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Embracing plant plasticity or robustness as a means of ensuring food security

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The dual challenges of global population explosion and environmental deterioration represent major hurdles for 21st Century agriculture culminating in an unprecedented demand for food security. In this Review, we revisit historical concepts of plasticity and canalization before integrating them with contemporary studies of genotype-environment interactions (G×E) that are currently being carried out at the genome-wide level. In doing so we address both fundamental questions regarding G×E and potential strategies to best secure yields in both current and future climate scenarios.

The vast majority of crops and vegetables that we currently eat were domesticated from their wild ancestors in the past 10,000 years[1]. Indeed, it has been widely reported that domestication was controlled by several key genes. For example, only five-six genes induced the dramatic changes occurring on the long domestication of cultivated corn with a similarly low number of genes being suggested for many other grain crops, as well as for other crops such as beans and tomatoes[2]. During the process of domestication, our ancestors simply chose what they needed for living. Such simple choices essentially led to the pyramiding of valuable mutations and recombinants, which rendered cultivated crops easier to breed, culture and store seeds from. That said the goals on domestication of different crops also varied greatly. In rice and wheat, the seed number was greatly enhanced during domestication while the weight of a single kernel was not dramatically changed[3,4]. By contrast in corn, the weight of the single kernel increased more than 10-fold during domestication[5]. Additionally, in tomatoes and eggplants, the number of fruits per plant was not increased greatly, but the size and weight of the individual fruit were altered (sometimes dramatically so), over the processes of domestication and improvement[6,7]. These represent only a few examples among the several hundred plants commonly cultivated today. Seventy percent of the calories consumed by humans come from only 15 crops[1], of which five (rice, wheat, corn, sugarcane, and barley) contribute more than half[8]. Indeed, while diversification at the level of our food crops is clearly warranted, we still need to secure their yields.

In contrast to their ancestors, the growth environments and conditions of currently grown plants are highly divergent[9]. Most crops are grown in temperate zones—flowering in spring and being harvested in autumn. However, some crops are sown in the fall, go through vernalization in winter and mature in the following spring or summer. With the development of molecular genetics and more recently genomics, we begin to learn much more about the mechanisms underlying the domestication process[10–14]. This has started to bring great insight into the adaptation of plant genotypes and phenotypes over evolutionary time[15–17]. Adaptation in crops involves a dynamic interplay between genetic variations and environmental pressures. This process is driven by specific genotypes that confer a selective advantage to plants in their respective environments. Adaptation can begin with plastic phenotypic changes in response to environmental shifts, followed by genetic changes. During the initial phase, the environment may induce phenotypic alterations, while in a subsequent phase, phenotypes are modified by mutations that accumulate through adaptive evolution[17]. Therefore, during the process of domestication, particular genotypes were selected for their notable plasticity[18,19]. This included enhanced agronomic characteristics, such as increased fruit and seed size, as well as the ability to adapt to diverse environments, thereby broadening their area of cultivation[1–4,7,9,10,20–23].

Reflecting on this, a range of studies have delved into how crops respond to environmental shifts, especially those concerning temperature, water content, soil conditions, and atmospheric variations[24–28]. For instance, research by Piperno et al. shed light on how teosinte and *Zea mays* ssp. *parviglumis* adapted to the climatic conditions of the Late Pleistocene and early Holocene periods, respectively. Their findings revealed significant morphological changes, including alterations in plant architecture and seed dormancy[24]. In

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a similar vein, Matesanz and Milla examined how wild ancestors and their domesticated counterparts, across various crops like cabbage, pea, and durum wheat, reacted under different nutrient and water conditions. Their research highlighted that both plasticity effects and trait averages can vary markedly between domesticated crops and their wild precursors, contingent on the specific trait being analyzed[25]. The distribution of major crop areas (Fig. 1A), and regions vulnerable to extreme weather (Fig. 1B) underscores the critical need for such studies, in terms of climate change. Understanding potential plastic responses at multiple levels, from metabolic pathways to morphology and covering key agronomic traits such as yield, is hence crucial for ensuring long-term food security.

Given that the demand for food production on a per land area basis is higher than ever due to the booming human population, environmental degradation and ever-increasing competition for land[29,30], we believe it is an opportune moment to place G×E in focus with regard to securing yield stability. In the context of plant breeding two divergent strategies are followed either (i), plasticity is minimized to develop a cultivar with satisfactory performance (phenotypically robust or canalized) across a range of environments[31] or alternatively (ii), performance is maximized by enriching environment-specific beneficial alleles that are neutral or even unfavorable in other conditions (phenotypically plastic)[32,33]. The second of these is akin to how natural selection has acted on wild populations[34].

Considerable insights into the genomic events underlying natural selection, domestication and improvement-driven selection have recently been uncovered in most of our major crops[2]. Moreover, insights into plasticity and canalization in plants have recently undergone a renaissance with (i), the application of -omics level profiling methods[35–37]; (ii), the development of ever-more sophisticated field phenotyping[38] and (iii), the collation of various environmental data from enviro-typing technologies[39], meaning that we have recently begun to acquire data with which we will be able to address a range of important questions. These questions include: (i), How do crops respond to changes in the environment? Which climatic factors will crops respond to and produce phenotypic changes, and what are the genetic mechanisms underlying such changes? (ii), How can we identify the most suitable crops and genotypes for different environmental conditions, and what is the best basis for such predictions? and (iii), How should we carry out crop genetic improvement in order to future-proof our food resources? Addressing such questions will clarify the fundamental nature of phenotypic variance, the roles of phenotypic plasticity and canalization in plant evolution and adaptation, and the potential strategies they offer for developing climate-resilience and sustainable crops to secure our food supply in the face of environmental challenges. In the current article, we will begin by providing original definitions and some historical background for both terms. We will then discuss recent scientific discoveries related to the aforementioned questions, taking into account advancements in molecular biology, multi-omics technologies, field phenotyping and enviro-typing technologies, and data analytics. Finally, we will assess the merits of embracing plant plasticity or robustness as a means of ensuring food security, or if we would be better off adopting a bet-hedging strategy incorporating both strategies under different circumstances.

The concepts of plasticity and canalization

Phenotypic plasticity is defined as the ability of a genotype to produce more than one phenotype when exposed to different environments (Figure 2A, Box 1). It is multidimensional, encompassing physiological, morphological, developmental, and biochemical aspects[40–42]. It is also multifactorial, with the plasticity of the investigated trait depending on genetics and the environmental factors. This complexity is further illustrated by the relationships with other traits. For example, it has been demonstrated that under acute abiotic pressures, the flexibility of one characteristic might even be diminished due to tight interconnectedness with other traits[43,44]. From a developmental perspective, Smith-Gill categorized plasticity as comprising two different subclasses: developmental conversion and phenotypic modulation[45]. The former subclass is genetically controlled and plays a role in adaptation to particular environmental condition. It follows that if a character is variable, selection must be maintaining that variability. The latter subclass is not necessarily genetic based and adaptive, but may exist because of a failure of the organism to completely buffer development against environmental perturbation. The plasticity associated with developmental conversion has attracted greater attention than the other subclass because of its genetically controlled, adaptive, and selectively maintained properties. Indeed, the prominent role of plasticity as an adaptational factor to environmental conditions in many organisms[46] has been topic of several articles[47,48] (Box 2).

Although there are many cases, in which plasticity is stated to be beneficial – either as a fitness advantage on the individual or an ecological success on the population level - it is also important to consider cases in which this is not the case. Here the concept of canalization is important. Canalization was initially defined by Waddington as the ability to produce a consistent phenotype in spite of variable genetic and/or environmental features[49,50]. As would be expected in light of the era he worked in, this theory was based on developmental phenotypes which were visible to the naked eye. He later broadened his definition to focus on phenotypes that, if not strictly invariable are “to some extent resistant to modification”[51,52], as well as developing the idea of canalizing selection thereby implying a genetic control of canalization. Similarly to plasticity, canalization was re-defined in the 1990´s, with the essence of all definitions, being similar to that of Wilkins et al., i.e., that canalization is the genetic capacity to buffer phenotypes against mutational or environmental perturbation[53].

The situation is further complicated by the fact that both canalization and plasticity are often hereditable and can therefore evolve (Fig. 2). Within the last couple of decades, molecular developmental genetics has provided new perspectives concerning the mechanisms underlying canalization. Indeed, Rutherford and Linquist identified an increase in morphological variation in Hsp90 mutants in Drosophila[54], with similar results being found in plants with Arabidopsis deficient in Hsp90 being similarly morphologically compromised[55]. Moreover, as detailed below, quantitative trait loci mapping revealed that chaperones of this family also resulted in the canalization of tomato metabolism[35].

