

Gene-by-environment interactions in plants: Molecular mechanisms, environmental drivers, and adaptive plasticity

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Abstract

Plants demonstrate a broad range of responses to environmental shifts. One of the most remarkable responses is plasticity, which is the ability of a single plant genotype to produce different phenotypes in response to environmental stimuli. As with all traits, the ability of plasticity to evolve depends on the presence of underlying genetic diversity within a population. A common approach for evaluating the role of genetic variation in driving differences in plasticity has been to study genotype-by-environment interactions ($G \times E$). $G \times E$ occurs when genotypes produce different phenotypic trait values in response to different environments. In this review, we highlight progress and promising methods for identifying the key environmental and genetic drivers of $G \times E$. Specifically, methodological advances in using algorithmic and multivariate approaches to understand key environmental drivers combined with new genomic innovations can greatly increase our understanding about molecular responses to environmental stimuli. These developing approaches can be applied to proliferating common garden networks that capture broad natural environmental gradients to unravel the underlying mechanisms of $G \times E$. An increased understanding of $G \times E$ can be used to enhance the resilience and productivity of agronomic systems.

Introduction

Across space, time, and levels of organization, plants demonstrate a wide array of responses to their environments (Aitken et al., 2008; Anderson et al., 2012; de Lafontaine et al., 2018; Napier et al., 2019). In particular, the ability of plants to thrive despite being sessile and thus, unable to choose their environment, is remarkable. One important way that plants respond to environmental changes is through phenotypic plasticity, the capacity of a single genotype to produce multiple phenotypes (Schlichting, 1986). Plasticity can generate phenotypic shifts that are adaptive, neutral,

or actually reduce fitness (e.g. maladaptive plasticity; Van Kleunen and Fischer, 2005; Ghalambor et al., 2007; Crispo, 2008; Velotta and Cheviron, 2018). Adaptive phenotypic plasticity is a multi-faceted process of sensing, responding, and ultimately persisting through a wide range of conditions (Bohnert et al., 1995; Zhu, 2016; Lamers et al., 2020) that is often driven by shifts in metabolism, development, growth, or physiology. Importantly, plasticity at lower levels of organization can facilitate homeostasis (i.e. lack of plasticity) at higher levels of organization. Whether and how phenotypic plasticity evolves will depend on, among other things, the

degree to which plasticity enhances fitness and the presence of genetic variation in plasticity within populations. As anthropogenic climate change rapidly pushes us into conditions with no historical precedent (Tierney et al., 2020), phenotypic plasticity will be a key factor in determining plant success across spatial scales, from individual populations and communities to the global distribution of vegetation (Woodward and Woodward, 1987; Kelly and Goulden, 2008; Parmesan and Hanley, 2015; Byrne et al., 2017; Feeley et al., 2020). Understanding the molecular mechanisms and environmental drivers underlying variation in plasticity will be essential for anticipating whether plant populations can adapt to future change and evaluating the need for potential mitigation actions.

As with all traits, the ability of plasticity to evolve depends on the degree of underlying genetic variation present within populations (Via, 1987). To evaluate the role of genetic variation in driving differences in plasticity, many studies have focused on detecting genotype-by-environment interactions ($G \times E$; Van Kleunen and Fischer, 2005). As implied by the term $G \times E$, there are two elements to understanding the variation of plastic responses in a population: genotypic and environmental variation. Both genotype and environment can contribute individually to changes in a measured phenotype, and these factors can also interact in complex nonadditive ways. $G \times E$ occur when genotypes produce different phenotypes in response to environmental change—for example, when there are environment-dependent genotypic values. $G \times E$ studies have revealed that plastic responses can have a genetic basis (e.g. Schlichting, 1986; Pigliucci, 2005), but the amount of genetic variation in a plastic response and corresponding ability to respond to selection varies greatly across species and traits (Murren et al., 2014). The strength and patterns of $G \times E$ for ecologically important traits across plant populations represent a pool of plastic responses to ongoing and future environmental change, and the subset of these responses that are adaptive could have crucial implications for how plant populations will respond to environmental shifts (Saltz et al., 2018; Prakash et al., 2022).

Traditionally, studies evaluating $G \times E$ have been conducted at an aggregated level. For instance, all aspects of the environment are often combined into a single “site” effect, and individual gene or allelic effects are binned into an aggregate genotype value. However, without understanding the specific environmental cues that trigger plastic responses, it is difficult to predict responses to shifting or variable climates (Bonamour et al., 2019), especially when climates are novel or become more extreme. Likewise, our understanding of the genetic aspects of plasticity is often poorly resolved: although plastic responses must be mediated at the molecular level (Schlichting and Smith, 2002), most quantitative genetic methods do not identify specific genes or their mechanism of action. Even when several candidate genes can be proposed, they are difficult to validate due to inconsistent and often small effects. Moreover, the

lack of follow-up genomic manipulations make inference about molecular mechanisms highly speculative (see Ioannidis et al., 2009; Curtin et al., 2017; Evans et al., 2021). Functionally validating specific genes linked to variation in plasticity will enable the use of population genomic tools to study the mechanistic dynamics of adaptive evolution (Lee et al., 2014). Moreover, working below the level of a whole-genome genotype may help avoid some of the limitations that genetic architecture (e.g. degree of nonadditivity, effect size distribution of genes, and patterns of pleiotropy) imposes on breeding; for example, artificial selection may fail to produce desired outcomes because pleiotropy can constrain certain trait combinations and facilitate others. Strengthening our ability to resolve key environmental gradients and genetic variation underlying $G \times E$ is an important step toward predicting how plants will respond to novel and extreme environmental conditions.

In this review, we survey recent literature and emerging perspectives across the molecular and ecological disciplines to assess the current state of $G \times E$ research in plants. Moving the field beyond simply recognizing the theoretical importance of $G \times E$ for the future persistence of plant populations will require a renewed focus on linking gene-level processes to shifts in specific environmental gradients. Marrying insights across disciplines and levels of organization will allow for the prediction of adaptive plastic responses to the quickly emerging novel environments of the Anthropocene.

