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Wheat genetic resources have avoided disease pandemics, improved food security, and reduced environmental footprints: A review of historical impacts and future opportunities

Julie King[1] | Susanne Dreisigacker[2] | Matthew Reynolds[2] | Anindya Bandyopadhyay[2] | Hans-Joachim Braun[2] | Leonardo Crespo-Herrera[2] | Jose Crossa[2,3] | Velu Govindan[2] | Julio Huerta[2,4] | Maria Itria Ibba[2] | Carlos A. Robles-Zazueta[5] | Carolina Saint Pierre[2] | Pawan K. Singh[2] | Ravi P. Singh[2,6] | V. Mohan Murali Achary[2] | Sridhar Bhavani[2] | Gerald Blasch[2] | Shifeng Cheng[7] | Hannes Dempewolf[8] | Richard B. Flavell[9] | Guillermo Gerard[2] | Surbhi Grewal[1] | Simon Griffiths[10] | Malcolm Hawkesford[11] | Xinyao He[2] | Sarah Hearne[2] | David Hodson[2] | Phil Howell[12] | Mohammad Reza Jalal Kamali[2] | Hannes Karwat[2] | Benjamin Kilian[13] | Ian P. King[1] | Masahiro Kishii[8] | Victor Maurice Kommerell[2] | Evans Lagudah[14] | Caixia Lan[6] | Osval A. Montesinos-Lopez[15] | Paul Nicholson[10] | Paulino Pérez-Rodríguez[3] | Francisco Pinto[16] | Kevin Pixley[2] | Greg Rebetzke[14] | Carolina Rivera-Amado[2] | Carolina Sansaloni[2] | Urs Schulthess[2,17] | Shivali Sharma[13] | Peter Shewry[11] | Guntar Subbarao[8] | Thakur Prasad Tiwari[2] | Richard Trethowan[18] | Cristobal Uauy[10]

Correspondence
Julie King, Room C26 Plant Sciences, Sutton Bonington Campus, Sutton Bonington, Leicestershire LE12 5RD, UK.
Email: julie.king@nottingham.ac.uk

Susanne Dreisigacker and Matthew Reynolds, International Maize and Wheat Improvement Center (CIMMYT) and Affiliates, El Batan, CP 56723 Texcoco, Mexico.
Email: s.dreisigacker@cgiar.org and m.reynolds@cgiar.org

Abstract

The use of plant genetic resources (PGR)—wild relatives, landraces, and isolated breeding gene pools—has had substantial impacts on wheat breeding for resistance to biotic and abiotic stresses, while increasing nutritional value, end-use quality, and grain yield. In the Global South, post-Green Revolution genetic yield gains are generally achieved with minimal additional inputs. As a result, production has increased, and millions of hectares of natural ecosystems have been spared. Without PGR-derived disease resistance, fungicide use would have easily doubled, massively increasing selection pressure for fungicide resistance. It is estimated that in wheat, a billion liters of fungicide application have been avoided just since 2000. This review presents examples of successful use of PGR including the relentless battle against wheat rust epidemics/pandemics, defending against diseases that jump species barriers like blast, biofortification giving nutrient-dense varieties and the use of novel

Julie King, Susanne Dreisigacker and Matthew Reynolds contributed equally.

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genetic variation for improving polygenic traits like climate resilience. Crop breeding genepools urgently need to be diversified to increase yields across a range of environments (>200 Mha globally), under less predictable weather and biotic stress pressure, while increasing input use efficiency. Given that the ~0.8 m PGR in wheat collections worldwide are relatively untapped and massive impacts of the tiny fraction studied, larger scale screenings and introgression promise solutions to emerging challenges, facilitated by advanced phenomic and genomic tools. The first translocations in wheat to modify rhizosphere microbiome interaction (reducing biological nitrification, reducing greenhouse gases, and increasing nitrogen use efficiency) is a landmark proof of concept. Phenomics and next-generation sequencing have already elucidated exotic haplotypes associated with biotic and complex abiotic traits now mainstreamed in breeding. Big data from decades of global yield trials can elucidate the benefits of PGR across environments. This kind of impact cannot be achieved without widescale sharing of germplasm and other breeding technologies through networks and public–private partnerships in a pre-competitive space.

KEYWORDS
climate resilience, input use efficiency, less fungicide dependence, rust epidemics, widening crop gene pools

1 | INTRODUCTION

The use of plant genetic resources (PGR) in wheat breeding has improved the nutrition and livelihoods of resource-constrained farmers and consumers in the Global South, where wheat is often the cereal of choice. Wheat is the staple food for ~1.5 billion people in Asia and Africa. Maintaining genetic resistance to a range of diseases improves yield stability and avoids epidemics. Furthermore, post-Green Revolution genetic yield gains are generally achieved with less (in the Global North) and often no fungicide (in the Global South), and without necessarily increasing inputs of fertilizer (Voss-Fels et al., 2019) or irrigation water (Pask & Reynolds, 2013) except in some high-production environments (Fischer et al., 2022). Due to the increased grain yield, millions of hectares of natural ecosystems have been saved from cultivation (Swaminathan, 2013). This review examines the impacts of utilizing PGR, particularly those related to the International Wheat Improvement Network (IWIN), coordinated by the International Maize and Wheat Improvement Centre (CIMMYT).

Significant impacts have primarily centered around the provision of new rust resistance genes to replace those that became ineffective, alongside the introduction of polygenic (durable) resistance. For example, the global wheat crop was heavily reliant on a single resistance gene (*Sr31*) for stem rust for over 50 years, until it failed in Uganda in the 1990s, almost causing a global pandemic had it not been for coordinated action under IWIN. Screening of PGRs routinely identifies new sources of disease resistance to other common wheat diseases, as well as new diseases like blast that broke the species barrier from rice. Without the disease resistance conferred by PGR, fungicide use globally would double at least, increasing selection pressure for fungicide-resistant disease strains.

In terms of quality, PGRs have been used to increase nutritional value and end-use quality. Some translocations resulted in unexpected yield gains (Singh et al., 1998), indicating the likely value of a wider exploration of PGR. More recently, translational research has facilitated identification among PGR of new sources of complex physiological traits—related to radiation use efficiency and climate resilience—incorporating them into good agronomic backgrounds for use largely as parents by IWIN breeders. As weather becomes more extreme, crop breeding gene pools will need to be further enriched with new adaptive alleles coming from PGR.

The review is structured into six main sections: (1) Introduction; (2) Extent and relative underutilization of the genetic resources held in collections globally; (3) Impacts from wheat wild relatives on food security and nutrition; (4) Forward-looking technologies for more efficient use of genetic resources; and (5) The power of international collaboration, germplasm, and data exchange to expedite solutions for farmers and the environments; and (6) Conclusions. Section 2 outlines the status of wheat genetic resources globally and the vast potential they embody for expanding wheat gene pools, especially given molecular tools and phenomics. Section 3 considers the impacts of breeding with PGR on maintaining disease resistance, including avoiding a stem rust pandemic; combatting blast disease that jumped the species barrier from rice; increasing the nutritional value and end-use quality of wheat, delivering novel sources of climate resilience and yield potential from PGR in high-yielding backgrounds; and the first translocations in wheat to modify rhizosphere microbiome interaction, reducing biological nitrification, greenhouse gases, and increasing nitrogen use efficiency (NUE). Section 4 describes the methods and challenges of phenotyping PGR in the field; next-generation sequencing for gene and haplotype discovery; big data analytics of PGR impacts from historical, IWIN nursery data; introgression strategies of PGR for

mainstream breeding; and gene editing to further harness impacts of PGR in wheat improvement. Section 5 estimates fungicide saved from PGR-derived disease resistance in wheat globally and highlights the power of international collaboration, where data and PGR are shared freely to expedite solutions to common problems.

Given that PGR are relatively untapped, more systematic characterization and introgression, supported by advanced phenotyping and genotyping tools, are likely to provide solutions to many emerging challenges. Phenomics and next-generation sequencing have already elucidated exotic haplotypes associated with complex traits (e.g., Molero et al., 2023) for a range of biotic and abiotic factors and mainstreamed in breeding.

2 | EXTENT AND RELATIVE UNDERUTILIZATION OF THE GENETIC RESOURCES HELD IN COLLECTIONS GLOBALLY

Plant genetic resources include wild relatives (Figure 1), their derivatives, landraces, distinct/isolated breeding gene pools (e.g.,

winter vs. spring wheat), and obsolete cultivars. Bread wheat itself is the product of a handful of outcrosses between the wild goat grass *Aegilops taschii* and tetraploid durum wheat approximately 10,000 years ago, effectively creating a genetic bottleneck in terms of access to diversity from millions of years of adaptation of its progenitors. Over the last century, PGR have been employed to widen the wheat genepool, developing cultivars with different maturity classes, improved resistance to disease and pests, and better nutrition and quality characteristics (Laugerotte et al., 2022; Salvi et al., 2013). This also led to the Green Revolution (Swaminathan, 2013) that boosted wheat productivity around the globe through the development of adapted high-yielding semi-dwarf varieties coupled with international exchange of knowledge, ideas, and germplasm (Lumpkin, 2015). A concerted effort to conserve pre-Green Revolution landraces, and ongoing conservation of wild relatives, has placed 100s of thousands of PGR in genetic resource collections, which have been tapped in some cases as valuable trait sources, indicated by the pedigrees of modern cultivars. This highlights the importance of conserving, characterizing, and evaluating PGR. More than 770,000 accessions from eight wheat-related genera, stored in 155 germplasm banks in 78 countries, are available
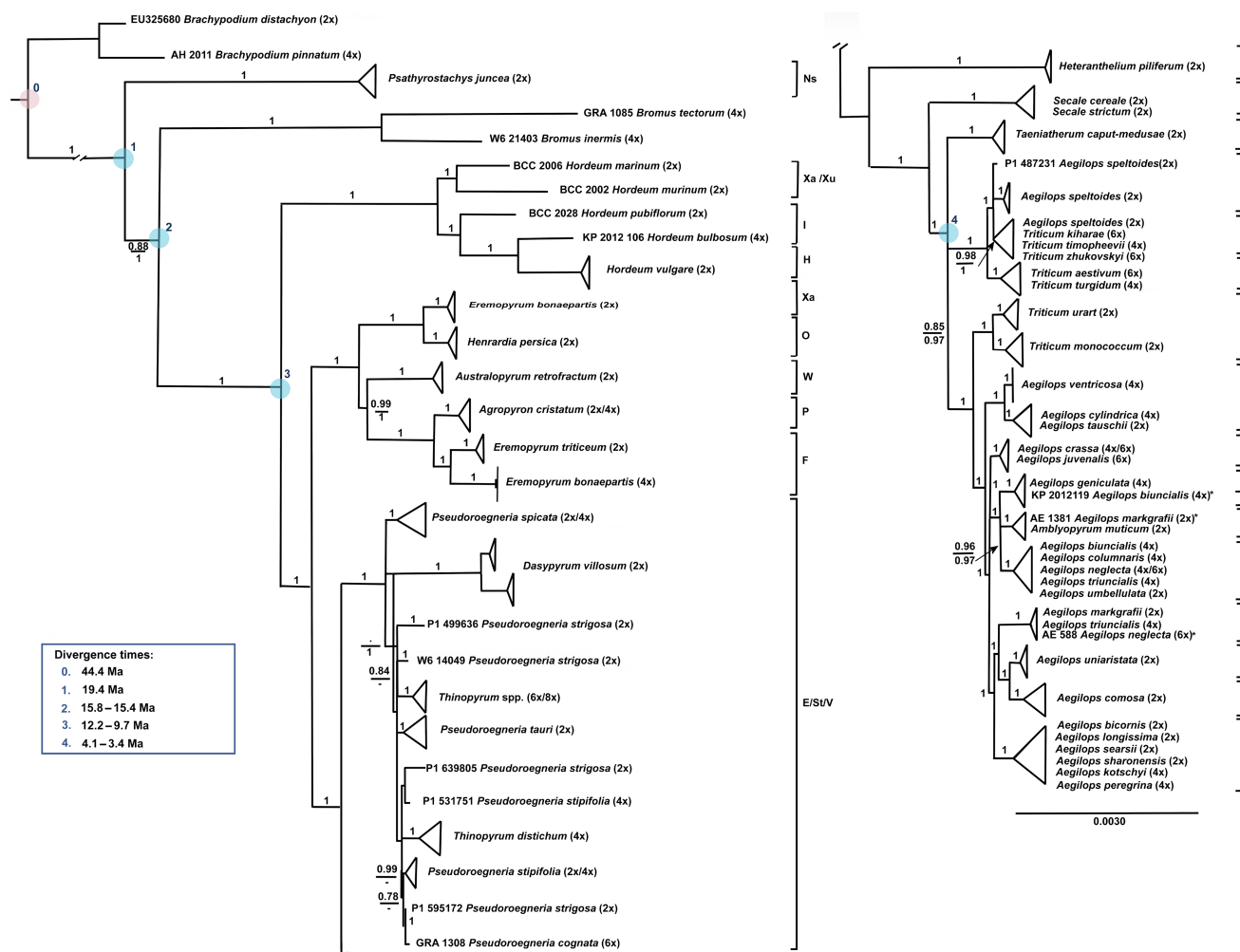

