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The Plant Genome

SPECIAL ISSUE: GENOMICS OF ABIOTIC STRESS TOLERANCE AND CROP RESILIENCE TO CLIMATE CHANGE

What plant breeding may (and may not) look like in 2050?

Filippo M. Bassi[1] | **Miguel Sanchez-Garcia**[1] | **Rodomiro Ortiz**[2]

[1]International Center for Agricultural Research in the Dry Areas (ICARDA), Rabat, Morocco

[2]Department of Plant Breeding, Swedish University of Agricultural Sciences, Lomma, Sweden

Correspondence
Rodomiro Ortiz, Department of Plant Breeding, Swedish University of Agricultural Sciences, Box 190, SE 23422 Lomma, Sweden.
Email: rodomiro.ortiz@slu.se

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Abstract

At the turn of 2000 many authors envisioned future plant breeding. Twenty years after, which of those authors' visions became reality or not, and which ones may become so in the years to come. After two decades of debates, climate change is a "certainty," food systems shifted from maximizing farm production to reducing environmental impact, and hopes placed into GMOs are mitigated by their low appreciation by consumers. We revise herein how plant breeding may raise or reduce genetic gains based on the breeder's equation. "Accuracy of Selection" has significantly improved by many experimental-scale field and laboratory implements, but also by vulgarizing statistical models, and integrating DNA markers into selection. Pre-breeding has really promoted the increase of useful "Genetic Variance." Shortening "Recycling Time" has seen great progression, to the point that achieving a denominator equal to "1" is becoming a possibility. Maintaining high "Selection Intensity" remains the biggest challenge, since adding any technology results in a higher cost per progeny, despite the steady reduction in cost per datapoint. Furthermore, the concepts of variety and seed enterprise might change with the advent of cheaper genomic tools to monitor their use and the promotion of participatory or citizen science. The technological and societal changes influence the new generation of plant breeders, moving them further away from field work, emphasizing instead the use of genomic-based selection methods relying on big data. We envisage what skills plant breeders of tomorrow might need to address challenges, and whether their time in the field may dwindle.

1 | INTRODUCTION

Twenty-five years ago, it is 1998, nearly the turn of the century. The vision for global agriculture was to deploy all available innovations to maximize farms productivity per unit of land to overcome the risk of food insecurity in the face of a growing population. Three years prior (1995), the Environmental Protection Agency had approved for farming in the USA the genetically modified (GM) insect resistance *Bacillus thuringiensis* crops, such as corn, cotton, potato, and tobacco (Abbas, 2018). By 1997, GM crops have already taken up large market shares and will continue to climb. Five years before (1993), Kary Mullis and Michael Smith were awarded the Nobel Prize in Chemistry for the invention of the polymerase chain reaction, inspiring millions of

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Abbreviations: DH, doubled haploid; G × E, genotype by environment interaction; GG, genetic gain; GM, genetically modified; GS, genomic selection; MAS, marker-assisted selection; NIRS, near-infrared reflectance spectroscopy.

potential applications by geneticists worldwide. Two years before (1996), the first eukaryotic genome (*Saccharomyces cerevisiae*) was successfully sequenced, and the *Arabidopsis* sequencing consortium was just formed to achieve its full genome sequencing few years after (2000).

It is also at the turn of the century when many authors were quested by editors to unveil their vision for the next millennium of plant breeding. With the many breakthroughs of genetics in the 1990s it is then unsurprising that one of us in 1998 (Ortiz, 1998) declared that in the next century plant breeding would become highly dependent on molecular markers, GM, and whole genome sequencing. At the time, also the surge of double haploid techniques and the undeniable increase of computational capacity had captured the attention of this author. This was certainly not the only review foreseeing that genetics and genomics would eventually lead the next breakthrough toward a food secure World (Borem & Kothe Milach, 1998). Bosemark (1995) and Lee (1998) suggested that the use of molecular markers could lead the way for an increase in selection intensity and the possibility to explore wider variability than ever before. Cooper et al. (1999) took a slightly different stance by suggesting how molecular markers could be used to statistically model the complex quantitative genetic interactions between traits and environments, and eventually become able to use computational models to take more efficient breeding decisions. In line with this, Hill et al. (1998) in their quantitative genetics book defined the importance of adopting the latest biometrical approaches to model genotype by environment interaction (G × E) to achieve higher genetic gains (GGs, Safi & Price, 1998). The great success of hybrid crops had also inspired several authors at the turn of the century to call for another attempt at converting more self-pollinated crops to hybrid systems (Ratnalikar & Singh, 1998). However, genetics was not the only aspect that attracted authors. Some innovations in plant physiology also prompted a new vision for phenotyping methods that breeders could deploy (Jackson et al., 1996), including the use of some novel laboratory equipment to predict industrial suitability at the plot level, like the near-infrared reflectance spectroscopy (NIRS) for replacing wet chemistry (Batten, 1998). It is also the time that agronomists started promoting widely the concept of zero tillage and conservation agriculture (Avery, 1997; Plucknett & Winkelmann, 1995).

