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Opinion

Heritage genetics for adaptation to marginal soils in barley

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Future crops need to be sustainable in the face of climate change. Modern barley varieties have been bred for high productivity and quality; however, they have suffered considerable genetic erosion, losing crucial genetic diversity. This renders modern cultivars vulnerable to climate change and stressful environments. We highlight the potential to tailor crops to a specific environment by utilising diversity inherent in an adapted landrace population. Tapping into natural biodiversity, while incorporating information about local environmental and climatic conditions, allows targeting of key traits and genotypes, enabling crop production in marginal soils. We outline future directions for the utilisation of genetic resources maintained in landrace collections to support sustainable agriculture through germplasm development via the use of genomics technologies and big data.

Reintroduction of genetic diversity

Agriculture faces a triple challenge of increasing food security with progressively marginal soil conditions in the face of climate change, while also reducing its impact on the environment. Maximising grain yield remains the main breeding target for all cereal crops; however, there needs to be a transition to breeding crops for sustainability as current approaches are showing maladaptation to stress [1], including late-season heat and early-season frost, variability in water availability, nutrient deficiency, salinity, and toxic elements found in some marginal soils [2]. This is exacerbated by **genetic erosion** (see [Glossary](#)) seen through domestication *per se* [3] and the subsequent breeding process in many species, including barley [4]. Barley is currently the fourth-most-widely cultivated cereal and constitutes one of the major sources of global feed, food, and malt. Breeding to maintain levels of production across soils with contrasting fertility and in marginal environments is therefore critical. Making the most of our soils and implementing farming systems with reduced inputs is key to environmental sustainability, emphasising the need to exploit better-adapted and more resilient varieties of our major crops.

Barley has a very broad ecogeographic range compared with most other crop species [5] and has therefore evolved tolerance to a wide variety of environmental conditions. For millennia, natural and farmer-driven selection during cultivation under adverse environmental conditions has resulted in the emergence of varied adaptive traits. The resulting architecture of genotypes provides a promising solution to secure future crop stability [5,6]. Numerous wild and cultivated barley accessions have been collected and conserved in gene banks [7–9], which await geographic, phenotypic, and molecular characterisation. Collections of **landraces** are therefore an important source of germplasm, genes, and traits to improve the sustainability of agriculture in the face of climate change and other environmental perturbations [10–12], while also having value in the assessment of the impacts of climate, migration, and trade in agrarian history [13,14]. Collectively, this can be used to infer and predict which landraces, wild relatives, and

Highlights

Growers need to produce increased crop yield to use resources more effectively and be resilient to abiotic stress and changing climates; however, current approaches are leading to maladaptation to stress.

Bottlenecks in the selection of barley varieties have resulted in a reduction of genetic diversity that is obstructive to climate-smart agriculture.

To reverse genetic erosion and identify novel sources of variation, we are re-examining and reintroducing crop landraces.

Landscape genomics can add a new dimension by modelling potential adaptive responses to a specific environment or global climate change.

In a conceptual model, we outline a targeted breeding programme connecting old cultivar collections with state-of-the-art gene discovery and phenotyping, necessary to provide new resources for future needs.

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progenitor species have the ability to yield under specific environmental constraints and act as donors of useful genes and traits to current elite varieties [15–17]. One example of this approach is **genome–environment association (GEA)** [18], or **environmental genome-wide association analysis (envGWAS)**, which is gaining popularity and has been used to assess barley and wheat for adaptive traits [19]. Specifically, genes involved in frost tolerance in barley have been found through allele mining of exome sequencing data from a population of landrace cultivars [20]. For this reason, locally selected landraces have received renewed interest across all crops [11].

Landraces have previously been recognised as an important genetic resource to reveal adaptation to traits such as high soil boron in wheat [21], aluminium tolerance in barley [22], **manganese (Mn) deficiency** in barley [23], and phosphorus efficiency in rice [24]. However, the potential of landrace collections has not been fully harnessed in modern plant breeding [6,25–28]. Exploiting the genetic control that has evolved through adaptation to distinct geographical zones will help in planning more effective breeding strategies for crop production in marginal environments and in reintroducing beneficial traits.