$G \times E$ background

Studies of phenotypic plasticity are often designed using common garden or lab experiments that replicate the same genotypes across different environments or experimental treatments. Frequently, phenotypic data collected from this style of experimental design is analyzed using a factorial analysis of variance (ANOVA) framework that tests for the effects of different genotypes (G), environments (E), and their nonadditive interaction ($G \times E$). Significant $G \times E$ occur when unique genotypes respond differently to environmental variation (Falconer and Mackay, 1996; Lynch and Walsh, 1998). The simplest way to depict these main and interactive effects is a function, called a reaction norm, that relates the mean phenotypic response of a genotype to a change in the environment (Schmalhausen, 1949; Schlichting and Pigliucci, 1998). Broadly, the genotype can influence a phenotypic value independent of the environment (Figure 1A), the environment can directly alter phenotypic expression similarly for all genotypes (Figure 1B), or these two effects can interact, causing the relationship between measured phenotypic values of each genotype to shift between environments (Figure 1, C–F; see Muir et al., 1992). For example, if a phenotypic trait is measured in multiple genotypes and two environments (1 & 2), rank-changing $G \times E$ occurs when some genotypes have relatively high phenotypic values in environment 1 and other genotypes have relatively high phenotypic values in environment 2

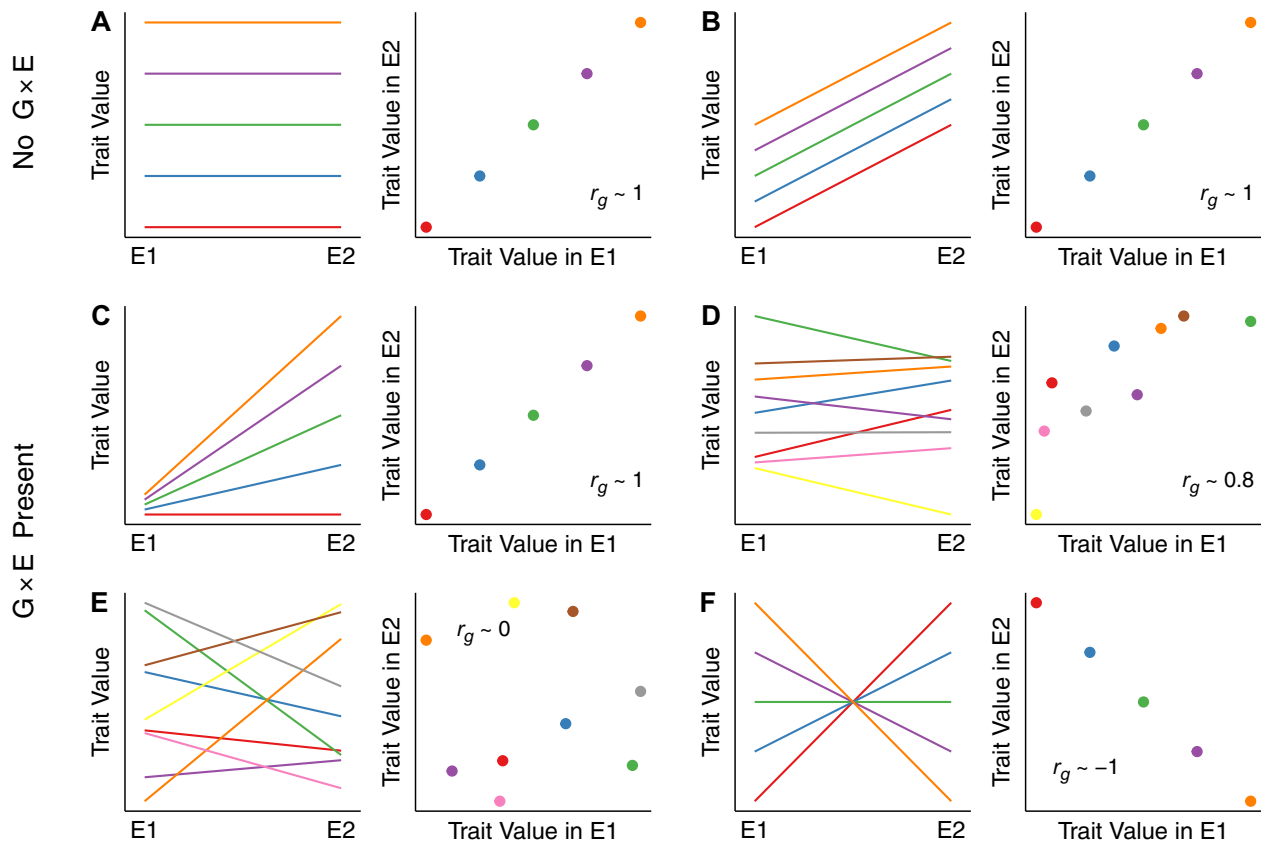


Figure 1 Six possible scenarios depicting the influence of genotype and environment on a trait of interest. In scenarios (A) and (B), $G \times E$ are absent, while scenarios (C)–(F) depict significant $G \times E$. For each scenario, the left column depicts the reaction norms for multiple genotypes measured in two environments. Nonparallel reaction norms indicate significant $G \times E$, while parallel reaction norms indicate a lack of $G \times E$. The right column depicts the corresponding genetic correlations of the trait. In nearly all instances, no $G \times E$ exists when genetic correlations (r_g) are approximately 1. In scenario (A) the genotypes have different trait values that are consistent between environments, indicating a significant genetic effect but no environmental effect. In scenario (B) the genotypes have different trait values that change by the same amount between environments, indicating a significant environmental effect and a significant genetic effect, but no $G \times E$. In scenario (C) the relative rankings of genotypes are constant between environments, but the difference in trait value changes between the environments, indicating variance-changing $G \times E$. This type of $G \times E$ can take many forms, all of which are characterized by nonintersecting reaction norms. Variance-changing $G \times E$ is a unique case where $r_g \sim 1$, but significant $G \times E$ exists. This significant $G \times E$ is driven by differences in scaling between environments. In scenarios (D), (E), and (F), the relative rankings of genotypes change between environments (i.e. the lines intersect). These scenarios differ in the degree of genetic control.

(Figure 1, D–F). In contrast, variance-changing $G \times E$ occurs when the same genotypes have relatively high phenotypic values in both environments, but the reaction norms are heteroskedastic (Figure 1C). Importantly, the outcomes observed at this phenotypic level, as represented by reaction norms, result from the combination of the $G \times E$ occurring at all the underlying genetic loci impacting the trait of interest (e.g. gene-by-environment interactions). $G \times E$ occurring at each individual locus can take the same form as $G \times E$ at the phenotypic level; genetic effects that change the sign or direction of impact depending on the environment (often termed antagonistic pleiotropy), or, perhaps more commonly, genetic effects that change in magnitude depending on the environment but with a consistent direction (often termed differential sensitivity; Des Marais et al., 2013; Figure 2).

Another compelling viewpoint considers the results from these factorial experimental designs as genetic correlations.

This approach, first introduced by Falconer (1952), treats the same phenotype measured in different environments as distinct traits that share genetic underpinning and are genetically correlated. These correlations can vary between -1 and $+1$. A positive value close to 1 indicates similar genetic control of the trait across environments (i.e. no $G \times E$; Figure 1, A–B). Genetic correlations less than a value of 1 suggest that $G \times E$ is present within the population. For instance, positive genetic correlations that are <1 suggest a mixture of common and unique genetic controls in each environment (Figure 1D); a genetic correlation near 0 implies novel genetic architecture across environments or a balance of positive and negative pleiotropy across loci (Figure 1E); and a value near -1 suggests a trade-off or antagonistic pleiotropy (Des Marais et al., 2013; Figure 1F). These genetic correlations are directly related to $G \times E$ reaction norms, and this relationship can be generalized across continuous

