University of Dundee

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Review

Active and adaptive plasticity in a changing climate

Rob Brooker [1,2,*] Lawrie K. Brown,[2] Timothy S. George,[2] Robin J. Pakeman,[1] Sarah Palmer,[3] Luke Ramsay,[2] Christian Schöb,[4] Nicholas Schurch,[5] and Mike J. Wilkinson[3]

Better understanding of the mechanistic basis of plant plasticity will enhance efforts to breed crops resilient to predicted climate change. However, complexity in plasticity's conceptualisation and measurement may hinder fruitful crossover of concepts between disciplines that would enable such advances. We argue active adaptive plasticity is particularly important in shaping the fitness of wild plants, representing the first line of a plant's defence to environmental change. Here, we define how this concept may be applied to crop breeding, suggest appropriate approaches to measure it in crops, and propose a refocussing on active adaptive plasticity to enhance crop resilience. We also discuss how the same concept may have wider utility, such as in *ex situ* plant conservation and reintroductions.

What is plasticity, and why does it matter?

Despite considerable research effort examining the occurrence and mechanisms of plasticity across many species, crossover of understanding from ecology and evolutionary biology to crop breeding appears limited. Knowledge of this lacuna is not new. Nicotra and Davidson [1] identified the need to bridge the gap more than a decade ago and argued that 'we are now at the threshold' of advances. Unfortunately, little progress has been made (Box 1); we contend that progress has been partly impeded by conceptual differences over the importance, meaning, and value of plasticity; by divergent and inconsistent use of terminology; and by a failure to recognise commonalities in high-level research objectives and approaches. We aim to help bridge this gap and highlight the importance of doing this to address issues of future food security and because of wider environmental and scientific benefits that will accrue. We first consider some of the key concepts and terminology involved. We then consider the importance of a key component of plasticity – **adaptive plasticity** (see Glossary) – that is widely studied by ecologists/evolutionary biologists and has particular relevance for crop breeding's attempts to address challenges arising from climate change. Finally, we consider how adopting a more harmonised approach may benefit *ex situ* conservation of rare wild species and crop relatives.

Phenotypic plasticity can be driven directly by growth-limiting resource shortages (e.g., lack of light, water, or essential nutrients), known as **passive plasticity**, or can be a manifestation of physiological response mechanisms activated by the plant as it adjusts to cope with a variable living environment, known as **active plasticity** [2,3]. It can be difficult to distinguish between these forms of plasticity [3–6], so most studies focus on the collective concept of phenotypic plasticity, which incorporates both forms. Phenotypic plasticity can result in profound changes to the appearance and metabolism of an individual, such as changes to the common ice plant *Mesembryanthemum crystallinum* L. that occur in response to salt or water stress [7,8] or to semiaquatic plant species in response to submersion [9]. Although generally less dramatic than these examples, phenotypic plasticity is often sufficient to influence **fitness** (for review, see [10]).

Highlights

Increasing environmental uncertainty is focussing research interest on plant plasticity. But despite calls for plasticity concepts to be adopted in crop breeding, this does not appear to have happened.

Plasticity is a broad and multifaceted concept, making it potentially difficult to identify those aspects of previous research most relevant to the crop breeding context.

Given the challenges posed by climate change and the different evolutionary contexts in natural and crop systems, we identify active adaptive plasticity as a key issue for further investigation by crop breeders.

We outline and illustrate the experimental and statistical analytical approaches necessary to begin to assess active adaptive plasticity, and we highlight benefits that might arise in other fields from a fuller understanding of the role and regulation of this aspect of plasticity.

[1]Department of Ecological Sciences, James Hutton Institute, Aberdeen, UK
[2]Department of Ecological Sciences, James Hutton Institute, Dundee, UK
[3]Institute of Biological, Environmental, and Rural Sciences (IBERS), Aberystwyth University, Plas Gogerddan, Aberystwyth, Ceredigion, UK
[4]Institute of Agricultural Sciences, ETH Zurich, Zurich, Switzerland
[5]Biomathematics and Statistics Scotland, Aberdeen, UK

*Correspondence:
rob.brooker@hutton.ac.uk (R. Brooker).

