Plant Genetic Resources: Characterization and Utilization

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Rethinking phenotypic evaluation in plant genetic resources: Environmental mismatch as a hidden source of bias

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Critical Review

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Abstract

The evaluation of plant genetic resources underpins crop improvement and adaptation. However, current phenotypic screening approaches, whether conducted in controlled environments or limited-location field trials, often expose diverse germplasm to standardized growing conditions that do not reflect their ecological origins. This leads to systematic bias in trait evaluation, particularly for adaptive traits shaped by local environments. Genotypes may be incorrectly rated as inferior when assessed outside their optimal growing conditions, leading to underutilization of valuable genetic diversity. Here, we argue that environmental mismatch represents a fundamental limitation in plant genetic resource screening. Drawing on evidence from genotype by environment interactions, phenotyping research and ecological genomics, we highlight how current practices can misrepresent adaptive potential. We propose a shift towards environment-aware phenotyping frameworks that incorporate ecological context, genomics, multi-environment testing and reaction-norm approaches. Addressing this issue is critical for unlocking the full value of plant genetic resources in the face of changing agro-ecological conditions and practices.

Introduction

Plant genetic resources constitute the foundation of global food security, providing the raw material for crop improvement and adaptation to evolving environmental conditions. Phenotypic characterization is central to identifying useful sources of germplasm for breeding programmes, yet a critical conceptual limitation persists: the environments in which genotypes are evaluated rarely reflect the ecological conditions under which they evolved or are best adapted. This challenge is particularly acute in global plant germplasm collections, where accessions originate from diverse agro-ecological zones but are often assessed under a narrow set of experimental conditions. Recent analyses highlight that climate-smart breeding requires aligning genotypes with their agro-climatic zones, reinforcing the risks of evaluating diverse germplasm under uniform or standardized growing conditions (Garcia-Oliveira *et al.* 2025). Phenotyping platforms, whether growth chambers, glasshouses or limited-location field trials, prioritize environmental uniformity to enhance reproducibility. While this reduces experimental noise, it introduces a more subtle but profound bias: environmental mismatch between genotype origin and evaluation conditions (Figure 1A).

The importance of genotype by environment (G × E) interactions in shaping phenotypic expression is well established (Cooper *et al.* 1997; Des Marais *et al.* 2013). Ecological genomics further demonstrates that adaptive variation is often environment-specific and linked to local selective pressures (Lasky *et al.* 2014; Exposito-Alonso *et al.* 2018). Despite both, phenotyping assessments frequently assume that performance in limited test environments reflects general genetic value, an assumption that risks underestimating adaptive diversity (Figure 1B), particularly in crop wild relatives and landraces. It is important to note that the extent to which environmental mismatch affects trait evaluation depends on the genetic architecture of the trait. For qualitative traits controlled by major gene(s), such as quality traits, phenotypic evaluation tends to be more stable across environments and environmental mismatch is less of a concern. But for quantitative traits such as adaptation to abiotic or resistance to biotic stresses and yield with low heritability and strong G × E interactions, environmental mismatch is a major concern. Phenological traits such as flowering and maturity times are also particularly sensitive to environmental mismatch, as they are strongly regulated by photoperiod and temperature.

The importance of environmental mismatch in plant genetic resource evaluation is well recognized by plant breeders and crop scientists but remains frequently overlooked, particularly in genomics-centred approaches. Recent advances in high-throughput plant phenotyping