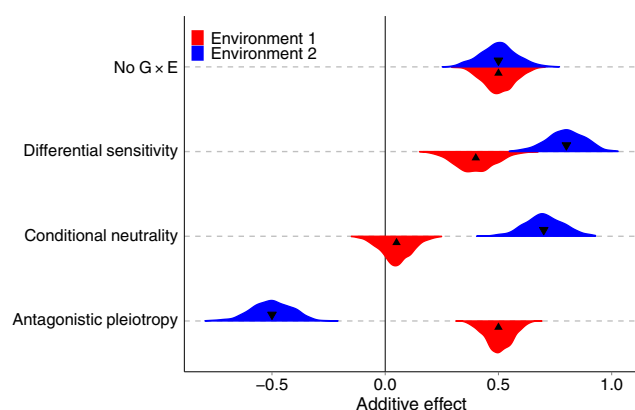


Figure 2 $G \times E$ results from the aggregated additive effects of quantitative trait loci (QTL) across the genome. These effects occur in four classes: antagonistic pleiotropy results when the sign of additive effects differs across environments; conditional neutrality ensues when effects occur only in particular environments; differential sensitivity occurs when the magnitude, but not the sign, of additive effects changes with the environment; no $G \times E$ arises when additive effects are not environmentally dependent.

environmental variation (Gomulkiewicz and Kirkpatrick, 1992). Broadly, the shift from working with reaction norms to genetic correlations is often advantageous for breeding programs. Using genetic correlations enables breeders access to well-established and highly effective quantitative genetics tools to predict responses to selection (Walsh and Lynch, 2018).

Environmental drivers

Plant breeding has a long history of using multi-environment field trials to evaluate $G \times E$. Often, these studies focused on the performance of specific genotypes at sites that represented the planned production environments (Comstock, 2007). For this reason, as well as the inherent complexity of deciphering the environmental component of $G \times E$, many statistical frameworks conveniently bin all environmental and local factors (e.g. weather, soil type, and presence of pathogens) into a single categorical “site” effect variable. Similarly, the practice of using a site effect is common in evolutionary and molecular ecology, where a wide range of field studies combine sources of environmental variation to understand local adaptation (Anderson et al., 2013). These approaches have generated important insights on yield in planned production locations and differences in fitness between local and foreign environments (Kawecki and Ebert, 2004; Fan et al., 2007; Hereford, 2009; Ågren et al., 2017). But, these studies were not designed to identify specific environmental drivers of plastic responses. To better quantify the environmental aspects of $G \times E$, several approaches of varying complexity have been utilized throughout the history of the field.

Researchers have used a diverse array of primarily mixed modeling approaches to understand $G \times E$ in plant experiments (e.g. Finlay and Wilkinson, 1963; Eberhart and Russell,

1966; Becker and Leon, 1988; Yau, 1995; Piepho and Pillen, 2004; Xavier et al., 2018; Wilson et al., 2021). One such approach is a special case of the classic reaction norm framework that swaps the site effect for the environmental mean (Finlay and Wilkinson, 1963). Specifically, this approach and its extensions, often termed “Finlay–Wilkinson regression,” show that $G \times E$ is easily quantified by the slope of the regression of genotype-specific performance across environmental gradients (Figure 3). Basic models of this form can generate estimates for quality gradients based on the average performance of all genotypes, using the plants as a phytometer to provide a measure of the aggregate environmental impact. Moreover, the environment-specific performance of any genotype can be estimated as long as it occurs within the range of test locations (de Leon et al., 2016). The most straightforward extension of this approach is to model the reaction norms that describe the phenotypic expression of the target genotypes by random regression on actual measured environmental descriptors (Fikse et al., 2003). For example, average growing season temperature or precipitation at each location could be used instead of “site” or the environmental mean performance. By directly evaluating target environmental descriptors, it may be possible to determine what factors have a significant impact on detected $G \times E$ and whether they contribute to changes in variance or a re-ranking of the genotypes. One drawback of the standard Finlay–Wilkinson approach is that it does not explicitly account for the possibility of nonlinear $G \times E$. A potential solution for this issue is to estimate nonlinear plasticity parameters from the residual errors (see Kusmec et al., 2017).

A modern extension of the reaction norm perspective uses algorithms to identify environmental drivers underpinning $G \times E$ in large-scale multi-environment data. These algorithmic approaches consider how genetic effects vary in size and direction along key environmental gradients (see Savolainen et al., 2013; Wadgymar et al., 2017; Li et al., 2018; Guo et al., 2020) and whether the temporal windows over which these gradients occur are important (i.e. development stage). One approach (Environmental Covariate Search Affecting Genetic Correlations [ECGC]) examines the similarity between an environmental covariance matrix and a multi-site genetic covariance matrix (Onogi et al., 2021). The base for ECGC is still a conventional reaction norm model (van Eeuwijk et al., 2005; Hayes et al., 2016), but, by associating the similarity matrices of environmental covariates and the genetic correlation matrix, this approach hopes to isolate the environmental gradients directly related to $G \times E$. Onogi et al. (2021) used this approach to identify the meteorological factors that shaped the $G \times E$ detected in tens of thousands of soybean (*Glycine max*) records collected in >50 environments. Specifically, they found precipitation around sowing dates and hours of sunshine just before maturity affected $G \times E$ involving yield. Subsequent genome-wide association mapping on the sensitivities related to the

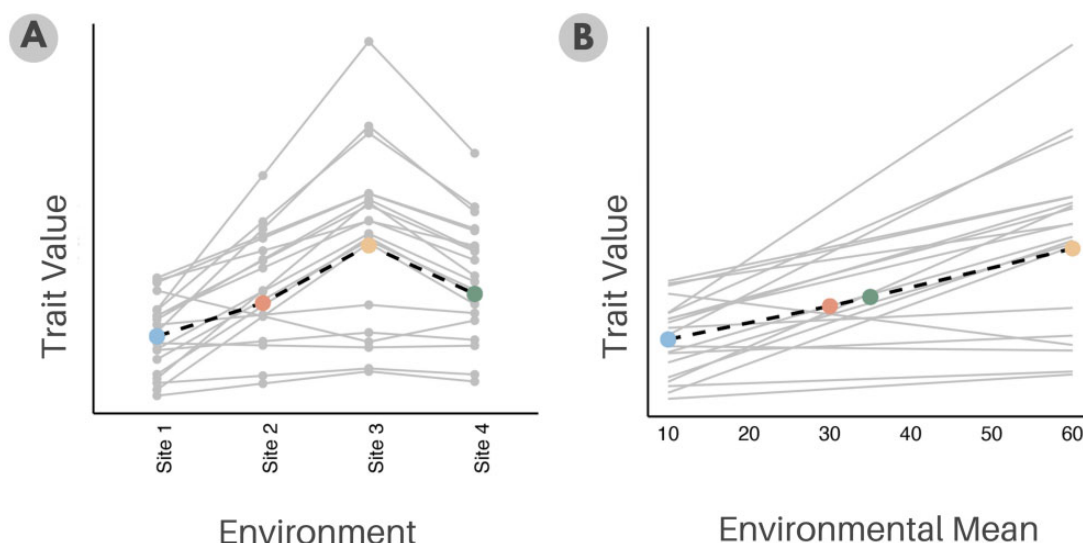


Figure 3 A, Depiction of the traditional approach for analyzing data from multiple sites. Along the x-axis, the sites are unordered or ordered based on the intuition of the researcher or a commonly used classification scheme (e.g. latitude). The gray dots connected by lines are individual genotypes, while the larger dots represent the site average for the trait across all genotypes at a site. Moderate amounts of $G \times E$ are depicted by the gray lines. This ordering scheme fails to adequately explain the primary environmental driver of the trait of interest as evidenced by Site 3 having a higher trait mean than Site 4. B, Here, the x-axis is reordered by the environmental mean (e.g. the average performance of genotypes at a particular site). Along this gradient, Sites 3 and 4 have now switched places, and the environmental similarity between Sites 2 and 4 is much higher than expected based on the original ordering scheme.

environmental drivers allowed them to identify candidate genes underlying the $G \times E$.