2 | WHAT WORKED AND WHAT DID NOT

Fast forward 25 years, it is now 2023, and you are probably reading this article on your laptop computer or on your smartphone, we have lost count of the number of plant genomes that have been sequenced, and talking about molecular markers have become as mundane as talking about the weather, which in the meantime has become much less mundane. At the same time, oil prices have increased fivefold, climate change is no longer a "debate" but a "certainty" (Easterbrook, 2006), and the World has experienced the global pandemic of SARS-Cov-2 (COVID-19). So, are all the predictions of a genomic revolution in plant breeding become a reality?

Core Ideas

- A genomic revolution in plant breeding shall become a reality from parents selection to variety commercialization.
- Higher rates of genetic gain can be achieved via the deployment of the latest plant breeding methods.
- These higher genetic gain rates are costly and promise to put out of business those that cannot afford them.
- Providers of several services are due to enter the commercial space, changing forever the figure of a plant breeder.

The vision for global agriculture has changed severely in a quarter of century, shifting away from the 1990s idea of seeking maximum farm outputs, to a new sustainable goal of minimizing the use of inputs and reducing environmental impact (Mba et al., 2012). In the process, the concept of achieving global food security has been turned toward a new vision for a more profitable, nutritious, and sustainable future. Interestingly, it is the wide adoption of GM crops, one of the most supported breeding technologies by authors in the 1990s, which has been suggested as a major cause of this rapid ideological shift. Consumers were probably not ready for the fast appearance of GM harvests in their grocery stores and reacted in many cases by putting pressure on their regulators to control their spread. As such, the GM technology has been an undeniable success with vast areas being cultivated today, but also a failure since their associated legal restrictions have impacted the ability of breeders to deploy it. In fact, only few field crops (canola, cotton, maize, and soybean) are currently cultivated in large global acreages as GM, their harvests mostly not meant for direct consumption by humans. Moreover, the expensive legal process for GM registration limits their deployment to mostly large private multinational enterprises capable of affording them. Public GM ventures have been almost negligible; the few cultivated ones such as "Golden Rice" are not yet covering sufficient area to be considered a true success (Wu et al., 2021). The complexity of deploying GM crops has also reduced the public research investment, hindering the discovery of novel and useful constructs, so that only few transgenes are deployed thus far.

The DNA marker technology was also seen in the 1990s as the key for plant breeders' future successes. In two decades, the price per molecular datapoint has been driven well below the wildest expectations, thereby making the adoption of this technology extremely affordable. Furthermore, the figure of the plant breeder has deeply changed, with the younger generation being fully trained in the deployment of genomic-based breeding methods (Baenziger et al., 2008). Moreover, the use of genomic tools in breeding has promoted a vast increase in the number and quality of publications made by plant geneticists, truly moving upward the level of knowledge in the field. Despite all this positive shift, it is quite evident that the DNA marker technology has only resulted in few documented cases of cultivars released, failing to impact plant breeding at the scale that scientists were predicting at the turn of the century. The reasons can be found in the fact that it took long time for plant breeders to accept and later embrace the technology. Moreover, the cost, complexity, slow turnaround time, and low number of samples that could be processed until recently were not meeting the needs of plant breeders. Furthermore, the discovery of useful DNA markers to be deployed was too slow for plant breeders to get interested, and the relatively few validated DNA markers became available well after the same loci that these tagged had been widely introgressed via phenotypic screening, thus making them virtually useless. In addition, the vast literature produced via the discovery of quantitative trait loci (QTL), despite almost always declaring in their conclusion section that "this QTL is now useful for marker-assisted selection (MAS)," authors rarely confirmed this statement by running a step of marker conversion and validation, making their discovered QTL "not ready for MAS." Although it is true that recently there has been a true shift and revamping of the DNA marker technology to serve breeders, their deployment has not yet reached on a vast scale farmers' field.

Linked to DNA markers, another technology that was expected to be disruptive was genome sequencing. In particular, the use of model organisms was envisioned as a strategic solution to rapidly build knowledge that could be transferred to crops. Indeed, model organisms have helped developing knowledge and gene models, but to date their impact in plant breeding has been extremely limited (Matthews & Vosshall, 2020). With the exponential reduction in cost and turnaround time for de novo sequencing, nearly all crop species dispose today of at least one reference genome, if not thousands (Lewin et al., 2018). These reference genomes are ideal for anchoring and comparing information across research groups, and they also favor the faster discovery of useful genes. However, the slower than expected adoption of MAS and the legal limitations on GM deployment have in turn prevented the adequate exploitation of the genomic sequences by breeders. As such, also this technology has not yet had the impact on plant breeding those authors were predicting in the 1990s.

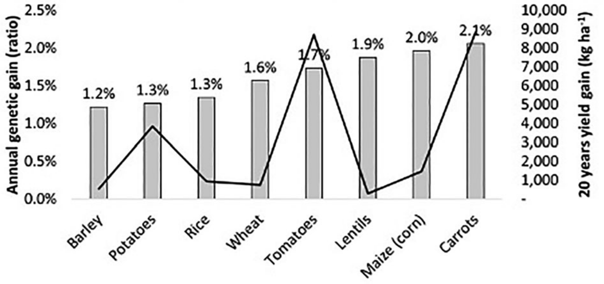

FIGURE 1 Global yield gain in the past 20 years presented as annual rate (primarily vertical axis-gray bars) and total yield gain (secondary vertical axis—black line) for some representative crops estimated by FAOSTAT data. The annual rate of yield gain is reported as a value above the bars and it combines genetic and management gains. To be noticed that potatoes, carrots, and tomatoes are reported as fresh weight yield.