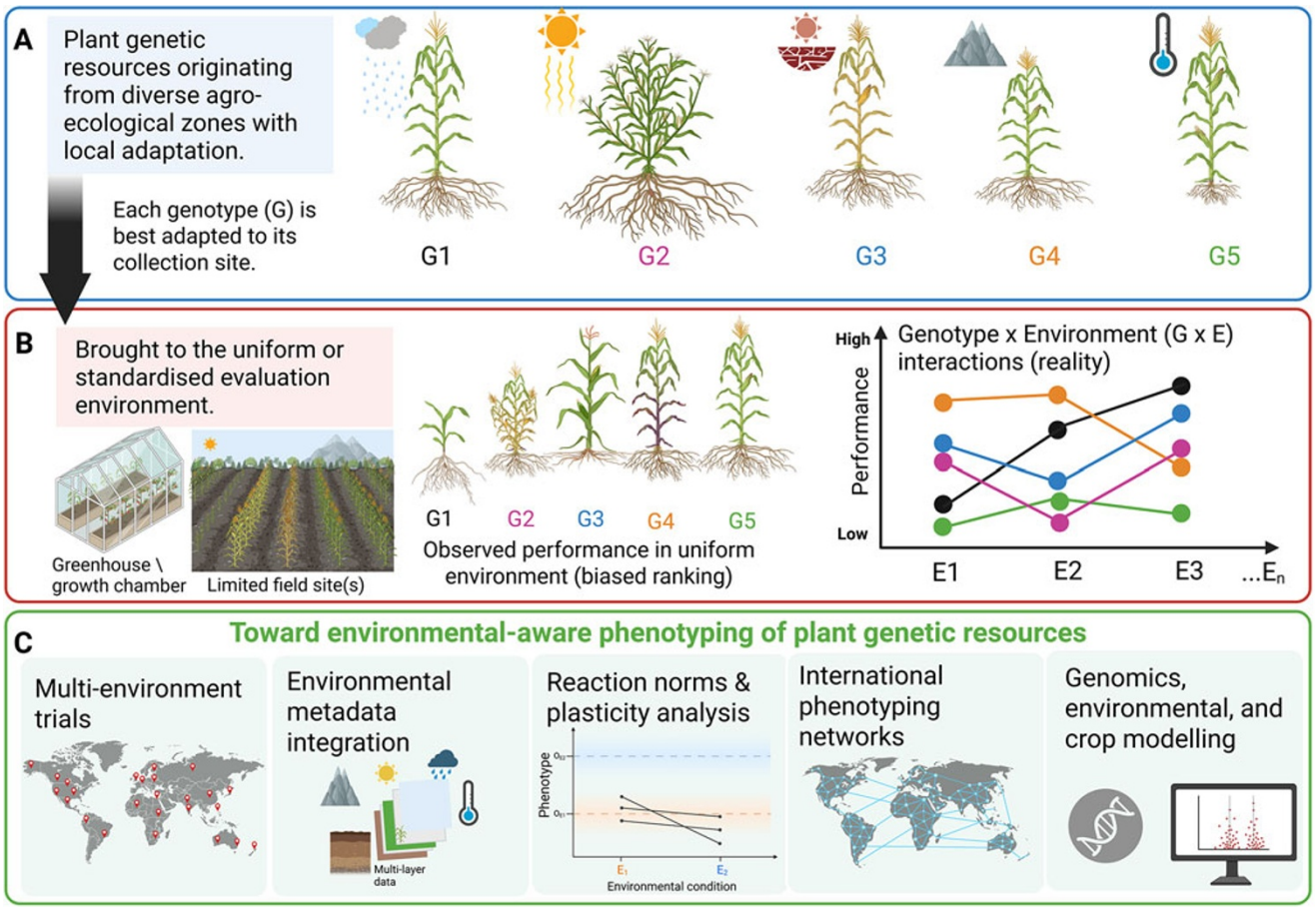

Figure 1. Conceptual illustration of environmental mismatch in phenotypic evaluation of plant genetic resources. Germplasm collected from diverse agro-ecological zones often having adaptations to the collection site growing conditions (A). Genotypes adapted to contrasting environments are often screened under a same or standardized environment. Consequently, phenotypic rankings may reflect adaptation to the testing environment rather than genetic potential (B). Environment-aware phenotyping frameworks are needed to better capture adaptive diversity and identify germplasm relevant for climate-resilient crop improvement (C). The crop (here, five maize genotypes) and rankings are used as examples in this figure. The sources of environmental mismatch illustrated here are temperature, photoperiod, rainfall and moisture regimes, soil type and nutrients, radiation, natural selection and local management practices. The figure was created using BioRender (www.biorender.com).