A related approach aiming to integrate an explicit environmental dimension (Critical Environmental Regressor through Informed Search) works by generating environmental indices that combine an environmental parameter and a growth window (Li et al., 2021; Mu et al., 2022). By creating a quantitative index for a measured environment (i.e. an environmental index), $G \times E$ can be modeled as performance curves of genotypes along this index (Li et al., 2018). This approach can also go beyond the aggregate genotypic level to quantify effects at different genetic loci along an environmental gradient (Li et al., 2021). For example, Mu et al. (2022) found that diurnal temperature range during the rapid growth period of sorghum (*Sorghum bicolor*) development was an informative environmental index. They demonstrated that combining the environmental index with genomic prediction could lead to improved performance prediction. In general, the continued development of these association approaches will provide the means to generate explicit testable hypotheses about environmental drivers of $G \times E$.

Perhaps the most promising designs for implementing these algorithmic approaches and studying the environmental drivers of $G \times E$ are large-scale common garden plantings (Johnson et al., 2022). Utilizing many disparate sites allows the inclusion of a wide range of variability by capturing key environmental gradients in a realistic manner. These designs are also easier to maintain than traditional experiments that require sustained treatment applications. For instance, as part of the Genomes to Fields initiative ([https://](https://www.genomes2fields.org/)

www.genomes2fields.org/), common garden efforts in maize (*Zea mays*) have revealed the importance of $G \times E$ in explaining phenotypic variation in yield traits. This suggests that measured environmental covariates can help improve predictions of future performance (Falcon et al., 2020; Rogers et al., 2021). At a broader scale, the potential of global common garden networks was recently illustrated by a study of white clover (*Trifolium repens*) that included 160 distinct sampling locations on six continents (Santangelo et al., 2022). Santangelo et al. (2022) found that urban plants produced less antiherbivore chemical defenses than rural plants. Genomic data suggested that this was an adaptive response linked to lower levels of drought stress and herbivory pressure in urban centers. Furthermore, ongoing multinational collaborations, such as the Arabidopsis (*Arabidopsis thaliana*)-focused GrENE-net (<https://grenenet.wordpress.com/>), have the potential to elucidate the genetic basis of adaptation by linking key environmental drivers, such as weather and soil data, to shifts in allele frequency over time and space through evolve-and-resequence experiments (Czech et al., 2022).

While dense common garden networks will continue to provide many insights, there have also been significant advances in experimental approaches for studying environmental effects. Traditionally, many empirical studies have compared a control to a single treatment level of an environmental factor. However, there are substantial limitations to these simple experiments, including an inability to mimic the complexity of nature and difficulty in choosing the correct levels for experimental treatments. This is one reason that Shaw and Etterson (2012) advocate studying climate

change in multi-site common gardens rather than experimentally. However, tremendous amounts of complexity can be summarized by reduced representations of reality (see Bergelson et al., 2021). The complexity of experiments has begun to increase, possibly representing the appropriate balance between interpretable reductionism and the intricacy of reality. One important advance has been incorporating multiple treatment levels into experiments. This is crucial because phenotypic responses to environmental gradients are often nonlinear (Knapp et al., 2017; Kreyling et al., 2018; Arnold et al., 2019). For instance, responses to changes in temperature are often concave, with a substantial drop in performance at very high temperatures (Arnold et al., 2019); plant responses to precipitation may be asymptotic, with little increase in production under very wet conditions relative to slightly drier conditions (Knapp et al., 2017). Experiments that include only two treatment levels (e.g. treatment or control) will fail to detect these effects. Adding even a single additional treatment level can capture far more of the true reaction norm (Aspinwall et al., 2017; Knapp et al., 2017; Monroe et al., 2021). Perhaps the best way to detect the shape of phenotypic responses to environmental drivers is a gradient design (Kreyling et al., 2018). This approach involves low or no replication of many treatment levels along an environmental gradient. Importantly, this alleviates the challenge of picking informative treatment levels (realistic values versus detecting effects, see Cottingham et al., 2005 for a discussion of design considerations) and allows the detection of subtle or nonlinear patterns when moving between treatment levels.

Another key advance in enhancing the complexity of experimental studies is incorporating multiple stresses into a single study. There are a few reasons that this is valuable. First, some phenomena that experiments attempt to manipulate are complex processes whose effects might be difficult to replicate accurately (Knapp et al., 2008). These effects can be underestimated by simply isolating differences in a single variable. For example, most field experiments seeking to understand drought will manipulate soil moisture but not vapor pressure deficit. Second, some important environmental gradients do not occur in isolation from others. For example, many natural droughts occur during heat waves (Knapp et al., 2008; Kreyling et al., 2017). Together, this may explain why field drought experiments elicit, on average, much smaller effects on plant performance than natural droughts (Kröel-Dulay et al., 2022). Moreover, stresses that alone would have minimal impact on plant performance can drastically reduce performance when combined, either simultaneously or in rapid succession (Rillig et al., 2019; Zandalinas et al., 2021). As climate changes and plants are increasingly exposed to multiple stresses simultaneously, understanding these combined impacts will become more important for enhancing our mechanistic understanding of $G \times E$ (Des Marais et al. 2017; Zandalinas et al., 2021).

To that end, future experiments could combine two or more stresses to better understand the degree of synergy,

additivity, or antagonism between different stress combinations. At the most basic level, this could include a factorial design of multiple relevant stresses (two levels for each stress: control versus stress). As adding new levels to factorial designs can quickly make the study intractable, this may require multi-staged studies. Several (3–5) relevant stresses that may act in combination could be identified and included in a factorial experiment or in an experiment that only allows pairwise combinations of stress, but not higher-order interactions. Then, follow-up experiments could manipulate the most important synergistic stresses (i.e. significant stress $\times$ stress interactions) at multiple levels. This would allow a better understanding of both the combined effects of relevant stresses and the impact of different levels of the stresses. Increasing the complexity of field experiments can be challenging at numerous levels, but the payoff of incorporating more realism into these experiments will be an improved understanding of the environmental drivers of $G \times E$.