FIGURE 1 Phylogenetic tree based on whole chloroplast genome sequences of 222 Triticeae and outgroup taxa (originally published by Bernhardt et al., 2017). *Aegilops*, rye, and *Triticum* have had a significant impact.

for wheat improvement (FAO, https://www.fao.org/wiews/data/ex-situ-sdg-251/overview/en/). These PGR offer potentially beneficial genetic diversity through introgression breeding and strategic inclusion of "forgotten," for example, underutilized or niche food crops, for example, einkorn wheat (*Triticum monococcum*) (Guzzon et al., 2022; McCouch & Rieseberg, 2023), if they are well characterized and easily accessible. Tools like FIGS (focused identification of germplasm) use "passport" information of accessions in terms of the environmental characteristics of their collection sites, to facilitate the identification of new and better sources of trait expression (https://www.icarda.org/research/innovations/focused-identification-germplasm-strategy-figs). DNA fingerprinting is another tool that enables more focused searches based on the genetic relatedness of accessions (Sansaloni et al., 2020).

Although wheat genetic resources are relatively well conserved in most national and international seedbanks and are available according to the standard material transfer agreement, their use is underwhelming compared with conservation efforts. Harnessing the massive potential value of these PGR (Dempewolf et al., 2023; Pisupati, 2015; Sharma et al., 2021; Singh, Vikram, et al., 2018) requires their improved access and systematic phenotyping and genotyping (Kilian & Graner, 2012). Several databases for germplasm collections provide information on germplasm held in ex situ collections and pre-breeding lines, for example, Genesys, WIEWS, GRIN-Global, and Germinate, but a common platform is needed to link data generated by all germplasm users (Shaw et al., 2023). Special attention must also be paid to accessing genetic resources held by academic institutions and research laboratories, as these collections are often poorly documented and unavailable for distribution (Dempewolf et al., 2023).

Pre-breeding or de novo domestication plays an essential role in transferring beneficial genetic diversity to the elite gene pool. Important traits include disease and pest resistance, nutritional quality, yield potential, input use efficiency and tolerance to drought, heat, and other abiotic stresses (Kilian et al., 2021; Leigh et al., 2022; Ortiz et al., 2008; Reynolds et al., 2021; Sharma et al., 2021; Zeibig et al., 2023). It is clear that wild relatives have been used more in hexaploid wheat breeding than in other crops (Bohra et al., 2022; Sharma et al., 2021). For example, introgression lines derived from *Aegilops mutica*, *Ae. speltoides*, and *Thinopyrum bessarabicum* have been developed to introgress the entire genome of these species into wheat in small chromosome segments (King et al., 2017, 2018, 2019; Iefimenko et al., 2015), while resynthesized or "synthetic hexaploid" wheat provides bridges to the entire genetic diversity within a compatible genome, *Ae. tauschii* being the most widely used source (Dreisigacker et al., 2008; Kishii, 2019; Villareal et al., 1991; Wright et al., 2024), and variation from tetraploid wheat can be introduced through direct crossing with hexaploid wheat (Horsnell et al., 2023).

The wild relatives of wheat, of which there are many genetically diverse accessions (Figure 1), evolved several million years ago unlike wheat itself which apparently evolved only once or twice 10,000 years ago through hybridization between tetraploid wheat

and the wild diploid *Ae. tauschii* (Charmet, 2011). As a result, the wild relatives provide a vast reservoir of genetic variation that is largely absent in cultivars. Even though the genetic variation of the wild relatives shows such promise for wheat improvement, we have barely scratched the surface of the available variation. However, the recent availability of new sequencing and marker technologies to identify, characterize, and track transfers of the variation into wheat systematically at high throughput will allow vastly more utilization of PGR in breeding (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023).

New tools applied at the Wheat Research Centre at Nottingham (WRC) focused on the use of the Axiom® Wheat-Relative Genotyping Array (King et al., 2017; Winfield et al., 2016) containing approximately 36,000 single-nucleotide polymorphisms (SNPs) polymorphic between wheat and 10 wild relative species (Wilkinson et al., 2012, 2016). This technology enabled the identification of 1000 new introgressions from several wild relative species (Baker et al., 2020; Devi et al., 2019; Grewal et al., 2018; King et al., 2018, 2019). However, while this technology has been extremely useful, it was unable to discriminate between lines carrying either one or two copies of the same introgression. In order to overcome this, the WRC has developed chromosome-specific Kompetitive allele-specific PCR (KASP) markers based on single-copy regions of the wheat genome (Grewal, Hubbart-Edwards, et al., 2020). These highly robust markers are diagnostic for each introgression and can be used to track their presence in breeding programs (Grewal et al., 2021, 2022; Grewal, Othmeni, et al., 2020; King et al., 2022). The development of the KASP markers has been facilitated via the skim sequencing of the wild relatives and the development of a bio-informatics pipeline able to identify SNPs between the wild relatives and single-copy regions of the wheat genome (Grewal et al., 2022). Skim sequencing also allows more in-depth analysis of individual introgression lines and the allelic variation they carry (Coombes et al., 2023). The introgressions can also be visualized cytologically using genomic in situ hybridization (Grewal, Othmeni, et al., 2020; King et al., 2019).

In summary, PGR have provided value to wheat breeding on a massive scale, with only a small fraction of the vast collection even having been characterized, suggesting considerably more potential.

3 | IMPACTS FROM WHEAT WILD RELATIVES ON FOOD SECURITY AND NUTRITION

This section summarizes the impacts of breeding with PGR. The largest has been maintaining disease resistance for decades, including avoiding a stem rust pandemic; PGR provided resistance when blast unexpectedly jumped the species barrier. Sources from PGR have increased the nutritional value and quality of wheat and delivered novel sources of climate resilience and yield potential in high-yielding backgrounds, as well as the first translocations to modify rhizosphere microbiome interaction.

3.1 | Stemming the tide of wheat rust epidemics and pandemics over four decades

The three rust fungi—leaf rust (*Puccinia triticina*, *Pt*), stripe or yellow rust (*Puccinia striiformis* f. sp. *Tritici*, *Pst*), and stem rust (*Puccinia graminis* f. sp. *Tritici*, *Pgt*)—pose a significant threat to global wheat production, with estimated annual losses ranging from US\$ 4.3 to 5.0 billion, representing between 5.9% and 7.7% of the total trade of wheat in 2021 and 2022, respectively (Huerta-Espino et al., 2020; Singh et al., 2016). However, the cultivation of resistant varieties, facilitated by international wheat improvement efforts, has mitigated these losses (Singh et al., 2008, 2016).

The quest for rust resistance began in the early 1900s, leading to the introgression of resistance genes from related species into bread wheat (Biffen, 1905; Hayes et al., 1920; McFadden, 1930; Stakman, 1955). This effort expanded genetic diversity and supported rust control globally (Mondal et al., 2016; Singh et al., 2008). Rust-resistant semi-dwarf wheat varieties, pivotal to the Green

Revolution, further underscored the importance of rust resistance (Rajaram et al., 1998).

As of 2023, 84, 86, and 67 formally cataloged resistance genes for *Pt*, *Pst*, and *Pgt*, respectively, have been identified, (https://wheat.pw.usda.gov/GG3/wgc) (R.A. McIntosh, personal communication). Over a third of these genes originate from 21 wild species and genera (Table 1). Cataloged genes are largely major or race-specific genes, and their deployment as single genes can lead to resistance breakdown, highlighting the ongoing challenge of rust management.

Genes from wild species that have been widely used in wheat breeding include *Sr24*, *Sr26*, *Sr31*, and *Sr38* for stem rust, *Lr9*, *Lr19*, *Lr26*, and *Lr37* for leaf rust, and *Yr9*, *Yr10*, *Yr15*, and *Yr37* for stripe rust (Singh et al., 1998). The wheat-rye translocation 1BL.1RS, containing *Lr26*, *Yr9*, *Sr31*, and *Pm8*, gained global popularity, but *Sr31* lost efficacy in Africa due to the emergence of UG99 (Pretorius et al., 2000). Another translocation, 2NS, carrying *Lr37*, *Yr17*, and *Sr38*, is widespread, particularly in CIMMYT elite lines, also offering improved yield and resistance to wheat blast (Cruz et al., 2016;

TABLE 1 Cataloged genes for resistance to the three rust fungi and their origin.

