacts on the other two factors.

Background

In essence the breeders' equation goes back to Galton's observations on the regression of quantitative variation among offspring to that of their parents and to Fisher's analysis of variance. In this sense the breeders' equation can be viewed as a fundamentally pre-Mendelian approach. It is all about correlations: correlation between the phenotypic values of the parents and the variation among selected individuals. For nearly a century, heritability has been estimated in replicated breeding trials where the data is subjected to an analysis of variance. In this analysis, the variation that is between the replications is taken to represent the genotypic component of the variance. This is a useful simplification, but it is a simplification; factors other than genotype may determine the replicated differences between varieties, genotypes or accessions. These include, for example, the age and provenance of the seed. This approach is

purely selection and describes how to manage selection for a single trait, but it misses some very important issues.

Using as an example the genes underlying beak shape variation in Darwin's finches - perhaps the most famous example of adaptive phenotypic variation - several genes are known to be associated with this variation (Palmer and Kronforst, 2015). Blunt vs pointed beak shape is controlled by *ALX1*, a gene involved in aspects of face development throughout the vertebrates, and allelic variation in this gene is responsible for beak shape variation within at least one species of Darwin's finches. This shows two things; one is that allelic variation in genes where mutations have major effects can be responsible for subtle or useful variation and this gene may be known from a wide range of species. The second is that allelic variation at a single locus can be responsible for quantitative phenotypic variation. Note that if allelic variation at a single locus is responsible for phenotypic variation, then no matter how heritable or variable the trait, or how intense the selection, we are stuck with the existing alleles and the variation they confer. Genetic analysis can therefore tell us which genes are important and also whether the way a trait is controlled in a given species is amenable to genetic improvement.

We should also consider linkage (meaning that allelic forms of two genes remain associated with each other because they are close together on a chromosome), which is quite common, especially when multiple loci (and /or traits) are involved. In the case where we are interested in two (or more) different traits and the beneficial alleles are linked in repulsion, this means that the beneficial characteristic of one trait in either parent is difficult to disentangle from the detrimental character of the other trait. Crosses are usually performed to combine beneficial alleles from different sources, but because of linkage in repulsion, combining beneficial alleles can prove difficult.

Box 1 On the frequency of linked loci.

This is analogous to the chance that among a group of people any two share a particular birthday https://en.wikipedia.org/wiki/Birthday_problem

If we are interested in G genetic loci, then there are

$G(G-1)/2 = P$ possible pairs to consider.

In a genome of 1000 cM we can say that there are 100 non-overlapping 10 cM blocks.

The chance that any two genes are in the same block is $1/100$.

The chance that two genes are not in the same block 0.99

The chance that none of P pairs are in the same block is 0.99^P

The chance that at least one pair of genes are in the same block is $(1 - 0.99^P)$

For $G = 12$ the chance is 0.48

(In the figure the x axis is G and the y axis is the chance that at least one pair of genes are in the same block given these criteria.)

Given that most traits of interest to breeders are polygenic and many traits are of interest, unwanted linkage is a huge problem. Buckler et al., (2009) for example identified more than 300 QTL determining variation in flowering time in maize and provided evidence for multiple alleles at these loci. For this number of genes the genetic interval into which a 1000 cM genome would need to be divided for a 50% chance of avoiding linkage is ca. 0.015cM.

The interesting question is therefore how to go about selecting those individuals that will have a heritable improvement in the desired characteristic. What breeding programmes need to do is identify alleles of interest and 'manage recombination' (de Vienne 2003) events in breeding programmes to accumulate desired alleles.

This leaves two questions 1) How can we identify useful alleles? and 2) How can we follow these in breeding programmes? The role of genetics in breeding and germplasm maintenance will therefore be discussed in past, current and future perspectives, below.

Supplementary Mat. 4 Crop Physiology

Jana Kholova, Milan Oldřich Urban, Francois Tardieu

Introduction

Crop physiology studies and describes live plant processes and functions, the interactions within plants and the plant behaviour in the context of different growth environments. Important part of crops physiology is evaluation of intra- and inter-specific variability in plant traits and functions. Crop physiology expands from the individual plant cell molecules on the one end to plant functional eco-physiological interaction with environments on the other hand (Supplementary Fig. S1). In close association with plant and crop modelling, it can be seen as an “interdisciplinary integrator” which could provide the answers to “which traits and environmental conditions result in yield” thus contributing to r component of “breeding equation” (Formula 1).

Past and current status

Crop physiology essentially deals with causal relationships between environmental conditions, genetic information and the dynamic changes in trait values. For its contribution to plant breeding, it has gained a reputation of being essentially retrospective, by explaining the successes and failures of breeding rather than contributing to a forward-looking strategy. Because current breeding essentially relies on yield, there is little evidence of plant physiology's contribution to development of crop products within CI (Tardieu et al., 2018, Sadras&Richards 2014, Reynolds&Langridge 2016). However, when describing the

development of the varieties that led to the green revolution in rice, the breeder, Peter Jennings, pays tribute to the contribution of Akira Tanaka, a physiologist for his pivotal role in defining the plant type (https://www.youtube.com/watch?v=OxdJ_wiimc0&t=1717s). Furthermore plant and crop physiology has provided many breeders of many crops with vital information that has helped them develop varieties and cultivars. The most striking example for that is probably the tolerance to submersion in rice, via an allele of the gene Sub1, present in the natural diversity and whose effect has been described in both physiological and genetic ways. Other examples are, photoperiod insensitive rice, sorghum, maize and soybean varieties based on an understanding of the control of flowering by day length; slate branching high harvest index cassava varieties were identified as higher yielding by physiologists manipulating the plants; vapor pressure deficit sensitive stomata for drought tolerance were shown by physiologists to improve water use efficiency and this trait has now been incorporated into commercial maize cultivars (see Supplementary Mat. 12) . Furthermore, we point out that explaining where and when a particular trait contributes to yield improvement gives breeders confidence that they can incorporate the trait advantageously. Especially attractive is the knowledge of the plant processes identified by plant physiologists and directly involved in yield formation, as was the case with reduction of anthesis-silk interval to reduce abortion in maize (Edmeades et al., 1993).

Because most adaptive traits affect yield in a context-dependent way (with positive, neutral or negative effects depending on environmental scenarios) only few adaptive processes and traits related to plant interactions with the environments are currently being investigated as a potential candidates (transpiration efficiency; carbon discrimination, root/stem conductivity in wheat, ABA in maize in EU are some positive examples). These, and many others, could well provide breeders with new traits to identify in the available germplasm and then to incorporate them into their breeding objectives. This would enhance the selection accuracy (\underline{r} component in Formula 1) for specific TPEs, knowing that expected positive effects are probabilistic, depending on the frequency of scenarios in which adaptive traits have positive effects (Tardieu et al., 2012, 2018; Hammer et al., 2006, 2010, Millet et al., 2019, Garin et al., 2020). Of interest is the example of maize stomatal response to vapor pressure deficit (see above). We suggest that in the future information exchange across crops will become more important, especially in those crops which have been the subject of intense selection and have relatively little genetic variation in the mainly elite lines used for crossing.

In the past paradigm crop physiologists were not able to do detailed studies on a large number of genetic materials. Recent technological advances from the early years of the 2000s made high -throughput sensor-based phenotyping, available to crop improvement programs. This high-throughput (HTP) technology now often labelled as phenomics has the capacity to provide information on 100s-1000s of genotypes. This removes one of the major restrictions on the work of physiologists with their previously limited capacity to study a wide range of genotypes either for direct measurement of traits or for establishing response curves to environmental conditions (Tardieu et al., 2017). Currently, the phenomic community begins to emphasize the usefulness of the phenomics data and a few of the physiology teams have begun aligning their research portfolio with the CI rather than serving purely the academic purposes (for detailed

information about see Supplementary Mat. 5). Nevertheless, CI requires solid quantitative evidence of the value delivered in terms of contribution to the genetic gain for target trait in the target environments (Supplementary Mat. 12). Additionally, the traits which might be in the frontline for usage (rev. by Tardieu 2012, 2018, Kholova et al., 2014, Tharanya et al., 2018, Sivasakthi et al., 2019) are frequently polygenic with gene-to-gene interactions depending on the environment (e.g. Kholova et al., 2012, Tharanya et al., 2018). There has to be mutual understanding that evolution has been molding plants to develop and survive in often harsh environments for millennia. The scope for building on these highly evolved processes of adaptation in CI is immense (e.g. concept of “Darwinian Agriculture” by Denison et al., 2012, recently e.g. vonWettberg et al., 2019).

Future perspectives

Phenomics is likely to undergo a transformation similar to that of genomics with a massive reduction in phenotyping cost and more rapidly available data as the technology advances (Vadez et al., 2015, Tardieu et al., 2017, Schmidt et al., 2020). Crop physiology measurements will largely be limited by both the capacity of researchers to formulate hypotheses and quantitatively define, defend and justify the tangible phenotyping targets for use in CI and also the ability of HTP systems to mimic the target environment. The latter may ultimately be the major limitation on the utility of HTP. The balance between the screening power scale (tens, hundreds, thousands lines), accuracy and cost will have to be well-defined. The engagement with other disciplines which were not classically considered in biological sciences will gain importance; e.g. physics (optics, particle physics), quantitative chemistry, computation sciences and information technology (machine learning, information systems, big data analytics). However, the traits to be analysed through HTP will almost certainly continue to depend on an intimate understanding of plant growth and development processes provided by physiological studies.

Physiology approaches can also resolve the bottleneck of the genomic selection (GS) based methods (see Supplementary Mat. 3), which are, at least for now, restricted by its reliance on large, precise datasets from a limited number of, often artificial, environments. This particular limitation of GS approaches can be overcome precisely by combining the GS with the modelling of plant functional interaction with environments (Millet et al., 2019, Technow et al., 2015). The investment into new tools and fit-for-purpose technology and long-term experiments should be recognized by funding agencies as extremely important. The technology advancements should come hand-in-hand with structured data to enable meta-phenomics approaches.

Practical support to CI teams

Given the tech-advancements, plant physiology is positioned to enable regular, rapid screening of 1000s of lines to support selections early in the (pre-)breeding process. This will be possible once the phenotyping target for environmental context is well defined and its value for CI quantitatively justified (e.g. ROI). Another key contribution of crops physiology disciplines to CI is the functional crops-in-system design - this is being recently done in conjunction with

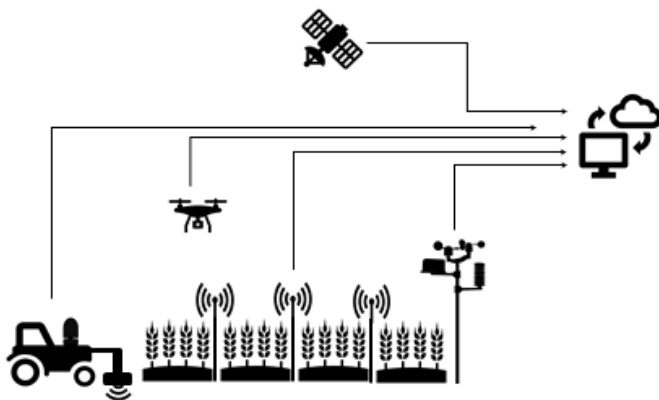
cropping system modelling approaches. Cropping system design also involves important evaluation of functional trade-off; e.g. in some context higher yielding high harvest index crop types may have slower ground cover and hence suffer more from weed competition, or compromise the stover production required by farming systems to feed the livestock (e.g. Kholova et al., 2014). Similarly, the traits that allow cassava to survive and yield something with uncertain rainfall may reduce its yield when water is readily available during the whole growing season (Cock and Connor, in press).

Supplementary Mat. 5 Crop Phenomics

Sindhuja Sankaran, Michael Gomez Selvaraj

Introduction

Phenomics refers to the evaluation of phenotypes through the acquisition of phenotypic data with high dimensionality (Großkinsky et al., 2015). The term ‘phenomics’ – an analogy of genomics – involves the systematic study of phenotypes at different levels that can scale from cellular level to organism level. Although alternatively it is also referred to as high-throughput phenotyping (HTP) technologies, in most cases, the throughput is associated with phenotypic data acquisition process. In our perspective, phenomics tools can assist in accurate, non-destructive, automated, cost-effective, or high-throughput characterization of phenotypes, that allow exploration of traits aided with sensing, automation and data mining approaches with capabilities beyond standard methods. Although several phenomics approaches are explored in controlled environmental conditions, in this manuscript, we will focus on field phenotyping efforts that strengthen CI research activities.



Future phenomics approaches may involve a combination of multiple sensors (multispectral, thermal, hyperspectral imaging; ground penetrating radar; LiDAR; soil sensors; weather data; etc.) mounted on multiple platforms (IoT, tractor, unmanned aerial system, low orbiting satellite) integrated with edge/cloud computing environment to acquire data in an intelligent manner and process data in near-real time or real time with visualization tools for breeder guidance.

Past and current status

In regard to the field phenomics systems, several platforms such as tower, hand-pushed platform, tractor-based system, autonomous platform, blimp, unmanned aerial vehicle (UAV) and manned aircraft integrated with RGB, thermal, light detection and ranging (LiDAR), multispectral/hyperspectral sensor systems, etc., have been developed and explored in recent past (Derry et al., 2014). The applicability of the systems depends on the purpose of research, a crop of interest, and growing conditions (acreage, plot size/design, etc.). Amongst these systems, two commonly used platforms include tractor-based systems and UAVs. There are many different forms of tractor-based systems developed/adapted and utilized for field phenotyping applications. Some of these platforms include sprayer-modified (Andrade-Sanchez et al., 2014; Barker III et al., 2016) and tractor integrated (Nguyen et al., 2016 a, b; Fernandez et al., 2017; Vuong et al., 2020) systems for phenotyping field/row crops. Such platforms differ in complexity and capabilities (sensors). Nevertheless, more recently, advancements in sensor technologies (lightweight, higher spatial/spectral resolution, etc.) and associated electronics, have enabled the dramatic use of UAVs for field phenotyping applications. Field phenotyping using UAVs has inherent benefits such as higher operational flexibility, rapid data acquisition, and capabilities of acquiring high-quality data (Sankaran et al., 2015; Shi et al., 2016) complementing field CI research studies. Given the continuing advancements in sensors and software technology, the applications of UAV-based systems will continue to develop. For example, integration of high-resolution RTK global position system (GPS) with UAV system (e.g. DJI Phantom 4 RTK), real-time in-field analysis (e.g. DJI P4 Multispectral with live RGB or normalized difference vegetation index/NDVI map feed), etc.

In addition to the above-described systems, several autonomous systems (e.g. Sun and Li, 2016; Shafiekhani et al., 2017; Pérez-Ruiz et al., 2020) have also been investigated. Much of these developments are from the public sector and/or universities working towards a solution for a specific crop and growing condition to assess specific crop trait/phenotype (biomass, architectural traits, crop status/health monitoring using indices such as NDVI, plant height, etc). One of the most sophisticated system for field-based phenotyping comes in the form of Field Scanalyzer (Virlet et al., 2017; LeBauer et al., 2017; Burnette et al., 2018), where the system integrates a range of sensor systems including fluorescence, RGB, multispectral, hyperspectral, and LiDAR sensors, alongside weather sensors. In more recent years, private companies have shown interest in agricultural applications, in terms of both system/technology development and novel data mining tools that include cloud computing, artificial intelligence (AI) and machine learning (ML) approaches. Some examples of system development include the development of Farmbeats units at Microsoft (<https://bit.ly/3mSJ3aA>) and agricultural robots at Google X (<https://bit.ly/330gMGW>).

One of the critical aspects of field phenomics efforts is data mining and analytics. Given the diversity of crops, cropping systems, and CI efforts that are phenotyped worldwide, developing standard data analytical tools can be challenging. Within the last year, there have been efforts towards developing analytical pipelines to allow automated or semi-automated extraction of features that represent crop phenotypes. Few such tools for UAV data analytics include pheno-

image analysis (Selvaraj et al., 2020), ImageBreed (Morales et al., 2020), FIELDImageR (Matias et al., 2020), drone processing pipeline (Schnauffer et al., 2020), Plot Phenix™ (<https://www.plotphenix.com>), etc. The deep learning approaches (Namin et al., 2018; Singh et al., 2018) are also enabling direct image-based analysis. Besides, several technical/data analytical tools (systems, cloud computing, AI/ML tools) for ag-data analysis are also available through Intel (e.g. Infiswift Internet-of-Things/IoT platform, development of sensors and systems/platforms), IBM (e.g. Watson Decision Platform for Agriculture), Google (e.g. Google Engine), Microsoft (e.g. Farmbeats, Microsoft Azure), Amazon (e.g. Amazon Web Services), etc. With more integrated and collaborative efforts between disciplines, and private-public partnerships, we can anticipate a perfect union between plant science, technology, and data mining approaches.

Future perspectives

Currently, most of the phenomic efforts are defined by a project, which is mostly short-term (3-5 years). Given that most CI efforts have a long-term goal and it takes three to five years to establish phenomics protocols, long-term projects supporting these efforts are desired. Moreover, it should also be taken into account, although several aspects in sensor-based phenotyping can be automated, there is still going to be a human element for cross-verification, refinement, and adapting the phenomics solutions for a well-defined research question.

The multi-disciplinary collaboration and cooperation (plant science/horticulture, engineering, computer science, data science, crop modeling, ecology, environment, physics, mathematics, etc.) will define the future of phenomics. Given the diversity of sensors and data mining approaches for field phenomics applications integrated with CI efforts, in future, it can be deduced that multi-scalar technologies need to be merged to develop a robust, fail-safe phenomics system. For instance, a CI field site can incorporate solar-powered IoT devices (RGB, multispectral, thermal, depth cameras, soil sensors) integrated with weather stations that can continuously monitor the dynamic crop responses (to capture $G \times E$ effects with micro-climate changes). At a critical time-point as computed using weather data, IoT data, and phenological crop stage, the IoT device can trigger a data capture using (i) a robotic self-autonomous UAV (multispectral, thermal camera) in a secured chamber and (ii) high-resolution satellite imagery using low-orbiting satellites (multispectral images), with the aid of geo-referenced plot map with predefined shape files. The self-wireless charging of UAVs is becoming a reality (e.g. Junaid et al., 2017) and is likely to advance in years to come. Similarly, low-orbiting satellites can capture multispectral imagery at high resolution (e.g. ~30 cm/pixel spatial resolution, ~1 day temporal resolution) that can be utilized for phenotyping applications (Sankaran et al., 2019; Zhang et al., 2020). The satellite image spatial resolution is anticipated to improve with years to come. The IoT and remote sensing data can further be integrated to autonomous ground-based systems for leaf-level measurements (e.g. close-range hyperspectral data, leaf sampling for biochemical parameter estimation, etc.), non-invasive measurement of physiological traits (e.g. porometer), extraction of soil data/root phenotypes (e.g. electromagnetic conductivity mapping, ground-penetrating radar/ Delgado et al., 2017), and other new technologies, yet to come (e.g. Terahertz imaging) for extracting multiple traits. We

can also anticipate the development of more apps (e.g. Field Book, phenoapps.org/apps/; Canopeo, canopeoapp.com) with potential phenotyping applications that may become an integral part of CI efforts.

Regarding all forms of data, there is continuing interest in real-time analysis to extract useful information. With developments in hardware/software technologies – both in terms of sensor development and computing (e.g. quantum computing) – on-board image/data processing and real-time analysis will become a reality. We anticipate that the breeder will have data-driven AI/ML tools that can assist in their CI efforts. Some of these tools can be associated with accurate AI-driven yield prediction models to predict various crop responses in simulated environments that represent different geographical locations or climate-change scenarios. Such datasets need to be integrated with genomic and other datasets (metabolomics, proteomic, etc.) as possible. Such advancements are only possible through collaborative efforts, not only across different disciplines and private-public partnerships, but also across other CI programs.

Practical considerations

In general, optical/remote sensing techniques associated with phenomics applications, especially under field environment, are subject to differences in reflectance resulting from various factors – e.g. sunlight, shadow-effect, wind, and sometimes growing conditions. It is critical to evaluate the effect of these factors during data acquisition, and apply controls (e.g. radiometric correction, data preprocessing/normalization techniques) to ensure that the quality of data is high to achieve interpretable results. Utilizing phenomics techniques, it takes few experiments/iterations prior to establishing a protocol for crop trait evaluation. This step is often ignored in practice, which needs to be accounted for in phenomics applications. In addition, there is a strong interdisciplinary communication necessary to define and refine expectations from the technology, for the successful implementation of a solution. The adoption and economic benefits of applying phenomics technology in CI programs would depend on genetic gain, costs and returns, technological advancements, and breeder's comfort level with the technology, among other factors (Awada et al., 2018).