These newer approaches will allow $G \times E$ research to move away from expansive “site” effects and consider the specific environmental drivers involved in plastic plant responses. The focus on environmental stimuli is crucial to future research efforts for two primary reasons. First, they allow for the identification of genomic regions linked to a specific abiotic stress or climate gradient of interest. Combined with existing annotation resources from many model systems, this will significantly reduce the number of candidate genes of interest for follow-up molecular studies aiming to identify genes involved in adaptive plastic responses. Second, even if a breeder’s goal is only to understand $G \times E$ across target growing sites, rapidly changing climate regimes will produce future growing conditions that may be out of the environmental bounds measured in a single $G \times E$ study. Put simply, predicting genotype performance in response to measurable changes in specific environmental stimuli will improve breeding success in untested or future climates.

Genetic drivers

To understand the genetic basis of plasticity, it is important to briefly examine how plasticity can evolve and why standing genetic variation in plasticity (i.e. $G \times E$) within populations is critical for this. Since plants cannot move to track suitable conditions, they must be able to cope with stressful environmental conditions. Consequently, plants often respond to these environmental shifts by changing their phenotype (i.e. phenotypic plasticity). These plastic responses can be passive, such as when growth declines due to resource limitation or when the rate of a biochemical reaction changes with temperature. Plastic responses can also be active. Active responses often allow plants to alter their development via a specific signal perception-transduction system (Gilroy and Trewavas, 2001; Van Kleunen and Fischer, 2005). To avoid costly evolutionary constraints and detrimental effects to plant fitness, active responses to stressful environments will often need to be dynamic. As such, plants must

finely tune responses rather than simply switching a pathway off or on (Kong et al., 2021). This highlights an important mechanism by which plasticity can evolve: when genetic variation in these finely tuned responses is present within populations, and natural selection favors certain genetic variants that exhibit $G \times E$, plasticity can evolve (Pigliucci and Byrd, 1998; Pigliucci, 2001; Matesanz et al., 2010).

How plants tune active stress response pathways is likely the product of sustained selective pressure. To generate an adaptive plastic response to shifts in environmental conditions, all the timescales related to signaling, integration, downstream processing, and elicited responses need to occur in a coordinated way that allows for adaptive outcomes in the context of the environmental challenge. If the timescales are mismatched due to the plant lagging, missing a cue, or over-responding, the response will be maladaptive and detrimental to overall plant fitness. Across a population, there can be genetic diversity in key genes mediating the different steps of this process, and the effects of these differing alleles can cause rank- or variance-changing $G \times E$ across measured environments. A recent framework proposed to understand how plants perceive, process, and act on environmental stimuli compared plastic responses in different environments to behavior patterns (Karban and Orrock, 2018). Crucially, plants must first sense environmental stimuli and pass “judgment” on how to respond (Trewavas, 2005). This step is perhaps best encapsulated by a simple question: how do plants sense their local environment? Although plants do not have a central nervous system, they possess receptors that allow them to sense stressful environments, including high temperature (Penfield, 2008; Lamers et al., 2020), herbivory (Arimura, 2021), and shading (Schmitt et al., 1995). For instance, phytochrome B is the primary photoreceptor controlling the growth of Arabidopsis seedlings exposed to variable shade conditions (Casal, 2013). This photoreceptor can not only read red/far-red light to sense shifts in shade conditions, but it also acts as a temperature sensor through temperature-dependent reversion of its active to inactive state (Legris et al., 2016).

After perceiving these environmental signals, plants use electrical, hydraulic, and chemical signaling pathways to transmit information across the plant body (Huber and Bauerle, 2016). The best-known signal transduction pathways include responses such as membrane depolarization, Ca^{2+} influxes, mitogen-activated protein (MAP) kinase cascades, phytohormone biosynthesis and catabolism, and reactive oxygen species (ROS) signaling. Crucially, signals triggered by similar stressors can be integrated and amplified to increase the mobilization of downstream effectors and enhance response effectiveness (Choi et al., 2016; Duran-Flores and Heil, 2016; Shinya et al., 2018). The propagation of these wavelike signals means that the plant has completed the judgment portion of the pathway. In plants experiencing herbivory, evidence suggests that phytohormones, such as jasmonic acid, abscisic acid, and ethylene,

accumulate, which in turn activates signaling cascades that regulate downstream transcriptional responses (Nguyen et al., 2016). These signaling responses and related shifts in gene expression indicate that the plant has perceived the environmental change. But, when the hormonal response is inappropriate and the genes expressed fail to maintain plant homeostasis, this process can result in increased susceptibility to environmental stressors (Karban and Orrock, 2018). Work by Orrock et al. (2015) articulated how these outcomes are linked to the principles of error management theory. Specifically, evolution by natural selection favors plants that make errors related to stress responses if they reduce the likelihood of making a costlier error (e.g. failing to respond to an environmental cue such as herbivory could be worse than responding to a “false” herbivory event).

The cost of responding or not responding to cues can also differ between environments. Hence, genotypes from some environments may experience selection that promotes earlier responses to a stimulus, while genotypes from other environments may experience selection for a later response tied to higher response thresholds. This pattern could be responsible for driving observed $G \times E$. This theory further suggests that plants respond based on the reliability of cues and the amount of time it takes to respond. For instance, some environmental changes are gradual and predictable, such as the seasonal change in photoperiod or the slow decline of soil water availability across the growing season. In contrast, other environmental changes are rapid, fluctuating, and unpredictable. Leaf temperature or light intensity may rapidly shift from one extreme state to another because of sun flecks caused by clouds or complex leaf canopies. Heat waves or cold snaps may occur rapidly with little warning and last only hours. Recent studies have shown that plants can mount remarkably rapid molecular responses, often within seconds, to some of these environmental changes (Kollist et al., 2019). These responses often exhibit several peaks in response to stimuli, including rapid (seconds), intermediate (minutes), and longer term (hours) changes in gene expression, metabolite production, or pulses in systemic signaling pathways (e.g. ROS, calcium waves, and electric signals). Thus, cues related to more temporally consistent and reliable processes are more likely to elicit a response (Alpert and Simms, 2002). However, even when a cue is less reliable, plastic responses that are easily reversible may still be preferentially implemented. For instance, osmotic adjustment and reduced stomatal conductance both happen rapidly in response to water stress (e.g. Blum, 2017; Nolan et al., 2017), and both actions have low associated costs as they are easily reversible. Conversely, more involved responses, such as building xylem conduits that are less susceptible to cavitation, are much slower and significantly less reversible (e.g. Fonti and Jansen, 2012). Triggering this type of response may require more intense or longer signal duration.

These patterns beg several important questions: what are the key molecular drivers of this decision framework? How does genetic variation underlying these drivers impact a

plant's ability to effectively tune responses to the environment once it passes judgment? Recent plant molecular research has aimed to answer this question by studying changes in transcriptional, proteomic, and metabolic networks linked to environmental stress perception and response (Ahuja et al., 2010). Results from these studies have led to many breakthroughs in our understanding about plant stress response. These include: the roles of chromatin remodeling factors in regulating the distribution of nucleosomes to influence general transcription (Song et al., 2021); protein post-translational modifications, like phosphorylation and methylation, in response to environmental alterations (Hu et al., 2017; Kong et al., 2021); epigenetic upregulation and downregulation of transcription factors in response to environmental stress (Chang et al., 2020); and the interplay of gene regulatory networks involved in plant responses to stress (e.g. MADS-box gene family; Castelán-Muñoz et al., 2019).