We argue that there is substantial and novel genetic diversity present in landraces awaiting to be unlocked and suggest strategies for targeting and utilising this diversity more efficiently and effectively. These perspectives are included in a conceptual model for predicting gene combinations by the integration of highly descriptive agronomic and genomic data to guide germplasm utilisation in future crop breeding.

Adaptive traits of barley landraces in marginal environments

The impacts of reduced diversity in modern breeding are becoming more evident [29] and are here exemplified in a case study characterising phenotypic and genetic variation. We examined both modern cultivars and locally adapted ancient genotypes of barley grown in alkaline marginal soils with inherent limitation of plant-available Mn [23]. Mn deficiency in barley and other staple crops is a worldwide problem [30,31] affecting large areas of southern Australia, Texas, regions of China, and northern Europe, including Scandinavia and the UK [23,32–38]. Soils particularly prone to Mn deficiency include calcareous, alkaline, and sandy soils with high porosity, where Mn is primarily present as oxides, which cannot be utilised by plants.

Under such conditions, the performance of a range of spring barley cultivars and landraces, representing the breeding history of barley in the UK and Northern Europe, was evaluated [23] (Box 1) and genotypes screened for their ability to perform optimal photosynthesis for biomass production (see Figure IA in Box 1) [39]. **Chlorophyll (Chl) a fluorescence analysis** was used to derive the quantum yield (F_v/F_m) of photosystem II (PSII), which is a proxy for plant Mn status [30,39]. Remarkable differences in F_v/F_m among the barley varieties were observed (see Figure IA in Box 1) [23], with values ranging from 0.30 (severe Mn deficiency) to 0.76 (mild Mn deficiency). The two Bere landraces, collected from Shetland and Orkney, had superior PSII efficiency (F_v/F_m of 0.75 and 0.76). By contrast, all other barley accessions, including recently recommended UK and Scandinavian varieties and other Scottish landraces, had F_v/F_m values ≤ 0.40 , indicating severe Mn deficiency [40]. The poor PSII efficiency of the UK elite varieties struggling with Mn deficiency was fatal, causing total crop loss as they failed to set seed. By contrast, the two Bere landraces produced a grain yield of 2.7 t ha⁻¹, demonstrating local adaptation to marginal soil conditions (see Figure IB in Box 1). This is a striking illustration of how locally adapted landraces can generate reasonable yields in challenging soils. The ability to produce grain on alkaline soils with low Mn availability has been enhanced in some Bere landraces by years of selection and adaptation but lost in elites, with no advantage in having the trait on fertile soils. Most beneficial adaptive phenotypic traits are considered to be controlled by multiple **polymorphic**

Glossary

Chlorophyll (Chl) a fluorescence analysis: a highly sensitive methodology that provides a non-destructive tool for measuring various key parameters related to photosynthetic efficiency.

Clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR associated

(Cas): CRISPR guide editing by Cas enzymes, one of a number of genome-editing tools.

De novo domestication: domestication is defined as the process whereby wild plants have been evolved into crop plants through human selection. *De novo* domestication maintains desirable traits, such as environmental adaptability, of the wild plants to enhance production in crop plants, using marker-based or gene-editing approaches.

Genetic erosion: loss of variation that may occur at the level of crop, cultivar, or allele. Reduction in allelic evenness and richness is the greatest concern in the agriculture of today.

Genome–environment association (GEA) and environmental genome-wide association analysis

(envGWAS): associations between SNPs and the environments from which the landraces were collected to uncover the genetic basis of environmental adaptation.

Genome-wide association studies

(GWAS): statistical associations between genetic markers and a trait of interest using a collection of diverse, unrelated accessions based on linkage disequilibrium.

Genomic selection: a statistical prediction of marker effects based on genotypic and phenotypic information from a calibration population used to train a prediction model.

Haplotype: a group of alleles in a cluster of tightly linked genes on a chromosome that are likely to be inherited together.

Landraces: genotypes of traditionally domesticated crops that are locally adapted, selected from diverse environments, and maintained by farmers over generations.