Supplementary Mat. 6 Phytopathology

Gloria Mosquera, Carlos Jara

Biotic factors reduce crop yield, resistance to specific diseases and pests is an integral part of many CI programs since resistant varieties provide economic, environmental, and health benefits not only for all-size farmers but also for consumers. Instead, chemical applications to control pests and diseases implies economic investments that usually increase production costs, are not environmentally friendly, and contaminate plant-derived products. Hence, Plant

Pathology (PP) main role should be to provide tools (knowledge, recommendations, germplasm, methods, etc.) to breeders or farmers to decrease crop losses and suggest what type of pest control is likely the most convenient. The germplasm development merely for disease resistance should not be the main target. Instead, PP should focus on the contributing to CI programs, with the tools required for development of elite germplasms by introgression of that particular source of resistance in different development stages. Under this scheme, besides germplasm, pathologists should include information about pathogen sources, and the conditions used during their screening. Perhaps this is one of the main challenges for an overall harmonic and effective collaboration since pathologists' point of view may not coincide with that of the breeders (pathogen sources truly require prioritization based on breeder's and field information according to intended regions for variety deployment).

Resistance to biotic stress genetics is highly complex in its composition and stability since there is no single gene or gene combination that could control several pathogens or even different races of the same species. In the past, pathology was one of the most active research areas inside crop research and its relevance was well recognized and supported by the amount of funds dedicated to this discipline. That allowed the development of many deliverables, including resistant germplasms, rating scales, pathogen management and inoculation protocols, and systematic training courses. In addition to funding, genetic resources from in-house gene banks were essential for pathologists' work, and lead – unfortunately - in an independent research area with few interactions with CI programs and even other disciplines. Research at that time was mainly applied and basic research was covered by academia.

This scenario started to change in the last 20 years, when other research areas gained relevance, and simultaneously, funding sources became more competitive. These challenges trigger for pathology transformation, which lead in more strategic PP work plans to maintain the pace of product production and respond to new demands including accelerated breeding for disease resistance by helping identify genetic variations in resistance among accessions. In this era, pathology's goal was to support processes required to move from conventional resistance selection to marker-assisted selection. Thus, pathologists might hold the optimal information about pathogen diversity in target regions and use it for taking decisions on strains or race selection for inoculations and disease phenotyping. Outdated information or not reliable, furthermore, phenotyping methods can create false expectations about resistance under artificial inoculations since pathogens evolve rapidly according to their environments. The use of the inappropriate strains or not correct phenotyping conditions put on risk the germplasm selection process. Despite these efforts, diseases remain as harmful factors for crop production since pathogen diversity and climate are crushing the best breeding bets for variety deployment.

There are frequent trade-offs between advances in one trait and another. There may also be trade-offs which are less obvious: for example, there may be a high metabolic cost to disease, pathogen evolution or insect resistance mechanisms. These trade-offs, which may sometimes be manifested as negative genetic correlations and slow progress, should be considered by breeders. In many cases it is preferable to manage diseases and pests with environmentally friendly means (phytosanitary practices, disease escape or eradication, biological control). A

beautiful example was one of the CGIARs most successful programmes: mealy bug control in cassava in Africa. Although host plant resistance was considered, bio control was deemed to be quicker and better.

Changes and re-structuralization of crop research will not stop, on the contrary new challenges are on board every day. Governments are becoming more aware of the necessities to protect their agriculture and genetic resources. Consequently, national plant health agencies are pushing new policies that limit traditional activities carried out by pathologists - mainly those involving pathogens and crop seed movement across countries, which is really a bottleneck for breeding programs with regional and global mandates (Supplementary Mat. 7 and 8). Furthermore, phenotyping is limited to pathogens or strains collected mainly locally, demanding capacity from international partners to carry out additional disease evaluations using their own local pathogen collections. Protecting national resources – in a global word - probably is a valid approach, even though farmers and consumers in developing countries can be directly affected since most NARs have reduced capacity to conduct disease evaluations and pre-breeding efforts on their own. This highlights an important potential role of the CGIAR in coordinating resistance evaluations to pathogens (or strains) not existing in some places.

Along with new regulations affecting germplasm and pathogen movement, the current phenotyping methods for disease resistance are also becoming a bottleneck for accelerating genetic gain (Araus et al., 2018). Currently used strategies based on manual evaluation (greenhouse and field) are costly, time consuming, and inefficient, limiting both gene discovery and germplasm selection for disease resistance. Technology based phenotyping replacing visual scoring should be the goal in the near future. Traditional scales for disease rating are subjective and were not developed for capturing minor differences between genotypes, which is the base of quantitative resistance. There are no doubts about the positive impact of disease scoring technology on crop improvement, but the solution is not straightforward since its development needs to overcome several challenges. The first step is to develop a reliable system with the capacity to specifically recognize disease lesions and differentiate them from those caused by other pathogens or even from affections caused by physiological or other (a)biotic stresses. Mahlein et al., (2019) have described different technologies, and some of them are already available for disease screening in other crops. Unfortunately, digital tools are so far pathogen-crop specific. Current strategies for modernization of breeding programs should include investments in PP-targeted technology (automatizing disease evaluation), which complements other tools being developed for agronomic traits. The advantages of a digital phenotyping system are multiple, including improved accuracy, high throughput, and wider phenotypic classification capacity that are ideal for improving qualitative genetic analysis. Once this type of technology is developed and implemented, the next step is to move from marker-assisted selection to a robust genomic assisted selection strategy for disease resistance and offer new challenges to CI strategies relying mostly on major resistance genes. The QTL-based resistance can then be the best option and its value could finally be exploited by breeders. Although QTL-based resistance has been a promising tool for a long time of which few successful stories can be told, they would become real help if: 1) the phenotypic effect is detected more accurately and 2) the tools for their pyramiding also improve. The QTL bad

name is unfortunate. This type of resistance is widely known to be more stable since it controls pathogens independently of their races, and if multiple QTL are pyramided have a reasonable resistance level. Poland and Rutkoski (2019) have described the advantages of genomic assisted-selection over conventional marker assisted strategy. Ultimately, multiple QTL controlling several pathogens could be evaluated at once, as has been described for maize and beans (Asea et al., 2012; Terán et al., , 2012), but using a genomic approach. Along with modern phenotyping tools, genetic resources from in-house gene banks will remain an essential resource for pathologists, breeders and physiologists. These two tools envision a bright future for gene discovery and deployment.

Supplementary Mat. 7 Genetic resources for a new agricultural environment

Daniel Debouck

At the turn of last century Russian agriculture was plagued by drought, cold and diseases, and revolts were frequent in rural areas (Nabhan 2009). At the age of 21 starting plant-collecting Nicolay Vavilov understood that drastic solutions could come from plant introduction and plant breeding: “Our exploratory work was pursued with a particular objective in mind: to utilize the plant resources of the world maximally for the purpose of plant breeding based on a global gene-bank” (Vavilov 1934). At 43 he was the director of the All-Union Institute of Plant Industry with 20,000 staff and 400 stations for one country (Hawkes 1990) (where is its modern equivalent?). Beyond his influential work on the origin of cultivated plants (1926), as lasting contributions from Vavilov one could cite: first, the novel concept that in order to find interesting traits for breeding the gene pool of a crop should be studied in its totality, and second, the documentation of the agricultural biological diversity in many places of the planet before it was changed forever. Along the former, he was among the first (and the few) to realize the scale of the diversity that piled up in thousand agricultural landscapes over the 8-10,000 years of domestication. Vavilov also understood the crop diversity as it was created over most of that duration, that is, across political borders, a dimension that we still struggle to articulate for breeding one century later.

With the release of the first cultivars resistant to diseases in 1910-1920 (e.g. potato: Ross 1986, wheat: Bonjean & Picard 1990) started the replacement of landraces by bred varieties. Erwin Baur in 1914 and Harry Harlan in 1936 were among the first to call attention to that replacement. It seems that the years 1950-60 were a landmark in that disappearance of landraces (van de Wouw et al., 2010). In the commodity centers of the Consultative Group on International Agricultural Research an indicator of impact and success of the Green Revolution was in the rate of adoption of improved varieties, that is, the level of replacement of the landraces (Pingali 2012, Lynam & Byerlee 2017). Garrison Wilkes in a conversation with Paul Raeburn (1995) nicely summed up: “it was taking stones from the foundation to repair the roof”. Breeding *per se* almost means replacement of an existing variety by a ‘better’ one, meeting farmer’s needs, and demands by distributors and/or consumers. But farmers have long rogued out less favorable genotypes in view of the needs of their families, communities and

local environments (Bunting 1990). A clear demonstration of these farmers' practices is the 'Columbus effect' or large-scale introduction and extinction of crops on both sides of the Atlantic in 1493-1600 (Butzer 1995). For example *Phaseolus vulgaris* won the race against *Lathyrus sativus* in the Iberian Peninsula, while *Vicia faba* won in the Andes as compared to the native tarwi *Lupinus mutabilis*, in both cases because of larger seed size and less detoxification process (Hernández-Bermejo & Lora-González 1992 and Gade 1969, respectively).

As an outcome of the UNCED of 1972, the IBPGR was created in 1974 and put emphasis on the rush rescue of landraces (Williams 1990). The Green Revolution was successful on diseases, and on yield because of work on growth habit and harvest index, and genetic gain came out because of the variation present in the germplasm collections. Which are the challenges of plant breeding by 2040 (two breeding cycles from now)? The same drivers that have pushed for yield increase in the period 1950-2020 are likely to push for the same, given the rising demands (Tilman et al., 2011). It might be however under decreasing gains (Ray et al., 2013), namely because of temperature increase beyond the appropriate ecology for the crop (Lobell & Gourdjji 2012). An important consideration is to not make the situation worse on the side of greenhouse gas emissions and pollution by nitrates (Tilman et al., 2011). Breeding priorities are the same while new strains of diseases will continue to appear and increase in yield is absolutely needed. Such new strains may mean that our germplasm collections may not have all the sources of resistance, and now there is little probability to find such resistances in landraces gone eighty years ago. Some hope might be on the side of wild relatives because coevolution has been acting for longer periods. Breeding priorities are different however because of environmental problems coming on the horizon. Good land in the past used for agriculture is now for non-agricultural purposes (Evans 1998); so new problems arise with crops being pushed into areas prone to drought, low phosphorus, or acid soils (Beebe 2012). Climates are likely to experience warming, drought or excessive rains, at levels several crops have never been exposed to (Beebe et al., 2011).

Solutions. Let us clarify first the prospects of 'new' crops: there is no seventh continent! Thus, no other 'Columbus effect' (the first one allowed half-billion: Evans 1998) is to be expected to give us some relief in the coming fifty years. 'New' crops might be old crops for which breeders eventually realize they have a tremendous head start in face of abiotic stress. A good example might be the tepary bean where shortcomings such as growth habit or seed size can be easily corrected with the experience gained on common bean and marker-assisted selection. Being not far away from the *P. vulgaris* phylum, an ample synteny is to be expected and thus the possibility of taking benefit of the advances of the bean map. Will we eat *Arabidopsis* as salad? Possibly not, in spite of all genomic progress. The crops we use and eat are the ones with domestication starting about 8-10,000 years ago. New crops would have to occupy a new niche in both agricultural systems and in consumers' preferences, and this way is uphill because of an 8-10,000 years head start by existing crops. In the New World we have unique botanical series (i.e. *Phaseolus* and *Solanum* section *Petota* with seven crops, *Annona*, *Capsicum* and *Cucurbita* with five, *Pachyrhizus* with three), where comparative mapping and synteny may

help discover homolog genes in the other species of the series, offering more ‘new crops’ to breeders and consumers.

So, a pertinent question is: are the germplasm collections with enough genetic diversity for environmental and physiological constraints? Possibly not, because the criteria for assembling such collections were focused on diseases and pests resistances and market classes, that is, the problems of the 1960s. About 2/3 of the bean collection kept in CIAT genebank have been evaluated for anthracnose, angular leaf spot and common bacterial blight but this figure drops to 18% for drought tolerance and 7% for low phosphorus tolerance (Hidalgo & Beebe 1997). For the basic crop machinery – efficiency of photosynthesis – only 150 accessions on over 37,000 in the bean collection have been evaluated (Lynch et al., 1992, González-Mejía et al., 1995). Jack Rodney Harlan (1972 p. 215) wrote: “The danger is that decisions are made and priorities are established out of *both* ignorance and prejudice”. So, keeping this in mind, two lines of action come to mind: i) collecting diversity *per se* independently from present uses, and ii) the development of new evaluation methods (during the Green Revolution the pace of evaluation by a multidisciplinary team including Genetic Resources + Pathology + Virology + Breeding was of aproxim. 1,800 accessions/ semester). To be on time with 2040, crop productivity in yield should progress at 2.4% per year (Ray et al., 2013), and right now for most crops we are far behind that speed, so both speed and scale are mandatory. Along the former line, one should not be afraid in going beyond the cultivated gene pools, but go for crop wild relatives in extreme environments, because with marker-assisted selection it will be possible to recover the trait of interest or to edit the gene(s) involved in a physiological pathway (Assefa et al., 2019, vonWettberg et al., 2019). Some may argue that filling gaps is fast (shall we send the drone?) and easy because there are tools to predict where gaps are (Ramírez-Villegas et al., 2010). But these tools are often built on average ecological behaviors, which are likely to be represented by at least a few accessions already conserved. What needs to be found and conserved are the ecological extreme behaviors. Further, these tools might not help much to find new species that are likely to be endemic or ecologically rare, since over the last 250 years the most common species have been found at least once. But because extinction is forever, and because collecting still depends on seasonal variation, it will take time and should be launched now. Along the latter line, given the size of the collections, the ‘classical’ multi-site testing with repetitions is beyond time and human resources available. Geographical approaches may help (towards the surviving germplasm where the stress has been present for thousands of years, and thus logically the wilds) but may not work in every case; for example they did not pick up outstanding wild forms under low phosphorus stress (eighteen accessions tested; Beebe et al., 1997), while there seems some promise for drought (eighty-six accessions tested: Cortés & Blair 2018a). Internally these approaches impose on the genebank to be strict on passport data (van Hintum et al., 2011) (to the extent possible, because hundreds of landraces were purchased on markets!). In some cases robotics and image analysis are applicable, because they can work non-stop. But an interesting approach might be in genomic signatures linked to a metabolic pathway involved in an abiotic stress (Cortés & Blair 2018b). Thus, new teams (Genetic Resources + Physiology + Bioinformatics + Breeding) in addition to the former should be established to screen the entire germplasm collections for markers that

have been proven to be associated with a physiological trait (following the example of the bruchid resistance in beans: Mbogo et al., 2009; also see part Supplementary Mat 3-5).

Candidate genes involved in physiological reactions to drought or heat will be disclosed, where the comparison with wild species from desert habitats that have for one million years passed the test of time, will give illuminating lessons on why some of our crops perform poorly in face of environmental challenges. Differences between species which are mostly in ecological competence will be better understood, and from there our ability to plant superior genotypes in each corresponding field. Gene edition may come to the horizon, but its efficiency will increase significantly with a model to copy. The major concern of this author is the non-realization of the full potential of the genomic breeding and comparative mapping, above all to address at last environmental and physiological constraints, as these technologies are applied to less-than-ideal or wrong materials, because in the meantime so many options have been lost, because one thought that time could be bought.

Epilogue

Plant breeding can bring some solutions to agricultural productivity but human societies also have to abandon childhood and understand their limits. Hugh Iltis (1988 p. 99) wrote: “the world hunger problem cannot be solved by growing more food, but only by growing fewer people”. Jared Diamond (2002 p.706) was more direct: “Only when crop and animal breeders take the lead in reducing our numbers and our impacts will they end up by doing us net good”. If in all recent years the ecological footprint of the planet is reached by mid-year, it is a clear signal that a current way of using the planet's resources is wrong. Reducing breeding cycle after breeding cycle the environmental footprint of production in our staple crops can be a step in the right direction. Plant breeders can take that challenge, they rightly will come back to germplasm conservationists asking for informed variation.

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Supplementary Mat. 8 Genetic resources

Peter Wenzl, Vania Azevedo

Introduction

Genebanks are the main source of new diversity to crop improvement. Created with the main objective to conserve the genetic diversity of the cultivated species, the genebanks conserve today a few millions of accessions of hundreds of crops and thousands of species, collected all around the globe, representing wild materials, landraces, breeding lines, genetic stocks and wild relatives. Genebanks provide breeding programs with the genetic variation (s_A) without which genetic improvement is impossible. Globally, more than 1,700 genebanks conserve approximately seven million accessions (FAO 2010), with CGIAR genebanks holding approximately 10% of these materials (Noriega et al., 2019). Much of this germplasm was collected last century (Halewood et al., 2012), starting in the 1970s when modern cultivars began replacing traditional landraces selected and shaped over millennia by agricultural communities living in areas where crops had been domesticated (Harlan 1972). Many landraces, as well as crop wild relatives growing in the wild, have gone extinct *in situ* since they were collected and today can only be found in *ex situ* genebank collections. Those that still exist *in situ* are now often more challenging to collect given the current regulatory environment (Halewood et al., 2012, Noriega et al., 2013). Landraces and wild relatives in existing collections are an invaluable source of unique alleles controlling traits such as nutrient density, abiotic-stress tolerance and disease and pest resistance (McCouch et al., 2020, Supplementary Mat. 4-6).

The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), which covers most of the major but only a subset of minor crops, regulates how this germplasm can be shared globally to contribute to crop improvement and how benefits arising from the germplasm's use should be shared (FAO 2009). The eleven international CGIAR genebanks, often located close to the centers of origin of the crops they conserve, are one of the main vehicles through which genebank germplasm is distributed globally (e.g. 80,000 samples in 2019; CGIAR Genebank Platform 2020). This is, in good part, the result of sustained investments in the regeneration and phytosanitary testing of accessions during the last decade and earlier work on developing phytosanitary methods to transfer germplasm safely. As their concerted effort to ensure the survival and availability of their accessions draws to a close, CGIAR genebanks can, to a degree, shift their focus towards helping breeders use the conserved germplasm more effectively. Enriching the collections with actionable information and bridging the 'genetic gap' between genebank collections and elite germplasm are perhaps the two most critical intervention points to lower the barrier to using genebank accessions as parents in (pre)breeding programs.

The expanding digital dimension of genebanks

More than just conserving everything that can be collected, genebanks have a critical role to play in generating precise information about the traits of interest so the adequate material can be made available to the crop improvement. A complete screen of a big genebank, with a few thousands of accessions, for all or for the majority of the important traits, is likely impossible. Millions of data points are generated every year by genebanks and partners to help understand the diversity conserved and identify more and more accessions that can be of interest for the breeding programs. However, compared to the amount of genetic diversity they contain,

genebank collections tend to be information poor, offering only limited actionable information for selecting accessions for crop improvement (McCouch et al., 2020). Passport data documenting taxonomy and provenance or collection sites, if available at all, are sometimes all that is known about certain accessions. Environmental parameters at accession collection sites can be used to identify accessions that are more likely to have alleles contributing to environmental adaptation or resistance to certain diseases (Khazaei et al., 2013). Where possible, genebanks record morphological and phenological descriptors during seed production, albeit primarily for the purpose of confirming the identity of accessions. Some genebanks also document morphological features using images (e.g. CIAT 2020). Only a few CGIAR collections, however, have been systematically evaluated for traits that are breeding targets (Upadhyaya et al., 2010), which is not surprising given the sizes of the collections.

The same way genomics is changing the breeding system it is also allowing the genebanks to very easily and rapidly identify potential sources of materials to be used in the breeding programs due to the possibility of linking molecular markers to the traits of interest. In contrast to phenotyping, high-density genotyping of entire collections is now entirely feasible, with costs ranging from less than a year to a few years of conserving a collection. Genotyping methods that are based on sequencing genome representations and use allele-calling algorithms that minimize ascertainment bias produce a future-proof and unbiased picture of the genetic composition of collections (Sansaloni et al., 2020). Genome-wide genotyping methods also identify potentially redundant accessions, provide a framework for identifying collection gaps and developing genetically balanced core collections, and can be used for association studies and genome-wide predictions of traits evaluated only for a subset of accessions (Ndjiondjop et al., 2017, Crossa et al., 2016, Yu et al., 2016). A strategy involving genotyping of entire collections, followed by phenotyping of accession subsets or core collections representing distinct gene-pools, therefore, could help genebank users select ‘best bet’ accessions for a variety of traits of interest, even if they have not all been phenotyped.

More than having the germplasm available, the information is equally important to be accessible (please, see detailed contribution on Crop Ontology in Supplementary Mat. 9). User friendly and open access databases are extremely important if the objective is to potentialize the use of the germplasm conserved in the genebanks and provide more sources of diversity to the crop improvement. Most successful examples of using landraces or wild relatives for introgressing desirable traits into elite germplasm are based on advanced backcrossing schemes targeting disease-resistance genes or other genetically simple traits (Bailey-Serres et al., 2010, Hajjar and Hodgkin 2007). Other approaches may be required to systematically exploit ‘exotic’ diversity for polygenic traits such as yield potential or abiotic-stress adaptations. Disentangling such ‘aggregate traits’ into genetically simpler physiological and morphological components that can be introgressed and selected for independently, is one possible approach (Reynolds and Langridge 2016; the other approach is discussed below). High-throughput, image-based methods for characterizing physiological/morphological features offer an expanding array of tools that could be used to mine genebank collections for component traits contributing to yield potential or heat/drought tolerance (Rebetzke et al., 2019).