Box 1. Is there a disconnect between ecology/evolutionary biology and crop breeding?

There have been previous calls for the understanding of plasticity arising from ecology and evolutionary biology to be transposed to crop breeding [1,5]. However, examination of recent crop breeding studies indicates that this has not occurred widely. We undertook a simple review of the literature, examining papers citing Nicotra and Davidson [1]. We identified 99 citing papers in the Web of Knowledge database. Within these, we then looked for papers that put their call into practice, specifically those papers that were (i) experimental studies, (ii) focussed on crop species, and (iii) measured adaptive plasticity as part of the selection process for a genetic population. This identified six papers (Table I), all of which use static environmental gradients to compare plasticity (a point we discuss in the section 'Measuring active adaptive plasticity' in the main text). Concurring with the results of our simple literature search, Arnold *et al.* [18], in a meta-analysis explicitly targeting studies of selection on plasticity in response to temperature, found no studies focussing on crops.

Table I. Examples of experimental studies focussed on crop species and measuring adaptive plasticity

Title	Crop	Refs
Root system plasticity to drought influences grain yield in bread wheat	Wheat	[82]
Genetic control of plasticity in root morphology and anatomy of rice in response to water deficit	Rice	[83]
Phenotypic plasticity of yield and agronomic traits in cereals and rapeseed at high latitudes	Cereals, oilseed rape	[84]
Plasticity of wheat grain yield is associated with plasticity of ear number.	Wheat	[85]
Oat phenotypes for drought adaptation and yield potential	Oats	[86]
Rice root architectural plasticity traits and genetic regions for adaptability to variable cultivation and stress conditions	Rice	[87]

Many animal and plant studies adopt the general concept of phenotypic plasticity given earlier and focus on the plasticity of **genets** (see, e.g., [11,12]). However, some ecological studies opt to consider the plasticity exhibited by entire populations [13,14]. This approach is useful for the study of some long-lived perennial species (see, e.g., [15]), although it is critical to recognise that this plasticity includes variation that is potentially attributable to population-level genetic variation. Such contributions should always be recognised and clearly distinguished from plasticity *sensu stricto* that occurs within the individual genotype.

Among ecological works, there is much interest in the potential for plasticity to confer selective advantage [2,16,17], and under particular conditions (Figure 1). Such adaptive plasticity is said to increase fitness [18] by allowing modification of the phenotype in response to the prevailing conditions so that the individual's contribution to the next generation is enhanced. Conversely, nonadaptive plasticity evokes no impact on fitness, and maladaptive plasticity reduces fitness, such as when the physiological costs of plasticity outweigh the gains in environmental 'fit' [18–21].

The agricultural literature has a marked tendency to view plasticity in a negative light and often encompasses aspects of plasticity into **G × E (genotype–environment interaction) effects**. G × E effects occur when different genotypes respond differently to environmental variation [12,22–26]. G × E effects are broadly analogous to the general concept of phenotypic plasticity, and, similarly, G × E effects do not differentiate between active or passive responses. Another factor not universally encompassed by G × E studies is whether the response enhances rather than decreases the fitness of the individual. To address this issue requires careful consideration of what constitutes fitness in an agricultural setting.

Contrasting fitness landscapes

Wild and cultivated plants grow in very different selection environments. In natural populations of perennial plants, life history theory dictates a trade-off between responses to enhance survival and to increase short-term reproduction [27]. A short-term 'fitness deficit' (e.g., reduced seed

Glossary

Active plasticity: strategic and physiologically regulated changes to phenotype in response to changes in environmental conditions, often involving stress response pathways.
Adaptive plasticity: changes in phenotype in response to changes in environmental conditions in a manner that enhances fitness, including stabilising fitness across environments and limiting fitness declines.
Ecosystem services: benefits (and occasionally costs) provided to humans by the activities or functions of an ecosystem, including food production and carbon sequestration.
Fitness: contribution of offspring to the next generation.
G × E (genotype–environment interaction) effects: contrasting response of differing genotypes to the same environmental variation.
Genet: plants that share a genotype.
Passive plasticity: changes to phenotype in response to changes in environmental conditions due solely to the imposition or removal of a growth-limiting factor such as light, water, or an essential nutrient.
Phenotypic plasticity: changes to phenotype in response to changes in environmental conditions.
Plant trait: a morphological, physiological, or phenological feature of an individual plant that is measurable.
Ramet: an individual propagule or plant of a single genet.