Studies of plasticity in plants

A myriad of studies on plant plasticity involving both the model plant Arabidopsis and various crop species have been carried out and extensively reviewed[56–58]. While these studies examine different traits in different species, they primarily focus on analyzing the genetic variations of phenotypic plasticity and uncovering the underlying causes of these variations[59–61]. Since genotype-environment interactions (G×E) are fundamental to phenotypic plasticity, and population-level variation in plasticity generates G×E in statistical analyses, methods for analyzing G×E often integrated with conceptual knowledges and molecular experiments to gain a better understanding of the sources and regulatory processes underlying complex trait variation[62–65]. One strategy in crop breeding is to maximize performance in individual environments by enriching environment-specific beneficial alleles that are conditional neutral or even unfavorable in other environments[32,33,66,67]. As Jin et al. previously commented[68], this mirrors the action of natural selection on wild populations wherein local adaptation results in optimized phenotypes in native environments that are often maladapted in other environments[34,69,70]. This strategy has high potential in the light of current climate change scenarios, given that genetic control systems can vary between optimal

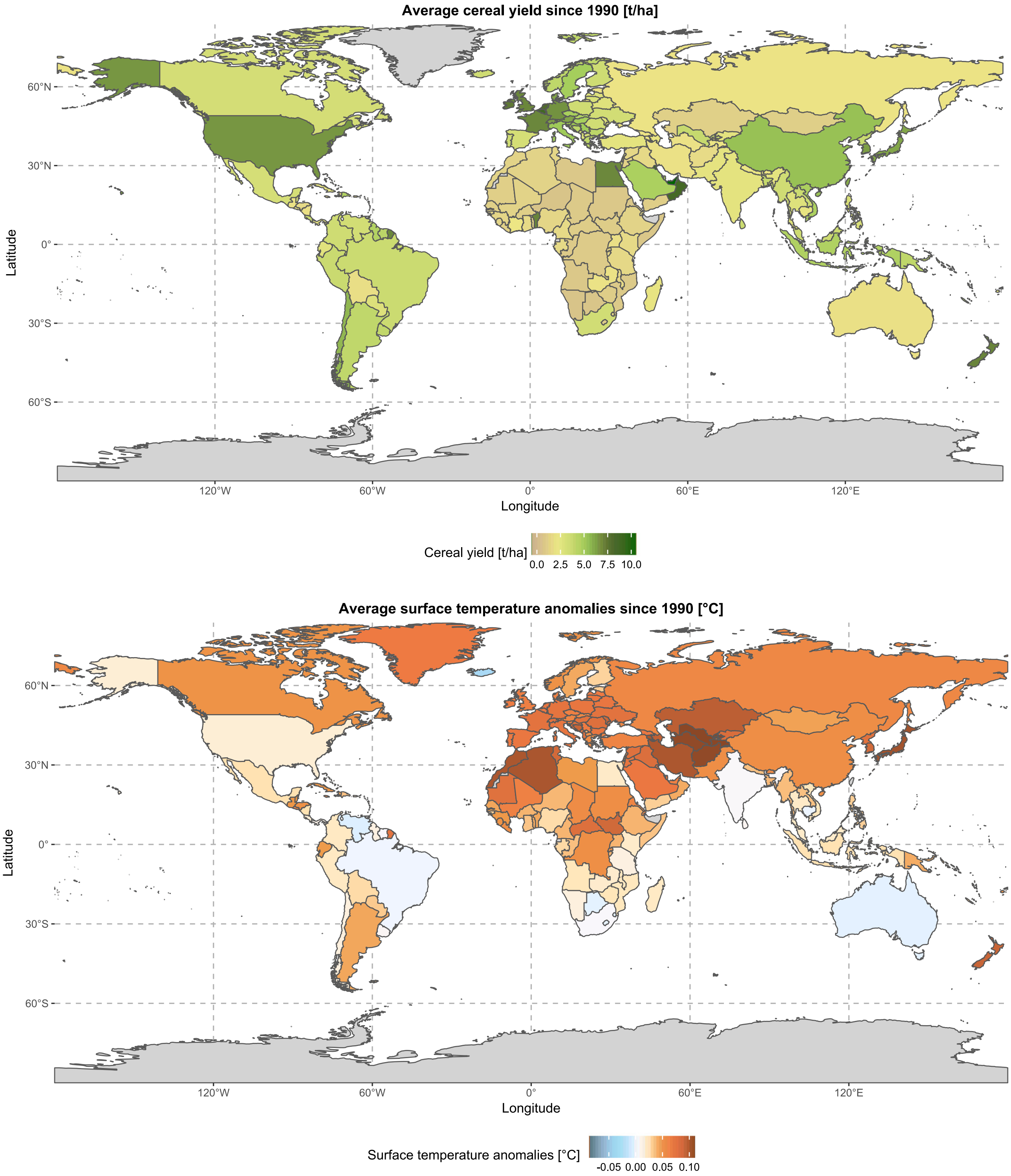

Fig. 1 | Global agricultural cereal productivity and global surface temperature anomalies since 1990. Both maps provide insights into agricultural productivity and climatic variations, both important for global food security and environmental dynamics. (A) Global distribution of cereal yield per country per year [t/ha] since 1990 [Food and Agriculture Organization of the United Nations (2023) – with major processing by Our World in Data. "Cereal yields – FAO". Food and Agriculture Organization of the United Nations, "Production: Crops and livestock products". Retrieved May 1, 2024 from https://ourworldindata.org/grapher/cereal-yield]. This visualization highlights key agricultural regions and shows geographical patterns in crop yield intensity, illustrating contributions to the global food supply. Dark green represents the highest cereal yield productivity, while sandy tones indicate the lowest. (B) Average surface temperature anomalies by country since 1990 [Copernicus Climate Change Service (2019) – with major processing by Our World in Data. "Global yearly surface temperature anomalies". Copernicus Climate Change Service, "ERA5 monthly averaged data on single levels from 1940 to present 2". Retrieved May 1, 2024 from https://ourworldindata.org/grapher/global-yearly-surface-temperature-anomalies]. Temperature anomalies were calculated relative to the 1960–1990 baseline by the authors of Our World in Data. The anomalies were furthermore averaged for each country from 1990 to 2023. Darker red regions indicate higher-than-normal temperatures, while blue regions indicate cooler-than-normal temperatures. White areas show no deviation from the baseline. The maps were generated using the R packages rnaturalearthdata (v1.0.0) and sf (v1.0.16).

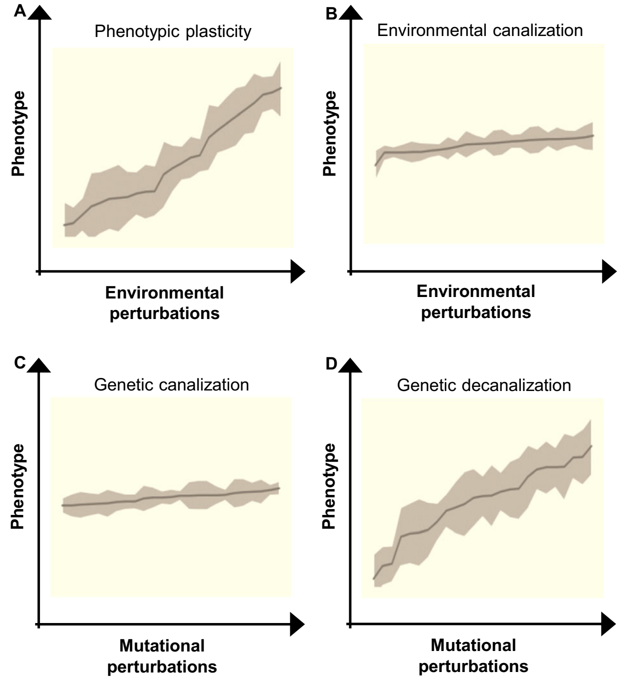

Fig. 2 | Responsiveness and robustness of phenotypes to environmental and genetic perturbations. (**A**) Phenotypic plasticity: the ability of an organism to adjust its phenotype in response to changes in its environment. (**B**) Environmental canalization: the ability of an organism to buffer phenotypes against environmental perturbations. Phenotypic plasticity (**A**) and environmental canalization (**B**) are two aspects of the same phenomenon. (**C**) Genetic canalization: the ability of an organism to buffer phenotypes against mutational perturbations. (**D**) Genetic decanalization: the ability of an organism to adjust its phenotype by potentiating mutational effects. Note: The environmental and mutational perturbations are organized in a sequence to demonstrate an enhanced phenotype.

and stressed environments. In such cases, highly plastic genotypes are particularly valuable due to their capacity to achieve optimal phenotypes in specific environments. For this reason, a considerable effort has been made in studying the genetic architecture of plasticity and dissecting the underlying quantitative trait loci[71–74]. Here we chose several papers as case studies to illustrate the insight achieved to date: approximately half of these in Arabidopsis, while rest describe work in our major cereal crops.