Varying subsets of accessions have historically been evaluated for a variety of traits by researchers who have received germplasm from genebanks. Yet most of the resulting data is dispersed across publications and institutions and cannot be easily linked back to the genebank accessions from which it has been derived and hence remains invisible to future genebank users. The ITPGRFA, as part of its Global Information System (GLIS), has started using digital object identifiers (DOI) to identify germplasm from genebanks and breeding programs (Alercia et al., 2018). DOI can be used (a) to locate on the internet data and publications linked to specific germplasm and (b) to define the relationships (genealogy) among distinct germplasm samples. If adopted broadly, GLIS would help create an information-feedback loop from germplasm users to genebanks, thus benefiting future genebank users.

Historically, genebanks often have had to focus on regenerating accessions to keep collections alive. Yet, the digital dimension of genetic resources is expanding at an accelerating pace and requires increasingly sophisticated tools and procedures. The new, so-called ‘Future Seeds’ genetic-resources center being built at the (ex-CIAT) CGIAR hub in Colombia, includes a ‘digital genebank’ module to accommodate the growth in DNA-sequence, phenotypic and environmental data linked to genebank accessions. The ultimate goal is to gradually assemble, for each crop conserved, a knowledge base that documents: (a) *ex situ* (compared to *in situ*) diversity; (b) environmental adaptation of accessions; (c) traits of interest for crop improvement (whether measured or predicted); and (d) the allelic composition of accessions for genes with known function with a particular focus on functional SNPs that could be potential targets for future gene-editing attempts.

Bridging the gap between genebanks and breeding programs

Besides enriching genebank collections with actionable information, bridging the ‘genetic gap’ between genebank collections and breeding programs is perhaps the other key intervention point for reducing the (career) risk of using genebank materials. Breeders tend to only ‘reach back’ to genebank materials if there is insufficient genetic variation for a trait in elite gene pools since linkage drag and genetic-background effects both reduce chances of success in wide crosses. This problem is less marked in crops like cassava which have only recently been the subject of intensive selective breeding.

The so-called pre-breeding, in consultation and collaboration with the breeders, can be done by genebanks, so it can complement and not compete with the breeders. More proactive and systematic pre-breeding efforts could ‘de-risk’ the use of novel genetic variation from genebanks. Core collections (or other succession subsets) could be systematically ‘reformatted’ into ‘bridging germplasm’ through crossing with elite germplasm. A good example for this kind of approach are the BC1-derived nested association-mapping (NAM) populations developed by the sorghum pre-breeding program at the University of Queensland whose products have been widely adopted by the seed industry (Jordan et al., 2011). Their NAM strategy effectively ‘filters’ exotic genetic variation for favorable allele effects in a 75% elite background. Some surprisingly large genetic gains have been observed, presumably by exposing cryptic genetic variation. These results suggest that for less bred/domesticated crops large and rapid genetic gains may be possible in such a system.

Harnessing polygenic variation from landraces or wild relatives requires different approaches because introgressing small-affect alleles, one-by-one, would be unmanageable. Recurrent selection-based approaches may be more effective in extracting small-effect alleles for polygenic traits from genebank materials into elite germplasm (Kannenberg and Falk 1995). Selecting progeny from exotic/elite crosses tends to favor the elite genetic background while eliminating favorable exotic alleles, so using origin-specific genomic selection instead of phenotypic selection may be advantageous (Yang et al., 2020).

There is a growing recognition that molecular-breeding strategies that not only rely on a product-development pipeline but also include an upstream population-improvement component are more efficient in terms of converting genetic diversity into genetic gain (Gorjanc et al., 2018). It remains to be seen how ‘bridging germplasm’ populations capturing novel variation from genebanks can be best linked to these breeding schemes to ensure the long-term sustainability of crop-improvement programs.

Breeding programs are primarily funded to release new, improved varieties that create tangible impacts in terms of yield or quality of produce. The genetic diversity present in elite gene pools often seems sufficient to drive genetic gains in the short to medium term; so injecting novel diversity from genebanks is only rarely considered a priority. Genebanks, on the other hand, are primarily funded to ensure the multi-generational conservation of the crop diversity that underpins food production. Making crop diversity easier to use in breeding programs, while highly desirable, is usually only tackled once long-term preservation of *ex situ* collections is assured. Incentive structures and funding, therefore, tend to create and sustain a gap in the ‘genetic value chain’ between genebanks and breeding programs.

Supplementary Mat. 9 The Crop Ontology: increasing reusability and interoperability of breeding data

Elizabeth Arnaud

The Crop Ontology today

The Crop Ontology (CO, <http://www.croponontology.org>), the oldest ontology developed by CGIAR, is a source of traits and variables validated and used by the crop improvement community that comprises today 4, 235 traits and 6,151 variables for 31 plant species. The CO stands among the most popular ontologies used in agriculture (Leonelli et al., 2017; Harper et al., 2018). Ontologies provide uniquely identified concepts linked with semantic relationships interpretable by computers therefore using ontology for the data annotation makes data content re-usable and discoverable online. Ontologies serve as standards for integration of a large and growing corpus of plant genomics, phenomics and genetics data (Cooper et al., 2018). Thanks to the Planteome’s ontology project funded by the National Science Foundation, US (IOS:1340112 award; <http://planteome.org>), the species-neutral Trait Ontology integrates the

CO (Arnaud et al., 2012; Laporte et al., 2016; Cooper et al., 2018), thus supporting data search for studies in comparative genomics or for grouping traits for a family or a clade.

Crop Ontology: A collaborative product for crop traits and variables

Crop improvement relies on collecting and aggregating consistent and comparable data on the desired traits for a new crop variety by testing it in multiple locations and diverse environments or experimental conditions, under various field management practices applied by farmers (Shrestha et al., 2012; Arnaud et al., 2020). The quality and consistency of the data has greatly improved since the crop improvement researchers use digital technologies that integrate the defined crop traits and variables provided by the Crop Ontology and adding now the cultural practices included in the Agronomy Ontology (<https://bigdata.cgiar.org/resources/agronomy-ontology/>; Devare et al., 2018). Long-term sustainable access to Crop Ontology has increased the research community's confidence in using it, in turn increasing data discoverability and value for re-use, thus contributing to the return on investment for their collection and storage (Arnaud et al., 2020).

By providing descriptions, measurement methods and scales of agronomic, morphological, physiological, quality, and stress traits along with a standard nomenclature for composing the variables (Supplementary Fig. S3), the CO supports the digital capture and aggregation of trait data into breeding databases such as the Integrated Breeding Platform (IBP; <https://www.integratedbreeding.net/>) and the Boyce Thompson Institute's Breedbase (<https://breedbase.org/>) (Shrestha et al., 2012; Arnaud et al., 2020). The CO offers the flexibility to store diverse variables for a given trait. Therefore, the IBP and Breedbase propose internal ontology management features guiding users to directly and immediately create formatted variables needed in their specific field books. Each CGIAR Center has designated a curator who maintains the CO for their mandate crops while the Alliance Bioversity-CIAT's ontology team provides helpdesk and maintains the guidelines to create new ontologies or add new concepts. The content of the CO is constantly evolving with new submissions done by centers and partners like Cornell University, John Innes Centre, INRAe, CIRAD, University of British Columbia or NaCRRI among many others, to create content for their crops.

Supplementary Fig. S3 – Trait and variable composition as displayed in the Crop Ontology

The image shows a screenshot of the Crop Ontology Curation Tool interface for the Cassava Ontology. The interface is divided into several sections, with numbered annotations (1-6) pointing to specific elements:

- 1. Cassava Ontology web page:** Points to the top navigation bar and the main header area.
- 2. Agronomic Trait:** Points to the 'Root Yield' trait category.
- 3. Methods of calculation or estimation:** Points to the list of methods under 'Root Yield', including 'Calculation :Dry Yield_method', 'Calculation :Fresh Root Yield_method', 'Calculation :Top Yield_method', and 'Estimation :plant yield_method'.
- 4. Unit:** Points to the units listed for the methods, such as 'kg/plant' and 't/ha/year'.
- 5. All Variables' names following the nomenclature – for fieldbooks:** Points to the 'Variables' section, which lists terms like 'RYield_Dry_t/ha', 'RYield_FreshAerial_t/ha', 'RYield_Fresh_t/ha', 'RYield_PerPint_kgPint', and 'RYield_PerYr_t/haYr'.
- 6. Full description of the method:** Points to the 'Term information' panel on the right, which provides details for the 'Estimation :plant yield_method' term, including its identifier, method class, description, and name.

Future perspectives of CO

The CO is open source, licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/), and available online for trait search or download using ontology look up services or through its Application Programming Interface usable by software and databases. The industry uses the Crop Ontology for their data management systems like Bayer Crop Science (Burkow et al., 2019), Syngenta, BASF and KWS, and should increase their trait concepts contribution to open public ontologies like PepsiCo Inc., owners of Quaker Oats, did in conjunction with their collaborators at NIAB, Cambridge UK, by publishing their oat ontology in CO for public access.

The CO format was adopted by both the metadata schema called the Minimum Information About a Plant Phenotype Experiment (MIAPPE; <https://www.miappe.org/>) (Ćwiek-Kupczyńska et al., 2016; Papoutsoglou et al., 2020) and also by the Breeding Application Programming Interface (BrAPI; <https://brapi.org/>; Selby et al., 2019) that enable the extraction of genotype and phenotype data across databases. The demand for new traits and variables remains high as the community needs to apply the CO format for their databases to be BRAPI-compliant. The limited side effect is the submission to CO of some very project-specific traits and variables. The CO community needs now to integrate, with the support of experts, methods

and scales used by high throughput technologies as well as the assessment methods for farmers, processors and consumers' varietal preferences.

When publishing peer-review papers, some researchers adopted the good practice of mentioning their studies' traits and variables with their CO identifiers and providing in the underlying data the links to the traits in the CO. They suggest approaching the journal editors to define together principles about a citation format of CO variables.

The breeding community does not fully embrace the importance of maintaining the CO as a global stand-alone reference and quality semantic resource outside the current breeding data management platforms that is the role of the CO coordination team and curators . In consequence, the development of a breeding programme does not always include direct contribution to the CO. However, the CO is the only ontology that offers a comprehensive list of defined traits along with their pre-composed variables, ready to use in field books or lab books. Maintaining such lists of traits, and particularly variables, per crop as a global public good and trusted shared service requires long-term curation abilities and distributed resources that are not systematically secured.

In 2017, the CGIAR's Platform for Big Data in Agriculture realized the importance of ontologies to support the interoperability of data and knowledge sharing, and is investing financially in the Ontologies CoP. The CoP plays an advocacy role in sensitizing stakeholders to the importance of this collaborative data curation effort, which contributes to breaking data silos and supports the growing use of digital tools in agrifood systems. The CoP webinar entitled 'The Crop Ontologies, the Integrated Breeding Platform and Breedbases: collaboration for Harmonizing Breeding Data' (<https://bigdata.cgiar.org/blog-post/webinar-crop-ontology-semantic-interoperability-of-breeding-data/>) will provide further detailed information.

Crop Ontology: semantics for digital tools in Crop Improvement

Varietal traits preferred by farmers, food processors, traders and consumers are compiled into products profiles: the breeding product profile with preferred agronomic and post harvest traits, and the food product profile produced by mixed teams of social and food scientists collecting preferences with surveys or measuring with formal sensory panels, biochemical analysis and near-infrared spectrum analysis. Both profiles should use the CO traits and variables so the food product profiles remain interpretable and actionable by breeders. Missing traits, methods and scales will be included into the CO thus enabling breeding databases to produce optimal variety profiles for a given region, without losing the primary meaning and the scoring given by the stakeholders. To support field books used in Participatory Varietal Selection (PVS) trials, farmers' preferences are being added to CO for the roots, tubers and bananas, with consideration for gender-sensitive variables. The triadic comparisons of technologies (TRICOT; Etten J. et al., 2019) used in citizen science-based varietal evaluation trials is added to support the selection of farmers' traits in ClimMob (<https://climmob.net/>), the related data

management and analytical platform, and enables its connection with breeding databases to complement the breeding product profiles promoted by the Excellence in Breeding Platform.

Supplementary Mat. 10 Agronomy and production environments

Phillip Thornton, Peter Craufurd

Agronomy is the science and technology of producing crops for multiple uses. Agronomic research typically navigates through the agi-systems at the higher level of soil-plant-atmosphere organization (GxExM) and more evidently tries to engage with the Society dimension of the continuum (i.e. GxExMxS). It ideally considers multidisciplinary input to design sustainable agricultural production practices under current and future environmental and socio-economic constraints. Agronomy is traditionally regarded as context- or site-specific, and a paradigm shift is needed to make agronomy more data-driven, more scale-appropriate and more predictive. Further, in the past climate change was not considered important but now agronomists have to take into account not only weather variance but also long term changes in the climate change, both in systems (e.g. through diversification) and fields (e.g. Conservation Agriculture).

Characterization of agricultural and crop production systems is a key element in guiding crop improvement programs and helping to provide answers to two key questions: which are the environmental and crop management factors that affect crop performance in different places, and where else do specific combinations of such factors occur? The first relates to the objectives of crop improvement programs (and agronomy) programs, the second to the size of the area or domain that specific crop improvement and agronomy research addresses. Both questions need answers if crop improvement is to be effectively targeted and justified. However, we have surprisingly little systematic or representative data on production environments (domains) and production practices (i.e. what farmers actually do in terms of crop management and which practices, if widely adopted, are proven to close the yield gap). There is a clear need for a more data-driven approach to agronomy and a more systematic approach to G x E x M x S.

Introduction

Despite supposedly targeting G x E x M in genetic gains programs (e.g. the CGIAR platform; <https://cgspace.cgiar.org/handle/10947/4314>), and the release of many varieties, on-farm yield gaps (e.g. <http://www.yieldgap.org/>) remain very large in many crops and countries (see part on yield gaps TEXT BOX 2). This might be seen as an indication that in the short to medium term there is no burning requirement for more yield potential - CI-teams probably need to better exploit the material available now and set the relevant technology to target G x E x M x S context. Typically, technical yield gaps (as opposed to policy or social factors; see Assefa et al., 2020) are posited as roughly attributable equally to G and M, and are perhaps often perceived as additive effects requiring no collaborative effort – or perhaps perceived as too

complex for systematic research. This has hindered more integrated thinking or research on this aspect by CI improvement and agronomy programs. In practical terms, there will always be a compromise between the desire from the breeders to test many genotypes and/or early generations versus the agronomists desire to test a potentially large number of crop management factors or the response to a single factor (e.g. nitrogen). From the agronomic side there is certainly a need to better define or prioritise the key management factors for which G x E x M can be investigated.

This might be, however, complicated because there has been very little systematic, quantitative work to define production environments and scalable production practices in this space in CGIAR. The last large-scale, relevant production environment characterization in CGIAR is from Bunting (1987) and contains a broad collection of CGIAR and FAO activity in the area up to the mid-1980s. Further research has ranged from informing research priority setting and resource-allocation decisions, including quantification of the potential for research to spill over from one environment to another (Wood and Pardey, 1998), to much more specific targeting of germplasm collection and improved crop management practices to specific environments to increase the effectiveness of publicly-funded wheat research (Hodson and White, 2007). Only recently the need for CGIAR-wide, systematic characterization of production environments regained the attention (e.g. Kholova et al., 2013, Hajjarpoor et al., 2018, Supplementary Mat 12).

Within the G x E x M paradigm the “E” variable is hard to alter but can be characterized but, in recent times, much effort in agronomic research has sought to address parts of the “M” which often provides half to two-thirds of the yield gain (Evans 1993; Lynam 2004). Too often the proposed M is visioned as a package (BMP or GAP; best management practice or good agronomic practice, respectively) that tries to solve the many constraints in individual farmers’ fields. Many studies, however, suggest that management factors are largely additive (Aune and Bationo, 2008) and effective at scale. For example, in sub-Saharan Africa (SSA) maize yields on farms are strongly correlated with plant population density. Typically, maize is evaluated and recommended to be grown at ~55,000 plants/ha, yet most farmers don’t achieve half that population (Nyagumbo et al., 2019). . Farmers may well take a stepwise approach to improving their crop management, improving one practice and then moving on to another. In some cases the first adopted practice may be management (see for example Fremont et al., 2009) and in others it may be varieties (Cock and Connor, 2021 in press). One might reasonably argue in these cases that the G x M should include a range of levels of management so as to provide a measure of system or management stability Thus, Agronomists need to identify and focus with CI on the solutions that work at scale, which should be defined by data and analysis. There is then a need for ‘intelligence’ and better data about what farmers actually do, how varieties perform and how farmers change their production practices, especially when adopting new varieties. This should facilitate a better understanding of and ability to predict yield and other outcomes.

The question and challenge is how, and indeed if, it is possible to better integrate agronomy and G x E x M into product design and testing? Do we need to rethink agronomy in terms of (i) the problem we are trying to solve and the appropriate scale at which a solution can be

solved at (i.e. what are the larger scale agronomic domains to breed or evaluate for? – or, in simpler terms, stop trying to solve for every problem at plot level); and (ii) the designs, processes, data and analytical tools needed for G x E x M (i.e. how can agronomy add real value to breeding programs and processes?)

Discipline's contribution

Although CGIAR centres continue to work in this space the efforts remain rather scattered. To form a coherent CGIAR-wide strategy, the community of practice, the Consortium for Spatial Information (CGIAR-CSI), which is now supported by CGIAR Platform for Big Data in Agriculture. For the same purpose the BMGF foundation heavily invested in establishment of the Excellence in Breeding (<https://www.cgiar.org/excellence-breeding-platform/>) and very recently an Excellence in Agronomy (EiA: see <https://www.iita.org/iita-project/cgiar-excellence-in-agronomy-2030-incubation-phase/>) cross-CGIAR platform. In the case of agronomy, EiA will generate common data collection protocols or methods, and analytics to design and use data across the CGIAR (and others) system. These efforts should contribute to crop product design and product marketability (targeting), provide feedback on G x E x M priorities (Supplementary Mat. 12 and 15) and should be systematically updated in the overall breeding schemes. Such connection will require homogeneity of the scales at which we should make decisions about G x E x M which might be a challenge. Still, we are not aware of any systematic assessment of the impact of agri-system characterization and agronomic research in the CGIAR – this would be challenging, given the difficulty of constructing a robust counterfactual. Nevertheless, it is very likely that such research has made a substantial contribution to crop improvement in particular and research targeting and prioritisation in general (for some examples, see Harwood et al., 2006; CGIAR, 2012; Eriksen et al., 2011). In the absence of any estimates of the costs and benefits of this kind of work over the last 40 years, an impact assessment is long overdue, challenging though it would be to carry out.

Past and current status and challenges

Agri-system characterisation in the past was beset by problems of data, both quality and availability. Although the situation improved beyond measure since Bunting (1987), even now most agronomy research remains very localised, in large part because agronomy has always been postulated as being context specific. Agronomy needs a paradigm shift in thinking and practice to become data-driven, and to identify the constraints and solutions that can be solved at scale. As a result, till date most breeding programs do not have a clear strategy for G x E x M (let alone x S!).

The positive development is seen in availability of the high-resolution spatial data sets of climate, weather, soils, production systems including multiple cropping systems, crop and livestock distributions and production variables, field sizes – the list is long and expanding, with high-resolution, cheap and frequent-interval satellite imagery, crowdsourcing, and big data approaches being routinely applied. Data storage and archiving present few problems nowadays, in view of open-source repositories such as DataVerse (<https://dataverse.org/>) offering free archiving of public data in perpetuity and the cloud offering massive data storage

opportunities at low cost. Quality issues remain a challenge, but one of the great benefits of widely accessible open-source data is their increased use and evaluation, so that data problems come to light relatively rapidly. Still, the substantial gaps remain; Most agronomic experiments are not designed to be spatially representative, nor in most cases socially or gender representative. Furthermore, most experiments do not collect or share the data needed for modelling. Therefore, most agronomic knowledge is still neither predictable nor scalable. Especially in the developing countries, the nationally representative panel (repeated) surveys that provide up to date intelligence on varieties and agronomy are rarely available; nor the parallel data exists to provide linkages to health and nutrition. This is the gap which has to be filled for definition and quantitative prioritisation of crop product design. The Excellence in Agronomy platform (<https://www.iita.org/iita-project/cgiar-excellence-in-agronomy-2030-incubation-phase/>) will address many of these issues by developing protocols and tools to collect data at scale, and the analytics to share, interpret and add value to these data.

Another major challenge has been the expansion of the remit of the CGIAR, particularly in relation to global climatic changes. Even in the mid-2000s, Hodson and White (2007) noted the growing importance of addressing how different agri-systems and their associated biotic and abiotic stresses might shift in the future in relation to changing climate patterns (and a globally connected world). The speed of change seems to have taken everyone by surprise, and there is now a broad consensus that agriculture and food systems are not on a pathway that will enable achievement of the Sustainable Development Goals by 2030, particularly in the face of anthropogenic climate change. Still, the challenge breeders and other climate change researchers face is to justify the pre-emptive climate-change research and show how it can result in better use of the same resources to do more and better field research NOW. Much of the work of CGIAR on climate change is framed as Climate Smart Agriculture (CSA), an approach for transforming and reorienting agricultural development under the realities of climate change (Lipper et al., 2014). The aim is to achieve sustainable agricultural development for food security via the three pillars of increased productivity in combination with reduced impacts to climate risks and shocks, and mitigation of climate change through reduced greenhouse gas emissions. Implementing CSA often involves addressing trade-offs between the three pillars, but this has to be done in a way that is equitable and inclusive. What is this likely to mean for crop improvement in the future?