Manganese (Mn) deficiency: symptoms in barley initially develop as interveinal chlorosis in younger leaves and eventually also as necrotic brown spots on older leaves, reflecting the indispensable function of Mn in photosynthesis.

genes [41], which is also likely for Mn efficiency observed in the responsive Bere landraces [23]. Genetically, these Bere landraces are distinct from modern and other old cultivars and landraces [23] (see Figure 1C in Box 1). Furthermore, within the Bere landrace group specific distinct geographical patterns can be observed, suggesting that they have developed independent equivalent strategies to cope with Mn deficiency [23]. This case study provides an exemplar of how locally adapted landraces can harbour genetic information that has been lost from the elite breeding gene pool but is critical for production on certain marginal soils.

Development of an improved and more resilient germplasm pool

The key challenge is how to translate and deploy these abilities from landraces into elite varieties to enhance yield in marginal soils, which are becoming more common in conventional and organic cropping systems. Landrace collections could enable farmers to select from and use a modern participatory breeding approach to identify the correct variety for specific locations and for specific value chains, including food, feed, or high-value malting and distilling uses. This 'modern landrace concept', along with future perspectives on using landrace material to generate plants adapted to climate change, is illustrated in a conceptual model (Figure 1, Key figure).

Genotypes with desirable traits selected for optimal performance in marginal soils and diverse environments are urgently required [42]. Landraces may be exploited directly as a source of genetic diversity for the development of new varieties expressing desirable traits that are adapted to specific agroecological zones (Figure 1). A complementary option termed 'survivalomics' is useful to identify parental material for introgression of abiotic stress tolerance based on the ability to yield in extreme habitats [43]. The positive alleles contributed by surviving landraces could be directly used in breeding to improve elite cultivars [44]. However, a major drawback of the direct use of landraces or wild relatives is their undesirable traits, such as excessive height in barley [45], which under high-input conditions induces lodging. By comparison, shorter modern elite cultivars have optimum performance under high nitrogen levels. Many of these issues can be overcome by using the correct sampling and statistical approaches to identify the beneficial alleles [46]. Another potential problem is accession heterogeneity and the potential mix of genotypes found in landrace populations, but this can be circumvented by the production of pure-line populations from single-seed descent [9].

The use of landraces as part of diverse panel populations for **genome-wide association studies (GWASs)** has enabled the identification of **quantitative trait loci (QTLs)** for a number of biotic and abiotic stress tolerance traits [47–49] and important physiological and development traits [50]. Similarly, multiple parent populations, such as **nested association mapping (NAM) populations**, **multiparent advanced generation intercross (MAGIC) populations**, and **multiple derivative lines (MDLs)**, which include landraces and wild relatives as parental donors, are yielding important diversity in phenotypes, which could improve sustainability of elite germplasm [51]. Identifying and transferring knowledge of new targets to the plant breeding community is essential to generate novel robust and high-yielding genotypes. Bi- and multiparent populations can be selected for desired traits in a target background by predicting genetic permutations that combine targeted traits (e.g., optimal flowering time and tolerance towards water and nutrient deficiency) (Figure 1; [48]). Knowledge and understanding of traits will assist in the identification of suitable parental lines for population development and sustainable (low inputs, stable yield in a variable climate) breeding programs [52], as will the combination of **genomic selection** and crop modelling, which has been used to ascertain environmental cues for flowering time in rice, for example [53]. The future breeding process will therefore benefit from advances in genome-enabled parental selection, identifying **haplotypes** and screening the progeny of crosses for desired recombinants whose performance can be predicted based on genetic information

Marker-assisted selection:

identification and use of genetic markers associated with desirable traits.

Multiparent advanced generation

intercross (MAGIC) populations: the use of multiple parents, where parents have been intercrossed to generate a genetic resource with increased recombination and variation for high-resolution QTL mapping.

Multiple derivative lines (MDLs): a combination of MAGIC, multiple parents, and NAM, a single common parent, crossed and backcrossed to develop a diverse population.

Nested association mapping (NAM)

populations: using a single common parent crossed to a diverse set of lines to create biparental populations, backcrossed or single-seed-descent populations, analysed together to improve the resolution of QTL mapping.