platforms, crop genomes and pan-genomes, and data integration have greatly expanded the scale of plant genetic resource evaluation, yet most phenotypic screening still relies on limited-environment testing. Additionally, our understanding of G × E interactions and ecological genomics has made the consequences of environmental standardization more explicit and quantifiable than in earlier work. This combination of increased analytical capacity and stronger empirical evidence has sharpened awareness that current evaluation frameworks may systematically bias the assessment of adaptive variation. This paper aims to highlight environmental mismatch in phenotypic evaluation and outlines environment-aware approaches to better capture adaptive trait diversity for crop improvement.

Controlled environments: Precision without ecological realism

Controlled-environment phenotyping platforms enable precise manipulation of environmental variables and high-throughput and precise data collection. However, their assumed environmental uniformity also constitutes a major limitation. Standardized environmental growing conditions enable meaningful comparisons among genotypes. However, by applying the same test environment across all genotypes, these systems implicitly assume that all genotypes respond optimally under the same settings, an assumption that is rarely valid for diverse germplasm, particularly for traits with strong G × E interactions. Genotypes from distinct ecological regions are adapted to specific combinations of photoperiod, temperature regimes, radiation intensity and soil characteristics. When evaluated under generic controlled conditions, such genotypes may exhibit reduced performance due to environmental maladaptation rather than genetic potential.

Controlled environments often fail to reproduce the ecological complexity of field conditions (Poorter *et al.* 2012; Langstroff *et al.* 2022). For example, previous studies have shown that phenotypes measured in controlled settings frequently diverge from those expressed in natural environments (Passioura 2006; Tardieu *et al.* 2018; Gomulkiewicz and Stinchcombe 2022), especially for stress-adaptive traits (Fiorani and Schurr 2013). Thus, while controlled environments provide precision, they may lack ecological validity, an important distinction when evaluating genetic resources intended for diverse agricultural systems.

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Field trials: Ecological relevance with inherent bias

Field-based phenotyping is often considered the gold standard due to its ecological relevance. However, field trials are not immune to environmental mismatch. Large germplasm panels are typically evaluated at a limited number of locations – sometimes for logistical convenience rather than ecological representativeness. As a result, only genotypes adapted to the local environment are assessed under near-optimal conditions, while other genotypes, particularly those from non-related environments, are evaluated under suboptimal conditions. This leads to location-specific selection bias, where genotype performance reflects environmental compatibility rather than intrinsic genetic potential.

Multi-environment trials (METs) consistently reveal substantial crossover G × E interactions (Cooper *et al.* 1997; Crossa *et al.* 2017). In crops, genotypes frequently change rank across environments, especially for drought, heat and nutrient-use efficiency traits (Varshney *et al.* 2014; Annicchiarico *et al.* 2017). Consequently, single- or limited-test environment trials risk favouring broadly adapted 'generalist' genotypes while overlooking specialized adaptations critical for resilience under specific stress conditions. It should be noted, however, that single test environment trials conducted over multiple years may capture environmental variation, as year-to-year fluctuations in biotic and abiotic pressure at a given site may reveal different growing conditions. Yet they often remain geographically constrained and may fail to represent the broader range of agro-ecological conditions from which diverse germplasm originates.

Environmental mismatch and plant genetic resource utilization

The effects of controlled-environment and field-based biases have important implications, summarized in Table 1. Of these, the misclassification of genotypes and the narrowing of the genetic base (Allaby *et al.* 2018) are perhaps the most consequential for long-term breeding progress. Once valuable diversity is overlooked in early screening, it rarely re-enters breeding pipelines, and the cumulative effect across generations can permanently reduce the adaptive potential available to plant breeders. This risk is particularly acute for crop wild relatives and landraces, which harbour specialized adaptations that broadly adapted elite lines cannot provide, yet are most likely to be undervalued under standardized evaluation conditions.