Future perspectives

The speed and extent of climate change impacts on agriculture and food systems have broad-ranging implications for the international agricultural research for development agenda, including for crop improvement. These impacts include increased frequency and severity of droughts and floods, pests and diseases that are becoming more prevalent and/or moving into new habitats, and changes in the start and length of growing seasons, for example. There are new needs for crop improvement, that highlight productivity, nutrition, and climate resilience as key dimensions for production systems in low income countries (DeFries, 2018; Davis et al., 2019).

An approach which is gaining momentum is to move away from identification of representative sites and scaling out from them towards use of the principles of precision agriculture. Precision agriculture is based on the principles of: (a) capture of data at an appropriate scale and frequency (b) analysis and interpretation of that information; and (c) implementation of a management response based on the analysis (National Research Council, 1997). These same principles have been used to determine which cultivars of sugarcane are well adapted to particular environmental conditions and how they respond to management. The system monitors weather, soil type, cultivars grown, cane yield and quality and several of the major management practices such as data of planting and harvest and use of ripeners of every sugarcane field in the major growing areas of Colombia. The data is then analysed and used by growers to determine, inter alia, which is the most suitable variety for their fields (Cock et al. 2011). As new varieties come available some early adopters try them and share their information so that other farmers can gain from their experience. Effectively every cane field becomes an experiment providing information on varietal performance, information grown to sugarcane for sugar production. In Australia a similar scheme was set up for rice (Lacy 2011). More recently within the CGIAR system the same approach has been used with small farmers to draw insights in the whole G X E X M continuum (Jimenez et al., 2016; Jimenez et al., 2019). In oil palm similar methodology based on commercial field data has been used to determine nutrient response under varying weather conditions. This approach moves away from the idea of context (field) specific solutions. This includes yield prediction and using survey data as a laboratory (e.g. nutrient response curves can be generated from production practice and yield data from farmer's fields), identification of constraints and any spatial patterns, and targeting (both domains of automated optical inspection (AOI) and potentially markets/returns on investment (ROI)) (e.g. Palmas and Chamberlin, 2020). To these can be added the spatial and temporal shifts in production environment characteristics that result from both fast and slow climate and atmospheric change. Production agri-system characterisation that addresses these changes, along with ex-ante (trade-off) analyses, is a key input to a re-evaluation and quantitative justification of priority setting and resource allocation decision-making processes in CGIAR (though there are other dimensions that have to be considered too, such as minimizing the environmental impacts of agricultural production and addressing rapidly-changing demand for quantity, quality and types of food).

In practice

Several actions can be highlighted that could enhance the contribution of agri-systems' characterization to climate- (and nutrition-) smart crop improvement (also in Balié et al., 2019).

The need for regular foresight and horizon scanning (Supplementary Mat. 15-16), to understand the rapidly-changing context of small-scale food producers in relation to breeding objectives and targets, coupled with better understanding of the potential role of changing diets and consumer demand on local food systems (Supplementary Mat 17-19). This might include re-consideration of the trialing sites, and treatments, for better capturing G x E x M which shall also represent relevant "S" components. CI-teams usually have the sites chosen (i.e. multi-location trials "MLTs") and this could be expanded to include sites or treatments important for

understanding and predicting G x E x M in context of S. These ‘sentinel’ sites should be properly instrumented and characterised. Furthermore, all advanced trials/METs should have minimum data sets that can contribute to spatial analysis and prediction (Supplementary Mat. 12, 15). Agronomy programs need to see the value of investing in sentinel sites so this becomes a shared enterprise. These should be complimented by a system of farm plot surveys and crop-cuts to drive predictions and insights (feedback) on what farmers actually do, what works and under what conditions can it be scaled. This would provide precious, real-time feedback, especially on varietal adoption but equally importantly on agronomic practice and the design of METs. This is not a new suggestion. What probably needs to be done is to demonstrate to CI programs the value of modelling and prediction, so that they might invest into the extra data collection. Likewise, agronomy programs might need to see the value of investing in sentinel sites so this becomes a shared enterprise.

Supplementary Mat. 11 Yield-gap analyses for prioritizing crop improvement strategies

David Connor

Food demand

Our world requires greater food production to better feed the 0.8 b who are currently underfed as well as the expected increase that will take total population from 7.9 b in 2020 to 9.7 b in 2050. Longer term projections are uncertain; population should stabilize then or soon after, and then decline. A reasonable objective is to obtain all future increase in food production, with yield increase decreasing from a current value of 1.2%/y to 0.66%/y by 2040 and 0.50%/y by 2050, on existing crop area, aided by less wastage, more intensive cropping and less area devoted to biofuel production (Fischer and Connor, 2018). In the last 10 y crop land is increasing at 0.05%/y although the area of major crops is increasing more, 0.97%/y. There is long-standing consensus that the challenge is great and will require a strong focus on maintaining crop yield increase (Hall and Richards, 2013; Cassman and Grassini, 2020). The question is how?

Farm yield, potential yield and yield gap

In any location, or averaged by region, the potential yield (PY) of any crop is the yield obtainable with the most adapted cultivar grown under the best management practices, meaning no biotic stress. This yield will be more variable under rainfed conditions (PYw) than under irrigation (PY) for reasons of year-to-year variation in rainfall. Best practice agronomy is not static but develops with time. The basic requirement to provide adequate nutrition, and water in the case of PY, together with control of pests, weeds and diseases remains but new fertilizers, other agrochemicals, and GPS-guided machinery together with practices such as zero tillage increase PY and PYw. Farmer skill in coordinating the many interventions in response to in-season weather is also required for successful cropping (Kirkegaard, 2019). Inputs and costs of management usually increase with yield such that farmers commonly identify an economic

yield which is less than PY, 20–30% (Grassini et al., 2011; Fischer et al., 2014). In some cases, farmers may choose cultivars which yield < (PY or PYw) for economic benefit associated with quality or processing-characteristics of products. For all cultivars, however, genetic progress will seek to increase PY which remains an important benchmark because it can be more closely achieved if prices for products increase sufficiently.

The difference between PY and what farmers achieve (FY) establishes a yield gap ($Yg = PY - FY$ or $PYw - FY$) that defines the yield gain that is possible with current cultivars; i.e. existing genetic potential. Breeding seeks to increase PY and Yg while agronomic practice seeks to increase FY and reduce Yg.

The status of crop improvement

Available data for FY and PY (or PYw) are collated and analysed for four major crops, wheat, rice, maize and soybean in Fischer et al. (2014). The authors present FY, PY and Yg (%FY) for 2010 with their progress (%/y) over the previous 20–30 y. The data are summarized here as averages and ranges for individual measurement sets for the regions unadjusted for crop area. The additional data for cassava are from experimental and survey work in Kenya and Uganda (Fermont et al., 2009) and Nigeria (Adiele et al., 2020). Presenting Yg as %FY allows quick assessment of possible yield gain to improved management relative to current performance. Yg = 100% reports a potential doubling of yield; Yg = 200% a tripling, depending on farmers' optimum.

Crop	Estimated values at 2010				Recent rate of change (%/y)		
	FY (t/ha)	PY (t/ha)	Yg (%FY)	Yg range (%)	FY	PY	Yg
Wheat	1.8–8.6 (4.3)	2.6–10.8 (6.5)	48	26–69	0.83	0.61	- 0.23
Rice	1.8–9.5 (5.0)	3.6–12.0 (8.1)	76	25–150	1.19	0.78	- 0.39

Maize	1.4–11.4 (5.6)	5.3–15 (11.4)	104	36–400	1.69	1.08	- 0.61
Soybean	2.3–2.9 (2.6)	3.0–3.8 (3.5)	31	30–33	1.30	0.50	- 0.80
Cassava	1.9–12.5 (7.5)	6.0–35.5 (20.9)	181	82–219	0.62 ^a	1.48 ^b	-

^a world value; current area increase is 2.3%/y (1998–2018) (FAOSTAT). ^b(Fischer et al., 2014)

These yield gap analyses describe and quantify the relative contributions of breeding and agronomy to FY increase of the major and some emerging crops. It reveals important features of the current status of crop improvement and the substantial differences that exist between and within individual crops. Even at a constant increase in PY (or PYw), the rate of gain decreases as yield increases.

Wheat is the most developed of the three main cereal crops with an average Yg of 48% compared with rice (76%) and maize (104%). The analysis indicates continuing progress in both FY and PY in most locations and opportunities to close Yg in each crop. For wheat, Yg was decreasing in all regions except Northern France and UK where Yg were 26 and 34%, and FY were 8.6 and 8.0 t/ha, respectively. For **rice**, Yg was smallest in Egypt (25%), Indonesia (30%) and Jiangsu, China (38%) and largest in Madhya Pradesh, India (150%) and NE Thailand (140%). Although the overall trend was to reduce Yg, it was shown to be increasing in Central Luzon, Philippines, (0.1%/y), Indonesia (0.6%/y), Japan (0.3%/y). For **maize**, the wide range of Yg (30–400%) reflects the environmental and socio-economic conditions under which the crop is grown. Yg was smallest for Iowa, USA, (36%) and largest for Eastern Africa (400%). Yg was decreasing strongly in Brazil (-1.8%/y) and Argentina (-1.3%/y) and even in Iowa (-1.0%/y), where maximum yields are achieved (11.4 t/ha) but was increasing in China (0.1%/y) and Eastern Africa (0.7%/y).

Yg for **soybean** (30–33%) reveal the high technical efficiency of production in three major producing countries. Despite being small, Yg was decreasing, fastest in China (-1.3%/y) and slowest in the USA (-0.2%/y). For Argentina, the rate was -0.9%/y. In all locations, FY was increasing faster than PY. **Cassava** is also a relatively new crop on the world stage emerging from a background of subsistence agriculture to be now the fourth largest carbohydrate producer after the three cereals discussed above. Yg (82–219%) express the undeveloped state of the crop, much of which is grown by smallholder farmers with low inputs on infertile soils that cannot be overcome without major attention to nutrition. In these African data, Yg are consistently large, average 181%, with ranges in Kenya (153–216%), Uganda (180%) and

Nigeria (82–219%). FY progress is slow with increasing production depending on expansion of crop area. Among major producing countries, FY is decreasing in Nigeria (-0.48%/y) but increasing in Thailand (2.4%/y). PY, in this case PYw, reveals that the crop is capable of high yields in favoured environments and the potential for substantial yield increase generally by improved management with existing cultivars (Cock and Connor, 2020).

Guidelines for the future

The urgent and enormous challenge to feed the world population during the next two decades as it increases towards a maximum requires focus on increasing FY in the most rapid way and so minimize the need for expansion of the crop area. The Yg analysis above identifies how existing crop improvement programs are increasing FY. It also provides guidance on ways to prioritize efforts to increase PY by breeding and/or FY by agronomy for individual crops and environments. It simplifies a more detailed analysis, including that of risk, by van Oort et al. (2017). In general terms, when Yg is small, greater PY can only be obtained from genetic gain and yet, while there is much hope for transgenic plants, there are yet no proven solutions to deal with the multi-gene complexity of yield response (Passioura, 2020). When Yg is large, a faster and surer route to greater FY is through improved agronomic practice and attention to social and economic factors that limit adoption by farmers. Both analyses reveal substantial potential of improved agronomy to increase FY by removing restrictions to expression of the genetic potential of current PY. More and better data are required at a smaller scale and could be usefully included in the developing Yield Gap Atlas (www.yieldgap.com).

The future for crop improvement is, therefore, one of cooperation. Where Yg are small, interaction between breeding and agronomy and the best farmers is essential because PY gains, inevitably small in the absence of some breakthrough, require skilled farmers to increase FY by careful agronomic management to improve resource-use efficiency. Such farmers also need help with new crops and new cropping systems to meet environmental standards. Where Yg are large, FY is more surely and rapidly increased by improved agronomy and a focus by breeders on maintaining PY. Studies have established economically feasible steps that farmers can follow on the pathway to greater yields (Fermont et al., 2009). Cooperation here extends beyond breeders and agronomists to include specialists in development of effective market chains to provide sale of inputs and purchase of products. An important focus for the next two decades must be Sub Saharan Africa where population growth is greatest and is outstripping agricultural productivity (van Ittersum et al., 2016). One can dream of more irrigation and intensification of cropping, but the soils and other resources are yet to be defined in many areas (Guilpart et al., 2017).

Strategic guidance is important, because recent developments and enthusiasm for new biotechnological and molecular methods are already confusing research efforts to increase crop productivity. A project, so far unsuccessful, to increase PY of rice by transforming to C4 photosynthesis could be defended for those rice systems with small Yg. But not so, a larger program to genetically modify both photosynthesis and starch storage of cassava (Sonnwald et al., 2020) where generally large Yg reveals that yields could be increased >2x by better

agronomy. Even if the project were successful, the hoped-for genetic yield benefit could not be expressed in FY without better agronomic support. Better to start first on that, now!

Conclusion

Success to properly feed a more populous world in 2050 on current agricultural land cannot be assured without greater cooperation between the various players (plant biologists, breeders, agronomists, soil scientists, adoption experts) and focus on areas and crops where major gains can be made now. The timescale is short, so major work must concentrate on applying known tools and technologies. PY will continue to increase but at a decreasing rate. Hoping for breakthroughs is allowed but the only evident step change in FY is that available from improved agronomy provided adoption can be hastened. Major advances are required in Africa where population growth is greatest, agriculture least developed, and agricultural resources insufficiently defined. Demonstrable success is essential by 2035.

Supplementary Mat. 12 Envirotyping & Crop Modelling

Charlie Messina, GL Hammer, Yunbi Xu

Introduction

Envirotyping (environmental characterization) can be defined as a technology to dissect, understand and characterize the natural or man-made environment (E or M) and its consequences on the crop (G X E X M interactions; e.g. Xu, 2011, 2012, 2016; Xu et al., 2012; Cooper et al., 2014). There is much of the static information available on G, E, M and GxExM interactions but often there is a poor understanding of the processes underlying these interactions.

CI faces dramatic environmental risks due to climate change which may be greater than expected (Saini, 2020; Searchinger et al., 2014). Breeders may have to develop climate-resilient cultivars to adapt the agri-systems to the severing environmental changes. For many breeding targets, the environment determines how the genotype will be expressed into a phenotype. Therefore, environmental characteristics of agri-systems will have to be reflected in the phenotyping protocols and the environmental context of phenotyping will also determine the relevance of a given phenotypic data to CI. In short, precision phenotyping needs to be coupled with precision envirotyping.

Past and current status

Envirotypes are influenced by several major categories of factors, including climate, soil, crop cultivar, crop management practice and companion organisms (Xu, 2016). Breeding programs, particularly in multinational seed companies, have benefitted from environmental data for their experimental stations, trial sites and multi-environmental trials (METs) across countries. This information has been used to (a) classify environments (eg. mega-environments, near iso

environments); (b) facilitate statistical analysis of environmental effects; (c) select test sites (Xu, 2016). For example, maize mega-environments in southern Africa were delineated by combinations of maximum temperature, season precipitation and subsoil pH (Bänziger et al., 2006; Xu, 2010). To control the error for CIMMYT maize sites, trials were placed to avoid/minimize field gradients. In stress prediction, wheat rust race UG99 has been predicted for its epidemic trends based on historical climate and crop production information (Singh et al., 2006). For in-vivo environmental characterization of agri-systems, a smart, large-scale data collection systems (e.g. internet of things; IoT) and information management system equipped with artificial intelligence will be needed to facilitate the management and conversion of the extremely complex data into the useful information to CI.

Envirotyping under controlled and managed environments is another option and has been largely used by geneticists and physiologists mostly for basic research. It can be expected that its applications in CI will become increasingly possible with established national phenomics facilities with improved envirotyping capacity.

The opportunities for environmental characterization were complemented and greatly expanded across spatio-temporal scales by agri-systems modelling tools. These in-silico methods can provide - if used appropriately - critical answers on “what is in the black box” (see introduction paragraph of this section), with the high spatial resolution and across temporal scales which is hardly possible to achieve otherwise. The need for crop models arose precisely from the above described apprehension that one has very limited insight into the dynamics of experimental or cropping systems by simply “running the trials” (De Wit 1965; Keating et al., 2003; Jones et al., 2016; Chenu et al., 2017, Kholova et al., 2020). Dynamic crop growth and development models were established to provide a transfer function that relates genotype, environment and management to yield (deWit 1970; Arkin et al., 1976; Vanderlip and Arkin 1977). Currently, crop modelling and simulation approaches provide an invaluable tool to CI-teams to quantitatively characterise the nature of the environment experienced by crops in a manner that connects more directly with crop status than raw climatic variables and across spatio-temporal scales. Environmental characterization is the base for designing the suitable crop type (G) and management (M) agri-system interventions.

Traditional CI-programs have been mostly sceptical towards integrating the in-silico modeling approaches into their portfolios. One of the reasons might be that many of the modelling teams operate incoherently with the CI-requirements. Other persisting hurdles compromising the modelling community are linked to the minimum, quality data requirements for model parameterization and model set-up evaluation as well as utilization of appropriate modelling tools to answer given questions with relevant simulations (common “modelling misconducts” are reviewed e.g. in Kholova et al., 2020). Still, advances in predictive agriculture are slowly but steadily changing the ways we view breeding and agronomy and the transition from decisions based on description of experiments to the use of predictive algorithms and simulation is imminent. Leveraging the on-going revolution of molecular breeding, prediction capabilities empowered by the integration of quantitative genetics theory with crop physiology and environmental science can improve productivity gains (Messina et al., 2020). Modeling

and simulation enable assessing and informing the creation of genotype-management technologies that help solve problems before these occur (Cooper et al., 2020). One of the methodologies underpinning the transition from descriptive to predictive agriculture is biomathematics that manifests in the form of crop growth models in agricultural science (Hammer et al., 2019). In advanced breeding programs, crop modeling already plays a pivotal role in the determination of the genetic gain (G) per unit cycle of selection (s) (see Formula below). The rate dG/ds depends not only on the decision made by the breeder today but on all prior decisions made since the inception of the breeding program (t_0), therefore the need to integrate decisions over time (t),

$$dG/ds = \int_{t_0}^t \int_c [i(c,t) \times r_a(c,t) \times \sigma_a(c,t)] dc dt$$

It also depends on how environment classes (c) are sampled by the testing system and how the outcomes of testing during the cycle of selection are weighted according to their frequency of occurrence in the geographies of interest. Therefore the intensity of selection is expressed as a function of c, and it is integrated over all possible environments defining the target population of environments. Podlich et al. (1999) demonstrates this framework and the advantages over other approaches in the presence of genotype x environment interactions. Crop models proved useful to reduce this theory to practice by enabling breeders to determine both the types of environment classes that define the target population of environments as well as their long-term frequencies (Chapman et al., 2000; Bustos-Korts et al., 2019 b), both of which are used to determine the weights to be applied in selection strategies. Intensity of selection (i) is a decision of the breeder that of course depends on both t and c, and when c is not considered, decisions at any point in time are influenced by the randomness of occurrence of c in the target geographies with the consequential reduction of dG/ds .

Because crop models encapsulate how plants respond to the environment, they play a critical role in the design of testing systems and phenotyping strategies (Messina et al., 2011; Cooper et al., 2014; van Eeuwijk et al., 2019; Bustos-Kortz et al., 2019 a). For example, simulations can enable detailed quantification of the soil-crop water status dynamics through the life cycle of a crop using the simulated daily soil water supply/crop water demand ratio as the crop water status index for target site-season combination and classified to form environment classes for the set of target environments. The water stress “envirotypes” are thus described as quantitative characters such as timing and intensity of crop water limitation on large scale (Chapman et al., 2000, Loffler et al., 2005; Chapman et al., 2000; Chenu et al., 2011; Hammer et al., 2014; Harrison et al., 2014; Kholova et al., 2013). Furthermore, when models are developed to capture genetic variation in adaptive traits at the right level of soil-plant-atmosphere organization (Hammer et al., 2019) these provide a means to undertake simulation studies and determine phenotyping targets. Precise phenotyping, in turn, enhances the rate of crop improvement by unravelling the gene and environment context dependencies underlying the genotype-by-environment interactions of TPE (Hammer et al., 2014; Harrison et al., 2014, Tardieu 2012). Such information is also crucial to design the testing systems and managed environments to consequently identify the adaptive traits for selection, not on themselves but through their integrated effects on yield (Supplementary Mat. 3-4). The practical application

of this approach has led to development of drought tolerant maize germplasm. In this case the modeling-led approach supported the design of phenotyping systems to improve rates of genetic gain (Cooper et al. 2014) by quantitative understanding the role of anthesis-silking interval (Edmeades et al., 1993; Messina et al., 2019), ear size at silking (Cooper et al., 2014), canopy size and radiation use efficiency (Messina et al., 2018), and transpiration response to vapor pressure deficit in TPE (Shekoofa et al., 2015). Since the introduction of drought tolerant maize in 2011, the area planted with this germplasm increased to about 20% (McFadden et al., 2019). In the context of the breeder's equation, the magnitude of σ_a depends on the germplasm and our ability to create the testing infrastructure in the form of managed environments and evaluation networks that generate repeatable data, and the ability of the breeder to implement agronomic management practices for the underpinning physiological determinants of yield to be expressed. Within this same framework, we consider the impact of crop models on the improvement of prediction accuracy (r_a), which depends on both c and t ; genetic variance could vary among environment types and changes as selection operates to increase the frequency of favorable alleles in the breeding populations (Cooper et al., 2014). By modeling genotype, environment and management components underpinning performance it was shown that crop models can increase r_a , where the improvement increases with increasing genotype by environment interactions (Podlich and Cooper, 1998; Chapman et al., 2003; Hammer et al., 2005, Technow et al., 2015; Cooper et al., 2016; Messina et al., 2018). Such modelling method application, however, requires trained transdisciplinary teams. There is mostly a clear gap in the trained workforce not only in breeding, but also in agronomy management, envirotyping, and data science and therefore envirotyping and the generation of quality data inputs for models remains an unresolved problem. Within hierarchical Bayesian frameworks it is feasible to estimate some environment parameters (Messina et al., 2018) but more research is needed both in the development of sensing capabilities and modeling.