Polymorphic genes: a gene is described as polymorphic where the presence of two or more variant forms of a specific DNA sequence occur among different individuals or populations.

Quantitative trait locus (QTL): a region of the genome associated with a particular trait; can be genetically or physically defined as an interval on a chromosome where the candidate gene for the trait lies.

Single-nucleotide polymorphism

(SNP): a position in the genome with a variable nucleotide.

Box 1. Visual illustration of contrasting response between barley landraces and modern cultivars to Mn deficiency

To demonstrate the superior performance of Beres on soils with low Mn availability in Orkney, a small field trial comparing commercially available recommended elite varieties with Bere and other local landraces was undertaken (Figure 1). The lines were screened visually throughout the growing season as well as being scored for photosynthetic ability and grain yield at harvest [23].

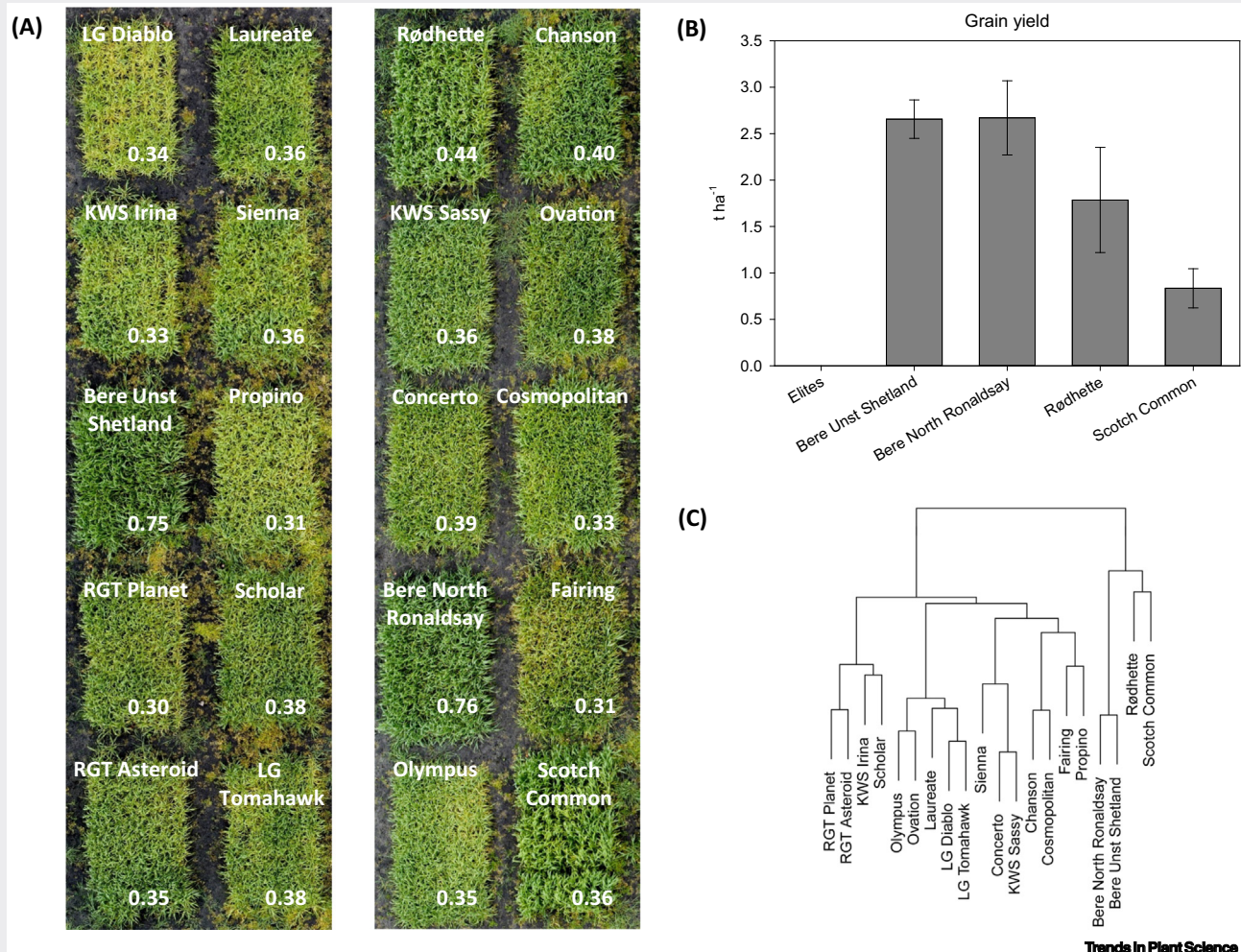


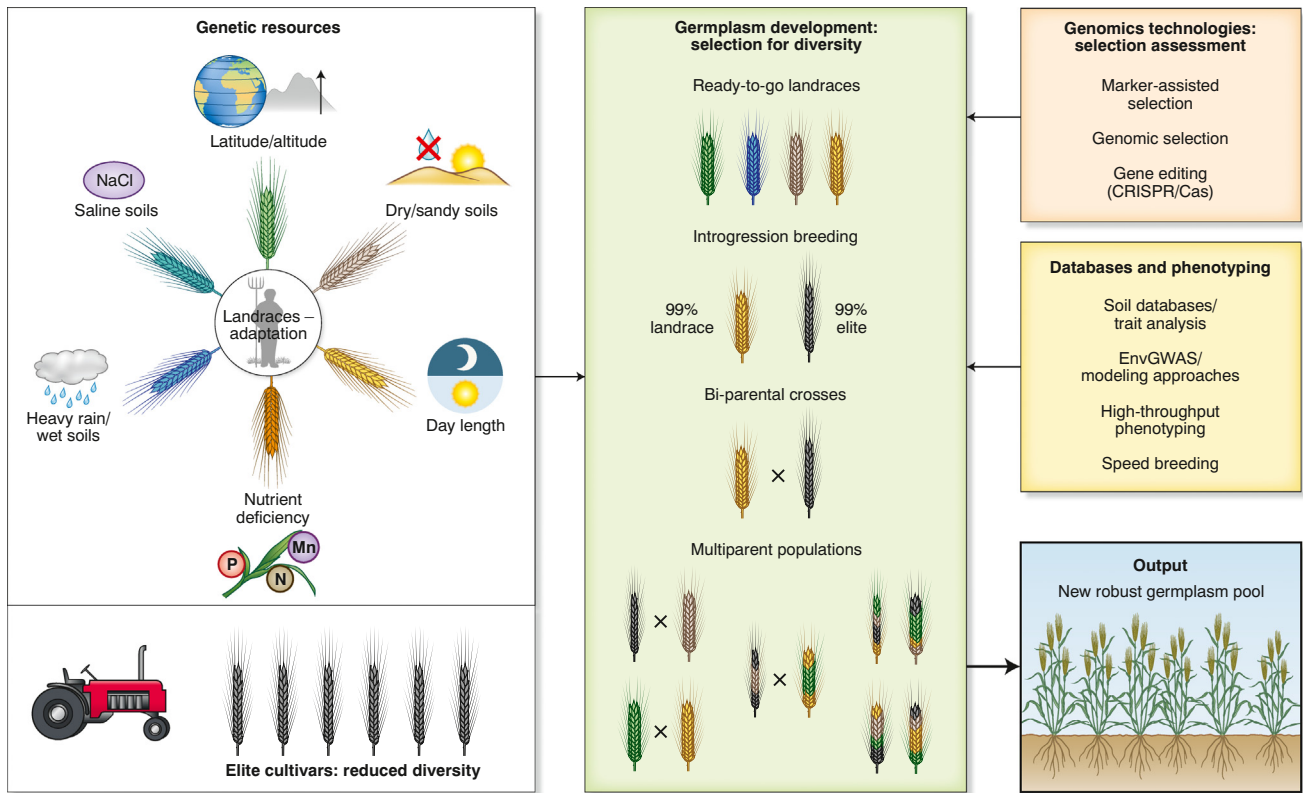
Figure 1. An overview of manganese response in the field and genetic diversity of a subset of Bere landraces and elite cultivars.