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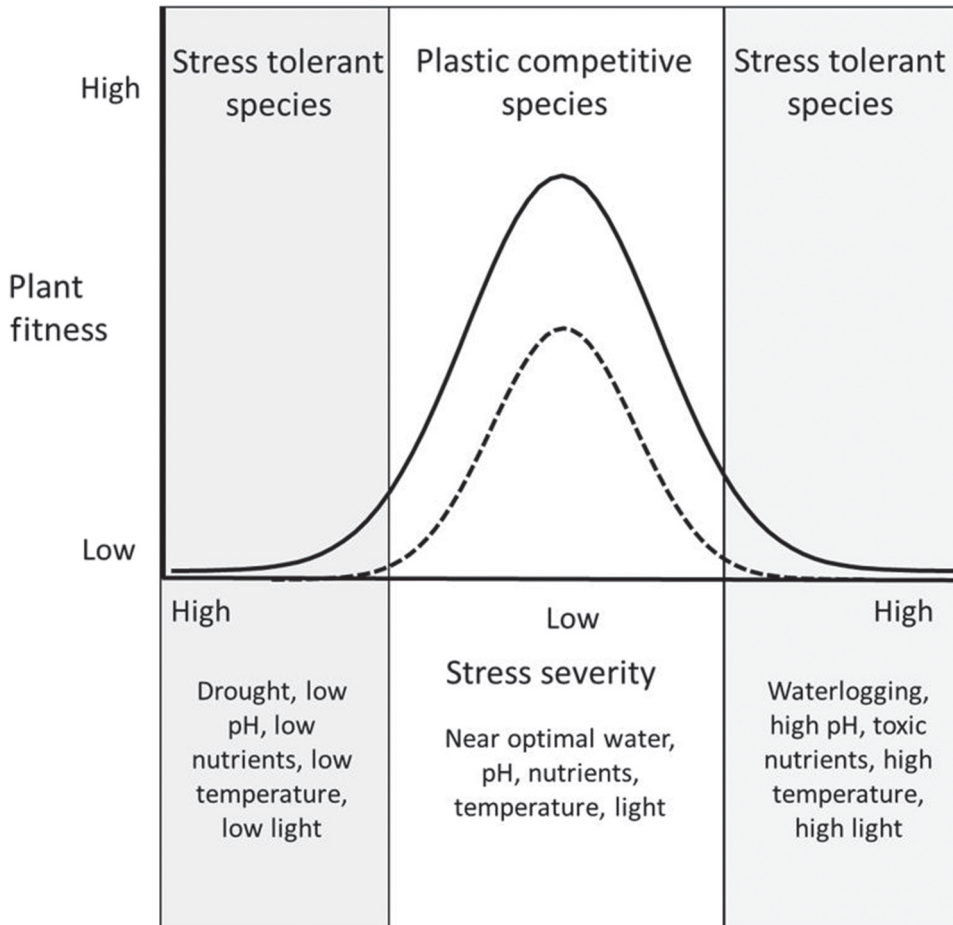
Figure 1. Proposed relationship between level of environmental stress (*x*-axis) and plant fitness, expressed both as total plant fitness (unbroken line) and the contribution to this of adaptive plasticity (broken line). In this simple model, plant species occupying and evolved to environments near to optimal conditions (e.g., plastic competitive species) are more likely to possess sufficient system redundancy in regulatory processes to allow high levels of adaptive plasticity. This means that the overall fitness of the individual will be as much set by regulation of the genes it possesses (adaptive plasticity) in response to prevailing environmental conditions as it is by the underlying genetic adaptation afforded by the alleles themselves. This is indicated by the high proportional contribution of adaptive plasticity to total plant fitness. By contrast, plants living in extreme marginal conditions (stress-tolerant species) possess far fewer regulatory options that would improve fitness. These plants will rely more on possessing alleles suited to the condition (stress tolerance) and on deploying regulatory settings that allow survival of the environment in which they live. At its most extreme, only the few genotypes containing the most stress-tolerant alleles and deploying the optimal regulatory regime will survive. In this case, there is no option for variation. It follows that any study seeking to measure the adaptive plasticity of a plant needs to consider whether the growing conditions for that species might be considered marginal for the species, or stressful overall relative to optimum conditions for plant growth, and the influence this could then have on the observed levels of adaptive plasticity.