Originating genus and species	Resistance genes		
	Leaf rust	Stripe rust	Stem rust
Triticum aestivum	Lr1, 2a, 2b, 2c, 3, 3 ka, 3bg, 10, 11, 12, 13, 14b, 15, 16, 17a, 17b, 33, 34, 46, 48, 49, 52, 60, 67, 68, 70, 73, 74, 75, 77, 78, 79, 80, 81, 82, 83	Yr1, 2, 3, 4, 5b, 6, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 25, 27, 29, 31, 32, 33, 34, 39, 41, 43, 44, 45, 46, 47, 48, 49, 51, 52, 53, 54, 57, 58, 59, 60, 61, 62, 63, 66, 67, 69, 71, 73, 74, 76, 78, 79, 80, 81, 82, 85, 86	Sr5, 6, 7a, 7b, 8a, 8b, 9a, 9b, 9f, 9 h, 10, 15, 16, 18, 19, 20, 23, 28, 29, 30, 41, 42, 48, 49, 54, 55, 56, 57, 58, 65, 67
T. turgidum	Lr14a, 23, 61, 72, 79, 84	Yr7, 24(=26), 30, 55, 56, 64, 65	Sr2, 9d, 9e, 9 g, 11, 63
T. comosum		Yr8	Sr34
T. dicoccoides	Lr53, 64	Yr35, 36, 84	
T. monococcum	Lr63		Sr21, 22a, 22b, 35, 60
T. spelta	Lr44, 47, 71	Yr5a	
T. timopheevi			Sr36, 37, 40
T. ventricosum	Lr37	Yr17	Sr38
Aegilops geniculata	Lr57	Yr40	Sr53
Ae. kotschyi	Lr54	Yr37	
Ae. neglecta	Lr62	Yr38	
Ae. perigrina	Lr59		
Ae. searsii			Sr51
Ae. sharonensis	Lr56		Sr62
Ae. speltoides	Lr28, 35, 36, 51, 65, 66		Sr32, 39, 47
Ae. tauschii	Lr21, 22a, 32, 39, 40, 41, 42, 43	Yr28	Sr33, 45, 46, 66
Ae. triuncialis	Lr50, 58	Yr42	
Ae. umbellulata	Lr9, 76	Yr70	
Dasypyrum villosum			Sr52
Elymus trachycaulis	Lr55		
Secale cereale	Lr25, 26, 45	Yr9, 83	Sr27, 31, 50, 59
Thinopyrum elongatum	Lr19, 24, 29		Sr24, 25, 26, 43, 61
Thinopyrum intermedium	Lr38	Yr50	Sr44, 64

Juliana, Poland, et al., 2019), while some genes from wild relatives, like *Sr32* and *Sr37*, were not widely used due to negative linkage drag (McIntosh et al., 1995; McIntosh & Gyarfas, 1971).

Race-nonspecific resistance, known as adult plant resistance (APR), remains crucial in rust control, often determined by various minor effect genes or quantitative trait loci (QTL). Alone, these APR genes offer modest rust resistance, but combinations of four to five can provide near-immune levels (Singh et al., 2000, 2014). Two pleiotropic multi-pathogen APR genes, namely *Lr34/Yr18/Sr57/Pm38* and *Lr67/Yr46/Sr55/Pm46*, were cloned and identified as ABC and hexose transporters respectively (Krattinger et al., 2009; Moore et al., 2015). Thus, they belong to a different class of resistance genes than race-specific genes. These genes, along with the pleiotropic APR gene *Lr46/Yr29/Sr58/Pm39*, and *Lr68*, also exhibit the morphological marker leaf tip necrosis that aids high-throughput visual selection (Singh et al., 2014). Varieties with *Lr34* and *Lr46* are common in semi-dwarf wheat, while *Lr67* is prevalent in tall varieties from South Asia (Lan et al., 2015; Moore et al., 2015; Zhang et al., 2022).

Stem rust gene *Sr2*, likely pleiotropic, provides partial resistance to multiple diseases, including yellow rust (*Yr30*) and powdery mildew (*Pm48*) (Singh et al., 2014). The *Sr2* gene, transferred from tetraploid emmer wheat (McFadden, 1930), provides partial resistance to stem rust, including Ug99 (Singh et al., 2011). CIMMYT's breeding efforts, starting in 2008, under the Borlaug Global Rust Initiative (BGRI), aimed to combine *Sr2* with other APR genes/QTL to enhance durable resistance in East Africa. Expanding from the Obregon-Toluca shuttle breeding to the Mexico-Kenya scheme increased resistance to Ug99 and rebuilt *Sr2*-based APR (Singh et al., 2015, 2016). This effort, including establishing a phenotyping platform in Njoro, Kenya, and shuttle breeding led to increased allele frequencies for stem rust resistance, enriching breeding lines with multiple R-genes, including *Sr2* (Singh et al., 2015). Kenya and Ethiopia have released Ug99-resistant varieties, including those carrying APR or varieties often combining *Sr2* with alien R-genes including *Sr13b* (Ethiopian varieties Ardi, Denbel 01, Kulumsa, Laku, and Shaki) *Sr22* (Asgori), and *Sr26* (Dursa).

Recently, a cassette of resistance genes, including five cloned ones, was developed via genetic engineering, promising enhanced resistance longevity (Luo et al., 2021). However, transgenic wheat cultivation is currently restricted in most of the Global South and Europe due to a lack of consumer acceptance and international regulatory differences. Future cassettes are likely to use more targeted integration technologies such as gene editing to enable R gene insertion. With the requirement of increased food production, these innovative approaches are urgently needed.

3.2 | Defending crops against diseases that jump species barriers in a changing climate: The case of rice and wheat blast

Wheat blast was first identified in Brazil in 1985, and then gradually spread to Paraguay, Bolivia, and Argentina (Singh, Gahtyari,

et al., 2021). Development of the disease in spikes is very fast leaving little time for taking remedial action (Cruz & Valent, 2017). In 2016, the first blast outbreak outside South America was reported in Bangladesh, followed by another intrusion in 2018 in Zambia (Singh, Gahtyari, et al., 2021) indicating the spread of wheat blast to Asia and Africa, greatly threatening wheat production in these continents.

The disease is caused by *Magnaporthe oryzae* pathotype *Triticum* (MoT), which is closely related to the rice blast pathogen *M. oryzae* pathotype *Oryzae* (MoO) and other pathotypes like MoL (for ryegrass) and MoS (for millet). Under natural conditions, these pathotypes do not infect their non-target hosts, but they can cross-infect under experimental conditions, especially under higher temperature (Pak et al., 2021; Paul et al., 2022; Shizhen et al., 2021). The origin of MoT is unknown. Recent analysis indicates that both MoT and MoL originated as a result of hybridization between a grass-infecting species endemic to Brazil and a signal grass (*Urochloa brizantha*), imported into Brazil as a source of fodder for beef production (Rahnama et al., 2021).

So far, 11 resistance genes have been identified in wheat, *Rmg1* to *Rmg9*, *RmgTd(t)*, and *RmgGR119*. However, most of the genes are for non-MoT isolates, and only *Rmg2*, *Rmg3*, *Rmg7*, *Rmg8*, and *RmgGR119* are effective against MoT, of which the first two have been defeated by newer MoT isolates and only the latter three showed effective resistance in greenhouse and still need to be validated in larger scale field experiments. Both *Rmg7* and *Rmg8* recognize the same effector (AVR-Rmg8) and so represent a single gene for breeding purposes (Anh et al., 2018). Apart from these genes, the 2NS/2AS translocation has been widely employed as a stable and effective resistance source, and most wheat blast-resistant varieties carry this translocation (Singh, Jighly, et al., 2021). The translocation was introduced previously from *Ae. ventricosa* to transfer the eyespot resistance gene *Pch1*. It also confers resistance against rusts (*Yr17*, *Lr37*, and *Sr38*), nematodes (*Cre5* and *Rkn3*), spot blotch, lodging, yield loss, and now wheat blast. Over 90% of CIMMYT elite germplasm harbors the 2NS/2AS translocation due to its multitrait utility. However, virulent MoT isolates have already emerged in South America (Ceresini et al., 2018), making the search for new resistant sources an urgent task. Large-scale screening of elite, landrace, and synthetic germplasm has led to the identification of some moderately resistant lines without 2NS, but none of them had a resistance comparable to lines carrying the 2NS translocation (Singh, Jighly, et al., 2021), highlighting the importance of the wild relatives.

Advances in genome sequencing enable combined genome-wide association studies (GWAS) with targeted gene sequencing in large wheat diversity panels. This approach was used to identify the two blast resistances, *Rwt3* and *Rwt4* (Arora et al., 2023). Resistance to MoT isolates from Bangladesh and Brazil was observed in accessions of Watkins landraces, collected in the early 1930s. The screen of the collection led to the identification of *Rmg7* and *Rmg8* (O'Hara et al., 2023). Surprisingly, it was shown that *Rmg7* and *Rmg8* are alleles of *Pm4*, a gene that recognizes isolates of wheat powdery mildew (*Blumeria graminis* f. sp. *tritici* [Bgt]), carrying specific alleles

of the effector *AVR-Pm4* (Sánchez-Martín et al., 2021). *Pm4* alleles have different origins with *Pm4d* introduced from *Triticum persicum* (O'Hara et al., 2023). The *Pm4f* allele, unique to Watkins landrace accessions, provides a new source of wheat blast resistance and, again, appears to originate from a wheat relative (O'Hara et al., 2023).

Changes in climate that result in increased humidity will exacerbate diseases like mildew that are favored by cool damp environments. To date, 74 mildew resistance genes/alleles have been reported, and among these, 41 originate outside the primary gene pool of wheat (Hafeez et al., 2021). Changes in weather patterns are already impacting wheat production in East Africa. Rain at anthesis has led to severe epidemics of Fusarium head blight (FHB), resulting in yield loss and contamination of grain with mycotoxins (Regasa, 2023). The most widely deployed and potent resistance to FHB is *Fhb1*, and it is suggested that this is situated in a region introgressed into wheat from an unknown source (Shimizu et al., 2021). Another potent FHB resistance gene has been reported from *Thinopyrum elongatum* and may provide an important partner to *Fhb1* in efforts to reduce the risk of mycotoxins reaching consumers (Wang et al., 2020).

The impact of climate change on crop pests and disease evolution is likely to overcome plant resistance faster, making the search for new sources of resistance among PGR all the more imperative.

3.3 | Mainstreaming biofortification for nutrient-dense wheat varieties for resource-poor producers and consumers

In 2022, over 9% of the world's population suffered from hunger, and almost a third could not afford a healthy diet, leading to widespread micronutrient deficiencies (FAO et al., 2013).