The area of phenomics has also achieved great advancements since the turn of the century. The use of remote sensing methods performed from the ground, below ground, the air or the space have found great appreciation and fast adoption by many breeders (Tao et al., 2022). Similarly, the deployments of artificial selection environments like rhizotrons, hydroponics, phytotrons, and other simulated systems have encountered strong appreciation in recent years. However, their validation for use in plant breeding is still ongoing, thereby making their overall impact in farmers' fields quite limited.

Overall, the omics tools in which so much hope was bestowed at the end of the century have delivered below expectations. Nevertheless, plant production globally has registered a clear upward trend for yield as shown for some representative crops in Figure 1 using global data generated by FAOSTAT (https://www.fao.org/faostat/en/#home). Although a large part of this yield improvement can be attributed to improvements in crop husbandry and resource management, a significant portion has been ensured by the ability of plant breeders to raise the GG rates. So, one could ask which factors contributed to it?

The deployment of the hybrid system has generated a steep gain already at the end of 1980s in most crops, and in some cases it has also resulted in better strategies for seed production (Ter Steeg et al., 2022). Unfortunately, several crucial factors determine its commercial feasibility, and its deployment in self-pollinated species is still minor. For crops like rice, barley, and wheat some promising results have been registered recently, but the adoption is still limited (Ortiz, 2015).

The use of accelerated methods to reach homozygosity, on the other hand, has become a gold standard for all crops. The doubled haploid (DH) technique has been widely adopted in nearly all breeding systems, especially for those crop types that require lengthy periods of cold accumulation before flowering (or vernalization). For spring types, the use of the shuttle breeding approach to double or triple the number of growth cycle per year has been often preferred to DH because it reaches inbred trialing substantially at the same time, for a fraction of the cost, and allowing for larger number of offspring to be. Recently, the advent of "speed breeding" to further increase the number of generations completed per year has also found a good level of adoption, and new varieties coming from this advancement strategy have been released (Srivastava & Bains, 2018). Certainly, these acceleration methods have contributed significantly to the increased GG rate since these intervene on the denominator of the GG equation, where small changes can have vast impacts.

One technology that was probably under-considered in the 1990s, but which resulted in a vast impact in plant breeding has been the engineering of specific field implements to conduct research. The deployment of affordable experimental planters, threshers, combines, and many critical laboratory equipment has profoundly impacted plant breeding. These implements have allowed to increase enormously the selection intensity by trialing more breeding materials while at the same time have dramatically improved the accuracy of the data gathered and have favored faster turnaround time necessary to deploy accelerated methods to inbreeding.

Probably the most disruptive technology that plant breeders have experienced in the past 25 years has been the democratization of statistical and biometrical analysis. The vast increase in affordable computational capacity has allowed each plant breeder to conduct complex analysis with extreme simplicity. The establishment of open-source statistical packages has dramatically increased the number of users relying on them to perform selection (Alvarado et al., 2020; Peternelli, 2011). In parallel, the simplification of statistical analysis into user-friendly packages has ensured that ever more complex analysis be performed routinely. G × E interactions can greatly mask the true value of a genotype, but now with the new bioinformatics tools it becomes the choice of the breeder if being fooled by it or correctly model it. Furthermore, data management has experienced its own revolution, making it extremely simple for breeders to utilize data across years, locations, and experiments to select the truly superior offspring in the nursery trials.

One element that geneticists writing their visions for the future of plant breeding in the 1990s probably were unable to account for, it is the vast adoption by farmers of zero (or reduced) tillage and resources-conservation technology practices. Research demonstrated that a certain degree of genotype by practice interaction exists (Joshi et al., 2007), which means that different breeding materials respond better or worse when grown following conservation agriculture practices. Some plant breeders have then switched to this methodology to align their selection fields to better mimic those of farmers, and others have decided not to. It remains to be seen if this fact has influenced the GG in the areas where conservation agriculture has been adopted, and if it will have an impact on others.

3 | WHAT MIGHT WORK

The world population continues rising, of which 1 billion humans suffer from hunger and 3 billions malnourished people live with less than US$2 daily. Today, many people live in areas affected by land degradation, frequent weather extremes, diminishing groundwater aquifers, pasture overgrazing, tropical deforestation, and loss of biodiversity. After the fast pace of technological and vision changes of the past 25 years, it is nearly impossible to predict with any certain what will happen in the next quarter of a century. In terms of global vision, there are concepts that are appearing with higher frequency, like the idea of a "carbon tax" that shall push toward ever more sustainable and local production, especially in association with the new model of "agroecology" (Dalgaard et al., 2003). In parallel, there is a growing appreciation for the concept of "food sovereignty" after the difficulties of provisioning staple foods some countries experienced after the COVID-19 pandemic and the war in Ukraine. Hence, the idea of "producing more, with less, and locally" is gaining momentum, despite the evident challenge in converting this nice statement into an actual farm solution. Adding to the mixture the deteriorating climates clearly shows the near-impossible challenge that plant scientists are called upon to solve. Plant geneticists have a key role to play within by providing ever-better cultivars, capable of withstanding the climatic stresses, yielding more and more nutritious harvests, while using less inputs and simultaneously enriching the soil in which they are grown.