Future perspectives & conclusion

There is a lot of interest to utilize genomic selection (GS) approaches in CI. However, GS based solely on statistical models (e.g. machine learning) for prediction of phenotype based on genotype are limited as they do not account to dynamic interactions of G with E and M (more in e.g. Hammer et al., 2020, Kholova et al., 2020). The emerging solution is to integrate the crop models with whole genome prediction as a specific case of a generalized additive model (GAM; Wood, 2017), where the crop model is one of the many possible functions one can consider for modeling the relationship between markers, traits underlying yield and environment. Importantly, crop modelling is a sole approach which can scale up testing the effects of future environments anticipated with anthropogenic climate change (Hammer et al., 2020; Harrison et al., 2014). Because mechanistic crop models encapsulate years of scientific progress, they provide a dynamic, knowledge driven representation of the terms in the traditional statistical model. Presenting the use of crop models as an integrator of knowledge, a tool to design systems to maximize the expression of intrinsic σ_a , and at the same time a function within a GAM, facilitates the dialogue between physiologists, quantitative geneticists, agronomists and breeders. Developing a common language and fruitful dialogues is necessary to create blueprints for the implementation of the technology. However, field programs that are

both resourced to understand and code the physiological underpinnings of adaptation, and to evaluate germplasm to make selection decisions based on this prediction capability are necessary. While some advocate this advanced technology is only feasible for application in large scale agriculture of developed nations, this is unlikely to be the case. Because smallholder systems are far more complex than developed agriculture and their breeding programs less resourced, digital technologies can bring significant relative value by reducing the amount of field testing in complex geo-political conditions, leveraging managed environments for prediction, and evaluating candidate genotypes for performance in a myriad of different socio-economic and physical environments characteristic of smallholder agriculture. It is not difficult to envision the net benefit of properly resourced programs structured around the use of advanced phenotyping environments, quantitative genetic algorithms and crop models.

Supplementary Mat. 13 On farm variety testing

Jacob van Etten

Introduction

On-farm testing of crop materials is a crucial aspect of the crop improvement cycle. Breeding is expected to contribute to improved performance of crop varieties in their target environments. Conventional plant breeding experimental designs are generally optimized to identify genetic effects and isolate them from environmental effects to accelerate selection. This also means, however, that these experiments can suffer from limited external validity, especially when they do not represent production conditions that are typical for the target environment, which may be highly heterogeneous (Atlin et al. 2001). On-farm testing complements on-station work to provide higher external validity to predict performance when the variety is grown by farmers on their own. On-farm testing is generally done on many farms under diverse environmental and management conditions that reflect the eventual use context of the final breeding products.

On-farm testing has a role during several stages of crop breeding. The focus of this chapter is mainly on on-farm evaluation of materials that are candidates for official release or already released varieties. The evaluation of pre-release materials generally includes released materials for comparison. During these stages, on-farm evaluation generates information for variety release decisions and variety promotion/marketing decisions. Information can also be used to assess the likelihood of farmer variety adoption and expected genetic gain (progress in productivity over time due to breeding efforts). On-farm trials are generally done in a farmer-participatory way, involving farmers in different stages of the experimental cycle and especially in the evaluation of the varieties. Farmer-participatory on-farm trials expose farmers directly to varieties growing in target environments. This provides a shortcut where other methods would mean much more trouble to fully represent all factors (crop modelling), mobilize tacit knowledge (trait prioritization exercises), or foster knowledge exchange between different professionals (farmers, breeders and others).

Past and current status

On-farm testing was not much different from work on agricultural stations before the advent of modern statistics in the agricultural sciences in the 1920s and 1930s. Randomized trials designs improved statistical inference but were difficult to implement by farmers, leading to a methodological and institutional divergence between experiments done on station and on farms (Maat and Glover 2012; Parolini 2015). Randomized designs on farms had to deal with balancing farmers' practical constraints and interpretation needs on the one hand, and the needs for scientific rigor and statistical validity on the other. In the 1980s, Farming Systems Research led to a new emphasis on on-farm trials and led to Farmer Participatory Research (FPR) as a focus in the 1990s. FPR faced logistical and methodological challenges, and presented high requirements for research skills (Martin and Sherington 1997). It has rarely led to 'institutionalized' long-term collaboration between research organizations and farmer organizations or civil society.

Many efforts in the period from 2000-2010 have addressed these constraints, including methodological ones. For example, Snapp (2002) developed the mother-baby trial format, which combined common "mother" plots (with a more complex design) with smaller baby plots on farms (having only a few treatments), allowing for different ways of engagement with the trial. Virk et al. (2009) showed that unbalanced trials can be analyzed using appropriate statistical methods (GLM, REML).

Despite progress, many issues persist. Misiko (2013) documented how participatory variety selection on common plots suffered from free-riders (participants who only show up when there is no work to do on the plot) and led to haphazard observation and low accuracy in variety selection. Almekinders et al. (2019) reviewed research that finds that on-farm trials do not always represent variation in growing conditions or cropping systems, and advise that researchers need to create a more reflexive way to design research, based on substantial dialogue with farmers. Kool et al. (2020) found that reports of on-farm trials performed in Africa rarely describe relevant yield-determining factors that affected the experimental results, the crop growing environment, how plots were selected, or the precise farmer practice that was compared with the experimental treatments. This limits reproducibility (the ability to generate a similar trial to verify results) and external validity (the degree to which the trial results can be confidently translated to real farming conditions). Brown et al. (2020) write that much on-farm trial data remains unpublished and that the rare datasets that are published are not standardized, making it difficult to aggregate and synthesize results. Data synthesis could facilitate the generalization of insights and improved understanding of interactions between genotypes and environments.

During the period of 2010-2020, however, a number of studies have started to address the remaining challenges. Several studies have suggested more farmer-led formats can work through trustful working relationships and methodological innovation (van Etten 2011; Waters-Bayer et al. 2015; Humphries et al. 2015). Making formats easier and handing trials more fully over to farmers could relieve many of the constraints noted above. Detailed studies have found that farmers can provide experimental data that is accurate enough for many research goals

(Steinke et al. 2017; Ochieng et al. 2019). New digital methods for data collection and communication can help to configure participation in different ways and facilitate two-way communication that overcomes many of the challenges of previous farmer-participatory formats (Steinke et al. 2020; van de Gevel 2020). Van Etten et al. (2019a) have shown how this could be done for variety selection by introducing an approach based on crowdsourced citizen science (digitally supported large-scale participatory research). It has been shown that the resulting trial data make it possible to analyze genotypes by environment interactions as they occur under farm conditions, by linking georeferenced trial data to daily temperature and rainfall data (van Etten et al. 2019b). Continued statistical innovation has helped to support more flexible on-farm trial formats (van Frank et al. 2019; Turner et al. 2019).

Future perspectives

Big data approaches are becoming more important in breeding through omics and high-throughput phenotyping. In comparison, on-farm testing has made much less technological progress from the beginning of the twentieth century. The current use of on-farm trials in the global South by CGIAR and NARS is in stark contrast with prevailing practices of large private seed companies in the North, which may cover thousands of farms every season for each crop and region, which can lead to detailed insights into GxE (Marko et al. 2017). By having much more detailed, biologically relevant feedback from farmers' fields, breeders would be much less groping in the dark about breeding goals and expected adoption of new varieties.

Only a fraction of the investment made in other aspects of the breeding process could lead to an accelerated methodological improvement in data collection, analysis and interpretation, which would ready on-farm testing for 21st century breeding [see Supplementary Mat. 6]. Investment should especially target the accelerated development of professional software to organize on-farm trials, including through crowdsourced formats (cf. <https://climmob.net>), to collect data (for example, image-based data collection, Makanza et al. 2018), label data with ontologies to allow for wide use in breeding software, and perform statistical analysis (following up on the work cited above). A full transformation of breeding to fully embrace on-farm trials will require capacity building and inserting the new ways of working into partnerships between breeders and other stakeholders in the seed system. As a result, on-farm trials could be more fully integrated into breeding product management cycles, providing not only information for “stage gate” decisions (moving breeding materials to subsequent phases), but also the constant redefinition of product profiles (breeding goals for new varieties).

Practical support to CI teams

Crop improvement teams could use support on various aspects to improve on-farm testing, making use of recent advances in digital tools and possibilities to do massified testing. Now, on-farm testing is still often done by breeding programs themselves and involves few other scientific disciplines.

CI teams will need to be supported through high-quality partnerships with stakeholders downstream from the breeding programs, such as extension programs, NGOs and farmer organizations, are crucial and need high-quality facilitation. Such partnerships could make on-

farm testing a more professional activity by building up the combination of expertise in logistics, data management, farmer engagement, and facilitation of the interpretation of information with multiple stakeholders. On-farm testing partnerships should bring different stakeholders together to interpret the information, including breeders, seed producers, product managers and seed marketing experts. This way, on-farm trials can become a crucial part of engagement with the overall seed system.

From a scientific point of view, on-farm testing can become an important focus for interdisciplinary dialogue to integrate insights and generate new hypotheses. On-farm trials should become a primary platform for interdisciplinary dialogue, not only with non-research stakeholders, but also between breeders, physiologists, crop modelers, agronomists, social scientists and others.

[1] An analogy for the current situation could be that of a postmodern guitar performer, sitting in the dark, who cannot see the faces of the audience, and is forced to play only with one hand. The music is beautiful and the finger picking very sophisticated, but the guitarist could have done much better with two hands and will never know if the audience liked it until reading the reviews much later.

Supplementary Mat. 14 Participatory plant breeding

Salvatore Ceccarelli and Stefania Grando

Introduction

A breeding programme becomes participatory when farmers (as the most common clients of the CI programmes), but also many other stakeholders, share with scientists - on an equal power-relationship - all major decisions made throughout all the main stages of a breeding programme shown in Fig. 1 (below as also in the main text). A distinction has to be made between participatory plant breeding (PPB) and participatory variety selection (PVS). The latter term is used when farmers' participation begins during testing of experimental varieties. PVS is technically easier to organize because farmers are involved only in expressing their opinion on the limited number of lines that usually reach that stage (Ceccarelli et al. 2000); however, they are left with a limited number of possible choices. Furthermore, with PVS there is the risk that breeding material that farmers might find desirable for adaptation to their social and physical environment, could be discarded during the selection in segregating populations and early testing stage, i.e. before it is even seen by them.

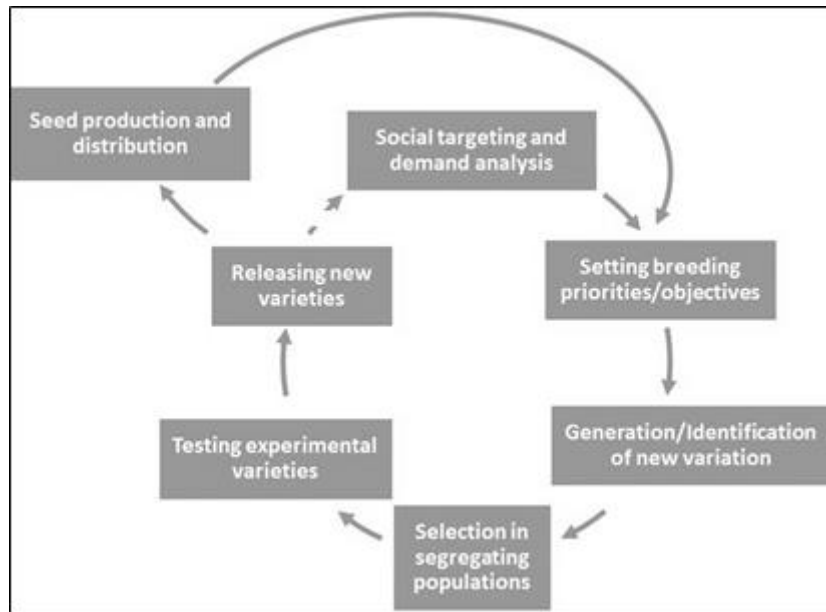


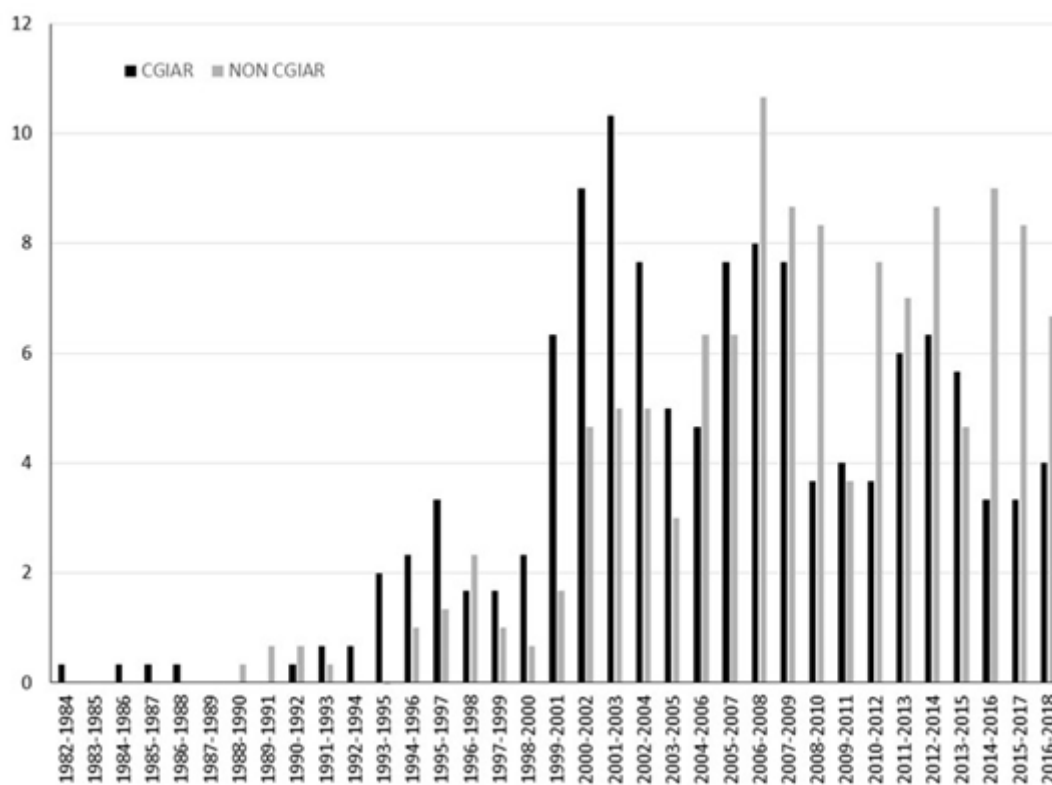
Fig. 1 Main stages of a breeding programme (Modified from Tufan et al. 2018)

A truly participatory breeding programme is implemented in a decentralized mode, namely the entire cycle in Fig. 1 (as in the main text) is implemented in the target environment; as such, it maximizes selection accuracy (r_{AI}) by exploiting the repeatability of genotype by location interactions. In its essence, the role of PPB in relation to farmers' rights is recognized in article 9c of the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO, 2009).

Past and current status

Participatory research, in a form, which has become known as the “Farmers First” concept, was initially proposed in two classic papers at the beginning and in the mid-eighties (Rhoades and Booth 1982; Rhoades et al. 1986). In the case of plant breeding, either PPB or PVS have been implemented in 69 countries, 10 of which developed, on 47 crops, including self-pollinated, cross-pollinated and vegetatively propagated, by different types of Institutions including CGIAR centers, Universities, and NGOs (Ceccarelli and Grando 2019).

While there is no indication of a decline in the use of PPB and PVS, a literature review shows that in the last 10 years there has been a shift in the number of papers published on the subject, changing from CGIAR centers contributing more up to about 2002-2004, to non-CGIAR Institutions/Organizations contributing consistently more after 2006-2008 (Supplementary Fig. S4) despite the PPB's greater demonstrated efficiency (Ceccarelli 2015).



Supplementary Fig. S4 Contribution to publications on PPB and PVS by CGIAR and non-CGIAR Institutions and/or organizations during 36 years' period (the data are 3-years moving means; from Ceccarelli & Grando 2019).

One of the criticisms moved to PPB and PVS is that by relying only on farmers' selection, it is neither efficient nor effective as it should include other stakeholders (Atlin et al. 2001); this criticism is unfounded because, in practice, PPB and PVS always include a range of relevant stakeholders (Bocci et al. 2020). A second criticism refers to the difficulty of releasing PPB or PVS varieties because of the false perception that PPB and PVS cannot generate uniform varieties. Actually, there are examples – though not many – of varieties released from PPB such as potato (Laurie and Magoro 2008), rice (Gyawali et al. 2010) and sweet potatoes (Gibson et al. 2011). There are also cases of varieties adopted without being released. For example, in Syria, and only with barley, there were 86 varieties selected by the farmers through PPB, adopted in different provinces on several thousand hectares (Communication Team ICARDA. 2009).

Furthermore, in the near future, the issue of seed sale of heterogeneous material will no longer be a problem, at least in organic European agriculture because of the new regulation of the European Parliament and of the Council on organic production and labelling of organic products to be implemented in 2021 (<https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32018R0848>), that will allow the marketing of plant reproductive material of organic heterogeneous material without having to comply with the requirements for registration and without having to comply with the certification categories of pre-basic, basic and certified material. Documented advantages of PPB/PVS are the production of varieties with a yield advantage over the best check ranging from 3.3 to 30.4% (Ceccarelli

et al. 2007), greater adoption rate (Galluzzi et al. 2014) even in the absence of formal release, increased genetic diversity (Joshi et al. 1997) and household food security (Joshi et al. 2012).

Future perspectives

One of the main global challenges is climate change. There are several examples of interactions between climate change, crop development and both pests and their natural enemies (Heeb et al. 2019). The complexity of climate change is made even worse by the fact that the changes in temperature and rainfall and its effects on biotic stresses are largely unpredictable and location specific. Therefore, the question is how a conventional and centralized breeding program, even if based on methodologies expected to improve selection efficiency such as genomic selection, can address what can be defined as a “moving target”? In other words, if in the next ten years, as a mounting body of evidence suggests, different locations will be characterized by a different pattern of rainfall, rainfall distribution, temperature, and, consequently, by a different scenario of pests and diseases, how do we choose the parental material to generate the genetic variation needed to respond to an ill-defined and changing objective?

A decentralized breeding program such as participatory plant breeding, which is already addressing location specificity, can be made even more effective by the use of heterogeneous populations, namely mixtures and evolutionary populations (Wolfe and Ceccarelli 2020) and by incorporating important tools in social targeting and demand analysis such as Customer Profile and Product Profile development. These tools, commonly used in private breeding, should be incorporated in the public CI programmes to address two key questions, namely breeding for whom and breeding what type of variety, respectively.

Developing a product profile is an important step in designing a breeding program because it contains a clear description of the characteristics of the variety to be developed. Within the target population of environments a breeding program is addressing, it is possible to develop different product profiles for the same crop grown within the same environment but for different end-uses – for example the case of malting, food and feed barley. The actual implementation of a given product profile can obviously benefit from a wide range of molecular tools and therefore participatory molecular breeding is quite possible.

At time, criticism is moved to PPB as a “fashion” or as “bandwagon” meaning that has become an easy way of attracting money. The “bandwagons” in science are well known. There has been a time in which biotechnology was labelled as “bandwagon” (Simmonds 1991). Simmonds wrote: “Biotechnology may be really useful sometime well into the next century but I’d want to see the crucial 10.000 ha passed before I’d agree that it were of any use at all; I’d require 10.000 hectares of an excellent cultivar, **freely** chosen by farmers and uniquely constructable by molecular tricks.” I highlighted “freely” because when this was taken up by Bernardo (2016) four years ago Bernardo forgot the importance of that word when he said that “Prof Simmonds grossly underestimated the utility and values of cultivars that carry single transgenes” meaning the several million hectares planted with GMOs. In fact, it is hard to believe that they were

freely chosen by farmers given that they are produced by the same companies which control the seed market.

We can understand thinking of PPB as a bandwagon – in the sense that it was an easy way to attract funds – twenty years ago, but not now, when there are many different buzzwords to attract funding. And yet, several institutions, including American Universities use PPB particularly in organic agriculture research (Ceccarelli and Grando 2019).