Significant progress has been made in developing and deploying wheat biofortified with increased concentrations of zinc (Zn) and iron (Fe), reaching millions of households in South Asia (Velu et al., 2019). This has been achieved by transferring high-Zn genes from selected landraces from Mexico, Iran, and Israel, spelt wheat and synthetic wheat derived from emmer, increasing grain Zn by 30%–40% while retaining good agronomic performance over a range of environments (Guzmán et al., 2014). More than 20 Zn-biofortified wheat varieties, all derived from crosses with exotic germplasm, have been released, with grain yields at least as high as the conventional varieties released in the same regions, and an average increase of 8–10ppm (25%–40%) of Zn in the grain (Govindan et al., 2022). CIMMYT-derived Zn-biofortified wheat varieties, such as the mega-variety Akbar-19 in Pakistan, are already grown on nearly 2Mha and their consumption is associated with a reduction in child morbidity and improvements in overall health outcomes of people who consume them (Sazawal et al., 2018). High-Zn is now mainstreamed in the entire CIMMYT spring bread wheat breeding program.

While biofortification with Fe and Zn has been very successful, it is important to continue to develop wheat varieties with even higher contents of these and other minerals, such as selenium and calcium and focus on the bioavailability of these traits by reducing micronutrient inhibitors like phytic acid. This can likely be achieved by exploiting currently unexplored diversity in gene banks and particularly landrace collections. The A. E. Watkins collection of landraces held at the John Innes Centre is the best characterized of these with full sequences available for over 800 accessions. Initial analyses of bi-parental populations between selected landraces and the modern UK cultivar Paragon have allowed the construction of an "atlas" of QTL for essential minerals (including Zn, Fe, Calcium [Ca], Magnesium [Mg], and potassium [K]) which can be stacked in future breeding programs.

3.4 | Novel genetic variation for yield improvement and climate resilience

Increasingly erratic weather is a challenge to yield stability (Xiong et al., 2021) and adaptation to climatic events such as heat waves, delayed rains, and warmer nocturnal temperatures has not been systematically addressed in wheat breeding or research (McAusland et al., 2023). However, superior sources of physiological traits for yield, input use efficiency (Murchie et al., 2023; Slafer et al., 2023), and climate resilience, have been identified among PGR (Reynolds et al., 2007, 2015, 2021) and used to improve yield and heat tolerance (Reynolds, Pask, et al., 2017; https://iwyp.org/). In the UK, the nationally coordinated project "Designing Future Wheat" has identified hexaploid landraces that harbor promising variation to boost yield potential under high-yielding temperate conditions (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023; Hawkesford & Griffiths, 2019).

At CIMMYT, PGR with outstanding expression of targeted physiological traits (e.g., Figure 2) enter physiological pre-breeding (PPB) pipelines where they are crossed and often backcrossed with elite lines, and the best PPB progeny tested globally. The PPB approach was boosted when ~60,000 PGR of the World Wheat Collection (WWC) were field screened under both heat and drought stress and the best-performing lines assembled as dedicated panels for marker discovery and pre-breeding (Sukumaran et al., 2021). The International Wheat Yield Partnership invested in the discovery of physiological and genetic bases of diverse high yield, high biomass advanced lines in terms of photosynthetic capacity (source) traits (Joynson et al., 2021; Molero et al., 2019, 2023) and spike fertility (sink traits) (Molero et al., 2019; Rivera-Amado et al., 2019), informing strategic source × sink crosses (Reynolds, Pask, et al., 2017).

The overarching strategy of PPB for complex traits is to achieve cumulative gene action for yield in respective environments via the enrichment of favorable new alleles in good genetic backgrounds. Complex traits do not necessarily stack up in a Mendelian way (Reynolds et al., 2022) because of trade-offs in expression (Rivera-Amado et al., 2019), that interact with growth stage, environment, and genetic background (Murchie et al., 2023; Slafer et al., 2023). As a result, progeny may not express the highest value of founder traits,

but their impact on yield-related traits such as growth rate, radiation use efficiency, evapotranspiration rate, hydration status, and green area duration for example, are all associated with improved growth and adaptive physiology and help select best progeny using high-throughput phenotyping (HTP, see Section 4.2).

CIMMYT PPB wheat nurseries are requested by public and private breeders for trialing at >200 sites annually. Returned data show no evidence of linkage drag from the use of PGRs as trait sources. On the contrary, globally the best-performing PPB lines show yield gains equivalent to elite CIMMYT checks, and some express significantly superior yield (10% or more) locally or regionally. The survey has confirmed that outstanding PPB lines are crossed to locally adapted cultivars (and occasionally released directly); seven PPB lines have been released directly as cultivars in Pakistan, Afghanistan, Bangladesh, and Egypt, respectively, in response to warmer conditions mainly (https://iwyp.org/; https://hedwic.org/). The PPB nurseries are helping expand breeding gene pools globally through dissemination via IWIN and their use by CIMMYT breeders as novel sources of trait expression and haplotypes. Recently, over 80,000 accessions from the WWC were genetically characterized to maximize novel diversity (Sansaloni et al., 2020), encompassing three categories: 4200 wild relatives, 20,000 tetraploid, and 60,000 hexaploid accessions. The analysis revealed landraces with unexplored diversity and genetic footprints defined by regions under selection and delivered a core subset for pre-breeding and GWAS, research that boosts PPB and breeding.

Synthetic hexaploid wheat made at CIMMYT—by combining the ancestral tetraploid and diploid genomes, namely durum wheat and *Ae. tauschii*, respectively, have contributed to the pedigrees of IWIN nurseries for decades (Rosyara et al., 2019). Their improved physiology has been documented under heat (Cossani & Reynolds, 2015) and drought (Lopes & Reynolds, 2011; Reynolds et al., 2007). They also contributed to the pedigrees of varieties released in Sichuan China, resulting in over 10% greater yield potential, based on traits such as high biomass and increased photosynthesis (Wan et al., 2023). Singh, Jighly, et al. (2021) and Molero et al. (2023) showed the contribution of an *Ae. tauschii* allele to heat tolerance as part of a haplotype originating from PBB. Most of these and other introgressions that resulted in yield gain (Singh et al., 1998) were serendipitous, giving an indication of the potential within PGR if yield and climate resilience are explicit targets.

Transfer of simple exotic genetics can also help improve climate resilience. For example, *Rht-B1b* and *Rht-D1b* dwarfing genes reduce plant height and allowed increased grain number and harvest index to increase grain yields globally (Flintham et al., 1997). However, these genes also reduce coleoptile length (Rebetzke et al., 2012), slow emergence and reduce establishment when deep sowing to access subsoil moisture (Stummer et al., 2023) and avoid high soil temperatures (Rebetzke et al., 2016). Alternative dwarfing genes, including *Rht18* transferred from durum to bread wheat (Rebetzke et al., 2022), increase coleoptile length to greater than 12 cm, thereby allowing emergence from sowing depths exceeding 12 cm (Zhao, Wang, et al., 2022). Climate and crop growth models predict an 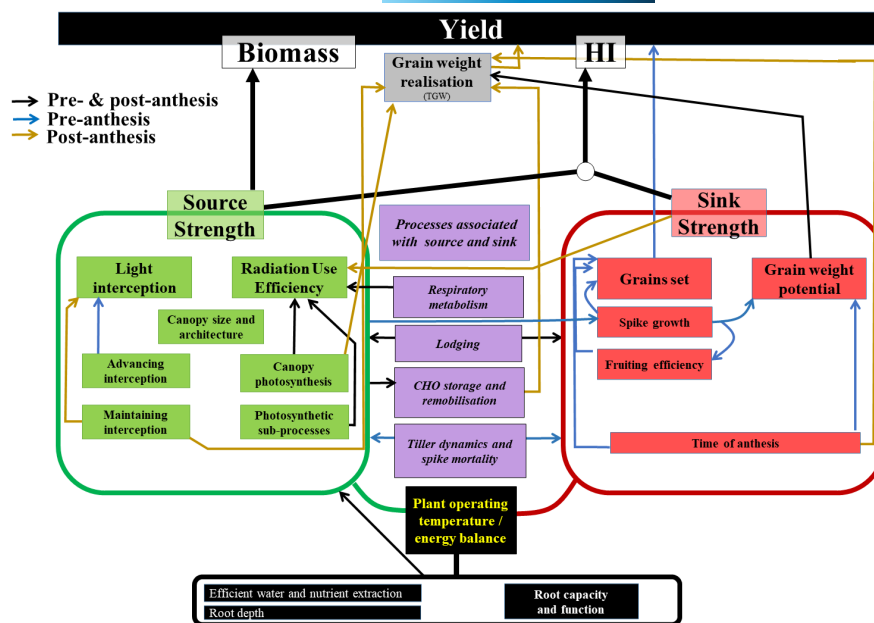average yield benefit with deep sowing in Australia of up to 20%, reflecting the importance of germination and early crop growth with warmer soil temperatures and less predictable rainfall (Zhao, Wang, et al., 2022). The *Rht18* dwarfing gene is now being used commercially in the release of long coleoptile milling quality wheat varieties.

In summary, climate resilience and yield potential can be boosted through judicious screening of PGR for new and superior sources of target traits and alleles, and their validation via PPB. A key trait to identify among PGR is final biomass (and its components) since this sets an upper limit for yield and is indicative of metabolic fitness in a given environment. For example, the best primary synthetic hexaploids may express 20% more biomass than elite checks under a range of environments including high temperature and drought (Reynolds et al., 2015). The challenge of PPB is to combine high biomass expression with partitioning traits that favor grain yield (Slafer et al., 2023; Figure 2). Another key trait is investment in root mass, especially for heat and drought adaptation to access subsoil water and match evaporative demand for water, respectively, and have been identified in PGR and PGR-derived elite lines (Ober et al., 2021; Reynolds et al., 2007). Nonetheless, the expression of favorable complex traits interacts with the environment and genetic background. While we are at a fledgling stage of understanding the genetic bases of complex trait expression, gene discovery in sequenced, well-phenotyped panels of "elite" genetic resources identify haplotypes for desired trait expression which can be validated for different target environments using IWIN trial data. It is expected that models like the wiring diagram (Figure 2), customized to target population of environments (TPEs) and using available data sets as inputs to deep learning (DL)-assisted simulations, will enable complex traits and their haplotypes to be included in next-generation breeding models to boost yield, climate resilience, and input use efficiency.

3.5 | Wide crossing for improved biological nitrification inhibitor enabled nitrogen efficiency in wheat due to reduced nitrate (NO_3) leaching and nitrous oxide (N_2O) gas emission

It is well known that modern wheat cropping, especially under humid conditions, shows a low NUE in terms of harvested N and grain yield relative to applied N fertilizer (Coskun et al., 2017; Omara et al., 2019; Talwar et al., 2020). This occurs even when fertilizer, largely ammonia-based, is managed as efficiently as possible. It is mostly due to leaching losses of nitrate, and gaseous ones of N_2 and N_2O under anaerobic conditions like waterlogging. The nitrate contributes to off-site water pollution, and N_2O very significantly to the estimated greenhouse gas intensity per kg of wheat produced (Leon et al., 2022). Biological nitrification inhibition (BNI) by root exudates has been recognized as markedly suppressing the soil microbial oxidation of ammonium to nitrate and reducing all N losses in some grasses, for example, *Brachiaria humidicola* (Ishikawa et al., 2003; Nuñez et al., 2018). This led to the search for the trait in wheat, primarily in its wild relatives from habitats where N supply would have been limited. The trait was found in one such relative,

FIGURE 2 Wiring diagram of tractable traits contributing to wheat yield (adapted from Reynolds et al., 2022).