There are many studies on phenotypic plasticity in Arabidopsis, however, we feel that five papers present a good coverage of the state-of-the art in the field. These papers shed light on regulatory genes and pathways that contribute to genetic variation in phenotypic plasticity in response to temperature or nitrogen. We start by reviewing the recent paper by Weiszmann et al., in which plasticity at the metabolomic level was investigated in diverse Arabidopsis accessions grown at different temperatures[75]. Their findings, which demonstrate that the plasticity of metabolism is both heritable and predictable, significantly advance our understanding of how plants reprogram their metabolic pathways to respond to temperature change. Furthermore, the molecular mechanism underlying plant responses to temperature can be understood through the case of the plasticity gene PHYTOCHROME INTERACTING FACTOR 4 (PIF4), which acts as a transcriptional regulator to the plasticity of shoot thermogenesis in Arabidopsis[76]. This finding highlights the role of PIF4 as a central regulator of temperature signaling, suggesting that molecular networks associated with this gene can be leveraged in breeding thermotolerant crop varieties. The other three Arabidopsis papers we chose to highlight deal with various aspects of plasticity in response to nitrogen supply[77–79]. One study clarifies the gene-environment interaction as the basis of phenotypic plasticity by elucidating how a REGULATOR OF CHROMATIN CONDENSATION 1 (RCC1) family protein interacts with nitrogen availability. Another study reveals that plasticity in shoot branching is more complex, as its genetic architecture varies between populations selected under high or low nitrate conditions, suggesting that the

BOX 1

Plasticity at the level of the individual and population

Plasticity is defined, at its simplest, as the ability of a genotype to produce more than one phenotype when exposed to different environments. Here we consider both the plasticity of the individual and plasticity at the population level.

Typically, an individual organism's plasticity is considered beneficial for fitness, allowing it to adapt to a wider range of environments by developing varied phenotypes[57,134]. Plasticity is pervasive: Forsman even argued that all organisms exhibit some degree of plasticity—if one key feature is not plastic, another will exhibit a broader reaction norm[135]. The concept of 'reaction norm', first defined by Woltereck[63] refers to how the phenotypic expression of a single genotype varies across environmental conditions. Furthermore, plasticity is multifactorial and multidimensional; while some phenotypic traits may be influenced by specific environmental factors, others may not. Similarly, different environmental factors may affect the plasticity of different traits[43,44]. The general importance of environmental influences for genotype-phenotype relationships has already been pointed out by Johannsen[136].

Plasticity at the population level can be divided into two types: discrete and continuous phenotypic control. The latter is based on quantitative qualities influenced by both plasticity and genetics. In contrast, discrete phenotypic control may be based either on polymorphisms, which originate from genetic variation, or on polyphenisms, which rely on the phenotypic regulation of variability. Polyphenism, in other words, is the phenotypic plasticity of one individual across different environments (Fig. 2)[137–139]. Plasticity at the population level primarily occurs in flexible traits, leading to small-scale adapted phenotypes[112,137,140,141]. However, there are cases where plasticity leads to large-scale changes in the population, for example, in adapting to climate changes by altering biochemical parameters[112,142] or in biotic competition by changing root system morphology[143]. Similar to the individual level, plasticity at the population level is mostly described as advantageous. This is particularly true in terms of a clade's survival for several reasons: 1) It allows the population to produce well-adapted phenotypes without undergoing genetic adaptation processes, thereby lowering the risk of extinction; 2) It can decrease susceptibility to abiotic and biotic changes due to its ability to occupy a wide range of niches; 3) It can increase the potential for invasiveness[58,144]. Since the scope of phenotypic plasticity of different genotypes can be under selection pressure, the corresponding germplasm pool may change in the long term. Environmental factors that promote plasticity may also restrict its evolution by limiting genetic diversity, impacting the development of phenotypes and their adaptive flexibility[145].

BOX 2

Glossary

Bet-hedging: Hedging a bet is a way to limit risk in sports betting. The most common way to hedge a bet is to place a smaller bet against the opposing team to that which you originally backed. This is essentially a risk-minimization strategy offsetting a part of the projected win on winning to ensure some guaranteed return.

Canalization: Canalization is the ability to produce a consistent phenotype in spite of variable genetic and/or environmental features.

Domestication: Domestication is the process of hereditary reorganization of wild animals and plants into domestic and cultivated forms according to the interests of people.

De novo domestication: De novo domestication is the incorporation of domesticated genes into the non-domesticated species to develop new crops.

Machine learning: Machine learning (ML) is a branch of artificial intelligence (AI) and computer science that focuses on the using data and algorithms to enable AI to imitate the way that humans learn, gradually improving its accuracy.

Phenotypic plasticity: At its simplest phenotypic plasticity is the ability of a genotype to produce more than one phenotype when exposed to different environments.

Synthetic biology: Synthetic biology (SynBio) is a multidisciplinary field of science that focuses on living systems and organisms, and it applies engineering principles to develop new biological parts, devices, and systems or to redesign existing systems found in nature.

regulatory network governing branching is subject to multi-level control[77,78]. Coming full circle, the final paper concerning Arabidopsis is developing condition- and accession-specific metabolic models to dissect and predict plasticity. The model-based analysis provides a stepping stone in understanding the molecular mechanisms and improving the predictability of plasticity for important traits[79].

Turning to crop species, there is a huge amount of work on phenotypic plasticity thus we took the decision to limit ourselves to the major cereal crops and the key traits, flowering time and plant height, where phenotypic plasticity has been most intensively studied. Flowering time, a trait that is responsive to environmental factors and of notable adaptive value, has demonstrated significant genetic variation in both trait mean and plasticity across four studies on maize[68,73,80,81]. These studies provide population-level support for the structure gene theory[82] by revealing distinct genetic architectures for trait mean and plasticity. This theory is further supported by the example of specific genes regulating other genes to exert plastic functions, as demonstrated by *ZmTPS14.1* whose effect is likely mediated by compensatory effects of *ZmSPL6* from a downstream pathway[68]. By contrast, the other two studies that investigate flowering time plasticity in rice and sorghum support the allelic sensitivity theory[83], as they identified the same sets of genes underlying both trait mean and plasticity[84,85]. Moreover, these studies illustrate how a common set of genes shape the observed G×E through incremental changes in the effects of genes or gene-by-gene interactions across environmental gradients. While a consensus on genetic architecture has yet to be reached, the environmental factors that influences flowering time plasticity remain relatively consistent across studies and species. Association analyses between environmental factors and flowering time plasticity indicate that sorghum, rice, and maize plants all detect and assess temperature and/or photoperiod during overlapping time windows (18–43 days after planting for sorghum[84], 9–50 days after planting for rice[85], and 22–37 days after planting for maize[81]) to anticipate future growth conditions and make the necessary developmental transitions. These studies on genetic architecture and environmental factors enrich our understanding of flowering time plasticity at the gene, genome, environment, and their interaction levels. Besides flowering time, plant height is another environmentally responsive trait. Its easily tracked trajectory provides an advantage for studying phenotypic plasticity from a developmental perspective. A study by Mu et al. on plant height plasticity in Sorghum examines the plasticity's expression over time from an ontogenic trajectory, including variation in the rates and the timing of the phenotypic response[86]. They propose a conceptual model to show the joint determination of phenotype by genotype, environment, and development through three-dimensional reaction norms, incorporating growth trajectories at multiple genetic levels with varied environmental inputs. This model contributes significantly to the integration of diverse perspectives and fosters a considerably deep understanding of phenotypic plasticity.

The above studies suggest that breeders can tailor regulatory and/or target genes to produce desired effects for particular environments, thus tackling the current grand challenge posed by climate change[68,71,73,80,84]. Moreover, incorporating environmental and genetic determinants into statistical models facilitates predicting phenotypic performance and identifying superior genotypes under various environmental conditions[87,88]. Pioneer studies have laid out conceptual frameworks for genotypic and enviro-typic breeding[89] and developed advanced models to predict trait performance with greater accuracy by including interactions between genetic markers and environmental variables[81,90,91]. Such research on plant phenotypic plasticity highlights the critical role of genetic and environmental interactions in enhancing crop performance and resilience, which will be especially crucial in addressing climate change challenges. This knowledge is foundational for crafting targeted breeding strategies to promote sustainable agriculture and ensure food security. However, we are still in need of more research with diverse populations and experiments exploring multifactorial environmental changes and the genetic potential for adaptation to these changes.

Studies of canalization in plants

Considerable studies of canalization in plants have also been carried out, though these are considerably less numerous than those of plasticity. It is important to note that this term is used for two widely different topics, i.e., the manner we have described above as well as in a highly specific and different manner to describe the behavior of the phytohormone auxin[92]. We will only discuss those based on the concept of canalization proposed by Waddington in 1942[49] who suggested that there must be some capacity of the genotype to buffer the phenotype against minor variations in genotype and environment[93].