We believe that the reluctance to implement participatory breeding programmes lies in the fact that in PPB, **sharing** is the name of the game. It is sharing not only with farmers and other stakeholders, but also with other colleagues because the ideal way is to implement PPB as a team made up of breeders (farmers grows several crops at the same time or in rotation), gender scientists, socio economists, pathologists, physiologist, entomologists, seed specialists and possibly others. Unfortunately, often there is a clash within CGIAR centers between a push for “interdisciplinary research” on one side and the allocation of funding, reward system and career paths on the other. Therefore, one of the reasons why doing PPB has never been popular is because of the high level of competition in science.

It is widely recognized that adoption has been and still is a major problem with conventional breeding (see for example Alary et al. 2020) and despite the higher adoption rate of participatory plant breeding, questions have been raised about its cost. As discussed in Mangione et al. (2006) and Ceccarelli et al. (2012), the issue is not simply the cost, but the cost-efficiency, which is much higher in PPB because it is extremely costly to produce varieties that nobody ever grows, a very common outcome of conventional public breeding.

Practical implications for CI programs

Wherever applied PPB has been capable to reach the most remote, less endowed, and poor farmers and to improve their livelihood by empowering them to become full partners of the scientists. The methodology could fit well with the CI programmes of the CGIAR given their structure, with access to a unique amount and diversity of germplasm and to a wide range of modern breeding techniques, a wide network of national partners, and a strong capacity building capability. Therefore, there are no real scientific reasons to reject PPB if not the reluctance to share with others the credit for obtaining a new variety.

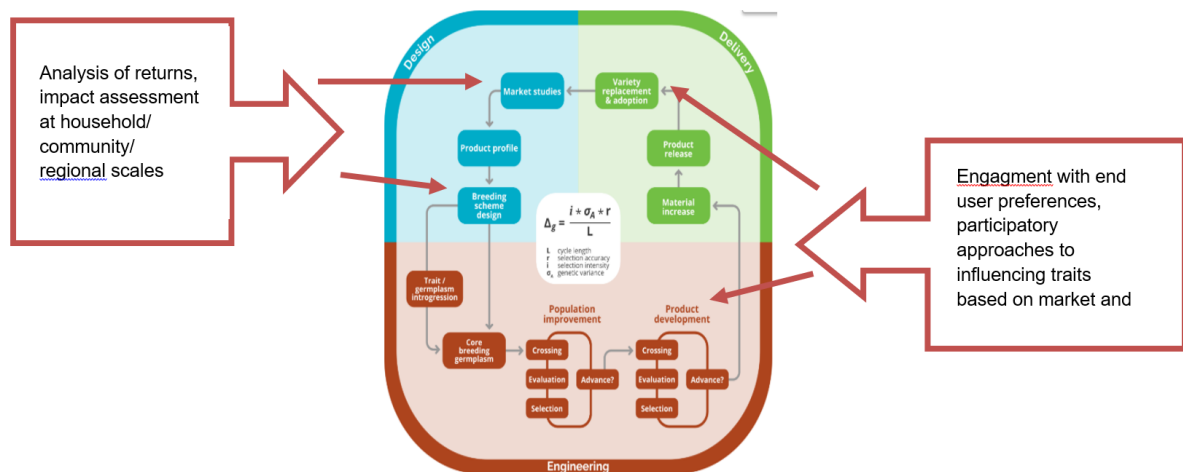
PPB is based on a methodology, which we have contributed to develop, and which includes the most advanced experimental designs and statistical analysis and therefore can generate papers for peer reviewed journals. It is very powerful in increasing agro-biodiversity because it is based on specific adaptation, thus increasing resilience, which is driven by crop diversity (Zampieri et al. 2020). Furthermore, by increasing agrobiodiversity, it becomes a breeding strategy capable of continuously adapting crops to the complexity of climate change particularly by incorporating mixtures and evolutionary populations.

Supplementary Mat. 15 Socio-economics: the specific role in CI programs

Andrew Barnes

Analysis of the socio-economic environment is critical to the success and maintenance of crop-improvement programmes. Socio-economic analysis covers a range of activities, from market assessment and market forecasting, assessing the influence of crop-improvement strategies across the supply chain and, more fundamentally, quantifying the economic impact from crop improvement investments (Alston et al., 2000; Alston et al., 2020). Hence, the broad spectrum of groups in which economists engage around crop improvement include the scientists but mostly the breeders themselves, agronomists who transfer the results of crop improvement programmes, as well as other industry representatives and government analysts.

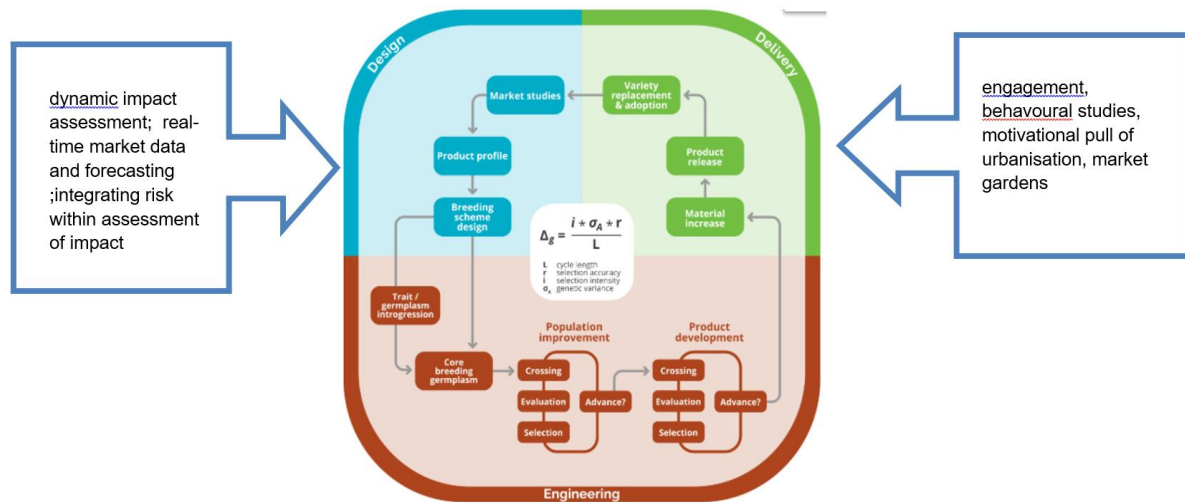
Socio-economics can drive and inform most aspects of the breeders' equation. The producer's desire for sustaining income from the land farmed is reflected in the desire for genetic gain to improve their resilience. Delivery of breeding lines which can offer a yield gain is highly lucrative for high income countries, but access is an issue in developing countries where inequalities are more acute. The promotion of non-yield enhancing traits, such as those around nutrition and drought-resistance, have driven selection intensity and has been led by desires from national and multinational global agencies. Hence, economists can identify the most cost-effective form of intervention, but also the relationship between public-private partnerships for development. This is an important distinction as aid budgets, and the underpinning research and advisory services, are under increasing pressures with high profile donor governments to reduce support for the global framework of agricultural research and development [note 1 below, Supplementary Fig. S5]. The question therefore centres around the attractiveness of traditionally 'non-economic' traits to the commercial sector. For example Syngenta's Foundation for Sustainable Agriculture work has partnered with the CGIAR system to develop drought-tolerant maize varieties [note 2 below, Supplementary Fig. S6].



Supplementary Fig. S5 Current status of socio-economics in plant improvement.

Socio-economics tends to occupy the top part of the breeders pipeline. Here the delivery is both influenced by agricultural economic studies (for market impacts and access) but also social-science based studies for improving delivery and engagement. On the design the study of

agricultural institutions both at the micro and macro level provides justification for continued investment but also cost-effective delivery.



Supplementary Fig. S6 Future status of socio-economics in plant improvement.

A range of social-scientific approaches have been applied to inform end-user preferences within crop improvement. These exercises within the farming community tend to assign weights to desired traits (see for example Duncan et al., 2016). Participatory plant breeding emerged in the last three decades (Sperling et al., 2001, Morris and Bellon, 2004) with the purpose of engaging end-user communities in the process of crop improvement programmes. This will temper the selection intensity (i) and the genetic standard deviation (σ_A) of the breeder's equation given the inclusion of wider, end-user identified, traits, such as ensuring consistent seed supply or compatibility with labour supply.

Past and current status

Since the 1950s agricultural economics has provided a solid empirical base for both supporting and justifying the research infrastructure around plant breeding (Byerlee and Moya, 1993; Stein et al., 2007), finding high returns to investment into plant breeding programmes which justify their continued investment by public agencies. However, whilst focused on productivity benefits and income growth these studies failed to provide much specificity for plant breeders per se. These were mostly focused on past achievements over a long time frame and did not respect the current changing political frameworks towards, for example climate change or support for sustainable livelihoods. More fundamentally whilst farm level studies find benefits of adoption of genetically improved material these have been mostly focused on productivity gains and only recently have begun to consider the role of different impacts which allow adaptation to climatic changes (Barnes, 2002; Dantsis *et al.*, 2010; Alston et al., 2020)

Given the increased pressures from climatic change varietal switching is slow in most developing countries due to, amongst others, lack of market access or a non-competitive private sector (Atlin *et al.*, 2017). Value chains, the process by which different 'actors' in the food chain add value to products, is a fundamental route to increasing access and one in which socio-economics plays a fundamental role (Trienekens, 2011).

Future perspectives

Most of these socio-economic domains still remain one-step away from the science of crop-improvement. The impact of market and policy signals that economic analysis focuses on is potentially diffuse for CI scientists to respond to. Similarly, the long time frames for new varieties to enter the market requires more precise forecasting tools. Hence, despite increasing challenges in developing countries, with population pressure and rural abandonment, opportunities exist through wider more holistic integration of socio-economic disciplines to shift CI science forwards. For instance agricultural economic studies can be augmented by real-time market data to support forecasts for desired traits for CI programmes. A further addition to impact assessment is the application of real-options appraisal (e.g. Zambujal-Oliveira, 2020). This allows flexibility for understanding the risks from different crop improvement investment strategies and therefore should lead to more information for the breeder and more effective uptake by end users as market conditions change.

Atlin *et al.* (2017) argue that more rapid uptake of new varieties could be achieved by convincing farmers through endorsement and aggressive promotion by aid agencies. Hence, a CI system could work in sympathy with the institutions delivering these new varieties, such as extension agents and donor agencies. The realm of institutional economics examines both these formal institutions but also informal institutions, such as how social networks influence choice of what to crop.

A constraint is the behavioural differences within these farmers and their differing motivations for farming, such as commercial or more family support objectives. Applying choice experiments, which trade-off a series of alternative traits or business choices, would allow us to understand the primary motivations of end users and their desired traits to direct CI strategies (e.g. Naico *et al.*, 2010). Further still behavioural economic approaches using simple games, have been applied with development settings (e.g. Claessens *et al.*, 2012)). These can elicit preferences under both present and future risks and how they influence decisions, as well as how market signals or policy interventions affect their decision-making.

An increasing desire to intensify production is a logical response to increasing urbanisation and more attractive urban jobs in growing service sectors. Mechanisation to replace labour should temper the product design towards crop improvement in the search for varieties which can be more usefully harvested at larger scale. This presents hazards however, as we need to avoid treadmill effects (Cochrane, 1958), evidenced during the green revolution of increasing demand for not only improved genetic stock but ancillary products to support these products. Current debt to equity in rural poor households is high (Barbier *et al.*, 2016) and borrowing to support on-farm production is a classic example of a poverty trap (Lipton, 1997). As

urbanisation increases there is also a growing trend for smaller scale market garden type approaches which again may result in changes and more niche growing opportunities for high value products.

Whilst farming and rural careers becomes an unattractive option for younger generations, the ancillary sectors which support CIs have developed substantially in high income countries and one would expect the same trajectory for developing countries. Thus, highly skilled jobs in data analysis, sensing and telecommunications would achieve some of the earlier needs for real-time data to inform CIs.

Practical support to the CI teams

In order to make CI more cost-effective requires continual improvements in cost-benefit analysis methodologies and data. This is in order to accommodate the evolving nature of breeding strategies to meet wider goals around income support and climate change. Within this, more nuanced and niche markets are appearing which support the diversification in incomes and diet as countries develop. Understanding adoption along these niche markets will be an important driver for directing effort in Crop Improvement. Lessons from ongoing economic surveys, such as the Living Standards Measurement Surveys of the World Bank (note 3 below), offer perspectives on how these low income households are changing. Economists, working with CI scientists, can therefore integrate and inform a more dynamic understanding of traits and how future scenarios will affect present crop adoption trajectories.

Notes:

[1] see for example:

<https://foreignpolicy.com/2019/08/13/how-to-save-foreign-aid-in-the-age-of-populism-usaid-dfid>

[2] <https://www.syngentafoundation.org/public-private-partnerships-crop-breeding>

[3] See <https://www.worldbank.org/en/programs/lsm> for further details

Supplementary Mat. 16 Foresight as a tool to help target breeding objectives

Steve Prager

Strategic foresight approaches support crop improvement decisions by helping breeders understand the context of their desired breeding objectives in relation to a series of systematically expressed plausible agricultural futures. Foresight approaches also facilitate the understanding of the potential long-term economic and nutritional impacts associated with investment in crop improvement. A major crop improvement initiative, the Crops to End Hunger program (CtEH), recently commissioned a foresight analysis to better understand potential outcomes of different investment possibilities (Wiebe et al., 2020).

Understanding foresight in the context of crop improvement

The acceleration of crop improvement through breeding is a core objective in many different breeding program modernization initiatives. Breeders often know what they would like to accomplish in long-term breeding strategies, but lack clarity in relation to how their future results interact with the future reality in either biophysical or social terms. One way to gain insight into this future reality is using quantitative strategic foresight models to understand the potential impact of different breeding objectives via simulation-based approaches. A use of strategic foresight models is to help to refine understanding of different potential crop improvement strategies in relation to different simulated future biophysical and socioeconomic conditions (Wiebe et al., 2018). The incorporation of crop modeling into strategic foresight models can help overcome a lack of adequate observations from field trials and, simultaneously, allows for the use of calibrated models to express crop response under future climates and different spatially explicit conditions, while also taking into account future demand and other socioeconomic or policy factors (Kruseman et al., 2020).

One of the most common applications of foresight is at the intersection of climate change and demand for the crop in question. The seemingly simple question such as “Will there be adequate demand for crop X in 30 years to make it worthwhile investing Y millions of dollars to achieve tolerance/resistance to Z condition?” is actually quite beguiling without the use of ex-ante foresight approaches. Numerous foresight studies show the complex spatial and temporal heterogeneity associated with “simple” answers to the above questions, whether looking at roots, tubers and bananas (Petsakos, 2019), or livestock and fish (Enahoro et al., 2019; Chan et al., 2019).

An obvious conclusion to the already initiated, the projected future value share of rice and wheat in 2030 (26.0% and 16.2%, respectively), immediately highlighted the potential for return on investment in crop improvement associated with these commodities. One of the advantages of foresight approaches, however, is that foresight approaches allow for consideration of a variety of potential outcomes, and upon further analysis, the original CtEH assessment also shows that, in a poverty weighted context, cassava and yams could also result in potentially very high returns on investment. Does this then suggest that we can simply invest our limited research funds in the crops that have the highest potential for return on investment at the global scale? Not so fast...

Foresight and breeding; awkward couple or elegant partners?

Two key observations in the state of the art as described above illustrate why we cannot simply look to return on investment at the global scale as the basis for deciding where we invest our limited crop improvement resources. The first is the sheer volume of assumptions and the spatial and temporal heterogeneity of the interactions occurring at the gene by environment by management (GxExM) nexus (Stöckle & Kemanian, 2020). The second relates to the desired outcomes; in an emerging perspective, this can be thought of as a socioeconomic extension to the previous paradigm, resulting in GxExMxS (and, with it, even greater increases in spatial and temporal heterogeneity).

Whether a participatory foresight approach, horizon scanning, scenario analysis or quantitative ex-ante modeling, the idea of foresight approaches are to explore plausible futures in order to overcome “presentism” and achieve desirable futures (Störmer et al., 2020). A conundrum thus arises. Even the futures we anticipate inject present bias into our futures perspective; if economic outcomes are seen as the main priority, foresight models will, predictably, suggest investment in crop improvement that targets many of the most widely consumed commodities (Wiebe et al., 2020). On the other hand, if the desired future is related to achieving a particular environmental outcome (e.g., eating within planetary boundaries), the corresponding recommendations can be substantively different (Springmann et al., 2018).

From a crop improvement perspective, does this mean foresight lacks relevance in the context of crop improvement? Not at all. Foresight helps us to gain targeted understanding about both the sensitivity of different investment strategies in crop improvement to exogenous factors such as population growth, changes in income and climate change, and even different investments in agronomic strategy such as sustainable intensification (Rosegrant et al., 2014). Similarly, foresight can be narrowed down to offer insight regarding potential returns on investment associated with a particular crop-systems strategy (Schiek et al., 2018).

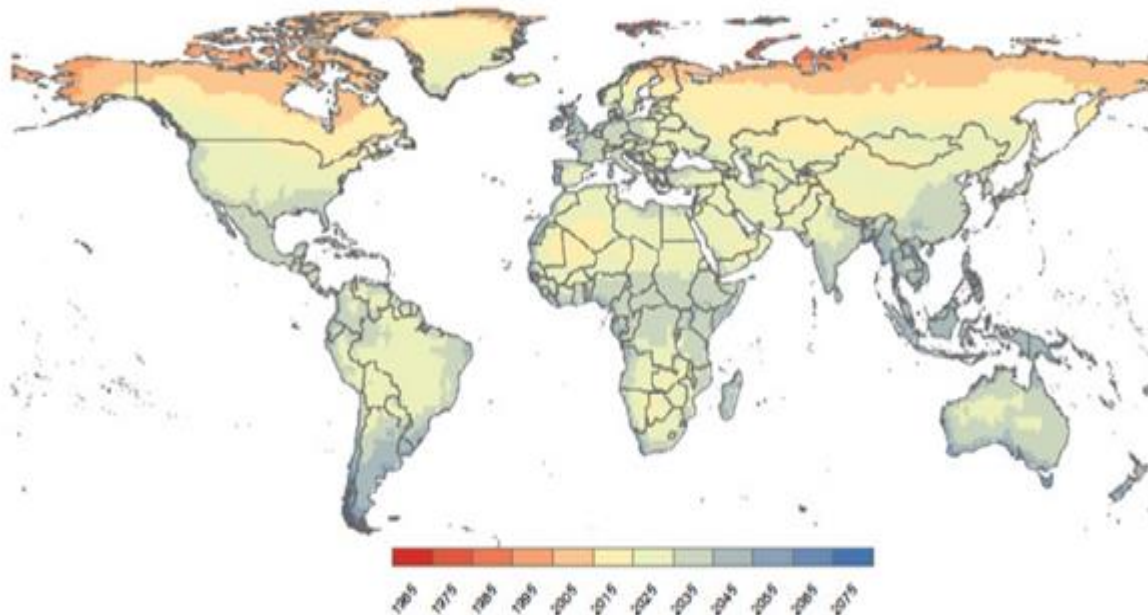
The almost infinite set of possibilities that emerges when we look at the astounding complexity of GxExMxS interactions shines a light both on the strength and the pitfalls of crop improvement strategies that leverage foresight approaches. The strength of strategic foresight is that it does, indeed, allow for systematic exploration of alternative futures. The pitfalls, like any science, are that if we make bad or unrealistic assumptions about the future (or our capacity to achieve a particular outcome), the results of foresight analysis could effectively support a nonsensical approach to prioritizing investment in crop improvement.

Importantly, foresight is not a magic bullet. Foresight approaches, whether quantitative or qualitative, are abstractions of reality and descriptions of plausible futures. While the science underlying foresight is fundamentally different from the science underpinning crop improvement, this does not mean that never the twain shall meet. Crop improvement and foresight specialists alike need to approach the integration of the two sciences with an eye toward co-production. Much of the legwork in crop improvement processes (e.g., field trials, consumer choice experiments, trait preference studies, etc.) could, with minor exception, become exceptional inputs into a structured foresight process. The take home message then is start early, iterate often, and exchange ideas as early as possible to include foresight in the design of crop improvement programs.

Practical foresight for crop improvement programs

The relatively long time horizons required to achieve major crop improvement outcomes all but require foresight as an integral input. Our ability to achieve desired outcomes is predicated on making good decisions now to anticipate the challenges we are likely to face in medium and long-term horizons. Crop modeling exercises simulating crop response to a 2 degree C temperature increase show potentially significant decreases in yield, especially in tropical regions (Challinor et al., 2014). From the perspective of a stage-gated crop improvement

breeding pipeline, this means an increasingly limited number of growing seasons in key regions in which the CGIAR is working prior to the expected onset of the anticipated 2 C increases in average temperatures around the world (see Supplementary Fig. S7, taken from Jarvis et al., 2019).



Supplementary Fig. S7 illustrates, much of the planet has, or will expect the 2 C threshold by around 2045 if not sooner, taken from Jarvis et al., 2019

As Supplementary Fig. S7 illustrates, much of the planet has, or will expect the 2 C threshold by around 2045 if not sooner. Given the need to accelerate advances in breeding-based adaptation strategies, quantitative foresight models are viable tools that can be used to understand potential implications and income of different breeding strategies. Using quantitative foresight models helps us to refine understanding not only of how intended improvements might affect crop performance in a spatially and temporally explicit manner (Kruseman et al., 2020), but also how these changes respond to (and affect) future biophysical and socioeconomic conditions (Wiebe et al., 2018).