"wheat grass" *Leymus racemosus* (Lam.) Tzvelev (2*n*=4*x*=28; genome JJNN) by Subbarao et al. (2007). After wide crossing and difficult chromosome manipulation, a decade later several elite modern CIMMYT wheat isolines having a chromosome arm from *Leymus* and BNI activity were delivered (Bozal-Leorri et al., 2022; Subbarao et al., 2021). In the meantime, BNI activity has also been found in some wheat landraces from the A. E. Watkins collection (O'Sullivan et al., 2016) and few modern cultivars like Sonora 64 and Roelfs F2008 (Subbarao et al., 2021), but currently, field testing has only comprised the *Leymus*-derived isolines (Bozal-Leorri et al., 2022; Subbarao et al., 2021). Preliminary results from Mexico, Japan, and India suggest that the trait carries no negative side effects on wheat growth and yield, reduces soil nitrate levels and N_2O emissions after ammonia-based N fertilizer application, and may improve NUE under limiting soil N conditions (Bozal-Leorri et al., 2022; Subbarao et al., 2021). At CIMMYT, we are currently exploring the BNI activity in other *Leymus* spp., such as *L. mollis*, and developing chromosome bread wheat translocations. The delivery of varieties to farmers with the *Leymus* BNI trait, or possibly a similar one derived from the wheat landraces showing nitrification inhibition, could be hugely beneficial in reducing wheat cost of production and negative off-site environmental effects.

4 | FORWARD-LOOKING TECHNOLOGIES FOR MORE EFFICIENT USE OF GENETIC RESOURCES

4.1 | Phenomics for physiological characterization and disease screening of PGR at field scale

Various proofs of concept in recent decades involving proximal (Babar et al., 2006), remote (Tattaris et al., 2016), and now satellite-based sensing (Pinto et al., 2023), combined with trait mining have provided the opportunity to pinpoint PGR with specific traits of interest (see Section 3.4). Currently, it is harder to gather HTP data on sink traits like harvest index and what underpins its expression, including most yield components and phenology (Slafer et al., 2023). However, image analysis coupled with DL models underpinned by rigorous field-based growth analysis will soon enable more sink traits to be estimated or modeled along with cardinal developmental stages. More complete data sets will allow breeding models to identify the need for PGR where genetic diversity is suboptimal in elite populations (Montesinos-López et al., 2023; Yoosefzadeh Najafabadi et al., 2023).

With PGR, it is essential to customize experimental design, due to the often-extreme variation in growth habit, phenology, and local adaptation of PGR, to avoid confounding effects that may be misleading (Reynolds & Pinto, 2019).

Nonetheless, well-designed HTP platforms lend themselves to discovery and validation of new levels of expression of physiological traits in PGR. Many radiation-use efficiency-related traits are well predicted among genotypes remotely, including light interception, photosynthetic capacity and architecture, pigment composition of leaves, biomass accumulation at early growth stages and under stress, and the dynamics of pigment content, which impacts light absorption and photoprotective mechanisms (Jin et al., 2021; Robles-Zazueta et al., 2022). Superior expression of many of these traits can be found among PGR. Canopy temperature can serve as high-throughput proxies for stomatal conductance (Amani et al., 1996), drought tolerance (Kim et al., 2023), and root mass at depth under drought as well as root capacity under heat stress (Pinto & Reynolds, 2015), all high priority targets for PGR screening. It has also been used to increase the predictive power of genomic selection (Juliana, Montesinos-López, et al., 2019).

Proximal spectroscopy was shown to estimate yield and a simple growth analysis among elite lines in the 90s (Babar et al., 2006). However, combined with machine learning (ML) and statistical methods such as partial least squares, the tool can be used stochastically

to identify multiple selection indices which would open up other new possibilities for PGR screening (Koc et al., 2022). Multispectral UAV and very high-resolution satellite imagery can already assess wheat rust severity at early growth stages, underlying the potential for detecting disease resistance derived from PGR at large scale (Figure 3) (Blasch et al., 2023; Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023).

These technologies have and will continue to provide breeding programs with opportunities to reduce resources and time spent in the field; for example, disease screening could be standardized using HTP sensors. Recent methodologies will allow for the use of RGB imagery coupled with artificial intelligence (AI) and ML algorithms to identify leaf and stem rust where images allow adequately high spatial resolution (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023). Another option is to use spectroscopy to train models associated with green pigment content or changes in leaf/stem biochemistry which often are a signal of pathogen infections (Koc et al., 2022).

Some of the challenges in using remote sensing techniques for breeding purposes are the scale of operability, access to research sites, and country restrictions for operations. To overcome these limitations, satellite imagery can be employed (Blasch et al., 2023; Pinto et al., 2023). Remote sensing at this scale will allow constant monitoring of disease incidence and the emergence of new pathogens. Since all the satellite data collected globally will come from the same platform, artifacts associated with instruments and human error will be substantially reduced when comparing genotypes among global sites.

4.2 | Post-genomics: Next-generation sequencing to harness novel haplotypes and candidate genes for greater genetic diversity and improved resilience

Research in genomics-driven approaches is progressing rapidly, with multiple ongoing efforts in wheat to address the significant challenges associated with crop improvement. One of the forward-looking objectives of this research related to the use of PGR is to accelerate the characterization and utilization of the preserved "evolutionary potential" of the wheat crop in seedbanks as demonstrated, for example, in the "Seeds of Discovery" project (https://seedsofdiscovery.org). Seedbank genomics have already demonstrated how "molecular passports" create value in seedbank management by providing precise knowledge that goes beyond the boundaries of classical descriptors (Mascher et al., 2019). Comparative (pan)genomic studies are also instrumental in providing insights into genomic variations in the cultivated gene pool for a given species. When compared to modern cultivars, the analyses of diverse PGR collections offer novel opportunities to identify genetic diversity that has been lost, selected against, or only rarely brought into the cultivated gene pool during the process of crop domestication. For example, the recent characterization of over 800 wheat landraces from the A. E. Watkins heritage collection and 200 modern cultivars showed that only two of seven identified ancestral landrace groups have been extensively used in modern breeding (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023). The primary aim of the analyses is to: (i) detect large-scale structural variations such as presence–absence variations or copy-number variations or inversions (where assemblies are available), (ii) clone and functionally annotate genetic factor(s) influencing the phenotypic expression of traits targeted by selection programs, and (iii) quantify the genetic effects of causal QTL across genetic elite backgrounds and multiple environments (Bayer et al., 2022; Bohra et al., 2022; Jayakodi et al., 2021; Varshney et al., 2021; Wang & Han, 2022). Taking this a step further, super-pangenomes, as defined by Khan et al. (2020), extend the genomic variations repertoire from the primary wheat gene pool to the broader *Triticum* genus by encompassing high-quality genome assemblies from diverse collections of diploid, tetraploid, and hexaploid species of wheat and its wild relatives (Figure 4).

FIGURE 3 Remote sensing-based rust disease severity screening at varying spatial resolutions in Ethiopia. Figure on the left represents data collected by the Parrot Bluegrass UAV system (5 cm pixel resolution), figure at the center represents data from the Skysat satellite (50 cm pixel resolution) and the right figure is an image from the Pleiades satellite (50 cm pixel resolution). All the figures are a false-color composite using NIR, red, and green bands to assess the level of infection at each plot. For further information on this work, see Blasch et al. (2023). Figure copyright: Gerald Blasch.

FIGURE 4 Timeline of the release of genome assemblies of bread wheat-related species.

Following skim or whole-genome sequencing, PGR collections can be underpinned by studying structured populations through GWAS, nested-association mapping or bi-parental QTL analysis. In the best case, these approaches directly lead to the discovery of candidate genes facilitated by the available assemblies and annotations. After causal genes have been identified, allele mining is an effective means to search for further useful variation and to ultimately identify and validate the novelty of haplotypes whose deployment could broaden the genetic variation in the elite pool. Recent examples in wheat include the population genomics analyses of various wheat accessions, 242 *Ae. tauschii* accessions, the diploid wild progenitor of the D sub-genome of wheat (Gaurav et al., 2022), 218 wild and cultivated einkorn accessions (*T. monococcum*), the first domesticated species in wheat (Ahmed et al., 2023), and the A. E. Watkins collection, a global repository of bread or durum wheat landraces (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023). Population genomics allowed rapid trait discovery in these studies. For example, k-mer association mapping identified discrete genomic regions with candidate genes for disease and pest resistance, including stem rust and curl mite resistance genes *SrTA1662* and *Cmc4* in the *Ae. tauschii* accessions. Furthermore, haplotype and allelic diversity analyses identified strong candidate genes for grain calcium concentration as well as nitrogen use and uptake efficiency on chromosome 5A in the bread wheat Watkins accessions in addition to a total of 143 prioritized QTL unique to the landraces (Cheng, Cheng, et al., 2023; Cheng, Feng, et al., 2023).

To elucidate how genetic information is translated into the traits and characteristics that an individual exhibits, genotype-to-phenotype maps are a fundamental concept (Mascher et al., 2019). Genotype-to-phenotype maps in the context of wild relatives refer to how genetic variation in these wild populations gives rise to the observed traits and characteristics of those wild species; however, they are equally relevant for introducing desirable traits into elite germplasm. Striving for a deeper understanding of how genomic information stored in seeds is translated into plant performance is crucial. Simple database queries on genotype-to-phenotype maps can lead to precise estimates of the genetic value of any given wild relative compared with elite wheat varieties as intended by the GlobalWheatG2B collaboration (https://www.g2b.com/).

The growing wealth of additional multi-omics data (e.g., genomics, transcriptomics, and metabolomics) from an increasing number of studies further provides an extraordinary opportunity to comprehensively understand the molecular mechanisms of complex traits (Mahmood et al., 2022). Multilayered information through high throughput and swift data generation in omics experiments can help to better interpret gene functions and build future dynamic models of gene and trait interactions to achieve crop improvement (Murchie et al., 2023; Slafer et al., 2023).

4.3 | Big data analytics of PGR impacts: Using historical, international breeding trial, and environmental data

Diverse PGR collections have been used in breeding for decades (see Sections 1 and 2) and extensive phenotype performance, pedigree, and genotypic data are available. The IWIN, initiated in the 1970s, has had substantial global impacts, contributing traits to at least half of the world's wheat production (Crespo-Herrera et al., 2018; Lantican et al., 2016; Reynolds, Braun, et al., 2017). The IWIN partners, comprising both public and private sectors, share key data with CIMMYT including on agronomic traits and disease resistance (https://data.cimmyt.org/dataverse/cimmytdatadvn). The recent release of the ERA5 (Hersbach et al., 2018) and AgERA5 (Boogaard et al., 2020) weather datasets has addressed the lack of weather data, allowing comprehensive analysis of large datasets.