There are accumulating examples of canalization of quantitatively characterized traits of single-celled organisms and land plants[94–97]. In Arabidopsis, the chaperone HSP90 has been shown to be a capacitor of phenotypic variation[98], providing an example of developmental canalization. Genes such as HSP90 are often considered as so-called gene network hubs, wherein the exponential distribution of connectivity is associated with robustness[93,99]. Put in simpler terms it is the power law distribution of network nodes that demonstrate robustness in perturbation i.e. few highly connected nodes, hubs, buffer the system from attack. As such these hubs are often considered as somewhat of an Achilles heel in the network. We describe below a couple of studies on these hubs; however, this is certainly an area that warrants considerable further research. For example, the *ELF3* gene was shown to have an effect on the canalization of both the circadian clock and glucosinolate levels[100]. Similarly, in tomato, researchers have used the variance of metabolites across environments to identify canalized metabolic QTL (cmQTL)[35]. Interestingly, these cmQTLs only partially overlapped with the QTL for the levels of the metabolites, suggesting different loci were related to variance and level, respectively. Further validation of candidate genes supports the idea that genes that affect cross-environment canalization do not necessarily also affect the inter-individual variance. The observation that loci responsible for variation in a trait are, at least in part, distinct and also fewer in number than loci responsible for the level of the trait is supported by a number of other studies[73,101–103]. Both the distinctiveness and the reduced number of loci could point to there being a few regulatory genes that simultaneously control several traits[35]. Depending on the trait, we can consider many different combinations of effects of loci on either the trait level or trait variance or both.

In this regard, datasets from large mapping studies that have previously been used simply to study the level of a given trait could be re-used to study the inter-individual or cross-environment variation. While this has been done in some cases[35,100,104–106] legacy data resources remain underutilized. Together with new data generated through the high-throughput platforms of the multiomics era, it can however be used to study canalization and variation more comprehensively[107]. In addition, the development and rapid uptake of the CRISPR/Cas gene editing techniques in candidate gene validation[108], has facilitated the rapid assessment of candidate canalization genes. Such studies confirmed the candidacy of *PANTHOTHENATE KINASE 4*, *LOSS OF GDU2* and *TRANSPOSON PROTEIN1* in canalization of tomato fruit metabolism[107]. Another example in tomato, and one that is even more relevant in terms of this review, focused on yield and is described across two papers. In the first a meta-analysis of 12 years of field harvest data of the 76 line *S. pennellii* introgression lines was conducted[109]. Five QTL affecting yield stability without affecting mean yield were identified. To address another aspect of the stability question the authors tested 48 morphological mutants and found one canalization mutant, *canal-1*, with a consistent effect in reducing the stability of a myriad of traits, including a snowy cotelydon phenotype. Further study revealed that green mutant leaves compensate for this impaired protein function by upregulation of transcription of photosystem assembly and photosystem component genes, thereby allowing adequate photosystem establishment, which is reflected in their wild-type-like proteome. White *canal-1* leaves, however, likely fail to reach a certain threshold enabling this overcompensation, and plastids get trapped in an undeveloped state, while additionally suffering from high light stress[110]. Collectively these studies demonstrate the identification of a wild species allele as a source to improve tomato yield stability. The above example, came from a much wider common garden experiment carried out at the same field site in which an unexpected bimodal distribution of stable and plastic traits were observed across 32 varieties of seven species grown under well-irrigated and dry field conditions[96]. In this larger study the authors compared 18 homologous phenotypes, including yield and seed production across the different crop species, which included varieties of tomato, eggplant, pepper, melon, watermelon, sunflower and maize. In doing so they were able to propose that canalization profiles of traits in a variety of taxa were ancestrally selected to maximize adaptation and reproductive success.

A similarly broad scope was used in a large synthesis of plasticity (and canalization), in plants which catalogued 31 reciprocal transplant studies into one of the following five categories: (i) canalized response mean phenotypes invariant; (ii) canalized response no plasticity mean phenotypes different; (iii) perfect adaptive plasticity; (iv) adaptive plasticity; (v) non−adaptive plasticity[111]. The analysis included a total of 362 records with 52% of these being non-plastic and over 30% of the plastic traits being adaptive suggesting that canalized responses are more common than adaptive plasticity as an evolutionary response to environmental instability. In a further study, a nested association soybean population, encompassing 5600 RILs was investigated. The authors found seven genomic regions, which display G×E interaction in terms of yield. Xavier et al. furthermore described multiple G×E effects in this population[112]. The model the authors used included the parental source, the regression coefficients of the marker effect and the allelic effect, all based on environment-centered principal components[113,114]. Some of the genes, which surrounded the significant peaks have previously been described to be involved in stress tolerance and thus linked to yield stability[115,116].

The above examples suggest that canalization plays a crucial role in enabling organisms to maintain consistent phenotypes despite genetic and/or environmental variations. For this reason, although admittedly far less common than for plasticity, some studies have focused on identifying canalized metabolic quantitative trait loci (cmQTLs) and their associated phenotypes. These studies have shown that canalization is as vital as plasticity, in that in controlling stable pathways, such as the circadian clock or glucosinolate levels, they ensure the consistency of phenotypic traits under diverse environmental conditions, even for complex compound traits such as yield. Understanding canalization thus also has considerable implications for enhancing crop resilience and yield stability.

How can we best ensure food security?

Having provided a historical overview of the study of plasticity and canalization, we will next return to the title of the article and discuss whether embracing plasticity or robustness represents the better strategy for food security (hereafter we use plasticity and robustness as two sides of one genotype that can be selectively bred, avoiding confusion with evolutionary and developmental implications). This question is particularly pertinent nowadays in the face of the rapidly expanding population alongside current and future climate change scenarios. Therefore, in the following section we will discuss the benefits and drawbacks of both strategies before discussing whether it would be prudent to solely adopt either approach or rather hedge our bets and adopt both.

The case for embracing plasticity

Modern agriculture is founded on the phenotypic plasticity inherent in plants. As we stated in the introduction seventy percent of the calories consumed by humans are provided by only 15 crops[1]. These crops have achieved global dominance despite largely being grown in environments, which are wildly divergent from those found in their center(s) of origin. This is perhaps most dramatically seen in the adaptation of crops from tropical to temperate climes, such as the considerable phenotypic differences between tropical and temperate maize[38,117–119], between upland and lowland rice and the massive adaptations found in potato and beans following the Colombian exchange[4]. These adaptations include photoperiod insensitivity, cold tolerance, stress resistance, short maturity duration, stay green, and enhanced yield potential[120–124]. Successes of exploitation of historical plasticity in plant adaptations and the dramatic increases in yield have been observed for the majority of these species over the last century. It is highly possible that historical plasticity has been fixed; nevertheless, integrating past observations with theories into applied research can offer a solid basis for understanding why embracing plasticity can be a sensible strategy in the face of the uncertainties of climate change.

As one of the most successful plant breeding endeavors, maize breeding has shown the tendency of embracing phenotypic plasticity, likely resulted from the disproportionate yield gain in low- and high-yielding environments (Fig. 3). In a long-term commercial breeding