(A) Field trial plots showing plant vigour and biomass production for 20 genotypes, including two Bere landrace lines (Unst Shetland and North Ronaldsay) (see materials and methods in the supplemental information online). Cultivars were recommended in the UK between 2009 and 2019 from major European breeding companies: RGT Seeds (RGT Planet and RGT Asteroid); KWS UK (KWS Sassy and KWS Irina); Limagrain Europe SA and UK (LG Tomahawk, Concerto, Olympus; LG Diablo, Ovation, and Sienna); Syngenta Participations AG (Fairing, Laureate, Propino, and Scholar); Sejet, Denmark (Cosmopolitan); and Saaten Union UK (Chanson). Chanson and Scholar are feed varieties and the other cultivars are recommended for the malting industry. Scotch Common is an old two-row landrace grown throughout Scotland during the 1900s and Graminor Rødhetta is a modern six-row cultivar from Norway. The soil type is a calcareous sandy loam, pH 7.8 with a low manganese (Mn) content of 1.7 mg l⁻¹. Numbers in each plot are the average Fv/Fm value measured in the youngest fully emerged leaf of the plants (n = 3), indicating plant tolerance to Mn deficiency (Fv/Fm < 0.5 = severe Mn deficiency). (B) Grain yield [t ha⁻¹; mean ± SE (n = 3)] for genotypes able to set seed. Control plots of the same genotypes were sown at the Agronomy Institute on Orkney, where we observed yields of 4.50–6.74 t ha⁻¹ for elite cultivars, 4.52–5.08 t ha⁻¹ for the Bere barleys, and 3.29 t ha⁻¹ for Scotch Common. (C) Neighbour-joining tree based on a similarity matrix prepared for the barley genotypes using the 50K SNP genotyping chip [78].

[6,54], playing a central role in securing food and feed production [55]. Elite barley cultivars lack haplotypic diversity at centromeric regions because of limited recombination, whereas landraces and wild relatives offer a source of alternative untapped haplotypes [56–58].

Key figure

Using plant genetic resources to develop new varieties with desirable traits



Trends in Plant Science

Figure 1. The barley genetic resources comprise landraces and modern elite genotypes. From this genetically diverse material, new germplasm can be developed or identified; that is, ready-to-go landraces can be selected, introgression breeding can be applied, or new germplasm can be developed from bi- or multiparental crossing schemes to move genes from landraces into elite lines and vice versa. Genomic technologies, available to assess and select from the different types of germplasm developed, include marker-assisted selection and genomic selection. In addition, the landrace source of genetic diversity may be used as inspiration when designing custom genetic modifications by the use of genome-editing tools such as clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR associated (Cas) systems to increase the precision with which new varieties can be created. We can search for traits that allow cultivation in extreme environments by linking trait information with environmental and soil data through environmental genome-wide association analysis (EnvGWAS). Phenotyping is still necessary to verify that the desired phenotype is achieved and may be facilitated by high-throughput/automated systems and by accelerating the breeding cycle (e.g., by the use of optimum light intensity, temperature, and daylength to increase the rate of photosynthesis and thus plant growth). Together, such strategies will lead to the development of an improved and more robust germplasm pool, which will yield more efficiently and sustainably in marginal environments. Illustration by Debbie Maizels, Zoobotanica Scientific Illustration.

Towards an environmental genomics approach

The availability of historical environmental data at specific georeferenced locations, along with predicted trends, will help to determine the role of climatic variables that have moulded the adaptation of landraces to different environments. It is now possible to systematically explore the genetic variation in local landraces in the context of climate maps to explore the drivers of natural selection for local adaptation [59]. Combining large-scale genomic, phenomic, and ecological data offers a framework to enhance our understanding of both the mechanistic basis and the evolutionary consequences underlying adaptation in landraces and wild relatives of a