By considering pedigree information, markers, and weather data, big data analytics can readily identify performance patterns related to PGR. Information on response to global warming is already available to breeders using this approach (Patidar et al., 2023; Xiong et al., 2021), and there are many more opportunities to detect local, regional, and global patterns of adaptation, as well as investigate hypotheses, such as whether introducing PGR improves yield stability for TPEs and beyond (Crossa et al., 2017). The IWIN has accumulated data from over 6000 site years from 12 targeted nurseries focused on strategic traits—that is, affecting regional or global problems—and each nursery of around 50 elite, disease-resistant lines, continues to provide a wealth of information that can be modelled.

While big data analysis was previously a tedious process, recent technologies now make such global data sets extremely valuable. Plant breeding techniques have already benefited from technological advances, particularly those derived from ML methods and other branches of AI, as highlighted by van Dijk et al. (2021). ML techniques, including DL methods, are widely applied in plant breeding studies to analyze and evaluate the transmission of information from DNA sequences to observable phenotypic traits in plants (Montesinos-López, Montesinos-López, Crossa, et al., 2018; Montesinos-López, Montesinos-López, Gianola, et al., 2018; Niazian & Niedbała, 2020). The widespread application of HTP and the promise of satellite phenotyping at plot scale (see Section 3) will, in combination with good environmental data, genomic data, and DL models, reveal the full impact that PGRs have had and may suggest new targets to help prioritize allele mining and wide crossing strategies.

4.4 | Introgression strategies of PGR for mainstream breeding

Designing PGR introgression strategies for mainstream breeding is not a trivial task, especially in the context of recurrent selection breeding schemes in which breeding populations are maintained genetically closed to maximize near-term rates of genetic gain. Traits from PGR must be introgressed as alleles or haplotypes, while minimizing the loss of progress within the elite germplasm pool. Introgression strategies for PGR therefore depend on several factors, including a trait prioritization process, the genetic architecture

of the traits (quantitative vs. qualitative traits), their source of the traits (wild relatives, landraces, and adapted germplasm), and the availability of resources and technologies.

For the introgression of new traits and/or genetic variation from PGR, the CIMMYT wheat breeding programs have established several trait delivery pathways. These pathways have three major components (Figure 5): (1) research and discovery often through collaboration with academia; (2) pre-breeding and parental development (e.g., see Section 3.4 for physiological traits); and (3) deployment (see Section 5.2). Each of these components contains elements that can be employed depending on the characteristics of the trait of interest. For instance, it is fundamental for the first component to have access to PGR, carryout the phenotypic characterization for the traits of interest and to develop selection tools (molecular or phenotypic) that allow the product and trait validation in pre-breeding products (second component). Modern technologies and analytical tools can be combined with each of these components. For example, the prediction of breeding values (Platten & Fritsche-Neto, 2023) and/or implementing other probabilistic algorithms (Moeinizade et al., 2022) in pre-breeding can accelerate the recovery of suitable parental lines for mainstream breeding. Furthermore, the development of HTP tools (see Section 3.2) applied to breeding can facilitate elements such as product and trait validation.

CIMMYT's wheat breeding program delivers about 1000 new genotypes annually via IWIN that constitutes National Agricultural Research Systems (NARS) and seed companies for use as parents in local/regional breeding programs or as candidates for varietal release (Lantican et al., 2016; Figure 6). For new product development,

Discovery

Embedded in individual research groups with specialized phenotyping capacity e.g., wheat rust, foliar diseases, quality, physiology,…

Groups make use of the current wheat trait discovery toolkit

- GWAS panels
- Mapping populations
- Phenotyping protocols
- Genotyping platforms
- Genebank
- Sequencing
- Data analytics,..

Parental development

Ideally centralized to establish standardized and optimized selection methods

1. Rapid trait introgression
Parent development and line augmentation via marker-assisted backcrossing and speed breeding

2. Strategic crossing
Parent development (donor × elite)

3. Population improvement

4. Wide crosses
Parent development (wild × elite) using conventional methods (colchicine, cytogenetics) or marker-assisted backcrossing

5. Gene editing

Deployment

Establish validation trials for the handover of products to mainstream breeding

1. YT- trials
Trials to test full agronomic performance of new parental/introgression lines, aligned with mainstream breeding YT-trials

2. Trait specific-trials
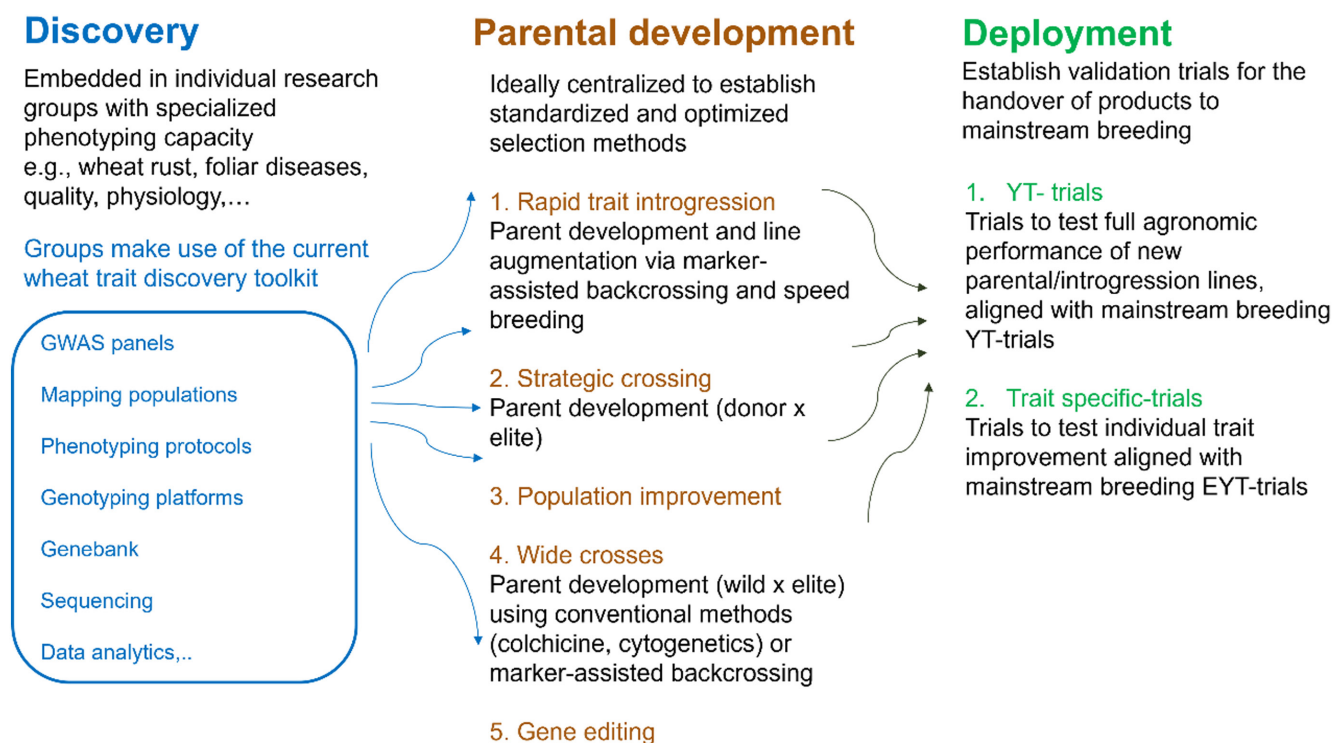Trials to test individual trait improvement aligned with mainstream breeding EYT-trials

FIGURE 5 Components of the overall trait delivery pathways in CIMMYT's mainstream breeding pipelines.
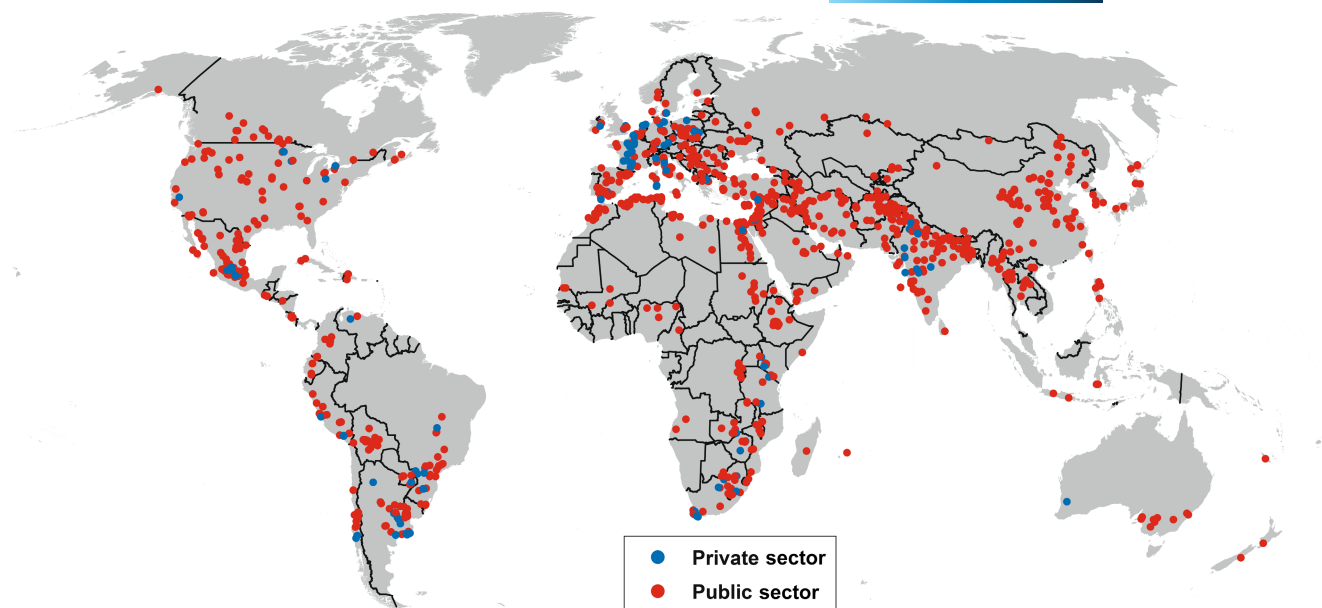
FIGURE 6 Public and private breeding programs that have received germplasm under the International Wheat Improvement Network (Kai Sonder, CIMMYT).

the breeding programs assign up to 10% of resources for crossing, advancing, and testing to incorporate new diversity in such otherwise closed populations or breeding pipelines (Singh et al., 2022). The bread wheat breeding pipelines at CIMMYT currently employ a rapid generation advancement scheme with a recurrent selection approach that integrates data-driven methods for parental selection (Villar-Hernández et al., 2018, 2021), implementation of genomic selection (Dreisigacker et al., 2021), earlier on station multi-environment testing and in TPEs (Costa-Neto et al., 2022; Crespo-Herrera et al., 2021), and with data derived from extensive international testing. Diverse new trait donors including PGR in elite backgrounds released from the trait delivery pathways are introduced in the elite breeding population of each pipeline.