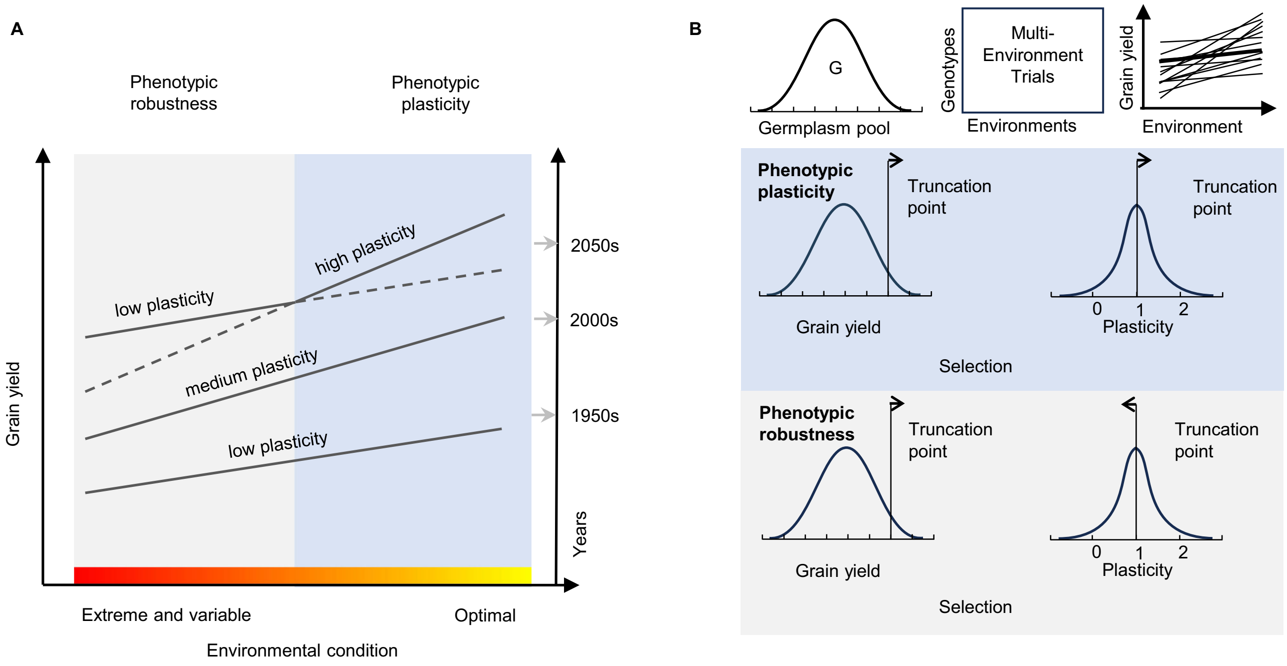

Fig. 3 | Leveraging phenotypic plasticity and robustness to increase grain yield in future climates. A Incorporation of environmental condition and variability into contemporary breeding strategies aimed at developing environment-dependent cultivars better than previous generations. **B** Implementation of multi-environment trials and selective breeding processes that prioritize yield optimization alongside phenotypic plasticity within a modern breeding program. The average of plasticity is 1, with values above 1 indicating high plasticity and values below 1 indicating high robustness.

program studied by Duvick et al., newer hybrids showed significantly higher yield plasticity compared to older hybrids[125]. This was evident in the greater yield differences observed between extreme conditions, the 1993 floods and the 2001 drought, and an ideal growing season in 1992. Analysis of yield data from trials conducted in 13 environments between 1996 and 2000 revealed that newer hybrids had a plasticity of 1.17 t/ha per unit change in environmental mean, compared to 1.02 t/ha in older hybrids and only 0.65 t/ha in open-pollinated cultivars. Such variation in phenotypic plasticity among era hybrids in this breeding program possibly bears a relation to the allocation of yield testing. Extensive testing in optimal environments, as opposed to limited environments, can lead to hybrids that are better adapted to optimal conditions and exhibit higher phenotypic plasticity. However, this uneven selection of testing environments may lead to greater yield variability when these plasticity varieties encounter unfavorable conditions. Therefore, embracing phenotypic plasticity necessitates a careful evaluation of production environments, making it advisable to apply this strategy in geographic locations characterized by high-yielding conditions and low environmental variability.

Embracing plasticity is essentially akin to the purchase of high-risk shares such as those in the high-tech or computer industries – whilst they will likely bring a high reward, they are more volatile than so-called blue-chip shares and as such these investments come with a higher risk of losses. Whilst all the above arguments provide a strong rationale for breeding for plasticity, the fact remains that breeding for robustness is a surer route to yield security in the long term. A potential risk of breeding for plasticity is essentially caused by the uncertainties and unpredictable nature engendered by our current climate change scenario. As such, going all in for plasticity does not seem to represent a good strategy.

The case for embracing robustness

As we detail above there are several strong arguments for embracing (and even attempting to augment) plasticity as a strategy to increase yield in the face of the challenges imposed by climate change. The argument for embracing robustness is far simpler – if you can fully buffer yield against environmental variation, then you can virtually guarantee food security[126,127]. This can be seen in Figure 3, which illustrates the relatively consistent yield performance of the low-plasticity cultivar compared to the high-plasticity cultivar across various environments. One advantage of cultivating low-plasticity cultivars is the ability to achieve significantly higher yield in adverse environmental conditions on condition that its genotypic value reaches the same level with the high-plasticity cultivar. Embracing robustness is a low-risk strategy somewhat analogous to the purchase of blue-chip stocks—as such the overall yield will not reach the highest possibilities which would be obtainable if one were to breed for plasticity (or purchase more volatile shares), however, the yield return is stable and therefore, by contrast to plastic populations, it will not fall much under adverse environmental conditions. Of course, one caveat of this logic is that we will not be able to fully buffer against environmental variation and that canalization may render populations more susceptible to the predicted increased incidence of extreme environmental events[128–130]. It is worth bearing in mind that the future climate predicted for a large proportion of arable land is similar to that currently experienced in other areas of the globe and this knowledge could be leveraged when designing strategies to "future-proof" crop yields that are based on breeding for robustness.

There are two strong counter-arguments that can be put forward against embracing robustness. One is the fact that whilst it will likely ensure yield stability it may well do so in a manner that restricts maximal yields under optimal conditions. As such it may not be the best strategy across the globe likely being an inappropriate strategy in areas where agriculture yields are generally very good. Another potential disadvantage of such a strategy is that it will likely compromise the adaptability of the crop in the future. Whilst the conservation of cultivars in global Genebanks means that such changes are unlikely to be irreversible—the recourse of rebreeding adaptability would mean a shift away from a pure breeding for robustness strategy. Thus, going all in for robustness also does not seem to represent a good strategy.

The case for bet-hedging

Having essentially already concluded that solely embracing plasticity or robustness would not represent sensible breeding strategies we are left with a mix-and-match strategy. To stretch the economics analogy further this would be somewhat akin to "hedging our bets". While this is in commonly parlance in English perhaps, we should outline it briefly. The idea is that you back both sides betting for one team and subsequently offsetting the risk in the initial bet by betting a smaller wager on the opponent of the team. Similarly, in economics, hedging is not the pursuit of risk-free trading but rather an attempt to reduce known risks during trading. An interesting study by Frank has analyzed phenotypic plasticity from perspectives of returns on investment, presenting that plants produce a stochastic response (i.e. bet-hedging) to new environment to increase the aggregate success of a genotype[131]. We thus propose that the best strategy for global agriculture in the face of climate change is to hedge our bets and to simultaneously embrace both plasticity and robustness (albeit in different populations) rather than betting everything on a single strategy. The advantages of such a solution are manifold but essentially come from the blending of the advantages and dilution of the disadvantages mentioned in the preceding paragraphs. In brief, in securing (an albeit lower) yield strategies incorporating the canalization approach would effectively act as a safety-first approach with a guarantee of a certain production irrespective of environmental changes whilst breeding for plasticity in a sub-set of the plants whilst being riskier also offers greater return under high-yielding environments. In doing so we should also consider the environmental range and homogeneity within it to adjust the strategy and achieve the maximum gain[132,133].

Conclusions and perspectives

Embracing phenotypic plasticity presents the opportunity to maximize the genetic potential of new cultivars and achieve multiplied increase in yield. This strategy benefits areas with well-understood, predictable, and controllable growing environments that are equipped with advanced enviro-typing technology and precision agriculture. On the other hand, embracing phenotypic robustness can lead to the development of stable cultivars that possess genes capable of buffering environment variations, but this may come at the cost of compromised yield production. This strategy benefits the vulnerable areas that frequently experience rising temperatures and extreme weather events, as well as in environments that are characterized by variability and unpredictability. Adoption of both strategies to an appropriate extent is likely to represent the optimal solution for any given crop type. It is important to stress that this opinion is partially based on assumptions we are making on extrapolations from the relatively small-scale experiments, which have been published to date. It will, however, be important over the next decade to empirically assess whether these hold-true in larger-scale experiments.

In addition, to bet-hedging in terms of whether to embrace plasticity or robustness within populations we additionally strongly believe in a broadening of the species basis on which we rely on for calories and nutrition. These arguments have been made elsewhere 1, so we will not reiterate them here but increased planting of the many under-utilized domesticates as well as de novo domestication of crop wild relatives with increased resilience to stress both represent powerful routes to achieve this goal.

Food security is one of the greatest challenges of our time and its importance is bound to increase over the coming decades. Drought, heat, salinity and biotic stresses, which are anticipated to increase in current climate change scenarios, have the potential to jeopardize crop yield stability. Whilst plasticity has been defined by multiple scientists for over a century; emphasis on its multidimensionality has only recently been considered with the majority of studies to date focused on single or at most a handful of traits and environmental factors. Multi-environment trials (MET) are, however, commonly used in plant breeding to estimate the mean of cultivars to predict their future performance. In the context of embracing plasticity or robustness in plant breeding, we should focus not only on the mean performance but also on the parameters of plasticity or canalization to evaluate the potential cultivar candidates. Embracing plasticity involves selecting candidates with high yield and high plasticity, whereas embracing robustness is to select candidates with relatively high yield and low plasticity (Figure 3). Additionally, conducting extensive assessments of breeding materials and environments are always valuable, including genetic canalization and environment canalization, environmental and mutational perturbation.