production) is adaptive if survival leads to increased lifetime fitness. Such a lifelong view of adaptive plasticity is clearly difficult to measure and may in part have driven the mistaken interpretation of any variation in fitness as being adaptively plastic [2,10]. The situation is marginally simpler for wild annuals: the fecundity–survival trade-off applies, but the fitness advantages of increased plasticity can be more directly linked to seed production. In a bad year, a more plastic individual may survive to yield some seed. However, this is not necessarily an indication that 'survival-orientated' plasticity is adaptive overall, depending also on long-term dynamics of the seed bank and whether benefits

from seed contribution in bad years outweigh seed yield deficits (compared with nonplastic genets) in good years. Thus, the adaptive significance of survival plasticity in wild annuals is still not 'simple.'

The selection environment experienced by agricultural plants is starkly different. Some processes simply will not operate, such as natural selection enabling passive plasticity to have evolutionary consequences [23]. The closest direct analogy to natural 'fitness' is commercial success of varieties arising from offspring, and thus there is a more direct link between agricultural fitness and parameters associated with marketable yield and/or crop quality. In a cereal food crop, for example, grain number, size, and nutritional quality relate directly to market value (e.g., [28]). In further contrast to natural populations, selection in an agricultural setting applies over the commercial longevity of the variety or breeding line, with even annual agricultural crops undergoing selection over many years or even decades (e.g., [29]). Thus, crops may be considered closer to wild perennials than annuals, noting that there is no trade-off between individual survival and fecundity. Instead, there is selection in crops for consistency of high yields, given the context of the prevailing conditions, which themselves have been highly modified to mitigate some of the many challenges faced by wild plants (e.g., [30]). In turn, this modified living environment also impacts the selection environment experienced by the crop: pests and diseases are controlled exogenously and/or through the introduction of resistance or tolerance genes to the crop, and nutrient and water shortages are mitigated by supplementation (e.g., [31,32]).

Another notable divergence is the strong selection applied against heterogeneity in crop varietal phenology and phenotype, ensuring 'distinctness' and 'uniformity' for varietal registration and ease of mechanised harvesting. As noted by Pigliucci [2], 'The agricultural literature has been dealing with plasticity for quite some time … but the interest there was in how to eliminate [author's emphasis] plasticity rather than in understanding where it comes from and how it works.' The divergent nature of the natural and agricultural selection environments also applies to fecundity. Fertility is of little or no importance if seed is not the harvestable product, and even for those food crops where the harvestable product is a seed or grain, selection – particularly in more intensive agriculture – does not usually relate strictly to the number of offspring that survive into the next generation. Instead, it applies to features associated with uniformity and total market value (seed/grain size, nutritional composition, yield per hectare, etc.) as discussed earlier.

Collectively, the above drivers are likely to diminish the potential fitness benefits of many aspects of phenotypic plasticity seen in wild species, reducing crop **plant trait** plasticity when compared with crop ancestors [33,34]. However, one driver stands out as a possible exception. The need to maximise marketable yield means successful varieties will have the ability to plastically moderate their phenotype to achieve this goal. It is arguable whether many breeding programmes are structured to optimise this feature, although selection from across sites and years would certainly contribute towards it.