New opportunities to optimize the introgression of PGR in mainstream breeding are explored and will be derived from harnessing aspects previously mentioned, such as the access to various sources of information (genomics, climate, soil, etc.) coupled with other modern analytical methods (such as AI) to aid predictive breeding to facilitate shorter breeding cycles and increased selection accuracy.

4.5 | Gene editing to harness PGR in wheat improvement

The precise introduction of new allelic variation from PGR to enhance agronomic traits in wheat across all three homologous chromosome copies is challenging due to wheat's large genome size and high frequency of repetitions. Novel plant breeding techniques are therefore needed to accelerate deployment. CRISPR/Cas9 genome editing systems including knockout, knockin, base editing, prime editing, and multiplex editing have been successfully applied to various

crop systems, offering targeted and precise genetic tools with unparalleled precision and efficiency for crop breeding applications (Chen et al., 2019; Zhou et al., 2023). Gene editing (GE) technology has several advantages over crossbreeding and transgenics by reducing the breeding cycle and cost. In wheat, GE has been successfully applied to improve disease resistance abiotic stress tolerance, grain yield, end-use quality, herbicide tolerance, and other agronomically important traits (Appendix S1).

There are only a few wheat genotypes that respond to genetic transformation, which currently constrains direct GE application to more diverse wheat germplasm. Transformation vector systems have been modified to express developmental regulators/morphogens, including *WUSCHEL2* (*WUS2*) and *BABY BOOM* (*BBM*) in maize and *GROWTH-REGULATING FACTOR 4* (*GRF4*) and *GRF-INTERACTING FACTOR 1* (*GIF1*) in wheat, which improves genetic transformation, plant regeneration, and editing efficiency (Debernardi et al., 2020; Wang, Ryan, et al., 2023). In addition to *Agrobacterium*-mediated gene delivery, biolistic, polyethylene glycol, and barley stripe mosaic virus-based delivery systems have been used (Appendix S1). Due to wheat's polyploidy, multiplex GE strategies, that can target the three homologous chromosome copies across the subgenomes A, B, and D could be efficient. Strategies which use multiple single guide RNAs to simultaneously edit multiple target sites or genes have already been tested (Zhou et al., 2023).

Chromosomal structural organization, such as translocations, inversions, deletions, and insertions, significantly influences agronomic traits in wheat (Zhao, Wang, et al., 2022; Zhao, Zheng, et al., 2022). GE has enabled scientists to manipulate meiotic recombination and chromosomal reorganization to overcome linkage drag and shape plant chromosomes for breeding. CRISPR tools have been used to induce chromosomal translocations in tomato (Filler Hayut et al., 2017; Roldan

et al., 2017), *Arabidopsis* (Beying et al., 2020; Filler-Hayut et al., 2021; Schmidt et al., 2019, 2020), maize (Rönspies et al., 2021), and soybean (Duan et al., 2021). The Spo11 protein initiates recombination and generates DNA double-strand breaks, which are repaired on homologous chromosomes to produce non-crossover and crossover molecules. Yelina et al. (2022) used coexpression of the dCas9::mTOPVIB fusion protein with six sgRNAs targeted to the 3ª crossover hotspot locus to monitor crossover frequency in *Arabidopsis thaliana*. If applied in wheat, this would greatly accelerate the use of beneficial PGR genes in breeding, which are often limited by undesirable linkage drag.

The WheatGmap database features over 3500 next-generation sequencing records from hexaploid wheat, comprising whole-genome sequencing, whole-exome sequencing, and transcriptome deep sequencing, and a high-quality genomic variation map from 145 wheat cultivars (Li, Zhang, et al., 2021). These genetic resources collectively aid in gene discovery and trait analysis, serving as a crucial foundation for selecting targets during wheat genome editing. Furthermore, genetic information associated with the desired trait value can be harnessed from the genetic reservoir of wild plant relatives to precisely generate new variations via gene editing directly in commercially cultivated landraces (Halewood et al., 2018). For example, using haplotype sequence analysis, 1632 wheat landraces and cultivars from 73 countries were identified with a genetic variation (752-bp deletion) at the *TaHRC* locus, which results in resistance to FHB in the haplotype Hap_Ning. CRISPR-Cas9-mediated mutations in the *TaHRC* gene resulted in dramatically increased FHB resistance (Su et al., 2019).

Up to date, the CGIAR and its partners have focused on site-directed nuclease (SDN) type edited varieties. Edited crops with SDN1 and SDN2 mutations have been widely adopted and classified as conventionally bred crops in many countries (Canada, USA, India, Australia, Japan, United Kingdom, Africa [Nigeria and Kenya] and many countries in Latin America) (Sprink et al., 2022). Recently, EU legislation has passed a favorable ruling for SDN1 genome-edited products. It is considered that this ruling of EU may pave the path for a universally harmonized framework for regulating gene editing. Novel applications of GE tools have already helped significantly in exploiting genetic resources toward enhanced breeding of wheat and future expanded use of CRISPR systems and allied editing tools will implement direct editing of elite cultivars toward faster development of important traits and reduction in cost.

5 | THE POWER OF INTERNATIONAL COLLABORATION, GERMPLASM, AND DATA EXCHANGE TO EXPEDITE SOLUTIONS FOR FARMERS AND THE ENVIRONMENT

5.1 | Estimates of fungicide saved from PGR-derived resistance in wheat on >200 mha

Worldwide one of the three rusts—and sometimes more than one—can occur and cause yield loss on 80% of the global wheat area. Beddow et al. (2015) estimated that 88% of the global wheat

production is vulnerable to yellow rust infection. Pardey et al. (2013) calculated that 66% of the global wheat area is climatically suitable for the disease. Braun et al. (2010) estimated that on the 112 mha wheat in low resource countries (LRC), leaf rust can occur on 69 mha, stem rust on 54 m, and yellow rust on 61 mha. Rust is difficult to control, since new virulent races are constantly evolving, and their spores can travel thousands of km in the jet stream in a few days. Breeding for rust resistance has been a top priority for over a century as there is a constant need to introgress new resistance genes to avoid or reduce foliar application of fungicides (Morton & Staub, 2008, https://www.apsnet.org/edcenter/apsnetfeatures/Pages/Fungicides.aspx).

Because of these efforts that continue to this day in wheat, less than 15% of farmers in LRCs and below 5% in Sub-Saharan Africa use fungicides routinely to control rusts (Sarkar et al., 2021; pers. comm. compiled by Braun with information from CIMMYT and ICARDA staff and NARS scientists) and rather rely on rust-resistant varieties. At CIMMYT, significant progress has been made in breeding for multiple disease resistance including all three rusts (Dinglasan et al., 2022). CIMMYT-derived spring wheat cultivars are grown on around 50% of the global wheat area rising to 75% in S-Asia and Sub-Saharan Africa. Breeding disease-resistant varieties has major implications for fungicide use in developing and developed countries. In high-resource countries (HRC), progress in resistance breeding for disease resistance has allowed farmers to reduce synthetic fungicide applications in wheat to an average of 1.25 times per crop cycle (Jørgensen et al., 2008). In LRCs, an estimated 85% of wheat farmers use no fungicide, 10% spray once, and less than 5% twice. The wheat area in developed and developing countries is about the same (110 mha). Estimating that 80% of the global wheat area worldwide is at risk from rust infections, farmers in HRC spray around 108 m times per season, while in LRCs 13 m times. At an average of 0.5 L per application per ha (Carmona et al., 2020), this translates to 92.5 million liters of fungicides applied to wheat worldwide, 54 million liters in HRCs, and 6.5 m in LRCs (and 32 million liters in China). Notwithstanding savings associated with genetic disease resistance in HRCs, the impact of PGR-based disease resistance in LRCs saves approximately 50 million liters of fungicide annually. Just since the beginning of this millennium, that is over 1 billion liters of fungicide application avoided.

5.2 | The IWIN and other networks that support international public goods

The generation of wheat cultivars adapted to the farming practices of the many wheat-growing areas of the world has been built upon the sharing of PGR and data. Exploitation of elite lines bred at one location, in other parts of the world, has been an essential part of wheat development throughout the ages. CIMMYT has served as a catalyst and leader in a global wheat innovation network focusing on the development, deployment, and sharing of elite germplasm for sustainable agricultural productivity, particularly for the Global South (Braun et al., 2010). Working closely with national and regional

breeding programs, the CGIAR breeding networks led by CIMMYT and ICARDA are the primary source of improved wheat lines used as parents or released as varieties across the Global South. As a consequence, improved wheat varieties developed using CGIAR breeding lines cover more than 100 mha (Lantican et al., 2016). Particularly in South Asia and Sub-Saharan Africa, CIMMYT-derived varieties are grown in nearly 80% of the world's wheat fields. These sorts of statistics demonstrate the value of sharing of germplasm.

CIMMYT elite germplasm has been freely distributed—as global public goods—to both public and private sector partners over the last 55 years, thereby enabling wheat scientists and breeders worldwide to access elite lines from different breeding pipelines (Figure 6). These wheat lines are annually evaluated in approximately 100 countries. Since the initiation of IWIN, there has been a growing trend in the release and adoption of more new and diverse wheat varieties (as a result of crosses with PGR) in the Global South (Dixon et al., 2006; Lantican et al., 2005). The use of alleles from PGR of wheat in CIMMYT breeding has been a common feature and is well documented (Ortiz et al., 2008) and herein. Between 2015 and 2023, more than 300 spring bread varieties were released in multiple countries and PGR were used in most to maintain disease resistance. The continuous supply of adapted germplasm from CIMMYT's wheat breeding program has been instrumental in addressing the growing demands of diverse wheat-growing regions globally. The rapid adoption of CIMMYT wheat germplasm was most notable in S-Asia, particularly in irrigated regions, and subsequently in the rainfed areas of Latin America, thereby paving the way for a more global impact of CIMMYT wheat breeding product (Pingali, 1999; Trethowan et al., 2001).