Relevance under climate change

Climate change will increase environmental variability, including temperature extremes, irregular rainfall and shifting pest pressures. Under such conditions, local adaptation and niche-specific traits become increasingly valuable. Ecological genomics shows that adaptive alleles are often associated with environmental gradients (Lasky *et al.* 2014; Exposito-Alonso *et al.* 2018). Predictive models integrating genomic and climatic data demonstrate that genotype fitness under future climates depends strongly on ecological matching (Hancock *et al.* 2011; Cortés and Blair 2018). These findings underscore the utility of evaluating genetic resources in environments that reflect their ecological origins. Recent work further emphasizes that genebanks remain underutilized unless genomic and environmental data are jointly considered to identify climate-adapted germplasm (Campbell *et al.* 2025; Cortés 2025). Beyond the breeding pipeline, increasing environmental mismatch under climate change may also compromise the reliability of variety trial data on which plant breeders, governments, NGOs, agricultural advisory services and development donors base their recommendations and investment priorities.

Strategies for environment-aware phenotyping

Addressing environmental mismatch requires environment-aware phenotyping approaches that better capture the agro-ecological diversity of both germplasm origins and target environments (Figure 1C). Key strategies include the following.

Multi-environment trials (METs)

METs enable explicit quantification of G × E interactions and identification of both broadly and specifically adapted genotypes (Crossa *et al.* 2017). For plant genetic resource assessment, evaluation across a minimum of two environments, whether two locations within the same season or the same location across two or more seasons, should be considered a baseline requirement rather than an optional enhancement. While two environments provide only a partial view of adaptive potential, they enable at least preliminary estimation of G × E interactions and reduce the risk of systematic misclassification of germplasm.

Integration of environmental metadata

Linking genotypes to their environments of origin (climate, soil, altitude) improves interpretation of phenotypic data and supports targeted testing (Hijmans *et al.* 2000; Meyer and Purugganan 2013). Despite its importance, environmental metadata remains incomplete or inconsistent across many genebank collections, limiting its practical utility. Systematic recording and integration of such data into genebank information systems, alongside phenotypic and genomic data, is therefore a priority for improving the utilization of plant genetic resources (Volk *et al.* 2021; Ghamkhar *et al.* 2025).

Reaction-norm and plasticity analysis

Reaction norms capture genotype responses across environmental gradients, providing a more comprehensive view of adaptive potential (Des Marais *et al.* 2013; Tardieu *et al.* 2017). Plasticity varies in its forms and adaptive value among traits, genotypes and environments (Schneider 2022; Napier *et al.* 2023). For plant breeders, two forms of phenotypic plasticity are particularly relevant. First, cryptic plasticity refers to cases where genotypes harbour environmentally responsive traits that are not expressed under standard evaluation conditions but become evident in ecologically matched environments. As a result, potentially valuable germplasm may be overlooked in conventional screening. Second, distinguishing between adaptive and maladaptive plasticity is essential: when genotypes are evaluated outside their native environments, observed plastic responses may not reflect performance in target conditions, leading to biased selection decisions. Reaction norm approaches, which quantify genotype-specific responses across environmental gradients, provide a robust framework for identifying both cryptic and potentially maladaptive plastic responses in diverse germplasm.

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Table 1. Potential sources of bias due to environmental mismatch in phenotypic evaluation of plant genetic resources and potential solutions. References are provided for each row to support the concepts summarized in the table