The data driven approaches that are driving many aspects of crop improvement programs can also benefit foresight. One promising area is the linking of foresight approaches directly to the design of the product profiles that support crop improvement. With a reasonable amount of research, we will soon be able to link characterization of future demographic trends (e.g., in relation to urbanization, income, farm size, and more) to how these trends drive trait future preferences. This represents a major opportunity to help guide the development of product profiles and, hence, the breeding process to not only be demand-led based on present understanding of demand, but also anticipatory in nature.

It should be clear that foresight analyses offer a great deal of insight to crop improvement programs. The key ingredients for a successful integration include early and ongoing dialog between the crop scientists and the foresight experts, co-development of shared understanding regarding what outcomes and what scenarios and outcomes are most relevant given breeding program objectives, and understanding that foresight is not a forecast. Foresight is, by its very nature, a science of integration. Disciplines from climate science and crop modeling to economics, spatial analysis and, critically, crop improvement, must come together to co-create robust and relevant foresight analyses. This final point is exceptionally important. Good integration of foresight into a crop improvement program will treat the foresight results as integrative “futures evidence” that serve as a decision support tool alongside complementary evidence such as priority setting and expert knowledge.

Supplementary Mat. 17 Gender

Eileen Nchanji

To what extent can the fully understood gender situation in one place help and direct breeders efforts in a more productive way? And how can changing demographics, the youth boom, persistent gender gaps and urbanisation change the global breeding effort?

Most women producers do not own land, and this probably accounts for less investment in innovation (Goldstein and Udry 2008). In addition, access to other productive resources like information, technology, and capital can quickly determine what they grow and what agricultural task they perform across different communities and regions in the world. Division of labour on and off-farm is also informed by socially constructed norms, where women are seen to do more labour intensive activities as well as systematically produce crops of lower value (wa Githinji et al., 2014). Interestingly, when these crops gain value, the men take over. Thus men and women control over such resources determines whether they benefit or lose out (Galiè et al., 2017).

The effects of gender inequality on the agricultural sector are not new; as supporting evidence has been generated for over two decades now and is still being generated (World Bank 2007). Gender inequalities are prevalent in smallholder agriculture due to women’s triple burden – reproduction, childcare, and domestic labour as well as the low value placed on female labour compared to their male counterparts. However, gender integration does not entail focusing exclusively on ways in which women differ from men but also how women and men differ amongst each other.

Integrating gender in any breeding program requires an understanding of how the different roles and resources of men and women affect their preferences and adoption or disadoption of any technology. It also requires a critical examination of how gender differences in wealth, age, education, geographical area and religion can influence the type and distribution of benefits among a targeted group of people expected to use a particular technology (Timothy

and Adeoti 2006). For example, wealth and education often mitigate the disadvantages of being a woman while poverty and illiteracy can wash out gender effects on both men and women.

Simple sex disaggregation might not provide enough explanation on how social behaviour can influence breeding. Sex-disaggregated data on what varieties or traits women or men prefer or who does what farm management tasks—will shed light on whether and what differences exist between the sexes. However, it will not necessarily tell you a lot about the effects of gender on technology choice. Thus, taking account of other social factors, such as income, religion, sex and education, geographical location provide an intersectional lens to understand the importance of gender relative to other factors (Kilic et al., 2013). For example, urbanization has pushed for fast cooking varieties and increased consumption of fresh beans in Uganda. Profiling users suitable for breeding programs is discussed in Orr et al. (2018).

The introduction of new technologies might require new management practices changing the type and amount of work to be done by different people (Doss et al., 2017). For example, the introduction of improved bean varieties had led to changes in farmer's practices. Gender decision-making processes – done individually or jointly on-farm tasks, management, marketing and income distribution from sales can fundamentally affect adoption (Gilligan et al., 2013).

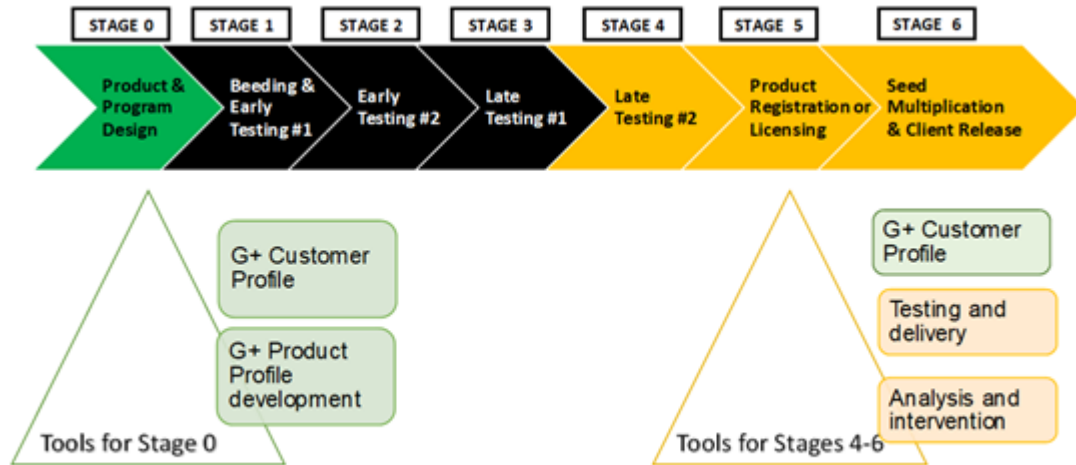
Interpreting gender differential traits in association with information of the assets and resources of the producer or other actors of the value chain is essential for a breeding program to decide on the most beneficiary group. Breeding programs face multiple demands from different actors in the value chain and sometimes have to be selective or trade off one trait over another.

Gender analysis is central in understanding trait and varietal differences between men and women value chain actors. However, it is not easy to bring out the social dimensions in biophysical research due to many reasons - lack of understanding, unavailability of standard tools, procedure, ownership of products etc. One of the challenges for gender scientists working with breeders is how to make gender analysis meaningful for biophysical scientists? In a way that it adds value to the breeding program but not necessarily more work to breeders; where a gender-responsive approach leads to greater adoption of their varieties.

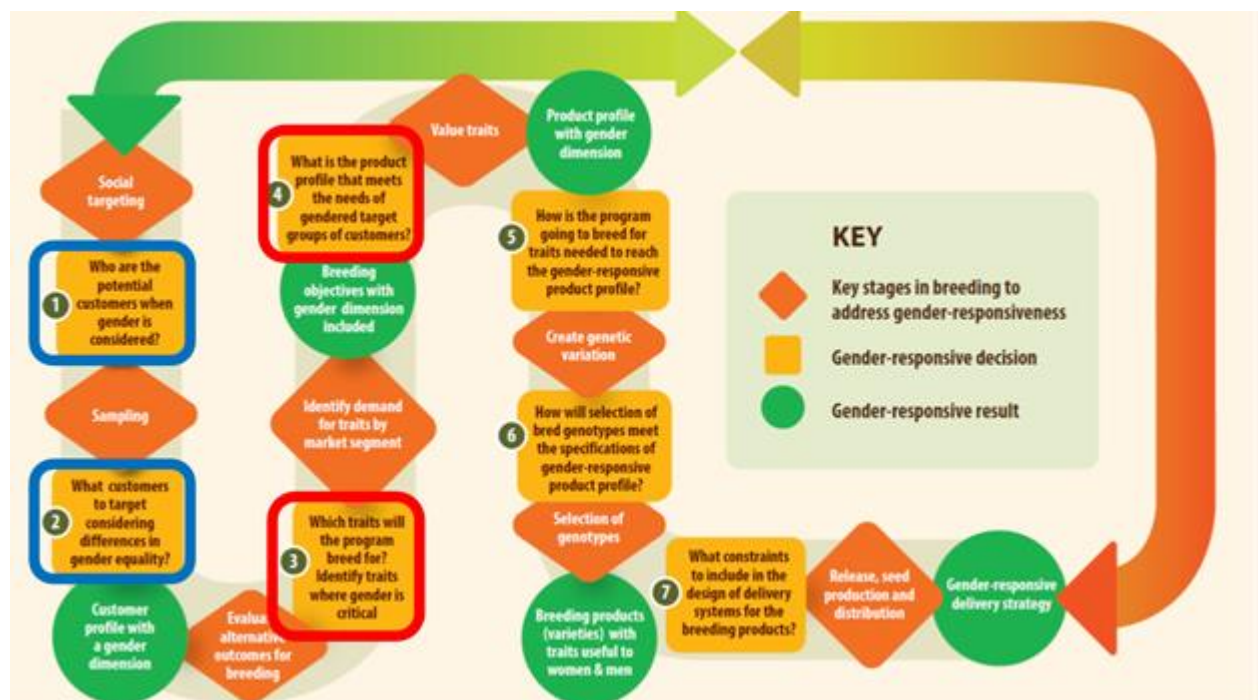
According to the Gender and Breeding Initiative Brief No. 1, for a breeding program to be gender-responsive, it has to: 1) Know when, where, and why women are an important beneficiary group. 2) Anticipate how design decisions (e.g., defining plant ideotype, prioritising of traits, targeting and testing varieties with farmers) may impact and be influenced by women's labour, available resources and opportunities. 3) Design breeding objectives specifically to benefit women farmers and consider their needs, constraints and knowledge more generally in the breeding program. 4) Be accountable, making sure success is measured in ways that include positive impacts for women”.

Most importantly “do no harm” to both men and women actors of the value chain. In every breeding stage, a decision should be taken that ensures gender is considered, as shown in Supplementary Fig. S8.

Supplementary Fig. S8 “Do no harm” to both men and women actors of the value chain. In every breeding stage, a decision should be taken that ensures gender is considered.



The Excellence in Breeding and Demand led breeding platforms have designed templates with inputs from gender scientists in the CGIAR on producing gender-responsive product profiles. To meet this goal, a G+ Customer profile and G+ Product profile has been developed and is being piloted by the Alliance (Bean team), IITA, CIP, ICARDA and ICRISAT in collaboration with breeders. Gender can be integrated at the different stages of the stage-gate process, as shown in the diagram below (Supplementary Fig. S9).



Supplementary Fig. S9 How can changing demographics, the youth boom, persistent gender gaps and urbanisation change the global breeding effort?

Supplementary Mat. 18 Strengthening the links between nutrition and crop improvement research

Robert Fungo

Introduction

Nutrition is the process by which individuals utilize nutrients obtained from food, playing a critical role in body functions supporting growth and development (Black *et al.*, 2008). Undernutrition negatively affects all aspects of an individual's health and development and, consequently, limits the community' and national economic and social development potential. The undernutrition can result from limited access to nutritious foods as well as from water, sanitation, hygiene (WASH) or feeding and caring practices (UNICEF, 1998). In low and middle-income countries (LMICs), inadequate intake of energy and micronutrients is one of the most important underlying causes of under-nutrition. Biofortification - i.e. nutritionally enhanced staples with increased nutrients content - can complement other strategies (e.g. chemical fortification, promotion of dietary changes etc.) by offering a sustainable and low cost way to reach people with poor access to health care systems (Council for Agricultural Science and Technology (CAST). 2020. Bouis, H. E., & Saltzman, A. (2017) Meenakshi et al., 2010).

The historical and current status

Historically, nutritionists have been addressing undernutrition by promoting micronutrient supplementation and fortification programmes targeting critical vehicle foods, e.g. the world-wide salt iodization program in nearly 150 countries have markedly improved iodine status of population over past two decades (https://www.ign.org/cm_data/idd_nov13_africa_overview.pdf) or the case of Guatemala which almost eliminated vitamin A deficiency by legislating that all sugar should be vitamin A fortified. While many of these programmes have been successful in some countries with advanced infrastructure, iron deficiency anaemia, vitamin A deficiency, and iodine deficiency disorders remain serious public health concerns in majority of LMICs (UNICEF, WHO and World Bank, 2020). The slow progress achieved to date relative to the immense resources that have been invested could be attributed in part, and among several other factors, to the strategies applied, which often rely on single or multiple nutrient supplementation, immunization and food fortification while insufficient attention is given to nutrient-rich food resources (Sommer et al., 1986).

A few decades ago, new approaches using CI techniques were piloted and later scaled to reach the rural poor. The CI intensification of agricultural systems (majorly rice, wheat and maize), through increased inputs, simplification and homogenization of ecosystems is correlated with

a concomitant decline in prices for high energy foods derived from them (Welch and Graham, 1999). Then again, population pressure fueled the demands for economic development and led policy-makers and research organizations to focus on the promotion of a few high-yielding crops and, in an alarming number of cases, promoted increased exploitation of calories rich but micronutrients poor foods. This trend has negatively changed the nature of diets in developed economies but spilled over to LMICs. These include not only problems related to undernutrition such as various vitamins and micronutrients deficiencies and increased rates of infectious diseases in one end of population section but also increasing rates of non-communicable diseases such as obesity, cancers, cardiovascular disease and diabetes mellitus on the other end of spectrum (Hawkes, 2006; Popkin, 2006).

It is important to note that the efforts to combat micronutrients deficiencies by fortification and supplementation haven't been effective especially in LMIC countries with inadequate food-chains infrastructure. In some cases, the biofortification of staple crops appears to be a more effective and sustainable strategy to reach the most vulnerable communities (e.g. vitamin A fortified sweet potato, cassava, rice and bananas, iron and zinc rich beans, wheat and millets, vitamin A rich maize). The idea is to provide high micronutrient accessions which are locally and culturally acceptable by local communities, for dissemination to the vulnerable communities. Furthermore, biofortification complements existing strategies by reaching populations who have limited access to health care systems. Biofortified staple crops present a better sustainability potential given the high production and consumption levels. Yet, while including biofortification traits into the CI program, CI-teams have to make certain to address these requirements with adequate CI-program design (also depending on the trait genetics, Supplementary Mat. 3-4) to ensure improvement of other important traits while including additional nutrition-related trait targets.

New approach needed. Is it worth the investment?

The impact of biofortified crops can be demonstrated on the example of high iron rich beans (HIBs) study conducted in Rwanda among female university students (Murray-Kolb et al., 2017). Here, the clinical trials revealed that the lethal consequences of anemia and iron deficiency could be averted by incorporation of iron rich beans in the diet of inadequately nourished females. A recent trial in India demonstrated that iron status, attention and memory among Indian adolescents can significantly improve, if they would include iron rich pearl millet in their diet (Scott et al., 2018). These findings provide quantitative evidence for CI-teams to investigate and deploy similar approaches in order to address undernutrition, improve cognitive performance and help ending the wicked cycle of poverty which is threatening the progress of LMIC nations.

One of the CI challenges is the combination of high-nutrient densities with yield, agronomic, and quality traits into a single package that can generate profitable varieties in country-crop specific contexts. Market, adoption, and acceptance research is crucial to guide CI teams in developing value propositions for all actors along the value chain. This is important in designing product profiles. Demand creation and awareness campaigns for biofortified crop varieties are supported by consumer acceptance and farmers adoption studies, and developing

novel food products in market development. For detailed information about Harvest Plus, written by Destan Aytekin, Jairo Arcos, please see Supplementary Mat. 19.

The nexus of crop improvement and human nutrition? Strategic partnerships are needed

There is enough evidence that CI interventions have a role to play in helping to reduce the wide spread of micronutrient undernutrition in LMICs (Scott et al., 2018, Murray-Kolb et al., 2017). This has been already noted by important donor agencies and, e.g. the Bill and Melinda Gates foundation has been funding the Vitamin A rich “Golden” banana initiative in Uganda and Great lakes region of East Africa since 2005 (Paul *et al.*, 2017; Paul *et al.*, 2018). This involves multi-disciplinary teams from Uganda and Australia, working in synergy to produce a marketable product ready for consumption in Africa and Australia. The critical role of nutritionists is to point out the intricacies of achieving a measurable impact on human health outcomes; e.g. the information including quantities of product consumed by target population, nutrients requirements, bioconversion and bioavailability of ingested nutrients and retention of the nutrients after storage, processing, and cooking (Nestel *et al.*, 2006; Stein et al., 2005). Importantly, for effective uptake of the biofortified products it is crucial to incentivize the product within the value-chains in form of e.g. nutrition education and awareness or demonstratable health benefits to growers and buyers without compromising agronomic and end-use characteristics (Pfeiffer and McClafferty, 2007; Underwood, 2000). Therefore, it's clear the impact of biofortified products can be delivered only with strong interdisciplinary coordination.

Supplementary Mat. 19 HarvestPlus

Destan Aytekin, Jairo Arcos

Introduction

Micronutrient malnutrition affects more than 2 billion people globally [1], causing significant health problems [3]. HarvestPlus and its partners improve nutrition and public health through biofortification, an intervention that increases the micronutrient density of staple crops through conventional breeding and agronomic practices, without compromising yields. It is an efficacious, cost-effective, sustainable, and scalable solution to tackle hidden hunger worldwide [4-6].

HarvestPlus works with over 600 partners, including the national agricultural research systems and CG centers, to develop and deliver these nutritious, high-yielding, and climate-smart crops to vulnerable populations [7]. HarvestPlus and its partners provide technical guidance and monitoring to support the scale-up and mainstreaming of biofortification in CGIAR and NARS breeding programs.

HarvestPlus facilitated the release of more than 240 varieties of 11 biofortified crops for consumption in 30 countries [7]. By the end of 2019, almost 8.5 million farming households were growing biofortified crops, benefiting over 42 million people [7].

Past and current status

Biofortification involves cross-breeding local, adapted crop varieties with parents that are more micronutrient-dense and selection for agronomic traits and end-use quality traits. This process takes approximately 6-8 years. After promising lines undergo multi-year, multi-location trials by the NARS and private sector partners, competitive varieties are released by national governments following official registration trials.

In 2005, HarvestPlus nutritionists, food technologists, and plant breeders established nutritional breeding targets. These target increments, set to have a measurable impact on human health, were based on nutrient bioavailability, food consumption patterns of target populations (non-pregnant, non-lactating women and children aged 1-6 years), dietary needs, and estimated nutrient losses [5]. Following efficacy and effectiveness studies confirmed that consumption of biofortified crops improves nutrition status as well as functional health outcomes. On-farm evaluations, monitoring surveys, and besides the farmers' adoption studies, consumers' acceptance studies have also been conducted to understand consumer preferences and willingness to pay [4]. Program evaluations and ex-ante and ex-post analyses have elucidated the cost-effectiveness and impact of the delivery models and programs.

The Copenhagen Consensus ranked interventions that reduce micronutrient deficiencies, including biofortification, among the highest value-for-money investments for economic development. As per their analysis, for every USD invested in biofortification, as much as 17 USD of benefits may be gained. Other ex-ante (before intervention) analysis conducted for several micronutrient-crop and country scenarios pointed out that biofortification is highly cost-effective according to the World Bank criteria of cost (in USD) per Disability-Adjusted Life Year (DALY) saved. More-in-depth studies modeling the micronutrient program portfolios looking at biofortification, fortification, and supplementation are also conducted in country contexts. They found that biofortification is one of the most cost-effective strategies for tackling the deficiency of the micronutrient which can be addressed through biofortification.

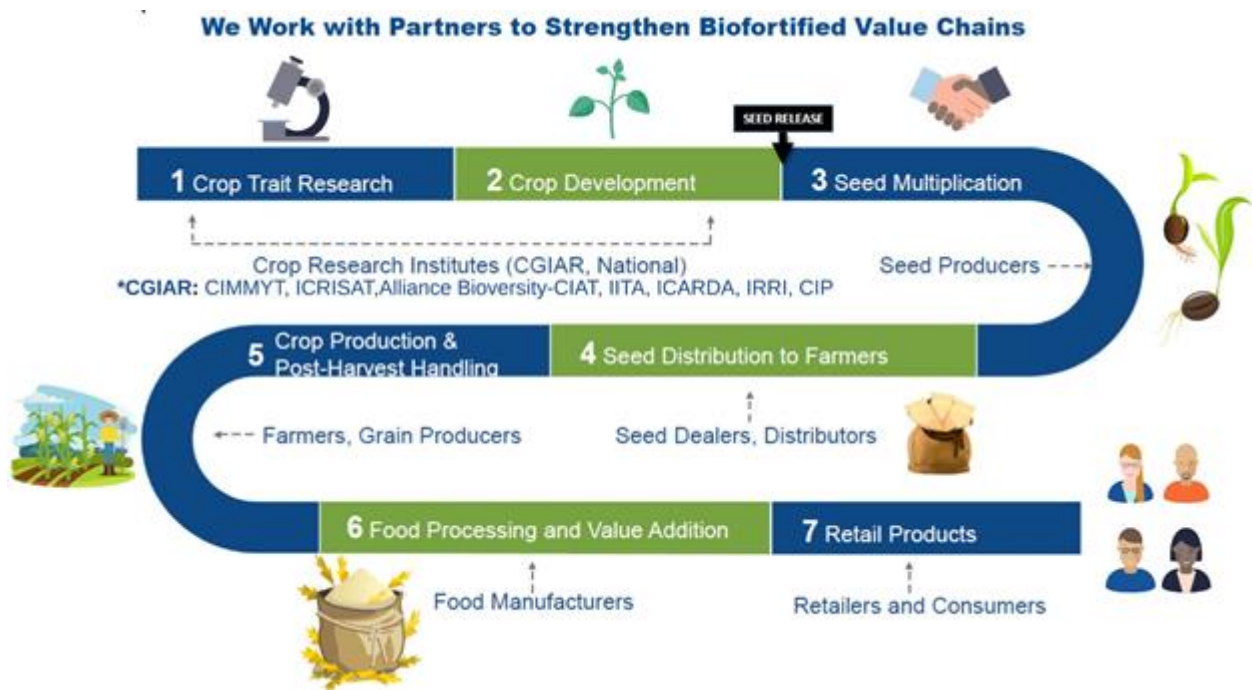
A recent example: An ex-ante cost-benefit analysis of zinc wheat variety that is resistant to wheat blast and other common diseases in Bangladesh showed a 5-8% better yield when compared with popular varieties, and that the potential economic benefits of delivering this zinc wheat variety was found to be far beyond the anticipated cost of the delivery, bringing USD 0.23-1.6 million of net benefits even in a worst-case dissemination scenario (citation: Mottaleb KA, Govindan V, Singh PK, et al. Economic benefits of blast-resistant biofortified wheat in Bangladesh: The case of BARI Gom 33. *Crop Prot.* 2019;123:45-58).