It is vital to note that the above points relate to crop breeding as it has been undertaken to date, focussed mainly on intensive agriculture with minimised variation in exogenous factors such that crops with limited plasticity are able to maintain fitness in multiple locations. However, climate change presents new challenges, with a predicted increase in both the severity and frequency of extreme weather events (e.g., [35]). Consequently, it is likely to be much less straightforward for farmers to control (and reduce the variability in) exogenous drivers. Harnessing agricultural adaptive plasticity may be critical for dealing with increasingly extreme and unpredictable environmental conditions under future climate change [5].

However, if the potential benefits of plant plasticity are to be integrated effectively into a breeding effort, it is particularly important to focus on active adaptive plastic responses of individuals rather than using the larger catchall umbrella of G × E effects. It is at the level of the individual genotype that plasticity can be selected for within breeding programs and where identification of underlying genetic mechanisms is possible (as per [1]). In turn, this may allow more interventive improvements to crop resilience. For example, the potential benefits of plasticity in polycultures are currently contentious [36]; it has been argued that plasticity may be detrimental if it prevents niche differentiation. However, specific targeting of adaptive plasticity among neighbouring species could facilitate more effective trait space partitioning, which enhances beneficial plant–plant interactions in communities [37,38].

Measuring active adaptive plasticity

Active adaptive plasticity is challenging to measure in natural ecosystems, although several works have proposed experimental approaches (for overviews, see [2,39]). Despite marked differences in selection landscapes experienced by wild plants and agricultural crops, shared fundamental aims and principles justify these studies being used as a platform to build a strategy to measure and then understand active adaptive plasticity in varieties and breeding lines.

First, it is important to control for genetic variation. This is achieved for wild species using clones or inbred lines [39,40], measuring genetic variability of a line/population [41], or standardising genetic variation between experimental groups [42,43]. Control of genetic variation in a wild species may be subject to many factors, including access to material, plant size, ability to multiply **ramets**, reproductive biology, seed dormancy, and time to phase change. The situation is simpler for an agricultural crop. Here, the variety forms the natural unit of genetic diversity for study, being the unit at which selection is applied. The amount of genetic variation contained in a variety varies according to the crop, but for the major crops, it is usually either none (clonal crops such as potatoes, apples), minimal (for inbred populations of cereals), or modest (self-contained outbreeding populations such as forage grasses) (e.g., [44]). Experiments should select a population size to use as a single replicate that is representative of that contained in a variety: for clonal crops, this would be a single plant as a single replicate of the variety. Decisions on the number of replicate plants (ramets) of this genet to use should also consider divergence in developmental or life experience between ramets, since this could change their initial physiological state at the start of the experiment. This would be especially true for ramets generated using tissue culture, where individual regenerated ramets may differ in genetic and epigenetic profiles (e.g., [45]), even when secured from meristem cultures [46]. Thus, replication must account for within-variety variation for plasticity, even when considering clonal material. The same reasoning applies to varieties containing even minimal genetic variation, where thought should also be given to the growing conditions of the parental plants. There is growing evidence to suggest transgenerational epigenetic inheritance of stress memory among filial offspring of inbred lines [47,48], giving scope for variation in plasticity between clones derived from the same genet (as per [49]). Thus, it is vital to source experimental material with sufficient within-variety replication, ideally originating from parental materials with identical provenance (or nearly so).

Second, while variation in plasticity between ontogenetic stages is not necessarily confounding, being a potentially important part of plasticity's expression [15,39], it needs to be acknowledged and (we suggest) controlled for in crop breeding studies. For annuals, including many crops, this can be accommodated by standardising experiment initiation at a specific life stage (e.g., anthesis). Perennials, particularly longer-lived species, may require distinction between seasonal cycles (e.g., leaf emergence, flowering time) and longer-term developmental phases and age. Ideally, experimental individuals will be from the same cohort and have near-identical life

experiences. Overall, results of experimental studies must be seen as being in the context of age, developmental stage, and prior (individual and parental) life histories.