Potential bias	Mechanism	Germplasm most affected	Potential solution	References
Misclassification of genotypes	Performance outside collection site underestimates adaptive potential	Crop wild relatives, landraces and breeding lines adapted for a specific climate	Multi-environment testing linked to environmental metadata	Lasky *et al.* (2014); Van Eeuwijk *et al.* (2016)
Narrowing of the genetic base	Selection may favour widely adapted germplasm	Diverse and underrepresented genotypes	Diversity-aware selection indices and allele frequency monitoring	Fu (2015), Allaby *et al.* (2018)
Failure to detect adaptive traits	Standardized growing conditions suppress expression of environment-specific traits such as photoperiod sensitivity, heat stress and drought escape	Genotypes with specific stress adaptation	Targeted phenotyping under conditions that trigger adaptive traits and stress response	Des Marais *et al.* (2013); Schneider (2022)
Underutilization of climate-resilient genetic resources	Niche-specific adaptations remain undetected under uniform or standardized screening	Locally adapted ecotypes and landraces	Integration of climate projections with genomic and phenotypic data	Cortés (2025); Campbell *et al.* (2025)

Decentralized phenotyping networks

While multi-environment trials provide the analytical framework for capturing G × E interactions, their effectiveness depends on both germplasm diversity and environmental coverage. Decentralized national and international phenotyping networks help address this limitation by distributing evaluation across a broad range of geographically and ecologically distinct sites. Unlike centralized trials designed primarily for experimental control, these networks are structured to capture the full breadth of agro-ecological variation relevant to target environments. Examples include those implemented by the CGIAR multilocation trials (Dhondt *et al.* 2025) that enable broader environmental variation to be captured. However, such large-scale networks depend on substantial and sustained financial investment that is not available to many research institutions or universities. In resource-limited settings, more accessible approaches, such as regional collaborations among breeding programmes and genebanks, coordinated evaluation across two or more representative environments and the sharing of phenotypic and environmental data through collaborative networks, can provide practical and scalable alternatives for improving the assessment of G × E interactions.

Simulation and modelling approaches

Crop models and genomic prediction frameworks incorporating environmental covariates improve prediction accuracy across environments (Cooper *et al.* 2014; Millet *et al.* 2019). However, when genomic selection is an appropriate breeding strategy, environment-aware genomic selection remains a significant challenge, particularly for complex quantitative traits under changing climatic conditions (Yan and Wang 2026). For traits with simple genetic architectures or where conventional phenotypic selection is sufficient, genomic selection may provide limited additional benefit. Together, these approaches align phenotyping strategies with the ecological complexity of plant agricultural systems.

Taken together, these strategies provide a practical framework for aligning phenotypic evaluation with the agro-ecological diversity of crop germplasm collections and the environments in which selected genotypes will ultimately be deployed. In practice, these approaches are most effective when used in combination and adapted to the specific breeding context. Realizing this transition will require coordinated investment across national and international genebanks, breeding programmes and researchers.

Conclusions

Phenotypic evaluation remains a cornerstone of plant genetic resource research, yet current approaches are constrained by a fundamental limitation: the mismatch between evaluation environments and the ecological contexts of genotypes. Both controlled-environment and field-based screening systems can introduce bias that obscures true genetic potential. Recognizing and addressing this limitation is essential for improving genetic resource characterization, enhancing breeding efficiency and unlocking adaptive diversity for climate resilience. Several practical recommendations follow from this critical and empirical analysis for greater precision. First, evaluation of plant genetic resources should span a minimum of two environments as a baseline for capturing G × E interactions. Second, environmental metadata describing genotype origins should be systematically linked to phenotypic records in genebank databases to support targeted evaluation. Third, breeding programmes may explicitly account for local adaptations present in crop wild relatives and landraces. Fourth, the integration of genomic and pre-breeding tools (including GenBank genomics, pan-genomes, genomics-assisted breeding, multi-omics approaches and the use of backcross-derived materials generated by crossing plant genetic resources with modern varieties) with phenotypic evaluation will improve the accuracy of identifying adaptive diversity across diverse environments. Fifth, investment in international decentralized phenotyping networks will be essential for capturing the full breadth of agro-ecological variation relevant to diverse germplasm. A shift towards environment-aware phenotyping that incorporates ecological and evolutionary principles will be critical for maximizing the value of plant genetic resources in the coming decades.

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