Recent progress in machine learning was already able to achieve relatively precise prediction values by considering the multi-dimensional characteristic or interconnecting transdisciplinary fields, such as quantitative genetics, genomics, evolution, breeding, and agronomy. To acquire training data for such simulations, one approach would be to conduct trials in ex situ conditions, that will be similar to future conditions in major cultivation regions. Furthermore, already existing databases with large-scale multi-omics data could be used for this purpose. We would additionally recommend to research wild relatives and landraces alongside to modern varieties due to their larger gene pool diversity. Such genotypes may encompass promising phenotypic characteristics, that were lost during the pyramiding of agronomically worthwhile traits during domestication. Regardless of the relative advances made in breeding for plasticity or canalization we would suggest to follow the bet-hedging strategy. Taking such an approach would both ensure robustness of yield, but also provide flexibility to face unexpected environmental fluctuations, which will occur due to climate change. It is, however, likely that the best ratio of plasticity to canalization is something that will need to be empirically determined depending on the crop in question.

References

1. Fernie, A. R. & Yang, J. B. *De novo* domestication: An alternative route toward new crops for the future. *Mol. Plant* **12**, 615–631 (2019).
2. Alseekh, S. et al. Domestication of crop metabolomes: Desired and unintended consequences. *Trends Plant Sci.* **26**, 650–661 (2021).
3. Si, L. Z. et al. OsSPL13 controls grain size in cultivated rice. *Nat. Genet.* **48**, 447-+ (2016).
4. Preece, C. et al. How did the domestication of Fertile Crescent grain crops increase their yields? *Funct. Ecol.* **31**, 387–397 (2017).
5. Liu, Z., Garcia, A., McMullen, M. D. & Flint-Garcia, S. A. Genetic analysis of kernel traits in maize-teosinte introgression populations. *G3 Genes|Genomes|Genet.* **6**, 2523–2530 (2016).
6. Zhu, G. T. et al. Rewiring of the fruit metabolome in tomato breeding. *Cell* **172**, 249-+ (2018).
7. Doganlar, S., Frary, A., Daunay, M. C., Lester, R. N. & Tanksley, S. D. Conservation of gene function in the solanaceae as revealed by comparative mapping of domestication traits in eggplant. *Genetics* **161**, 1713–1726 (2002).
8. Ross-Ibarra, J., Morrell, P. L. & Gaut, B. S. Plant domestication, a unique opportunity to identify the genetic basis of adaptation. *Proc. Natl Acad. Sci. USA* **104**, 8641–8648 (2007).
9. Zsögön, A., Peres, L. E. P., Xiao, Y., Yan, J. & Fernie, A. R. Enhancing crop diversity for food security in the face of climate uncertainty. *Plant J.* **109**, 402–414 (2022).
10. Meyer, R. S. & Purugganan, M. D. Evolution of crop species: genetics of domestication and diversification. *Nat. Rev. Genet.* **14**, 840–852 (2013).
11. Purugganan, M. D. Evolutionary insights into the nature of plant domestication. *Curr. Biol.* **29**, R705–r714 (2019).

12. Andersson, L. & Purugganan, M. Molecular genetic variation of animals and plants under domestication. *Proc. Natl Acad. Sci. USA* **119**, e2122150119 (2022).
13. Groen, S. C. et al. The strength and pattern of natural selection on gene expression in rice. *Nature* **578**, 572–576 (2020).
14. Purugganan, M. D. What is domestication? *Trends Ecol. Evol.* **37**, 663–671 (2022).
15. Hamann, E. et al. Rapid evolutionary changes in gene expression in response to climate fluctuations. *Mol. Ecol.* **30**, 193–206 (2021).
16. Groen, S. C. et al. Evolutionary systems biology reveals patterns of rice adaptation to drought-prone agro-ecosystems. *Plant Cell* **34**, 759–783 (2022).
17. Exposito-Alonso, M., Burbano, H. A., Bossdorf, O., Nielsen, R. & Weigel, D. Natural selection on the *Arabidopsis thaliana* genome in present and future climates. *Nature* **573**, 126–129 (2019).
18. Chrungoo, N. K., Dohtdong, L. & Chettry, U. Genome plasticity in buckwheat. *Gene Pool. Divers Crop Improve.* **1**, 227–239 (2016).
19. Shimizu, H. et al. Genetic control of phenotypic plasticity in Asian cultivated and wild rice in response to nutrient and density changes. *Genome* **53**, 211–223 (2010).
20. Gasparini, K., Moreira, J. D. R., Peres, L. E. P. & Zsögön, A. De novo domestication of wild species to create crops with increased resilience and nutritional value. *Curr. Opin. Plant Biol.* **60**, 102006 (2021).
21. Hufford, M. B., Berny Mier, Y. T. J. C. & Gepts, P. Crop biodiversity: An unfinished magnum opus of nature. *Annu Rev. Plant Biol.* **70**, 727–751 (2019).
22. Meyer, R. S., DuVal, A. E. & Jensen, H. R. Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *N. Phytol.* **196**, 29–48 (2012).
23. Zhang, J., Yu, H. & Li, J. De novo domestication: Retrace the history of agriculture to design future crops. *Curr. Opin. Biotechnol.* **81**, 102946 (2023).
24. Piperno, D. R., Holst, I., Moreno, J. E. & Winter, K. Experimenting with domestication: Understanding macro-and micro-phenotypes and developmental plasticity in teosinte in its ancestral pleistocene and early holocene environments. *J. Archaeol. Sci.* **108**, 104970 (2019).
25. Matesanz, S. & Milla, R. Differential plasticity to water and nutrients between crops and their wild progenitors. *Environ. Exp. Bot.* **145**, 54–63 (2018).
26. Roucou, A. et al. Shifts in plant functional strategies over the course of wheat domestication. *J. Appl. Ecol.* **55**, 25–37 (2018).
27. Gaudin, A. C., McClymont, S. A. & Raizada, M. N. The nitrogen adaptation strategy of the wild teosinte ancestor of modern maize, *Zea mays* subsp. *parviglumis*. *Crop Sci.* **51**, 2780–2795 (2011).
28. Lorant, A. et al. The potential role of genetic assimilation during maize domestication. *PloS One* **12**, e0184202 (2017).
29. Sun, Y., Alseekh, S. & Fernie, A. R. Plant secondary metabolic responses to global climate change: A meta-analysis in medicinal and aromatic plants. *Glob. Chang Biol.* **29**, 477–504 (2023).
30. Ripple, W. J. et al. World scientists' warning of a climate emergency 2021. *Bioscience* **71**, 894–898 (2021).
31. Lynch, M. & Walsh, B. *Genetics and Analysis of Quantitative Traits*. (Sinauer, 1988).
32. Gage, J. L. et al. The effect of artificial selection on phenotypic plasticity in maize. *Nat. Commun.* **8**, 1348 (2017).
33. Xiao, J. et al. Wheat genomic study for genetic improvement of traits in China. *Sci. China Life Sci.* **65**, 1718–1775 (2022).
34. Anderson, J. T., Lee, C. R., Rushworth, C. A., Colautti, R. I. & Mitchell-Olds, T. Genetic trade-offs and conditional neutrality contribute to local adaptation. *Mol. Ecol.* **22**, 699–708 (2013).
35. Alseekh, S. et al. Canalization of tomato fruit metabolism. *Plant Cell* **29**, 2753–2765 (2017).
36. Fernie, A. R. & Tohge, T. Plastic, fantastic! Phenotypic variance in the transcriptional landscape of the grape berry. *Genome Biol.* **14**, 119 (2013).
37. Dal Santo, S. et al. The plasticity of the grapevine berry transcriptome. *Genome Biol.* **14**, r54 (2013).
38. Liu, H. et al. Genomic, transcriptomic, and phenomic variation reveals the complex adaptation of modern maize breeding. *Mol. Plant* **8**, 871–884 (2015).
39. Guo, T. & Li, X. Machine learning for predicting phenotype from genotype and environment. *Curr. Opin. Biotechnol.* **79**, 102853 (2023).
40. Li, G. et al. Mechanisms of the morphological plasticity induced by phytohormones and the environment in plants. *Int. J. Mol. Sci.* **22**, 765 (2021).
41. Callahan, H. S., Pigliucci, M. & Schlichting, C. D. Developmental phenotypic plasticity: Where ecology and evolution meet molecular biology. *Bioessays* **19**, 519–525 (1997).
42. Ren, G. Q. et al. The effect of nitrogen and temperature changes on *Solidago canadensis* phenotypic plasticity and fitness. *Plant Species Biol.* **35**, 283–299 (2020).
43. Valladares, F., Gianoli, E. & Gómez, J. M. Ecological limits to plant phenotypic plasticity. *N. Phytol.* **176**, 749–763 (2007).
44. Morel-Journel, T. et al. A multidimensional approach to the expression of phenotypic plasticity. *Funct. Ecol.* **34**, 2338–2349 (2020).
45. Smith-Gill, S. J. Developmental plasticity: Developmental conversion versus phenotypic modulation. *Am. Zool.* **23**, 47–55 (1983).
46. Bradshaw, A. D. in *Evolutionary Significance of Phenotypic Plasticity in Plants* Vol. 13 *Advances in Genetics* (ed Thoday JM Casapari EW) 115-155 (1965).
47. Eshel, I. & Matessi, C. Canalization, genetic assimilation and preadaptation. A quantitative genetic model. *Genetics* **149**, 2119–2133 (1998).
48. Behera, N. & Nanjundiah, V. An investigation into the role of phenotypic plasticity in evolution. *J. Theor. Biol.* **172**, 225–234 (1995).
49. Waddington, C. H. Canalization of developmentand the inheritance of acquired characters. *Nature* **150**, 563–565 (1942).
50. Waddington, C. H. Epigenetics and evolution. *J. Exp. Zool.* **7**, 186–199 (1953).
51. Waddington, C. H. *The Strategy of the Genes*. (Macmillan, 1957). https://doi.org/10.4324/9781315765471.
52. Waddington, C. H. Genetic assimilation. *Adv. Genet* **10**, 257–293 (1961).
53. Wilkins, A. S. Canalization a molecular genetic perspective. *Bioessays* **19**, 257–262 (1997).
54. Rutherford, S. L. & Lindquist, S. Hsp90 as a capacitor for morphological evolution. *Nature* **396**, 336–342 (1998).
55. Sangster, T. A. et al. HSP90 affects the expression of genetic variation and developmental stability in quantitative traits. *Proc. Natl Acad. Sci. USA* **105**, 2963–2968 (2008).
56. Nicotra, A. B. et al. Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* **15**, 684–692 (2010).
57. Laitinen, R. A. E. & Nikoloski, Z. Genetic basis of plasticity in plants. *J. Exp. Bot.* **70**, 739–745 (2019).
58. Sultan, S. E. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* **5**, 537–542 (2000).
59. Assmann, S. M. Natural variation in abiotic stress and climate change responses in Arabidopsis: Implications for twenty first century agriculture. *Int. J. Plant Sci.* **174**, 3–26 (2013).