Having sourced material, the next challenge is differentiating active adaptive plasticity from other plastic responses. Phenotypic plasticity is commonly assessed through modelling reaction norms [2,50,51], with an assumed linear relationship between a trait characteristic and a static, often sparsely sampled, environmental gradient [52], sometimes with only a 'high versus low comparison' (e.g., [20]). Recognition that trait behaviour across environmental gradients is complex and nonlinear has prompted more advanced statistical modelling approaches such as random regression mixed modelling. However, these approaches 'have not yet been widely implemented in many disciplines of plant biology to analyse plasticity' [12] and alone are insufficient to measure active adaptive plasticity, probing neither the relationship between a trait's response and the individual's ability to maintain some (albeit proxy) measure of fitness or an individual's ability to actively respond to changing environmental conditions. This is not to say that important lessons cannot be taken from reaction norm modelling, as discussed by previous studies advocating this approach (e.g., [2]). This applies whether the measure of fitness is a more proximal metric, such as biomass or flower number in an ecological study, or a more direct measure of fitness, such as grain yield and quality for crop studies. From a crop breeding perspective, a simple comparison of lines that are able to maintain yield parameters in the face of a variable growing environment will permit crude selection of the most adaptively plastic lines, but it will not provide sufficient basis for the dissection of active adaptive plasticity that enables targeted selection within a modern breeding programme. In short, we need to identify which aspects of overall plasticity are actively contributing to the capability to maintain yields. It is here that agriculture can learn from the experiences of the ecological plasticity community.

To demonstrate the application of these modelling approaches to uncover contributing components of adaptive plasticity in a crop breeding context, we performed a typical trial that exposed cultivars of barley to a static environmental gradient (Box 2). We use a more complex, although still simplistic, modelling approach whose results indicate potential variation in active adaptive plasticity between barley cultivars. Despite its illustrative utility, our preliminary trial is inadequate for a full assessment of active adaptive plasticity due to a key limitation of this (commonly applied) approach: the absence of longitudinal environmental variation. This is particularly relevant when exploring responses to projected future climatic variability. Using the example of drought (with adaptive plasticity being particularly relevant to water use [1,33]), we know plant responses differ throughout the growing season [53,54] and that climate change projections indicate drought levels will vary increasingly across the growing season (https://www.metoffice.gov.uk/research/approach/collaboration/ukcp/index). In addition, nonstatic environmental gradients help us separate the effect of genetic tolerance (stress tolerance) and genetic flexibility (active adaptive plasticity).

To explore ontogenetic shifts in plasticity, careful thought is required over the life-stage timing, fluctuation frequency, and amplitude along the plant life history of stress exposure and response measurements. Snapshot exposure allows stress application to coincide with a particular life stage, but exposure must be sufficiently prolonged to evoke a response. There is also no single factor called 'stress' [3]; fuller understanding necessitates assessment of the simultaneous impact of multiple stress factors, which in turn may set limits on plastic responses to individual stressors [21]. Uncertainty over response lag periods also means longitudinal studies should track plant responses to stress conditions varying across scales and frequencies similar to those experienced in the environment or projected under climate change scenarios. Such work could use sequential harvests of clonal ramets, and proxy measures of plant physiological status

could be used to characterise which aspects of plant phenotype/physiology is largely responsible for any adaptive plasticity detected. These could include nondestructive phenotypic measurements by means of near-infrared reflectance spectroscopy [55] or limited tissue sampling for metabolomic, transcriptomic, or epigenetic profiling [43,56,57].

This takes us to the issue of what to measure in terms of both the potentially plastic response traits (e.g., root:shoot ratio) and components of adaptive plasticity (e.g., agricultural fitness). For response traits, it may be preferable to study physiological processes such as nitrogen, light, or water use efficiency rather than alteration of physical features (e.g., aboveground biomass) that may be proxies for such changes [58]. It is also unlikely that active adaptive plasticity involves variation in a single trait, and, indeed, evidence indicates differential plasticity between types of traits (see, e.g., [59]) and some plastic responses involving complex suites of traits (e.g., [60]).