range of crop species [60–62]. The use of geographic and agroecological information and past and future climate-predictive modelling, along with crop simulation and trait-based ensemble modelling, can focus the search for stress tolerance genes and provide support for environmental ideotype breeding [43,63–65]. In addition, landscape genomics (i.e., the combination of geographically available information on sampling points to compute ecophysiological indices, and genomics) has been productive in identifying signatures of selection [44,66,67]. For example, a detailed analysis of known flowering-associated genes has shown significant geographical structuring [68]. Optimised flowering time, specific for geographical regions, is crucial to allow plants to benefit from rainfall at early stages of development or avoid extreme weather late in the season [69], allowing not only better grain-filling conditions for maximum productivity but also crop resilience to extreme stress, providing greater opportunity to yield under such conditions. Positive alleles contributed by elite genotypes indicate genomic regions of landraces that could be targeted by pre-breeding programs to improve suboptimal landrace features [44]. New combinations of genes for adaptation to marginal soils would increase the diversity of the cultivated crop and deliver the biological resources required for such cultivation. Thus, a sensible strategy for plant breeding would be to introgress beneficial optimised traits from elite lines into locally adapted landrace germplasm or vice versa, to best match site-specific conditions [25]. Although the former has worked well for single genes or additive traits, the latter has been proposed as an approach for complex traits such as stress tolerance or components of yield and yield stability [28]. By transferring critical domestication and adaptive traits (i.e. alleles of key known genes) from elite germplasm into wild material, we can immediately produce germplasm that can be effectively evaluated for valuable complex traits. Judicious selection of parents could lead to candidate cultivars in a rapid manner [44]; for instance, Bere landraces and newly developed lines with introgressions of the Bere genome will have physiological traits for superior accumulation and utilisation of Mn (and other essential micronutrients) compared with elite varieties.

Established techniques, such as **marker-assisted selection**, marker-assisted backcrossing, genomic selection, high-throughput phenotyping, and speed breeding can accelerate plant breeding (Figure 1) [70–72]. The increasing availability of these methods and online informational resources provides the potential to mine alleles in locally adapted landraces and to use this information to generate improved crops. Improvements in DNA sequencing technologies have enhanced the capacity to identify and manipulate genetic diversity and thereby the choice of variation to be utilised (Figure 1). Even without mechanistic understanding, the identification of **SNP** markers that are statistically associated with desirable traits, owing to their close physical proximity in the genome and hence likelihood of being co-inherited, allows the prediction of phenotype from genotype [73]. Novel genome-editing techniques have recently been developed to facilitate accurate manipulation of target sequences [74], including **clustered regularly interspaced short palindromic repeats (CRISPR)** technologies available for precise genetic manipulation [72,75], and this could be applied to landrace and wild relatives in pseudo-redomestication approaches [10,29,76,77]. Moreover, increased knowledge of metabolic pathways resulting from genomic analyses will help in the design of new varieties with beneficial traits with increased precision [73].

Concluding remarks and future perspectives

Agriculture is facing a major challenge to maintain and enhance food production on increasingly marginal soils in the face of climate change while also reducing the impact on the wider environment. There exists a large amount of genetic and phenotypic diversity in landraces, wild relatives, and progenitor species that could be harnessed to tackle some of these challenges. While examples of such diversity in landraces is ever increasing, the difficulties of transferring such abilities to the elite germplasm remains (see [Outstanding questions](#)). However, by the judicious application

Outstanding questions

Which adaptive traits have the greatest impact on crop resilience in future climates?

How is loss of genetic diversity related to the intensity of the selection process, and is the information beneficial in helping to plan more sustainable and targeted breeding options?

How do we decipher highly descriptive genomic data to guide and improve landrace germplasm utilisation in crop breeding?

How specific will the target breeding environment need to be to enable tolerance of crops to future environments, or will it be possible to breed a 'stress-free' cultivar that copes under many conditions?

How do we improve landscape measurements and facilitate the integration of data sources from, particularly, environmental science?

Will pseudo-redomestication from a landrace background be an effective way to improve sustainability in crops?

of cutting-edge genomic and genetics approaches, such as genome editing, genomic selection, genome-enabling crossing schemes, and speed breeding, combined with information from crop, environment, and genome modelling to landraces, it will be possible to accelerate this process and overcome some of the bottlenecks.

We predict a future where gene pools of modern cultivars can be selectively expanded by manually directed genetic introgression from landraces for improved tolerances to manage the more intense stresses predicted with climate change.

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Declaration of interests

No interests are declared.

Supplemental information

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