Many disciplines associated with plant breeding would need to come together to deliver such germplasm. Luckily, there is an equation that helps define and monitor the progression toward these common goals: GG (Dwivedi et al., 2020; Rutkoski, 2019). GG is typically measured as "rate of gain per year," stemming from a linear equation measuring the interactions between three factors at the nominator (selection accuracy, intensity of selection, and genetic variance), divided by a fourth factor at the denominator (recycling time) as shown below. It is therefore useful to revise which technologies and innovations can be expected to have a positive impact for each factor.

$$Genetic\ gain = \frac{accuracy \times intensity \times variance}{recycling\ time}$$

3.1 | Accuracy of selection

Type I error in plant breeding can be seen as the advancement to the next generation of entries that were supposed to be performing but that are not, whereas type II error is the discard of entries deemed inferior that were not. Having high accuracy of selection prevents both errors and ensures hence that the truly superior entries are promoted. Since the 1990s, probably the largest advancement in GG has been made in this factor of the equation.

3.1.1 | Phenotyping accuracy

Since most plant breeding decisions are made based on phenotypic scores, the value of selection accuracy is often substituted by the value of phenotypic accuracy. However, selection accuracy and phenotyping accuracy are not the same even though their linkage is evident. Most traits in plants are controlled by multiple genes that interact in a quantitative fashion with the environments. This gives raise to the G × E interaction that can mask the true value of an entry, leading to low accuracy of selection. However, G × E is also a true biological effect that can be exploited positively by favoring the adoption of varieties specifically adapted to a given environment, effectively increasing performances. Several improved statistical models and approaches have been defined to increase the heritability of a trait and model the G × E (Bustos-Korts, 2017; Cooper & DeLacy, 1994; Crossa et al., 2004). It can be expected that the deployment of ever more complex spatial analysis and improved field designs shall further improve the accuracy of selection. Linked to this will be the deployment of better experimental machines and tools. Several companies have recognized the importance to serve plant scientists with improved tools; new versions of field and laboratory equipment are due to be the released in the next decades. A good example is the NIRS, which are now equipped with broader wave lengths, have improved prediction models, and can operate using just a single seed or directly on a combine during harvest. Coalitions of plant scientists are coming together to generate more comprehensive and vast datasets for NIRS, increasing the number of traits that can be measured and the accuracy of their predictions. Communities of practices for phenomics data management, processing, and analysis will be necessary to truly drive discovery using the new tools capable of generating millions of datapoints per plot (Khan, 2022).

3.1.2 | Stacking of major genes for accuracy increase

The largest increase in accuracy has been obtained via the deployment of genomics. The GM approach ensures the exact delivery of one gene controlling one trait of interest, avoiding the masking effect of the environment. GM crops revolutionized plant breeding in some crops, but their impact is still limited in staples consumed directly as food. More can be expected from the GM approach in the next decades, with novel constructs promised to deliver tolerance to climatic stresses or protect against specific pathogens. However, the current regulations will prevent most breeders to access this technology; although it can be hoped that the public opinion sways in favor of this approach in the next 25 years, there are no clear evidence to suggest this might occur. The use of artificial chromosomes has also been proposed to transform many genes at once, but it is unlikely that these would meet consumers appreciation (Kan et al., 2022).

On the other hand, the scientific community is carefully promoting the use of gene-editing technology, and so far, its regulation has been treated separately from the GM method (Sprink et al., 2022). Hence, there is true potential to achieve highly accurate introgression and modification of core genes using the gene-editing method. However, the success of this approach will be ultimately dependent on the capacity to obtain new functional traits by modifying few nucleotides, and hence on the ability of plant geneticists to identify the core set of nucleotides to modify. As for most crops only a small number of genes have been properly cloned and characterized, this knowledge gap represents a true impediment to the deployment of gene editing. The increased availability of plant genomes and pangenomes may accelerate the discovery and characterization of more genes, but more investments would be necessary to truly boost this aspect. In addition, there are some technical limitations on the number of genes or loci that can be edited in each callus generation, but there is evidence that this limitation might be surmounted in the next decades (Birchler, 2017; Rodríguez-Leal et al., 2017). In fact, the passage through callus culture is another limiting factor for this technology, as several generations are required to produce enough seeds to advance to yield trials, and only few offspring can be produced. On the other hand, DNA markers well designed to tag alleles of interest offer a faster, more scalable, and technologically simpler solution to pyramid major genes. Currently, a targeted pyramiding scheme using DHs can realistically deliver new lines with 20 introgressed alleles in as little as 2 years, and at relatively high-efficiency rates (Sanchez-Garcia & Bentley, 2020). Hence, gene editing would need to significantly improve to become superior to MAS. An alternative more exciting option would be to generate alleles that are not available in the primary gene-pool, or to target regulatory elements for which very little genetic variation exist (Li, Feng, et al., 2022), but more understanding is still necessary. Overall, the idea that plant breeders will design the next generation of cultivars combining several alleles via gene editing is unlikely to occur by 2050. MAS is likely to continue being the method of choice for pyramiding. However, it could be envisioned that gene editing might be used to correct several major alleles for few crossing parents, facilitating the subsequent use of MAS on a large set of their offspring.