Connecting these environmental sensing and responding pathways (i.e. molecular mechanisms) to detected patterns of $G \times E$ requires identifying the sources of underlying genetic variation. Evidence from an array of quantitative trait locus (QTL) mapping and genome-wide association studies (GWAS) suggests that stress responses related to many of these molecular mechanisms can exhibit differential sensitivity related to underlying genetic diversity (Davila Olivares et al., 2017; Thoen et al., 2017; Frouin et al., 2018; Luo et al., 2019; Ruggieri et al., 2019; Wen et al., 2019; Janni et al., 2020). One common trend that emerges from these studies is the importance of genes that show broad pleiotropic effects. These pleiotropic effects are often related to the seemingly disparate processes of flowering time, growth architecture, and environmental stress responses (Corrales et al., 2014; Yang et al., 2014; Kazan and Lyons, 2016; Kumar et al., 2019; Lv et al., 2021). Rather than thinking of these genes as mediating both developmental and stress responses, it might be more straightforward to classify these genes as “general environmental integrators” that trigger appropriate downstream responses when presented with key stimuli. These genes might represent the gatekeepers of plastic responses in plants and, as such, should be key targets for future $G \times E$ studies.

While many genes have been linked to both development and stress responses, there are several well-documented examples of broad integrator genes in plants that demonstrate response variability based on naturally occurring genetic diversity. In rice, Grain and heading date 7 (*Ghd7*) is a transcription factor involved in both the regulation of flowering time and stress response; its effects are directly related to genetic background and environmental conditions (Weng et al., 2014; Herath, 2019). Moreover, phenotypic shifts in heading date partially attributed to mutant alleles of *Ghd7* enabled the early expansion of rice into new cultivation regions with disparate environments (Fujino et al., 2022).

Two other genes that are very promising candidates for “general environmental integrators” are *GIGANTEA* and *FRIGIDA*. Both genes may act as scaffolds for protein

components capable of triggering and regulating the expression of genes directly related to development and stress response (Hu et al., 2014; Mishra and Panigrahi, 2015; Roeber et al., 2021). Specifically, *GIGANTEA* plays a key role in tuning plant development through photoperiod sensing pathways and mediating the impact of photoperiod on stress responses (Mishra and Panigrahi, 2015; Roeber et al., 2021) and exhibits natural variation in Arabidopsis (de Montaigu and Coupland, 2017). Analysis of chimeric and mutated *GIGANTEA* alleles in *Brassica rapa* identified the causal polymorphism responsible for shifts in circadian period, salt and cold stress tolerance, as well as red light inhibition of hypocotyl elongation (Xie et al., 2015). Likewise, *FRIGIDA* is involved in the recruitment of chromatin modifiers that epigenetically modify flowering time genes. It also plays a key role in regulating flowering during vernalization (Hu et al., 2014) and has recently been linked to several abiotic stress pathways (Lovell et al., 2013; Chen et al., 2018, 2022). Moreover, differences in the flowering time of naturally occurring Arabidopsis accessions are strongly associated with allelic variation in *FRIGIDA* (Johanson et al., 2000; Choi et al., 2011). New results also suggest that these two scaffold genes are involved in the formation of biomolecular condensates (i.e. membrane-less compartments that contain specific, concentrated collections of nucleic acids and proteins, see Banani et al., 2017), which seem to serve as centers of environmental integration (Pardi and Nusinow, 2021; Zhu et al., 2021). While the mechanisms and function of biomolecular condensation are still under investigation, it has been suggested that these scaffolds are necessary for condensate formation (Emenecker et al., 2020). Taken together, these findings indicate that scaffolding genes may play a role as integrators of broad environmental signals capable of triggering phenotypic responses of variable intensity based on the magnitude of environmental stimuli and underlying genetic variation. Evidence that naturally occurring or transgenic variation can tune the degree of stress response related to these genes suggests that breeders could target these genes as “plant rheostats,” effectively serving as dials that could be turned up or down to regulate the impacts of a given environmental stressor on plant development.

To understand the overall genetic drivers of $G \times E$, including the potentially pivotal role of “general environmental integrator” genes, there will need to be accurate identification of genetic diversity underlying the differentiation in measurable molecular responses to realistic environmental stimuli. This will require monitoring and recording the time scale and magnitude of these responses under realistic field conditions. While molecular genetic analyses of the past were largely performed under controlled laboratory conditions, recent technological innovations have enabled researchers to implement large-scale field trials that examine expression changes in thousands of genes in response to natural environmental fluctuations (Nagano et al., 2012; Izawa, 2015; Matsuzaki et al., 2015; Izawa, 2018). For instance, a field drought manipulation of two sorghum

genotypes—which comprised ~400 transcriptomic samples from multiple time points and tissues—revealed rapid, global, and temporally-structured transcriptomic responses, including regulation of established drought response pathways (Varoquaux et al., 2019). Varoquaux et al. (2019) reported molecular responses that helped explain differences in drought tolerance between the genotypes; 25% of genes significantly affected by drought were differentially expressed in only 1 genotype and 30%–50% of these genes were differentially expressed in both genotypes, but the response magnitudes differed (i.e. differential sensitivity). Results from this study contribute to growing evidence that large-scale field omics studies will help identify gene regulatory networks responsible for mediating environmental responses (Matsuzaki et al., 2015) and identify genetic variation responsible for changing the direction and magnitude of these responses (Varoquaux et al., 2019). Furthermore, using approaches such as phenotypic and polygenic selection analyses on these omics datasets, the type and strength of selection can be estimated for measured transcripts providing insight into the environmental selective pressures acting on gene expression (Groen et al., 2020, 2022). As data accumulate from these large-scale omics experiments, we will be able to quantify changes in expression in response to environmental stimuli and subsequently create $G \times E$ expression profiles for general integrator genes. Using these profiles, we will be able to generate candidate lists for novel integrator genes in an unbiased fashion, rather than studying well-documented gene examples from model organisms (e.g. rice [*Oryza sativa*] and Arabidopsis). Moreover, these natural field trials will be especially valuable because the plants will experience multiple stressors rather than exposure to a single prescribed experimental manipulation.

Future directions

Pushing our understanding of $G \times E$ through detailed exploration of the environmental and genetic drivers of adaptive phenotypic plasticity will play a key role in preparing plant systems for the increasingly stressful and novel conditions of the Anthropocene. Recently, there has been concern over projections that future crop yields will not keep pace with population growth due to the negative impacts of climate change on agricultural systems (Tripathi et al., 2016). This has led to increased discussion about potential genetic strategies for improving crop yields (Bailey-Serres et al., 2019). While $G \times E$ has traditionally been considered a burden for improving performance, recent synthesis suggests that in the age of big data, $G \times E$ now represents a blessing because genetic diversity underlying these interactions provides a path to increased resilience (Mulder, 2017). For example, breeding or engineering crops with increased resilience to climate will likely involve selecting or manipulating systems for adaptive plasticity at lower levels that lead to environmental stability at the level of biomass or yield. Thus far, this review has highlighted the components of $G \times E$ separately. This is a simplifying construct used to discuss recent

advances in identifying the constituent environmental and genetic drivers of this interaction. Integrating these advances should allow researchers to develop a holistic, hierarchical framework for studying $G \times E$ (Figure 4).