An ex-post example is from Rwanda. The iron beans in Rwanda yielded about 20% more than regular ones, resulting in USD 57-78 additional profit per hectare. From 2010 when the

program was established in the country to 2018, the total value of benefits was USD 25 million. USD 4.9 million of this was due to the reduction in the burden of iron deficiency, and the rest resulted from the increased production levels. The cost-benefit analysis showed that for every dollar invested 2.9 dollars' worth of benefits were reaped (citation: Lividini, Keith; Diressie, Michael. Outcomes of Biofortification: High Iron Beans in Rwanda. August 2019, Internal Resource Available upon Request. PowerPoint Presentation)

HarvestPlus takes a value chain approach to deliver biofortified crops at scale, within a holistic food systems context (Supplementary Fig. S10).

Supplementary Fig. S10 HarvestPlus collaboration with CG centers, and others through the value chain



One of the biggest crop improvement challenges is the combination of high-nutrient traits with yield, agronomic, and quality traits into a single package that can generate profitable varieties in country-crop specific contexts. Achievements are evident in the release of > 240 varieties and adoption by 8.5 million farmers.

Efficient diagnostic tools and methods are crucial to accurately and reliably analyze the micronutrient content of varieties and screen samples for the breeding process [9]. HarvestPlus and partners pioneered the development and implementation of non-contaminating equipment, improvement of analytical protocols, and high-throughput analysis of iron and zinc. Introducing the X-ray fluorescence spectroscopy and Near Infrared Spectroscopy (NIRS) as

cost-effective and time-efficient solutions to screen mineral levels and related organic compounds affecting mineral bioavailability of crops in plant breeding programs was a game-changer [10-12]. Similarly, NIRS was proposed for measuring carotenoids in particular for root and tuber crops [13-15].

To date, HarvestPlus has built capacity in 25 micronutrient analytical laboratories at nine CGIAR centers, 12 NARS, and four universities, and trained more than 100 laboratory staff in 13 countries in field sampling, sample preparation, equipment calibration, and routine analysis.

Future perspectives

Evidence shows that by 2050, the increasing CO₂ concentration will cause many crops – in particular, staple crops – grown under such conditions losing their nutrition levels by 3–17% [16]. Increased CO₂ concentration is expected to cause significant increases in the number of micronutrient-deficient people. Urgent action is needed.

In addition, COVID-19 impacts on human nutrition and health as people rely more on staples. Good nutrition and adequate micronutrient intake boost the immune system [17]. It has become even more vital to have nutrition-interventions integrated into a holistic food systems approach. Biofortified crops are produced locally, rely on short supply chains, and are therefore more resilient to global supply shocks amidst COVID-19. Innovative delivery strategies include the use of digital technologies [18], and blockchain technology for traceability of agricultural products. For example, HarvestPlus and The New Fork apply blockchain distributed ledger technology to track and authenticate the origin of biofortified seeds and foods through value chains.

Market, adoption, and acceptance research is crucial to guide breeding program breeding in developing value propositions for all actors along the value chain. This is important in designing product profiles [19]. HarvestPlus provides technical guidance to ensure improved quality and adoption for biofortified varieties. Demand creation and awareness campaigns for biofortified crop varieties are supported by consumer acceptance and farmers adoption studies, and developing novel food products in market development.

To overcome challenges such as β -carotene degradation and low retention in vitamin A food products [20-24], HarvestPlus, with partners, has been investigating and developing solutions through multidisciplinary studies, combining breeding and nutrition food science. Phytate causes a reduction in the bioavailability of iron and zinc and affects the absorption of the micronutrients in the human body [20, 25-28]. Solutions include breeding for low phytate or high phytase in combination with food technology/processing recommendations.

Mainstreaming biofortification into CGIAR and NARS breeding programs is a key strategy in scaling biofortification as all varieties grown will eventually be replaced once parents used to develop future varieties are converted into micronutrient dense, nutritious versions. It requires a holistic approach — especially in resource mobilization, micronutrient target setting, quality M&E, standards, advocacy, public commitment, and support. The CG centers and several

NARS made a commitment to mainstream biofortification in their breeding efforts, aligned with the rising importance of nutrition security within the CGIAR. HarvestPlus provides guidance for these institutes through technical assistance, advice, capacity development, and facilitates the exchange of germplasm between countries. Current targeted breeding also supports mainstreaming and, over time, will decrease with products becoming available. Moving forward, a solid M&E system needs to be in place to measure and monitor the impact of mainstreaming.

Practical support the CI teams

Harvest Plus would replace themselves providing support/technical assistance in the engineering part of the breeders' equation and actively can be involved in the design and delivery parts. Moving forward (in 10 years from now), H+ would like to position themselves as providing support/technical assistance for the engineering and design sections while focusing on the delivery and catalyzing the scaling up of biofortification.

There is proof of the concept of the efficacious and effective, sustainable, cost-effective, and scalable impact of biofortification on human nutrition and health. Biofortification does not compromise yields, and in certain cases, enhances productivity [8, 29-30].

There is robust evidence along the value chain of biofortification's impact on nutrition and health, as well as consumer acceptance, farmers' adoption, and cost-effectiveness of the intervention. HarvestPlus shares evidence and tools applicable to not only biofortified varieties but other crops/varieties. E.g., The Biofortification Priority Index has been shared widely and can be used by CG breeding programs as they consider nutrition as a core trait in their product portfolios. Biofortification has moved through the discovery, development, and adoption phases, and now the technology is ready to be scaled. To achieve this will require innovative partnerships and investments guided by efficacy and cost-benefit evidence.

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Supplementary Mat. 20 Synthesis & Conclusion

James Cock, Jana Kholova, Milan Urban + other co-authors

A multidisciplinary approach is needed to find solutions to the “mega-challenges” facing agricultural production (Gaffney *et al.*, 2019). Crop improvement (CI) is an integral of the CGIAR’s strategies to tackle the many facets of these multiple challenges. At the same time it is clear that there is not one single CI strategy that will meet all the challenges the CGIAR faces and, furthermore, CI may not be an appropriate tool to meet many of those challenges. The success of CI will depend on its ability to both assimilate knowledge from many sources and disciplines, and to integrate itself into an overall strategy CGIAR strategy that seeks the most appropriate means to resolve problems and open up new opportunities. Here we highlight the advantages of a multidisciplinary approach and some of the impediments to its achievement. We hope that bringing up these issues will catalyze and accelerate the discovery of solutions to the challenges facing CI.

Issues linked to human nature and fear to speak the “unacceptable”

Breeders are used to failure: of the progeny they produce only one in tens of thousands or more eventually becomes a successful variety. Breeders can however learn from negative results. When they rogue out materials that are not promising, they learn which parents are more or less likely to produce potential useful progeny. However, often important negative results, such as allelic variation in X that does not contribute to heritable variation in Y, are neither published nor systematically recorded. Nevertheless, these relationships gained through the experience of individual researchers contribute to their understanding of the issue in question. A multidisciplinary team needs to integrate such experience and understanding that can only be achieved where communication is open and unfettered. This means first that individuals should be encouraged to ask challenging questions or to be able to pose them in a way that reveals a lack of knowledge or understanding and second people should not be ashamed of apparently negative results and should openly discuss them and their significance for the program. Thus, for example, if no genetic variance is found for a desirable trait, this should be openly discussed so that a decision can be made as to whether to continue searching, or to decide not to work further with improvement of that trait. It is not the researchers fault if there is no genetic variation. The general management principle that looking for the guilty person in the team to

blame when things do not work out as expected is extremely unproductive and detrimental in crop improvement programs.

The 'culture' of a team or organization reflects how its collective experience, knowledge and understanding is maintained, nurtured and deployed, and this is of special relevance to succession planning. The quality of the succession planning ultimately reveals the priorities of an organization. One of us, who has been involved in both animal and crop improvement programs, has always insisted that there should be a backup leader of the breeding program who can step into the leaders shoes if, for any reason, the leader leaves the program or is no longer able to carry out his duties. This redundancy is increasingly difficult to achieve in the present, cost conscious, project based, environment of the CGIAR. However, it is vital to ensure the continuity of crop improvement programs that cannot simply be switched on or off.

An important, but little discussed topic in CI was mentioned in the socio-economic sciences contributions. These pointed out that improvement of cropping systems to meet world food demand are not likely to be successful unless population growth is curbed (Supplementary Mat. 13-17; also Nobel prize speech of N. Borlaug). Fortunately, as populations become better educated and more prosperous, the rate of population growth is declining in many parts of the world. Nevertheless, population growth is just one example of how the agri-systems interact with society at large.

Issues linked to the lack of focus

Darwin (1859) famously described the relationship between natural and artificial selection. The key feature of natural selection is that it is undirected, but accompanied by heritable bias for survival. This is the power of evolution by natural selection, but its randomness - a Brownian motion in an adaptive landscape - means that it takes a long period of time to shift from one state to another. Directed selection on the other hand has an objective (or purpose) and can be designed to take the most efficient route to a desired end. While exploration of the adaptive landscape is interesting and engaging, it is a distraction within a breeding programme. It is important to distinguish between the random walk of evolution and the choice of a specific breeding objective and the means to achieve that objective.

There is frequent confusion linked to the CI-programs target beneficiaries; are these women, smallholders, youth, underprivileged members of society, under-nourished or mal-nourished people, or particular value-chain players? These different stakeholders from diverse social sections ranging from rural to urban cannot be simply put into one category and they certainly cannot all be labelled as "farmers". Yet CGIAR crop improvement programs often appear to use a one size fits all strategy to meet the needs of all the target beneficiaries even though at times there may be tradeoffs which make it impossible to design such a strategy. Thus, for example, the CGIAR strategies geared to producing low cost nutritious food to the population at large conflicts with the goal of improved livelihoods of smallholders who produce that food. The crop improvement programs may require distinct strategies, including choice of crop to be improved, to meet the needs of the distinct target populations (indicated by disciplines in Supplementary Mat. 13-17 and some of the JC supplements). The adoption of distinct strategies

would be in line with the prioritization of the CGIAR Science Council (2005 – 2015) which identified reducing rural poverty through agricultural diversification and emerging opportunities for high-value commodities and products as a system priority (CGIAR Science Council, 2005). Furthermore, if the welfare of the rural poor who work on the land is to improve in a globalized world, crops with traits that facilitate increased labor productivity are a necessity. Thus, the current focus of the CGIAR largely on yield gaps should broaden to include the even larger labor productivity gaps. These examples indicate the importance of the definition of the beneficiaries and targets, which should reflect the overall country context, in-line with local government policies and the strategies to implement them.

It has been emphasized that further clarity of directions could come from the quantifications and geographical focus of the research targets including use of GIS approaches and econometrics as an evidence (e.g. return on investment [ROI], Supplementary Mat. 3-5, and 10-12). The targets - not only in CI but also institutional, should be regularly reviewed by the peer-review process (2). The “fashion” certainly does not help CI programs (Bernardo *et al.*, 2016; Sadras *et al.*, 2020; Supplementary Mat. 13-16). The emphasis on a mainly bio-physical (G, E) characterization of the production systems to include both the management (M) and society (S) components is seen as a massive step forward. To continue this trajectory and account for the complexity of both biophysical and social goals in a changing world in the CI program (which requires multiple years from the product conception to release and adoption) crop improvement programs must foresee what the world will look like in the coming decades. The foresight models which blend the multiple interactions ranging from increased urbanization to climate change impact on cropping systems will greatly facilitate this process (see Supp. Mat. 16).

Lack of focus could be also rooted in the oversimplified views on the breeding targets which classically are reduced to increased yield. A focus on a complex function such as yield may fail to identify an actionable breeding target. Crop improvement program targeting can be greatly improved if the underlying functions determining the breeding target (e.g. yield) are considered (Supplementary Mat. 4-5) while carefully accounting context dependency (Supplementary Mat. 6-12). TCI programs that omit the context dependency (i.e. GxExMxS interactions) of the breeding target will have limited value. The rapidly evolving methods and tools to characterize breeding target interactions with ExMxS context can greatly improve the program targeting. These methodologies should be embedded in the core CI-teams.

We have considered whether CGIAR CI-programs should focus on targets complementary to those that are successfully supported by the private sector. While this would be efficient, we should note that the drivers for the private sector are not automatically in the best interests of CGIAR target beneficiaries and markets. Thus, carefully designed overlap and partnership with the private sector is needed. Furthermore, it may not be of interest to the private sector to develop more nutritious staples, whereas it is a priority area of the CGIAR. In order to achieve a balance between the goal of more nutritious food staples and the desire of the farmer for crops that are more profitable, the CGIAR has to ensure that the new varieties are both more nutritious and more profitable for farmers. This may require policy decisions within the

breeding programs to only make available materials for final selection that meet both criteria. If farmers can get their hands on more profitable but lower nutritional value varieties they will surely grow them.

The CGIAR currently stresses genetic gain at the field level as the ultimate measure of crop improvement. This has two serious implications. First, to objectively evaluate genetic gain at the field level is extremely complex and requires subjective assessment of the relative importance of G, E, M and S in the gains at the field level. The E component may be puzzling, however, we point out that increased carbon dioxide levels in the atmosphere, will, *ceteris paribus*, increase both yield and water use efficiency of many crops. Improved yield resulting from improved genotypes is normally related to concomitant changes in the management, which in turn often depend on the socio-economic milieu. Second, there are many traits related to maintenance of productivity in a changing environment and improved quality that are both important and not readily quantified. The improvement of nutrient densities in staple crops for a better fed world should evidently continue, but we find it difficult to define the genetic gain at the field level.

Issues linked to booming technology, data & tech-transfer

Digital technologies are revolutionizing the sciences in response to increasing knowledge, complexity and interdependency of our world. Unanimously, all contacted researchers highlighted the ongoing digital and technological boom in agri-sciences. The advancing technology might, however, pose a substantial trap to the CI-programs if considered (i) without rigorous hypothesis, (ii) in irrelevant GxExMxS context, and (iii) without relevant econometrics (Supplementary Mat. 3-5, 13-16).

Digitalization and automation of systems and processes enables the access to a massive amount of data, some in the real time. In such a situation, more than ever, the importance of standardized and statistically sound data treatment pipelines became a necessary function of CI-teams. The importance of standardized processes are imperative and data sciences is mostly viewed as an important vehicle for cross-disciplinary collaboration.

Proliferation of novel technologies into agricultural sciences means a natural partnership with non-traditional disciplines (e.g. quantitative chemistry, particle physics, IT, software engineering etc.). At present, the technical expertise required for operating, maintenance and upgrading of such complex technological systems is scarce and highly centralized. Such technology options would be efficient for CI mostly if outsourced as compared to attempts to create in-house versions of systems already functional and implementable elsewhere (Supplementary Mat. 3-6). We noted that strategic CGIAR locations might be established as centralized hubs to support networking with partners who have the critical technology and expertise. This would avoid difficulty linked with technology transfer to each CI-team. Frequently enough, much of new technology leads in academically interesting publications but fails to translate into action within the CI-pipelines (Supplementary Mat. 3, Nature Editorials 2020); this outcome may even be driven by institutional policies.

There are enormous opportunities for crowd sourcing and monitoring of farmers` experiences to select improved varieties and to gain insights on where they perform well and how they respond to management (see Supplementary Mat. 13 and 14). These modern information technologies may lead to much greater farmer selection of varieties, questioning the need for rigorous multi-locational trials and official release of certified varieties.

Ultimately, the bottlenecks related to technology and the data generation boom are linked to our capacity to interpret and utilize the generated information. This leads us to the “issue of common scale”; this highlights incompatibility in the spatio-temporal resolution/scale at which the data is being generated and/or interpreted and the scale at which it is required to support application. The incompatibility of scales, which is quite common, further obstructs data interoperability, interpretation and interpolation (e.g. use of the data from the socio-economic dimension for CI; Supplementary Mat. 3, 16, and 17). Unfortunately, even in this modern era, the data quality and its timely sharing with key beneficiaries appears to be a constraint.

Issues linked to management, organization and funding strategies (focusing on CGIAR)

Since most of the contributors have had experience working closely with the CGIAR system, they have brought an invaluable, practical insight into the system's operation.

One of our common concerns is that the CGIAR seemed to be caught between being a development agency and a research institution. CGIAR seems forced to choose between competing with national institutions to be the engine of change or to be the powerhouse for the generation of new knowledge, which properly rests with academic institutions. It cannot be both and ideally should find a role, which is neither.

The CGIAR cannot be solely a research organisation because it has to identify and execute an implementation route. It has to find an effective position catalysing the translation of research from the well-funded academic labs to the networks of (often poorly funded) national research organisations on whom it depends for impact. The CI programme can despair for one or the other or realise its unique and important role as the interlocutor, able to call on a reserve of resources and expertise that can translate socio-economic problems into questions that can be researched and resolved. The current CGIAR needs to be strengthened in this area especially in crop improvement with better linkages to the social sciences (Supplementary Mat. 3, 15), and needs to be confident that this has a necessary and valuable contribution. The environment such a role creates might be confusing for CI managers and organizational leaders who need to provide a blueprint for teamwork that incentivizes CI teams to work collaboratively to achieve measurable impact on the farming system (not an impact factor).

Funding gaps in agricultural research for development complicate the matters further (e.g. Nature editorials 2020; Sadras *et al.*, 2020) – the phenomenon is commonly known as the “call for proposals syndrome” among CGIAR centres. The lack of targeted breeder oriented projects further fuels the vicious cycle linked to the necessity for “full cost recovery” (i.e. most of the personal, operational, capital even institutional charges have to be borne by projects). All institutions must raise sufficient finance to meet their operational costs. However, running the

CGIAR, as a system, on the basis of individual project costs is likely to lead to failure to achieve its purpose. The reason why a particular project can be effective if based within a CGIAR institution is that CGIAR has expertise and resources beyond the costed project that can be brought to bear on the issue being addressed. If there is no such expertise or resource augmenting the project then it is not particularly important that it is based within the CGIAR. If the CGIAR has nothing to contribute beyond a set of interrelated one-off projects then it has no unique value. The CGIAR must therefore finance its fundamental role as an interlocutor, that is as a fundamentally multidisciplinary player essential for the translation of knowledge into benefit for the resource poor.

The current structure based on short-term projects is incompatible with the long time frame of crop improvement and the importance of continuity. This structure with its associated call for proposal syndrome frequently distracts or even derails CI-efforts. Breaking this vicious cycle would probably require synchronization and tight dialogue between the donor agencies (Sadras *et al.*, 2020; Gaffney *et al.*, 2019), national-level research institution leads, and policy makers, together with the top-management of CGIAR institutions. The current movement towards “one CGIAR” aims to address the “political” component of \mathcal{S} sphere of the GxExMxS paradigm and might, at the end, ease the communication stream and bring the clarity and focus necessary for successful delivery on the CGIAR system goals and mission.

We express the sincere hope that research advancements, integration and focus, along with the CGIAR system reforms coupled to ongoing revisions of funding strategies from key donors will establish and renew global efforts to develop and sustain the world's agri-system in the upcoming decades.

Author Contributions

JK - Writing, original draft preparation, visualization, conceptualization, review & editing
MOU - Writing, original draft preparation, visualization, conceptualization, review & editing
JC - Writing, conceptualization, review & editing
AJ - Writing, review & editing
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CS - Writing, review & editing
CP - Writing, review & editing
CJ - Writing, review & editing
ConD - Writing, review & editing
CM - Writing, review & editing
CP - Writing, review & editing
DD - Writing, review & editing
EN - Writing, review & editing
FR - Writing, review & editing
GS - Writing, review & editing

HG - Writing, review & editing
HJ - Writing, review & editing
JC - Writing, review & editing
MS - Writing, review & editing
MG - Writing, review & editing
NE - Writing, review & editing
NgE - Writing, review & editing
PS - Writing, review & editing
SS - Writing, review & editing
SM - Writing, review & editing
TF - Writing, review & editing
TP - Writing, review & editing
VS - Writing, review & editing
VEJ - Writing, review & editing
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