3.1.3 | The stacking of minor genes for accuracy gain

The availability of affordable dense genotyping options, sophisticated biometrical modeling, and means for handling big data facilitates the use of genomic estimated breeding values for performing selection (hereafter genomic selection, GS) of minor genes. Managing quantitative progression toward GG will remain the prerogative of carefully designed recurrent selection schemes that accumulate multiple minor genes in the right allelic combination. To that end, GS has met increasing appreciation and adoption by many programs. Therefore, it is no longer a question of "if" but "when" all breeding programs shall rely on it. However, there are still some issues to be solved to avoid the same hype of 30-year ago when promoting MAS. In fact, while studying the accuracy of GS approaches, breeders have become aware of how inaccurate their phenotypic selection was and are now more enticed by the idea of selecting at 0.2 accuracy. There is still room to improve these low accuracy rates by using better statistical approaches, but a consensus has formed that the best gain will come from choosing the right training set, and therefore from the breeders' ability to design a suitable scheme for it (Bassi et al., 2016). In parallel, several authors believe that GS could be a disruptive technology capable of significantly increase the rate of GG (Crossa et al., 2017). In turns, that means that programs that do not apply GS would lose GG quickly each year as compared to the early adopters, to the point that their germplasm could soon become obsolete. It is for that reason that private breeding companies and the One CGIAR have committed in accelerating the adoption of this methodology.

Although there is a huge drive to adopt GS widely using a blanket approach, this breeding method requires strategic decisions and investments, making of it an elitist technology. GS requires human capacity to be performed, adequate big data management (Kim et al., 2020), and access to high throughput DNA markers. Because of the costs and knowledge associated with its adoption, it is rapidly widening the gap between larger breeding setups, and most of the small/medium private or public enterprises. This is particularly true in the Global South where the One CGIAR operates. The human capacity gap can be filled by targeted trainings, but it is not always possible to change the mindset of existing breeding leads. In the past, a vast generation of biotechnologists has been trained to conduct in-house marker analysis that no longer serve the scale, cost, and turnaround speed needed to deploy GS. Several service providers have established themselves to screen thousands of progenies with hundreds of DNA markers within 3–4 weeks of turnaround time. This effectively pushed the biotechnologists to migrate toward breeding jobs, bringing forth the needed mindset shift for the adoption of GS.

While the reliance on these providers of genotyping service will continue in the next decades, is it possible that more services will become available? The provision of full-scale de novo sequencing and assembly on demand is already a reality, and with the price of this service continuously dropping it shall soon become a routine approach. Similarly, the "Amazon approach" shall soon find its application also in plant breeding by offering simplified and affordable solutions for genomic and phenotypic data storage and management (Yan & Wang, 2023). Beyond, the vast datasets that are generated by breeding programs nowadays (i.e., genomic, phenomic, and environmental) require ever more complex statistical analysis to truly take full advantage, opening the possibility to providers to also offer analytical services. In particular, the use of artificial intelligence approaches has the potential to extract extremely useful information from breeding data (Harfouche et al., 2019), but the complexity of its deployment and the need for high computational capacity would be better served by a centralized approach with commercial providers rather than by each breeding programs individually. New solutions are being designed to facilitate the interpretation of the results like the Operations Research Approach, a technology originally developed to optimize decision in industry, that is, now being adopted to facilitate breeding decisions based on big data analysis (Beans, 2020). Hence, it is probably not farfetch to consider that the next decades will see the establishment of true "one stop shop" for genomic breeding, offering solutions from genotyping to data storage all the way to analysis and decisions. That would simplify the need of developing the capacities of the breeding team, while driving down costs and favoring the rapid uptake of innovations.

3.2 | Intensity of selection

The intensity of selection is a standard value defined by the rate of selected entries out of the total size of the original set, and it is influenced both by the actual number of entries and the rate itself (Hickey et al., 2017; Mackay, 2020). In that sense, it has often been associated with the ability of breeders to access sufficient funds to afford testing as vast as possible number of progenies. On the contrary, the use of more expensive testing systems results in a higher cost per progenies, and hence it would reduce the total number of progenies tested. Because of this, the intensity of selection has been in many ways the least favored of factors of the GG equation in the past decades. For instance, the use of MAS comes at a price; until very recently it was not economic to use markers if a qualitative phenotypic screening was available. Similarly, although it is true that predicting performances by GS of fixed material is often cheaper than conducting yield trials or time-consuming laboratory testing, for segregating generations it is true the opposite: thousands of F_2 or F_3 individual progenies can be advanced phenotypically at virtually no costs, while only a small number of progenies can be afforded to conduct genotyping for GS. In the next decades, it can be expected that the drive to increase the number of markers datapoint per unit invested will also be accompanied by a reduction in the cost of assessing a fixed number of markers. In fact, although increasing the number of markers tested can result in a small increase in accuracy (Zaim et al., 2020), it is by reducing the cost of genotyping one progeny with few hundred markers that breeders will be able to maintain or even increase selection intensity, ultimately achieving higher GG. An alternative breeders are using to maintain high selection intensity is to design recurrent full sib mating schemes (Bassi et al., 2016) or to perform GS at more than one segregating filial generation (Li, Kaur, et al., 2022), but both methods require targeted investments. Nevertheless, maintaining high levels of selection intensity in segregating generations is probably the biggest challenge that plant breeders are called to face in the next decades and it is unclear now what innovative solutions will be devised for it by 2050 (da Silva et al., 2021).