First, a holistic, hierarchical $G \times E$ framework should embrace complexity by incorporating genotypes with sequenced genomic data into field trials across a broad range of environmental conditions. Multi-site field trials can identify key environmental gradients by implementing new analyses, such as the ECGC algorithm, and molecular drivers of adaptive plasticity by incorporating repeated transcriptomic sampling. One particularly promising approach for analyzing these studies is multivariate adaptive shrinkage (mash), a broad empirical Bayesian approach that estimates and tests numerous genetic effects in many environmental conditions (Urbat et al., 2019). For instance, mash can be used to quantify the extent to which the effects of single-nucleotide polymorphisms (SNPs) differ across environments. An important aspect of mash is that it can synthesize data across multiple GWAS trials or environmental conditions, which could promote stronger inferences on current studies performed by different research groups (Mural et al., 2021) and also leverage the results of decades-old studies if germplasm still exists (MacQueen et al., 2020). This can be especially useful for identifying genomic regions associated with significant effects when target traits are collected from multiple GWAS trials. This approach also facilitates the discovery of SNPs with synergistic or antagonistic pleiotropic effects on traits related to key environmental drivers of $G \times E$ (Said et al., 2022). Recent work has proposed extending the utility of these mash analyses not only to explore important regions of genomic variation involved in $G \times E$ but also to isolate key environmental stimuli by specifying the ways genetic marker effects covary with environmental gradients (MacQueen et al., 2021). MacQueen et al. (2021) reported significant $G \times E$ related to the environmental cues and genetic variation affecting phenology in natural populations of switchgrass (*Panicum virgatum*). These results suggested that breeding for alleles at $G \times E$ -associated loci could change flowering responsiveness to environmental cues. When paired with replicated common garden designs planted across environments like the one highlighted here, approaches like mash will support the identification of environmental stimuli that predict plastic responses and provide new insight into the drivers of $G \times E$.

The next step in a comprehensive $G \times E$ framework is linking observed phenotypic patterns with underlying molecular mechanisms. Perhaps one of the most exciting research avenues for providing this link is single-cell transcriptomics (Rich-Griffin et al., 2020; Seyferth et al., 2021; Marand and Schmitz, 2022). Unlike other widely utilized RNA-seq methods that aggregate all cell types within a biological sample, single-cell RNA-seq can detect the expression patterns of important, low-abundance cell types that would have been obscured in previous approaches. Moreover, the ability of single-cell transcriptomic

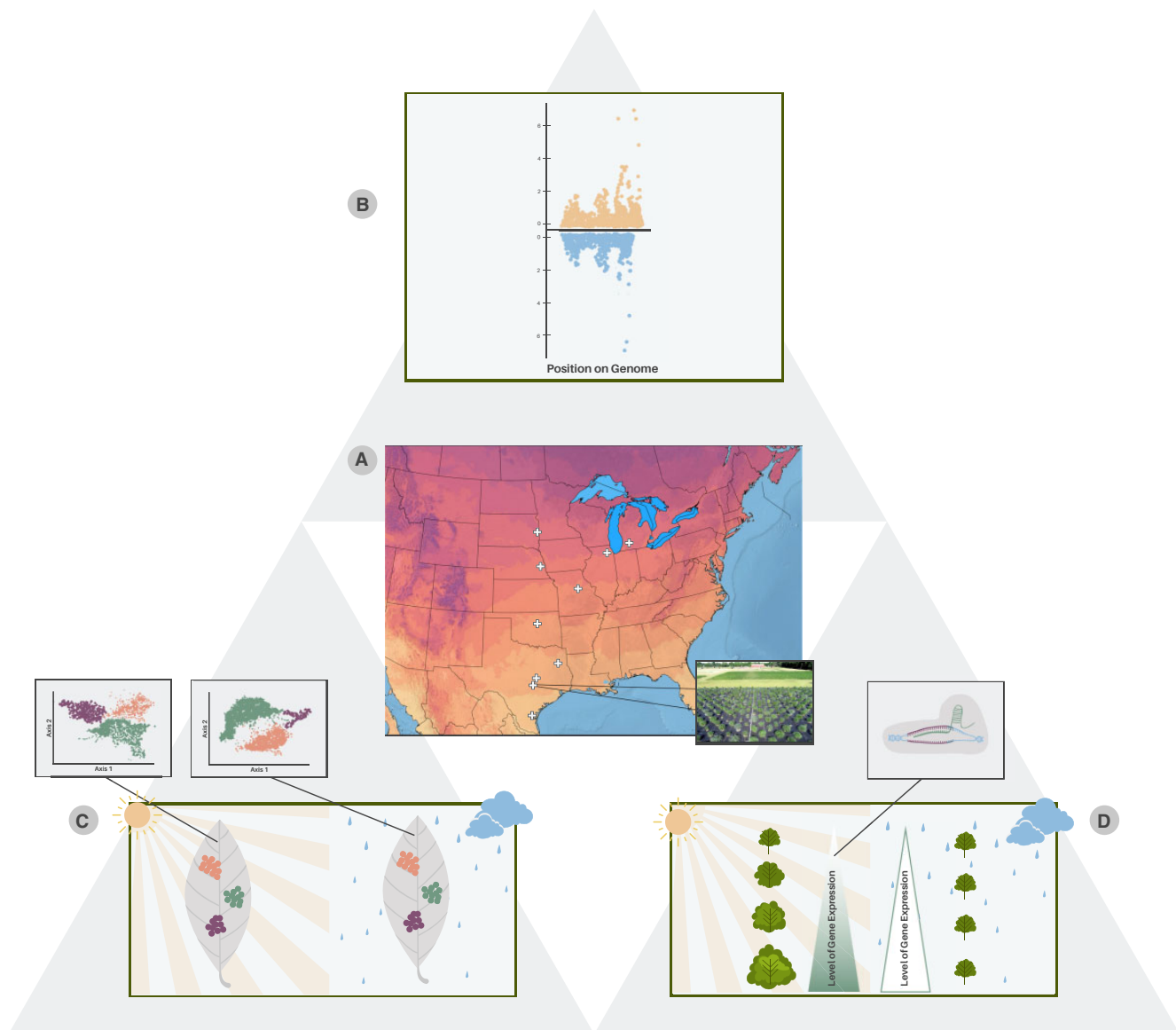


Figure 4 A proposed multi-stage, hierarchical framework for studying $G \times E$. A, This proposed framework begins with a sample common garden network (e.g. see Lovell et al., 2021) that spans a broad climate gradient (annual mean temperature depicted in the background color gradient) with many genotypes replicated across environments (see inset). Using information from the common garden network, researchers can take advantage of several recent advances to identify the drivers of $G \times E$. For simplicity, the subsequent panels demonstrate a series of approaches used in two environments to study $G \times E$. B, This panel depicts a simplified Miami plot showing the effect of genetic loci on a trait of interest measured in different environments. C, This panel shows how single-cell transcriptomics conducted in multiple environments can measure gene expression of different cell types in distinctive environments, which is commonly visualized using a Uniform Manifold Approximation and Projection. D, After identifying the key environmental and molecular drivers of $G \times E$ using the approaches described above, genome editing experiments can be performed to validate the drivers of $G \times E$. Here, the expression of genes can be tweaked to generate environmentally dependent phenotypic effects.