60. El-Soda, M. et al. QTL and candidate genes associated with leaf anion concentrations in response to phosphate supply in *Arabidopsis thaliana*. *BMC Plant Biol.* **19**, 410 (2019).
61. Sasaki, E., Gunis, J., Reichardt-Gomez, I., Nizhynska, V. & Nordborg, M. Conditional GWAS of non-CG transposon methylation in *Arabidopsis thaliana* reveals major polymorphisms in five genes. *PLoS Genet* **18**, e1010345 (2022).
62. Pigliucci, M. Evolution of phenotypic plasticity: Where are we going now? *Trends Ecol. Evol.* **20**, 481–486 (2005).
63. Mangin, B. et al. Genetic control of plasticity of oil yield for combined abiotic stresses using a joint approach of crop modelling and genome-wide association. *Plant Cell Environ.* **40**, 2276–2291 (2017).
64. Schneider, J. R., Chadee, D. D., Mori, A., Romero-Severson, J. & Severson, D. W. Heritability and adaptive phenotypic plasticity of adult body size in the mosquito *Aedes aegypti* with implications for dengue vector competence. *Infect. Genet Evol.* **11**, 11–16 (2011).
65. Vanous, A. et al. Stability analysis of kernel quality traits in exotic-derived doubled haploid maize lines. *Plant Genome* **12**, 170114 (2019).
66. Ge, J. et al. Genome-wide selection and introgression of Chinese rice varieties during breeding. *J. Genet Genom.* **49**, 492–501 (2022).
67. Jannink, J. L., Lorenz, A. J. & Iwata, H. Genomic selection in plant breeding: From theory to practice. *Brief. Funct. Genom.* **9**, 166–177 (2010).
68. Jin, M. et al. Complex genetic architecture underlying the plasticity of maize agronomic traits. *Plant Commun.* **4**, 100473 (2023).
69. Hereford, J. A quantitative survey of local adaptation and fitness trade-offs. *Am. Nat.* **173**, 579–588 (2009).
70. Blanquart, F., Kaltz, O., Nuismer, S. L. & Gandon, S. A practical guide to measuring local adaptation. *Ecol. Lett.* **16**, 1195–1205 (2013).
71. Li, C. et al. Genetic architecture of phenotypic means and plasticities of kernel size and weight in maize. *Theor. Appl Genet* **132**, 3309–3320 (2019).
72. El-Soda, M., Malosetti, M., Zwaan, B. J., Koornneef, M. & Aarts, M. G. Genotype×environment interaction QTL mapping in plants: Lessons from Arabidopsis. *Trends Plant Sci.* **19**, 390–398 (2014).
73. Kusmec, A., Srinivasan, S., Nettleton, D. & Schnable, P. S. Distinct genetic architectures for phenotype means and plasticities in *Zea mays*. *Nat. Plants* **3**, 715–723 (2017).
74. Schneider, H. M. et al. Genetic control of root architectural plasticity in maize. *J. Exp. Bot.* **71**, 3185–3197 (2020).
75. Weiszmann, J. et al. Metabolome plasticity in 241 *Arabidopsis thaliana* accessions reveals evolutionary cold adaptation processes. *Plant Physiol.* **193**, 980–1000 (2023).
76. Delker, C., Quint, M. & Wigge, P. A. Recent advances in understanding thermomorphogenesis signaling. *Curr. Opin. Plant Biol.* **68**, 102231 (2022).
77. Duarte, G. T. et al. Plasticity of rosette size in response to nitrogen availability is controlled by an RCC1-family protein. *Plant Cell Environ.* **44**, 3398–3411 (2021).
78. Tavares, H. et al. Artificial selection reveals complex genetic architecture of shoot branching and its response to nitrate supply in Arabidopsis. *PLOS Genet.* **19**, e1010863 (2023).
79. Tong, H., Laitinen, R. A. E. & Nikoloski, Z. Predicting plasticity of rosette growth and metabolic fluxes in *Arabidopsis thaliana*. *N. Phytol.* **240**, 426–438 (2023).
80. Liu, N., Du, Y., Warburton, M. L., Xiao, Y. & Yan, J. Phenotypic plasticity contributes to maize adaptation and heterosis. *Mol. Biol. Evol.* **38**, 1262–1275 (2021).
81. Li, X. et al. An integrated framework reinstating the environmental dimension for GWAS and genomic selection in crops. *Mol. Plant* **14**, 874–887 (2021).
82. Scheiner, S. M. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24**, 35–68 (1993).
83. Via, S. Adaptive phenotypic plasticity: Target or by-product of selection in a variable environment? *Am. Naturalist* **142**, 352–365 (1993).
84. Li, X., Guo, T., Mu, Q., Li, X. & Yu, J. Genomic and environmental determinants and their interplay underlying phenotypic plasticity. *Proc. Natl Acad. Sci. USA* **115**, 6679–6684 (2018).
85. Guo, T. et al. Dynamic effects of interacting genes underlying rice flowering-time phenotypic plasticity and global adaptation. *Genome Res* **30**, 673–683 (2020).
86. Mu, Q., Guo, T., Li, X. & Yu, J. Phenotypic plasticity in plant height shaped by interaction between genetic loci and diurnal temperature range. *N. Phytol.* **233**, 1768–1779 (2022).
87. Piepho, H. P. Prediction of and for new environments: What's your model. *Mol. Plant* **15**, 581–582 (2022).
88. Cooper, M. & Messina, C. D. Breeding crops for drought-affected environments and improved climate resilience. *Plant Cell* **35**, 162–186 (2023).
89. Resende, R. T. et al. Enviromics in breeding: applications and perspectives on envirotypic-assisted selection. *Theor. Appl Genet* **134**, 95–112 (2021).
90. Li, X. et al. Genetics-inspired data-driven approaches explain and predict crop performance fluctuations attributed to changing climatic conditions. *Mol. Plant* **15**, 203–206 (2022).
91. de Los Campos, G., Pérez-Rodríguez, P., Bogard, M., Gouache, D. & Crossa, J. A data-driven simulation platform to predict cultivars' performances under uncertain weather conditions. *Nat. Commun.* **11**, 4876 (2020).
92. Friml, J. et al. ABP1-TMK auxin perception for global phosphorylation and auxin canalization. *Nature* **609**, 575–581 (2022).
93. Alseekh, S., Karakas, E., Zhu, F., Wijesingha Ahchige, M. & Fernie, A. R. Plant biochemical genetics in the multiomics era. *J. Exp. Bot.* **74**, 4293–4307 (2023).
94. Alon, U., Surette, M. G., Barkai, N. & Leibler, S. Robustness in bacterial chemotaxis. *Nature* **397**, 168–171 (1999).
95. Lehner, B. Genes confer similar robustness to environmental, stochastic, and genetic perturbations in yeast. *PLoS One* **5**, e9035 (2010).
96. Fisher, J., Bensal, E. & Zamir, D. Bimodality of stable and plastic traits in plants. *Theor. Appl Genet* **130**, 1915–1926 (2017).
97. Lachowiec, J., Mason, G. A., Schultz, K. & Queitsch, C. Redundancy, feedback, and robustness in the *Arabidopsis thaliana* BZR/BEH gene family. *Front Genet* **9**, 523 (2018).
98. Queitsch, C., Sangster, T. A. & Lindquist, S. Hsp90 as a capacitor of phenotypic variation. *Nature* **417**, 618–624 (2002).
99. Lachowiec, J., Queitsch, C. & Kliebenstein, D. J. Molecular mechanisms governing differential robustness of development and environmental responses in plants. *Ann. Bot.* **117**, 795–809 (2016).
100. Jimenez-Gomez, J. M., Corwin, J. A., Joseph, B., Maloof, J. N. & Kliebenstein, D. J. Genomic analysis of QTLs and genes altering natural variation in stochastic noise. *PLoS Genet* **7**, e1002295 (2011).
101. Hall, M. C., Dworkin, I., Ungerer, M. C. & Purugganan, M. Genetics of microenvironmental canalization in *Arabidopsis thaliana*. *Proc. Natl Acad. Sci. USA* **104**, 13717–13722 (2007).
102. Joseph, B., Corwin, J. A. & Kliebenstein, D. J. Genetic variation in the nuclear and organellar genomes modulates stochastic variation in the metabolome, growth, and defense. *PLoS Genet* **11**, e1004779 (2015).