As stated for the "accuracy of selection," the introduction of several field and laboratory experimental equipment have significantly increased the number of entries that can be screened and hence the intensity of selection. Hence, the area of phenomics is of great value in terms of increasing intensity in the future by testing larger populations. Novel approaches to field testing using manned and unmanned vehicles carrying multiple tools have already demonstrated their suitability to increase accuracy of selection as well to test many thousands plots at virtually no added costs (Guo et al., 2020). However, the results of these tools are only as good as the environment in which these are deployed, and its ability to express traits of interests. Adaptation to climate change stresses is a major trait(s) of interest of breeding programs for the next decades. In that sense, the Global South is already affected by many of these climatic stresses and hence provides a valuable opportunity to test today against the issues of tomorrow. There are already several nice examples on the use of the Global South as a phenotyping platform for climate change adaptation, such as the case of International Center for Agricultural Research in the Dry Areas' durum wheat testing heat tolerance along Senegal River Basin (Sall, Bassi, et al., 2018; Sall, Cisse, et al., 2018; 2019), or the CGIAR WHEAT precision phenotyping platforms (Lopes et al., 2014; Reynolds et al., 2020). One future evolution could be the establishment of true certification processes for varieties, by which the achievement of certain results at specific sites would result in true labels of climate adaptation (i.e., "drought tolerant" or "heat tolerant") that breeding programs can use to attract farmers adoption. This approach could be expanded to all breeding programs to foster investments, help increase their selection intensity, while certifying for critical traits.

Another option to increase selection intensity is the incorporation of a citizen science approach in which farmers (i.e., citizens) are provided with germplasm for testing under their own conditions (Isaac & Martin, 2019; van de Gevel et al., 2020; van Etten et al., 2019). If enough citizens can be engaged (often as an act of kindness), a vast array of data of medium to low quality can be generated at virtually no added costs. Although several shortcomings exist in the quality and complexity of the data that could be generated, the citizen science approach holds the potential to increase the number of progenies screened and hence the selection intensity. It remains to be seen what level of engagement citizen would demonstrate if the process was to become regular and by public and private enterprises alike.

3.3 | Genetic variance

Since 1990s and the introduction of DNA markers, we have become increasingly proficient in assessing the level of genetic variability held by breeding programs. Unfortunately, the results are not positive, showing that most of the diversity is still stored within our genebanks, which luckily did an amazing job at conserving it until breeders become able to exploit it (Dempewolf et al., 2023; Salgotra & Chauhan, 2023; Khoury et al., 2022; Mazzucotelli et al., 2020). The relationship between "useful variance" for a trait of interest and "genetic variability" overall is not linear; nevertheless, it is generally accepted that a program with low variability would be unable to generate useful variance. The breeding process of continuously crossing the best by the best and select the best (van Ginkel & Ortiz, 2018) "eats up" very quickly variance, promoting the rapid fixing of preferred alleles, until breeders become unable to drive further progress. Many authors warned breeders of this negative trend but the change of mentality toward the use of more exotic mating parents is still not accepted by many. In fact, students have been taught for a long time that the use of landraces and crop wild relatives was a last resource that should be used only in extreme cases (Neumann et al., 2023). Recently, a new drive toward the incorporation of these into elites by dedicated pre-breeding pipelines has shown very positive outcomes (El Haddad, Kabbaj, et al., 2021; El Haddad, Sanchez-Garcia, et al., 2021; Renzi et al., 2022). Some authors have suggested that the "better than expected" results obtained when using exotic germplasm into their crossing programs can be attributed to the higher genetic variance generated, as no other evident explanation can be found (Neumann et al., 2023).

The concept of germplasm enhancement or pre-breeding has become generally accepted and more programs are adopting its principles. The genebanks are the obvious source of this novel diversity to be incorporated. Several are undergoing the hard work of characterizing better their accessions to serve targeted diversity on demand (Nguyen & Norton, 2020). In several cases, the genebank have initiated a process of skim sequencing or genotyping of their entire accessions (Nybom & Lācis, 2021; Schulthess et al., 2022; Singh et al., 2019). It is probable that in the next decades more genomic information will become available from genebanks, but also from other breeding programs. Hence, it is conceivable that the existing genebank databases like GeneSys (https://www.genesys-pgr.org), Germinate (https://germinateplatform.github.io/get-germinate/; Lee et al., 2005), ENSEMBLE (Birney et al., 2004), or NCBI would become in the near future the true holders of the global genetic diversity in the form of stored genomic sequences. Breeding programs at risk of losing variance in a specific region or for a specific trait would then become able to query these databases to identify the needed variance and acquire it from the genebank (Yu et al., 2016, 2020). In parallel, the use of approaches to maximize the likelihood of success when selecting mating partners like PopVar (Mohammadi et al., 2015) or artificial intelligence are likely to become gold standards in the next decades, and with them the management of variance will become a major focus of breeders. “Major focus” often equals to “investment,” so it is with some worry, to say the least, that we hope the exchange of germplasm aimed at replenishing loss variance will remain freely available to all for the greater good (Ghimiray & Vernooy, 2017; Lopez-Noriega et al., 2013; Winge, 2016), even though recent trends show that this might not be the case (Smith et al., 2021).