approaches to resolve differential responses of specific tissue types to environmental stressors suggests that this method could provide breakthroughs in our understanding of $G \times E$. It is likely that only certain cell types will be involved in responding to different classes of environmental stimuli and will allow us to create bins for targeted expression analyses. In fact, a recent single-cell transcriptomic study found that

abiotic stress stimuli primarily altered gene expression in a cell type-specific manner; within a given cell type, however, similar sets of genes were expressed in response to different abiotic stresses (Wang et al., 2021). Using this approach to isolate key cell types involved in environmental responses and, more broadly, identifying “general environmental integrator gene networks” that are routinely altered in response

to environmental stress has immense potential for advancing our understanding of the molecular basis of $G \times E$.

While these approaches will greatly increase our ability to identify important genetic diversity associated with phenotypic shifts across environments, there needs to be a concerted effort to validate these results experimentally and put the findings into practice. Accumulating results suggest that the most promising and efficient avenue for validation is to employ genome editing approaches (Lemmon et al., 2018; Chen et al., 2019; Liu and Yan, 2019). Specifically, CRISPR/Cas9, a common genome editing approach, has been used to engineer loss of function mutations to verify candidate genic regions. After verification, it was then used to induce weak transcriptional alleles that resulted in reduced gene expression providing increases in flower production (Soyk et al., 2017). CRISPR/Cas9 now offers many experimental applications in plants, including the ability to activate or repress genes, edit the epigenome, and perform DNA-free genetic modification (Moradpour and Abdulah, 2020). These diverse applications illustrate the utility of genome editing not only for validating candidate “general environmental integrator” genes, but also for upregulating or downregulating gene expression related to environmental stress responses (turning the “rheostat”). The use of genome editing is the crucial final step that will move $G \times E$ from being a breeding hindrance to a potential cornerstone of efforts to improve plant resilience.

The framework proposed here for studying $G \times E$ will also serve as a valuable next step for answering long-standing questions about the limits and costs of plasticity. Theoretically, plasticity can always produce a better match between phenotype and environment across variable conditions than a single fixed phenotype (Levins, 1968). This begs the simple question: why are all traits not plastic? The answer to this question was thought to primarily revolve around the failure of plastic traits to produce the optimum (i.e. a plastic trait is limited in its ability to produce the optimum trait mean for a stable environment compared to fixed trait development), or the inherent cost associated with sensing and processing environmental cues needed to invoke a plastic response (DeWitt et al., 1998). However, more recent syntheses suggest caution when discussing the limits and costs of plasticity (Auld et al., 2010). Some work advocates that the evolution of plasticity is constrained primarily by relaxed or variable selection intensities (Murren et al., 2015). Specifically, relative to specialist genotypes with fixed phenotypes, generalist genotypes with plastic phenotypes should experience less selective pressure on developmental pathways specific to the range of environmental conditions they experience. Conversely, compared with generalists experiencing multiple environments, specialists in a single environment should purge deleterious mutations and fix beneficial mutations more quickly (Kawecki, 1994). Thus, theoretical work postulates that the constraints imposed by relaxed selection will result in specialists out-competing more plastic generalists, but explicit tests of this are rare (Murren et al., 2015).

Field data linking specific genes to environmental drivers will be critical for testing these theoretical ideas. If there is simply a higher cost associated with maintaining the ability to respond plastically, then we should be able to quantify these costs in plants that have been modified to exhibit greater plastic responses to environmental stimuli (Schmitt et al., 1995). Conversely, if appreciable costs are not detected, it would suggest that selection gave a competitive edge to specialists in historically stable environments.

Another issue to which this framework can be applied addresses the role of $G \times E$ in local adaptation and the occurrence of trade-offs. A common perspective defines local adaptation as $G \times E$ for fitness or performance. Here, trade-offs would be identified by loci that show antagonistic pleiotropy (a sign change in effect on fitness) that leads to maladaptation across environments. Trade-offs in performance between environments can have severe consequences for crop production or maintaining resilience in response to climate change. However, antagonistic pleiotropy is not universal. Many recent studies have identified loci with fitness effects in one environment, but little or no fitness effects in alternative environments (e.g. Gardner and Latta, 2006; Lowry et al., 2009; Anderson et al., 2013; Gramlich et al., 2022), a pattern called conditional neutrality. $G \times E$ -based trade-offs that result from conditional neutrality are an ideal target for breeding strategies to break trade-offs (Verslues et al., 2022). A defining feature of conditionally neutral loci is that they produce no cost in disfavored environments and provide benefits in favored environments (Anderson et al., 2011).

Breeding approaches that combine many conditionally neutral alleles in a single genome can generate generalist genotypes that avoid trade-offs entirely. In a molecular context, Kudo et al. (2019) bred plants that co-expressed two growth-promoting genes, GA requiring 5 (*GAS*) and Phytochrome-interacting factor 4 (*PIF4*), to eliminate a trade-off between growth and drought stress tolerance caused by the stress-inducible gene dehydration-responsive element-binding protein 1A (*DREB1A*). Trade-offs driven by antagonistic pleiotropy may be more difficult to circumvent because each allele has negative impacts on performance in the disfavored environment. However, trade-offs can often be alleviated by consistent artificial selection that is orthogonal to the trade-off or through crosses between locally adapted genotypes that break genetic linkage (Conner, 2003; Agrawal et al., 2010). This may yield promising results in the case of antagonistic pleiotropy also. In more extreme cases, gene editing may be necessary to eliminate trade-offs. As Kudo et al. (2019) demonstrated with gene stacking in rice, and as would no doubt be the case with gene editing, success in breaking trade-offs will be most likely when the genetic and environmental bases of $G \times E$ are well understood.

Conclusions

A long history of studying $G \times E$ in plant field trials has provided many important insights about how phenotypic trait

values of different genotypes can shift along environmental gradients. Generalizing these findings to improve breeding programs and better understand evolutionary dynamics has been impeded by limited resolution in identifying key environmental variables and genetic diversity driving these interactions. However, recent advances in the availability and processing of environmental data combined with rapid improvements in transcriptomic and genome editing approaches suggest we are poised to harness $G \times E$ to improve the resilience of agronomic systems. The integration of these approaches will provide insight into the specific environmental gradients that drive these interactions and help to elucidate the key molecular mechanisms that determine responses to environmental stimuli based on underlying genetic variation. Moreover, using lessons learned from these emerging methodologies, it may be possible to generate “plant rheostats” that can broadly regulate response sensitivity to a wide range of environmental stressors. Such a powerful breeding mechanism will enhance the resilience and productivity of agronomic systems by conferring the ability to quickly scale phenotypic responses to increasingly unpredictable and novel climate conditions.

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