103. Li, B. et al. An integrative genetic study of rice metabolism, growth and stochastic variation reveals potential C/N partitioning loci. *Sci. Rep.* **6**, 30143 (2016).
104. Schauer, N. et al. Comprehensive metabolic profiling and phenotyping of interspecific introgression lines for tomato improvement. *Nat. Biotechnol.* **24**, 447–454 (2006).
105. Schauer, N. et al. Mode of inheritance of primary metabolic traits in tomato. *Plant Cell* **20**, 509–523 (2008).
106. Wentzell, A. M. et al. Linking metabolic QTLs with network and cis-eQTLs controlling biosynthetic pathways. *PLoS Genet* **3**, 1687–1701 (2007).
107. Wijesingha Ahchige, M., Fernie, A. R. & Alseekh, S. PANTOTHENATE KINASE4, LOSS OF GDU2, and TRANSPOSON PROTEIN1 affect the canalization of tomato fruit metabolism. *Plant Physiol.* **192**, 442–468 (2023).
108. Yan, J. & Fernie, A. R. Editorial overview: 21st Century solutions for crop improvement. *Curr. Opin. Biotechnol.* **83**, 102982 (2023).
109. Fisher, J. & Zamir, D. Genes for yield stability in tomatoes. *Adv. Genet* **2**, 2100049 (2021).
110. Wijesingha-Ahchige, M. et al. The variegated canalized-1 tomato mutant is linked to photosystem assembly. *Comput Struct. Biotechnol. J.* **23**, 3967–398 (2024).
111. Palacio-López, K., Beckage, B., Scheiner, S. & Molofsky, J. The ubiquity of phenotypic plasticity in plants: a synthesis. *Ecol. Evol.* **5**, 3389–3400 (2015).
112. Xavier, A. et al. Genome-wide analysis of grain yield stability and environmental interactions in a multiparental soybean population. *G3 (Bethesda)* **8**, 519–529 (2018).
113. Gauch, H. G. J. Statistical analysis of yield trials by AMMI and GGE. *Crop Sci.* **46**, 1488–1500 (2006).
114. Montazavian, S. M. M. et al. GGE biplot and AMMI analysis of yield performance of barley genotypes across different environments in Inran. *J. Agric. Sci. Technol.* **16**, 609–622 (2014).
115. Komatsu, S., Kuji, R., Nanjo, Y., Hiraga, S. & Furukawa, K. Comprehensive analysis of endoplasmic reticulum-enriched fraction in root tips of soybean under flooding stress using proteomics techniques. *J. Proteom.* **77**, 531–560 (2012).
116. Oh, M. W., Nanjo, Y. & Komatsu, S. Identification of nuclear proteins in soybean under flooding stress using proteomic technique. *Protein Pept. Lett.* **21**, 458–467 (2014).
117. Da Fonseca, R. R. et al. The origin and evolution of maize in the Southwestern United States. *Nat. plants* **1**, 1–5 (2015).
118. Yang, N. et al. Two teosintes made modern maize. *Science* **382**, eadg8940 (2023).
119. Swarts, K. et al. Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America. *Science* **357**, 512–515 (2017).
120. Doebley, J., Wendel, J. D., Smith, J., Stuber, C. W. & Goodman, M. M. The origin of cornbelt maize: The isozyme evidence. *Economic Bot.* **42**, 120–131 (1988).
121. Hung, H.-Y. et al. ZmCCT and the genetic basis of day-length adaptation underlying the postdomestication spread of maize. *Proc. Natl Acad. Sci.* **109**, E1913–E1921 (2012).
122. Huang, C. et al. ZmCCT9 enhances maize adaptation to higher latitudes. *Proc. Natl Acad. Sci.* **115**, E334–E341 (2018).
123. Hufford, M. B. et al. Comparative population genomics of maize domestication and improvement. *Nat. Genet.* **44**, 808–811 (2012).
124. Choquette, N. E. et al. Enhancing adaptation of tropical maize to temperate environments using genomic selection. *G3: Genes, Genomes, Genet.* **13**, jkad141 (2023).
125. Duvick, D. N. Biotechnology in the 1930s: The development of hybrid maize. *Nat. Rev. Genet* **2**, 69–74 (2001).
126. Ray, D. K., Gerber, J. S., MacDonald, G. K. & West, P. C. Climate variation explains a third of global crop yield variability. *Nat. Commun.* **6**, 5989 (2015).
127. Carena, M. J. Germplasm enhancement for adaptation to climate changes. *Crop Breed. Appl. Biotechnol.* **11**, 56–65 (2011).
128. Hallgrímsson, B., Willmore, K. & Hall, B. K. Canalization, developmental stability, and morphological integration in primate limbs. *Am. J. Phys. Anthropol.* **119**, 131–158 (2002).
129. Flatt, T. The evolutionary genetics of canalization. *Q. Rev. Biol.* **80**, 287–316 (2005).
130. Rice, S. H. The evolution of canalization and the breaking of von Baer's laws: Modeling the evolution of development with epistasis. *Evolution* **52**, 647–656 (1998).
131. Frank, S. A. Natural selection. I. Variable environments and uncertain returns on investment. *J. Evolut. Biol.* **24**, 2299–2309 (2011).
132. Ceccarelli, S. Wide adaptation: How wide? *Euphytica* **40**, 197–205 (1989).
133. Kusmec, A., de Leon, N. & Schnable, P. S. Harnessing phenotypic plasticity to improve maize yields. *Front Plant Sci.* **9**, 1377 (2018).
134. Gratani, L., Catoni, R. & Varone, L. Morphological, anatomical and physiological leaf traits of *Q. ilex*, *P. latifolia*, *P. lentiscus* amd *M.communis* and their response to Mediterranean climate stress factors. *Bot. Stud.* **54**, 35 (2013).
135. Forsman, A. Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity* **115**, 276–284 (2015).
136. Johannsen, W. The genotype conception of heredity. *Am. Nat.* **45** (1911).
137. Wennersten, L. & Forsman, A. Population-level consequences of polymorphism, plasticity and randomized phenotype switching: a review of predictions. *Biol. Rev. Camb. Philos. Soc.* **87**, 756–767 (2012).
138. Pfennig, D. W. & McGee, M. Resource polyphenism increases species richness: A test of the hypothesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 577–591 (2010).
139. Smith-Gill, S. J. Developmental plasticity: developmental conversion versus phenotypic modulaton. *Am. Zool.* **23**, 47–55 (1983).
140. Snell-Rood, E. C. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**, 1004–1011 (2013).
141. de Kroon, H., Huber, H., Stuefer, J. F. & van Groenendael, J. M. A modular concept of phenotypic plasticity in plants. *N. Phytol.* **166**, 73–82 (2005).
142. Kumar, R. R. et al. Biochemical defense response: Characterizing the plasticity of source and sink in spring wheat under terminal heat stress. *Front Plant Sci.* **8**, 1603 (2017).
143. Callaway, R. M., Pennings, S. C. & Richards, C. L. Phenotypic plasticity and interactions among plants. *Ecology* **84**, 1115–1128 (2003).
144. Pfennig, D. W. et al. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* **25**, 459–467 (2010).
145. Murren, C. J. et al. Constraints on the evolution of phenotypic plasticity: Limits and costs of phenotype and plasticity. *Heredity* **115**, 293–301 (2015).

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Competing interests

The authors declare no competing interests.

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