3.4 | Recycling time

Recycling is the time expressed in years that elapses between the moment a cross is made, and its resulting progenies are re-mated again. It is then a function of the time needed to complete a cross then advance the resulting progenies to a generation when the traits of interest can be measured with sufficient accuracy, and the number of successive tests needed before determining that a progeny is valuable as a new parent. A major advancement for this factor of the GG equation was already achieved by Norman Borlaug in the 1950s with the introduction of the concept of shuttle breeding, which allowed advancing to inbreeding at the speed of two generations per year. In the 1990s, the vast adoption of clonal propagation and DH achieved even faster rates of advancement. Recently, the approach named “speed breeding,” which is a method to accelerated glasshouse generation time using long artificial daylight and controlled temperatures, has found increasing appreciation as it matches the advancement time done by DH, but at a fraction of the cost and it is possible to conduct phenotypic selection while progressing to inbreeding (Ahlamad et al., 2018, 2020). Because of its many advantages, it can be expected that speed breeding will be met with even greater appreciation in the next decades. However, the cost of electricity for lighting and temperature control, and the working man hours it requires make it not suitable everywhere. In that sense, the Global South has access to longer sun hours, milder temperatures, and often more affordable costs. It can then be envisioned that service providers for this technology are established and operated there to serve the needs of programs worldwide.

Despite the accelerated time to inbreeding or to the testing generation, the need to conduct multiple-years and multiple-environments of testing before identifying the most useful progenies to be recombined remains the main limiting factor for truly reducing recycling time. In that sense, GS with its ability to predict the offspring performance before these are field tested offers the exciting opportunity to severely reduce recycling time (Bassi et al., 2016). Recrossing of selected F_2 is therefore a real possibility, that is unfortunately prevented by the need of feeding the GS model with training dataset related to the progenies (Zaim et al., 2020). Hence, it can be foreseen that the next decades will witness the development of new breeding schemes and statistical models capable of handling the issue of low relatedness between the breeding and training population to finally deliver denominators for the GG equation of size “1” or even fraction of it.

4 | DELIVERING CULTIVARS

The difficulty of deploying some of the novel approaches described above is envisioned it will favor the establishment of service providers capable of cumulating requests to drive down costs. A graph describing what future breeding with the inclusion of service providers might look like is provided in Figure 2 and explained extensively in this section. A service provider shall be contracted to design the best crosses using artificial intelligence approaches to mine for useful variance from global dataset. Another service provider shall be entrusted to advance the resulting progenies rapidly via speed breeding and ensuring the imposition of GS and MAS, also deploying the most advanced biometric models. Recycling of progenies would then occur rapidly based on their predicted performances, while in parallel the material shall be advanced to the first stage of testing. Another service provider will offer high-throughput phenotypic screening, probably integrating the use of field phenotyping platforms located in the Global South to obtain specific certified labels. The progenies undergoing yield trial would then be genotyped at high density to provide the basis for future predictions and imputations. The most interesting germplasm would then be advanced in the breeding pipeline to cultivar level and participatory

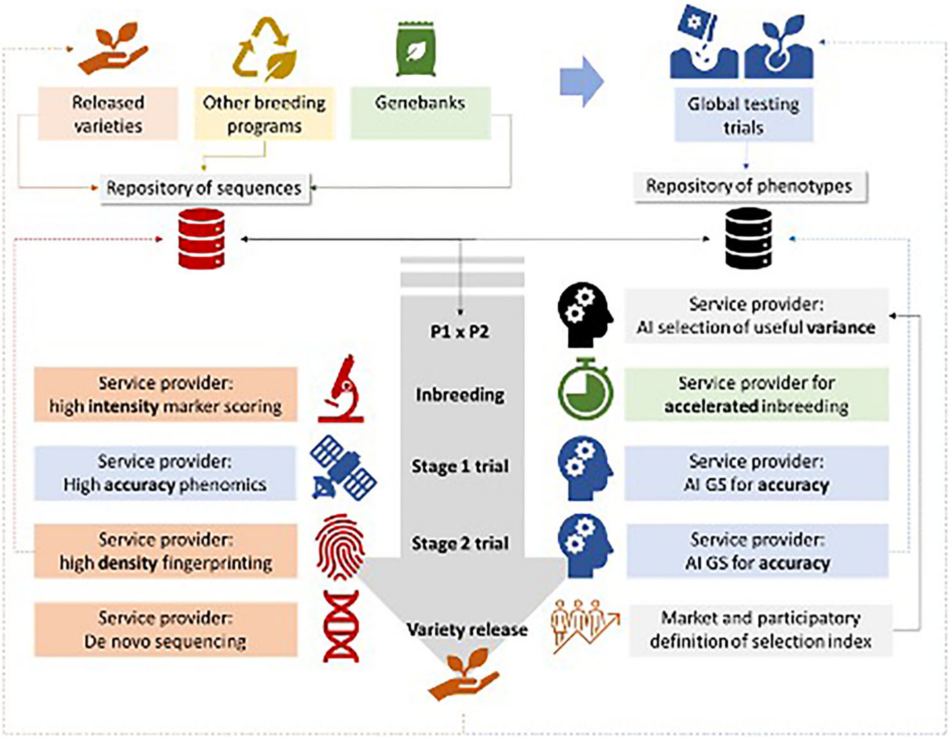

FIGURE 2 Tomorrow's breeding: a vision for 2050 plant breeding approach that relies on service providers for most steps, including the use of next generation artificial intelligence models, a global community of practice for the exchange of data and useful variance, accelerated schemes relying on providers in milder climates, and a strong integration of market intelligence, including the use of participatory approaches. For example, a shift to a citizen approach will allow released cultivars to be also sold as few seed bags and then each farmer becoming responsible for producing vast seed amounts.

approaches could be used to identify its appreciation by users. For instance, Alary et al. (2020) have proposed a participatory farmers' weighted selection index (PWS) to scale up the more classical participatory variety selection and define traits preferences that can be integrated at all levels of the breeding pipeline.