Numerous studies have demonstrated the contribution of CIMMYT-related germplasm to increased productivity around the world (Evenson & Gollin, 2003; Lantican et al., 2005; Ortiz et al., 2008). Genetic gains are well documented, most recently by Crespo-Herrera et al. (2017, 2018), Mondal et al. (2020), and Gerard et al. (2020). Notably, the findings from the Semi-Arid Wheat Yield Trials (SAWYT) conducted across 740 locations in 66 countries between 2002 and 2014 highlight the tangible impact, revealing an average yield increase of 1.8% in low-yielding environments and 1.41% in medium-yielding environments (Crespo-Herrera et al., 2018). Elite Spring Wheat Yield Trials tested across 180 optimal environments from 2006 to 2015 revealed genetic gains in the order of 1.63% when compared to the long-term CIMMYT check Atilla (Crespo-Herrera et al., 2017). While for High Rainfall Wheat Yield Trials conducted across 138 international environments from 2007 to 2016 an annual genetic gain of 1.17% relative to local checks was reported (Gerard et al., 2020). Studies also demonstrated the successful development and dissemination of CIMMYT- or ICARDA-derived heat-tolerant wheat varieties in the Middle East and North Africa (MENA) region, and notably, CIMMYT spring bread wheat varieties have been widely adopted in African environments. The enhanced yields from improved wheat varieties providing direct benefits for smallholder farmers and consumers in the Global South have been calculated (Lantican et al., 2016; Shiferaw et al., 2014) with the most recent estimates between 2016 and 2020 of US$ 11 billion annually

(Fuglie & Echeverria, 2024). Cost–benefit ratios of well over 100:1 have been calculated even at much more modest estimates for returns on investment (Lantican et al., 2016). These modest investments have played an essential role in preserving historically low food prices for decades (Evenson & Gollin, 2003).

Complementing IWIN, CIMMYT has a long history of networking with academia to deliver translational research, initially in understanding the genetics of disease resistance (see Section 3.1), later in adapting molecular biology technologies to practical breeding (see Section 4.1) and in deployment of complex physiological traits into elite germplasm (see Section 3.4). The latter typically involves the exploration of PGR for superior expression of desirable physiological traits and haplotypes (https://hedwic.org/), including through public–private partnership (https://iwyp.org/). These networks, along with many additional expert working groups, affiliated with the Wheat Initiative (https://www.wheatinitiative.org/) are collectively developing strategies and technologies to increase the use of PGR in wheat breeding generally (Langridge et al., 2022).

An additional important initiative is the CIMMYT Australia ICARDA Germplasm Evaluation (CAIGE) program, which has significantly enhanced the adoption of CIMMYT and ICARDA wheat and barley germplasm in Australia, supporting breeders and scientists for informed decisions on germplasm development and distribution (Mathews et al., 2007; Trethowan, 2014). Leveraging the combined expertise, CIMMYT-ICARDA collaborations in wheat research have generated positive outcomes, including enhanced crop productivity and improved adaptability, and have strengthened global food security through several joint initiatives (Lantican et al., 2016; Tadesse et al., 2019).

CIMMYT has and continues to be well-positioned to support the needs of growing wheat markets through (i) established breeding pipelines and (ii) the sharing/distribution of genetic resources through IWIN networks. This sharing has contributed enormously to the development of broadly adapted, high-yielding, disease-resistant, and climate-resilient wheat varieties grown by farmers around the world. The sharing of germplasm is supported by a seamless flow of information, and data exchange between NARS and CIMMYT breeding programs, reinforcing the network effect. The integration today of IWIN historical breeding trial data, comprising over 10 million raw phenotypic data points, with the new advancements in ML and DL techniques, will continue to provide novel and strategic approaches to effectively tackle the urgent challenges posed by climate change in agriculture (Reynolds, Braun, et al., 2017; Xiong et al., 2021) provided the sharing and exchange of information continues. Without them, wheat improvement for all the wheat-growing areas of the world will inevitably decline.

6 | CONCLUSIONS

The impact of international public-goods wheat breeding has indisputable benefits in the Global South, as well as globally. Fuglie and

Echeverria (2024) estimate an added value between 2016 and 2020 of \$11 billion per year, mostly benefiting resource-constrained farmers and consumers. The collection and storage of PGR (since early in the 20th century) have played a key role, especially through the maintenance breeding of disease resistance. Nonetheless, massive potential remains—there are estimated to be close to 0.8 m accessions in wheat collections worldwide and considerably more in situ—about which relatively little is known for the most part. However, wild relatives have survived millions of years of climate variance compared with our relatively recent crop species, so more systematic screening is recommended to identify new and better sources of needed traits. Given the major impacts from the use of PGR to date, that considered only a tiny fraction of PGR available, systematic, well-controlled screening of major collections is recommended using high-throughput genomic and phenomics tools and GIS information. Another reason to invest in wide crossing is that it is a proven and non-controversial technology with multiple impacts and substantial return on investment. With new technologies emerging all the time to facilitate its use in breeding, PGR should be considered the best bet for achieving "climate resilience" including its biotic and abiotic components. For example, HTP and next-generation sequencing substantially increase the probability of identifying and tracking valuable new alleles from PGR. Gene discovery—using sequencing combined with phenotypic data—is identifying novel loci and haplotypes deriving from PGR, and can help target allele mining among PGR for field validation as well as provide candidates for gene editing.

For heritable traits (involving a few genes like resistance to common diseases and some quality and nutritional traits), PGR screening, genetic analysis, and marker-assisted backcrossing are efficient ways to make considerably more options available to breeders. For complex traits related to climate resilience, yield potential, and stability for example, where genetic bases are more elusive, PGR trait sources can be crossed with complementary parental sources and high-throughput phenomic selection used to identify best progeny eventually combined with recurrent genomic selection approaches for the continued transfer of minor effect genes into the elite breeding pools (Sanchez et al., 2023). The use of wild relatives still represents a challenge for improving complex traits in terms of identifying and translocating chromatin for polygenic traits, although bridge species like synthetic hexaploid wheat allows complete access to *Ae. tauschii*, with excellent results (see Section 3.4).

Interestingly, crosses made with PGR expressing superior physiological traits such as radiation use efficiency, did not present problems of linkage drag. This further supports the case for the use of PGR in breeding and to broaden wheat gene pools generally, increasing the options for "climate proofing" future crops in new niches that the environment is carving out.

AUTHOR CONTRIBUTIONS

Julie King: Conceptualization; writing – original draft; writing – review and editing. **Susanne Dreisigacker:** Conceptualization; writing – original draft; writing – review and editing. **Matthew Reynolds:** Conceptualization; writing – original draft; writing – review and editing. **Anindya Bandyopadhyay:** Conceptualization; writing – original draft; writing – review and editing. **Hans-Joachim Braun:** Writing – original draft; writing – review and editing. **Leonardo Crespo-Herrera**: Writing – review. **Jose Crossa:** Writing – review. **Velu Govindan:** Writing – original draft; writing – review. **Julio Huerta:** Writing – original draft; writing – review and editing. **Maria Itria Ibba:** Writing – review and editing. **Carlos A. Robles-Zazueta:** Conceptualization; writing – original draft; writing – review and editing. **Carolina Saint Pierre:** Conceptualization; writing – original draft; writing – review and editing. **Pawan K. Singh:** Conceptualization; writing – original draft; writing – review and editing. **Ravi P. Singh:** Conceptualization; writing – original draft; writing – review and editing. **V. Mohan Murali Achary:** Writing – original draft. **Sridhar Bhavani:** Writing – review and editing. **Gerald Blasch:** Writing – review and editing. **Shifeng Cheng:** Writing – review and editing. **Hannes Dempewolf:** Writing – review and editing. **Richard B. Flavell:** Writing – review and editing. **Guillermo Gerard:** Writing – review and editing. **Surbhi Grewal:** Writing – review and editing. **Simon Griffiths:** Writing – review and editing. **Malcolm Hawkesford:** Writing – review and editing. **Xinyao He:** Writing – original draft; writing – review. **Sarah Hearne:** Writing – review and editing. **David Hodson:** Writing – review and editing. **Phil Howell:** Writing – review and editing. **Mohammad Reza Jalal Kamali:** Writing – review and editing. **Hannes Karwat:** Writing –editing. **Benjamin Kilian:** Writing – review and editing. **Ian P. King:** Writing – review and editing. **Masahiro Kishii:** Writing – editing. **Victor Maurice Kommerell:** Writing – review and editing. **Evans Lagudah:** Writing – review and editing. **Caixia Lan:** Writing – review and editing. **Osval A. Montesinos-Lopez:** Writing – review and editing. **Paul Nicholson:** Writing – review and editing. **Paulino Pérez-Rodríguez:** Writing – review and editing. **Francisco Pinto:** Conceptualization; writing – original draft. **Kevin Pixley:** Writing – review and editing. **Greg Rebetzke:** Writing – review and editing. **Carolina Rivera-Amado:** Writing – review and editing. **Carolina Sansaloni:** Writing – review and editing. **Urs Schulthess:** Writing – review and editing. **Shivali Sharma:** Writing – review and editing. **Peter Shewry:** Writing – review and editing. **Guntar Subbarao:** Writing – review and editing. **Thakur Prasad Tiwari:** Writing – review and editing. **Richard Trethowan:** Writing – review and editing. **Cristobal Uauy:** Writing – review and editing.

AFFILIATIONS

[1]School of Biosciences, The University of Nottingham, Loughborough, UK
[2]International Maize and Wheat Improvement Center (CIMMYT) and Affiliates, Texcoco, Mexico
[3]Colegio de Postgraduados, Montecillos, Mexico
[4]Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Campo Experimental Valle de México, Texcoco, Mexico
[5]Department of Plant Breeding, Hochschule Geisenheim University, Geisenheim, Germany
[6]Huazhong Agricultural University, Wuhan, Hubei, China
[7]Chinese Academy of Agricultural Science (AGIS), Shenzhen, China
[8]Crop, Livestock and Environment Division, Japan International Research Center for Agricultural Sciences (JIRCAS), Ibaraki, Japan
[9]International Wheat Yield Partnership, College Station, Texas, USA

[10]John Innes Centre (JIC), Norwich Research Park, Norwich, UK
[11]Rothamsted Research, Harpenden, UK
[12]National Institute of Agricultural Botany (NIAB), Cambridge, UK
[13]Global Crop Diversity Trust, Bonn, Germany
[14]Commonwealth Scientific and Industrial Research Organization (CSIRO), Agriculture and Food, Canberra, Australian Capital Territory, Australia
[15]Facultad de Telemática, Universidad de Colima, Colima, Mexico
[16]Department of Plant Sciences, Centre for Crop Systems Analysis, Wageningen University Research, Wageningen, The Netherlands
[17]CIMMYT-China Joint Center for Wheat and Maize Improvement, Henan Agricultural University, Zhengzhou, China
[18]School of Life and Environmental Sciences, Plant Breeding Institute, Sydney Institute of Agriculture, University of Sydney, Narrabri, New South Wales, Australia

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study. The data shown in the Figure 6 is not accessible publicly as it comes from the seed requests institutions make to CIMMYT for the IWIN materials which is in an internal database that contains confidential information like contact data of the people making the request such as phone numbers and emails. Whether an institution is public or private sector is derived from that list. The results from the wheat trials that these collaborators perform at the sites represented in the map with the IWIN materials are publicly available under: https://orderseed.cimmyt.org/iwin-results.php.

ORCID

Matthew Reynolds https://orcid.org/0000-0002-4291-4316

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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