A revision is likely also to occur to the variety release system, moving away from the very costly and time consuming distinct, uniform and stable system toward a more genomic-enhanced approach. An example could be that each breeder deposits the de novo genomic sequence of its new cultivar in a centralize repository, which could then be used to trace back genomic contributions and relative importance of different loci. For livestock, their genomic predicted contribution to the next offspring generation has become enough to sell the semen of selected male parents for artificial insemination (Romadhonny et al., 2019). It is not unlikely that the genomic sequence of new cultivars will also become sufficient to determine their predicted value for farming and for mating, to sell their pollen to other programs. In parallel, a global drive to accelerate and improve the breeding approach is likely to promote a revision of several legal aspects currently governing plant variety releases (Yang et al., 2021). The genomic repository of cultivars could also serve as a new global catalogue, replacing the time-consuming need of country-specific releases. The sequence itself could be used to determine the genomic contribution of different cultivars and breeding materials and eventually recognize the rights and royalties of each breeding program. Furthermore, the use of DNA markers to test the seeds would allow to rapidly identify the cultivars, so deploying these at collection site (i.e., mills, grains elevators, and others) could serve to track their commercial use. In that vision, the current certification process of seeds would become obsolete. The large-scale production of quality seed seems to be still a limiting factor for the uptake of newly released cultivars. It takes about 2 years to achieve enough homogeneity to submit seeds to the cultivar catalogue, 2 more years of field testing across sites, another 4–6 years to produce enough seed for their commercialization, and 3 or 4 more years for reaching vast adoption. This timeframe needs to be rethought and warrants a paradigm shift to improve the delivery of higher rates of GG to farmers. A solution could be a decentralized shift toward the "community seed enterprise" strategy (Vernooy et al., 2022), with one farm per community becoming responsible to serve the local seed needs, whereas DNA markers applied to harvests would serve as the true measurement of royalties to be paid to the original variety developer. Such a change would be also perfectly aligned with the new agroecological vision to serve locally adapted varieties to each community (Nishikawa & Pimbert, 2022).

5 | PLANT BREEDERS OF TOMORROW

The 2003 article “A dying breed” stated “Public-sector research into classical [field] crop breeding is withering, supplanted by ‘sexier’ high-tech methods” (Knight, 2003). Twenty years ago, this article highlighted already how field-based research was losing traction in favor of more “high-tech” breeding methods. So, who might be the plant breeders of tomorrow and will this trend away from field work continue (Repinski et al., 2011)?

Breeding for the remaining of this 21st century requires engaging in more participatory approaches to meet the changing market’s needs, while promoting the strategic deployment of novel traits for the sustainable intensification (or extensification) of agriculture, and at the same revamp the cultivar development pipeline to deliver higher rates of GG into farmers’ fields. Therefore, we envisage that the plant breeders of tomorrow will need to dialog as equal with socio-economists to define achievable product profiles and understand market’s whims ahead of time. The tomorrow-breeders will also need to know the most recent advances in agronomy to suggest and integrate traits suitable for novel farm management practices. Within our vision of a more “service-based breeding,” in which the progression toward inbreeding shall be performed in artificial environments, the integration of on demand genomic models to preselect candidates done by service providers, and even the selection of parents taken away from the breeder’s subjective preference, it is possible that breeders’ biometrical skills will become less required than today. Instead, the plant breeders of tomorrow will need to design strategic pipelines, allocate resources effectively, and handle all logistics. Ensuring the right balance of high selection intensity vis-à-vis the possibility to raise selection accuracy at higher costs per individual can be foreseen as the true challenge of the next century of breeding. A challenge that might be better resolved applying the principles of logic typical of engineers, rather than the rules of genetics more familiar to plant breeders. Nevertheless, once the best approach is designed and refined, plant breeders might find themselves with enough free time to enjoy again “field walking” and “crop whispering,” learning things about plants that only the human mind is capable of fathom, finally breaking the trend and pushing back some “art” into the work of plant breeders.

AUTHOR CONTRIBUTIONS

Filippo M. Bassi: Conceptualization; investigation; writing—original draft; writing—review and editing. **Miguel Sanchez-Garcia**: Conceptualization; investigation; methodology; writing—original draft; writing—review and editing. **Rodomiro Ortiz**: Conceptualization; investigation; project administration; resources; supervision; writing—original draft; writing—review and editing.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

Not applicable for a perspective article.

ORCID

Filippo M. Bassi https://orcid.org/0000-0002-1164-5598
Rodomiro Ortiz https://orcid.org/0000-0002-1739-7206

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