Numerous studies describe molecular stress responses leading to a particular trait change. This detailed level of understanding is required for the targeted selection of enhanced plasticity. Examples include modulation of meristem determinacy [61] and stomatal guard cell density [48]. Several works have similarly highlighted diverse molecular responses to pathogen attack (for reviews, see [62–64]). Viewed holistically, genetic control of trait plasticity is clearly complex (see, e.g., [65])

Box 2. Analytical strategy for assessing adaptive plasticity: results of a preliminary trial

A preliminary trial conducted in January/February 2020 focussed on the response of plant phenotypic traits to different levels of water stress. Comparison of barley cultivars is not an obvious approach, as crop selection and breeding, focussing on yield quantity, quality, and uniformity, may have led to selective loss of traits such as adaptive plasticity [33,34]. However, this makes the test conservative, and, at the same time, crop cultivar collections can provide isogenic seeds generated from common parental stocks.

The experiment used five barley varieties, including modern elite varieties (Irina and Concerto) and ancient Scottish landraces of bere barley with contrasting rhizosheath sizes (Bere 2426, Bere 59A37 Unst, Bere 16 Bernaray, Bere_SASA_818). Five replicates of each variety were grown under common conditions throughout: soil was field soil, a clay loam, with a pH of 6.0; experimental setup, watering, and nutrient regime followed [88], but with water stress values of 50%, 62.5%, 75%, 87.5%, and 100% field capacity, as calculated by gravimetric water content. After 4 weeks of growth, the individual plants were harvested. Aboveground dry biomass was measured at harvest by weighing all the shoot material after oven drying at 70°C for 4 days. Intact plants were carefully removed from the pots by knocking the contents of the pot out and lifting the plants free of the surrounding bulk soil. Dry root mass was measured using the methods of [89].

We chose total biomass as our measure of success, reflecting a measure of a plant's ability to use the resources available in its environment. We fit the total biomass measure of success response with a generalised logistic function given by the equation;

$$y = A + (K - A) / \left(C + Qe^{-B(x-M)} \right)^{1/v} \tag{I}$$

where A is the lower asymptotic value, K is the upper asymptotic value (if $C = 1$), B is the growth-rate, M is the shift of the curve midpoint along the x-axis, v defines where maximum growth rate occurs, Q is a scaling parameter related to $y(0)$, and C is related to the upper asymptotic value. We fix $C = Q = v = K = 1$ and $A = 0$, which reduces Equation I to;

$$y = 1 / \left(1 + e^{-B(x-M)} \right) \tag{II}$$

with the parameters B and M as fit parameters that define two key aspects of a plant's ability to maintain success, the level of environmental stress beyond which plants no longer maintain peak success (as indicated by maintenance of peak production M; Figure IA), and sensitivity to increases in stress beyond this point (as indicated by the collapse rate B; Figure IB). We fit the measure of success data from each cultivar in R using the nonlinear least-squares fitting package 'nls,' with initial values of $M = 0.6$ and $B = 15$. We model the suite of trait reaction norms with simple linear models and contrast the fit parameters against those for the measure of success. Contrasting the key model fit parameters for the paired measure of success and trait models across genotypes allows us to simultaneously measure which genotypes are best able to maintain success under environmental stress and which traits are correlated with this.

Larger changes in root:shoot ratio across the drought gradient correlated with longer maintenance of peak biomass production (Figure IA) and less rapid decrease in biomass in response to stress beyond the threshold point (Figure IB). This means that cultivars best able to alter their root:shoot ratio were also best able to maintain overall biomass production under increasing drought, matching results from previous studies showing yield stability is positively associated with plasticity [90]. From this preliminary trial, we interpret root:shoot ratio as a candidate adaptively plastic trait for drought for the success metric of biomass and conclude that some barley cultivars (such as Concerto) are more adaptively plastic than others (e.g., Irina).
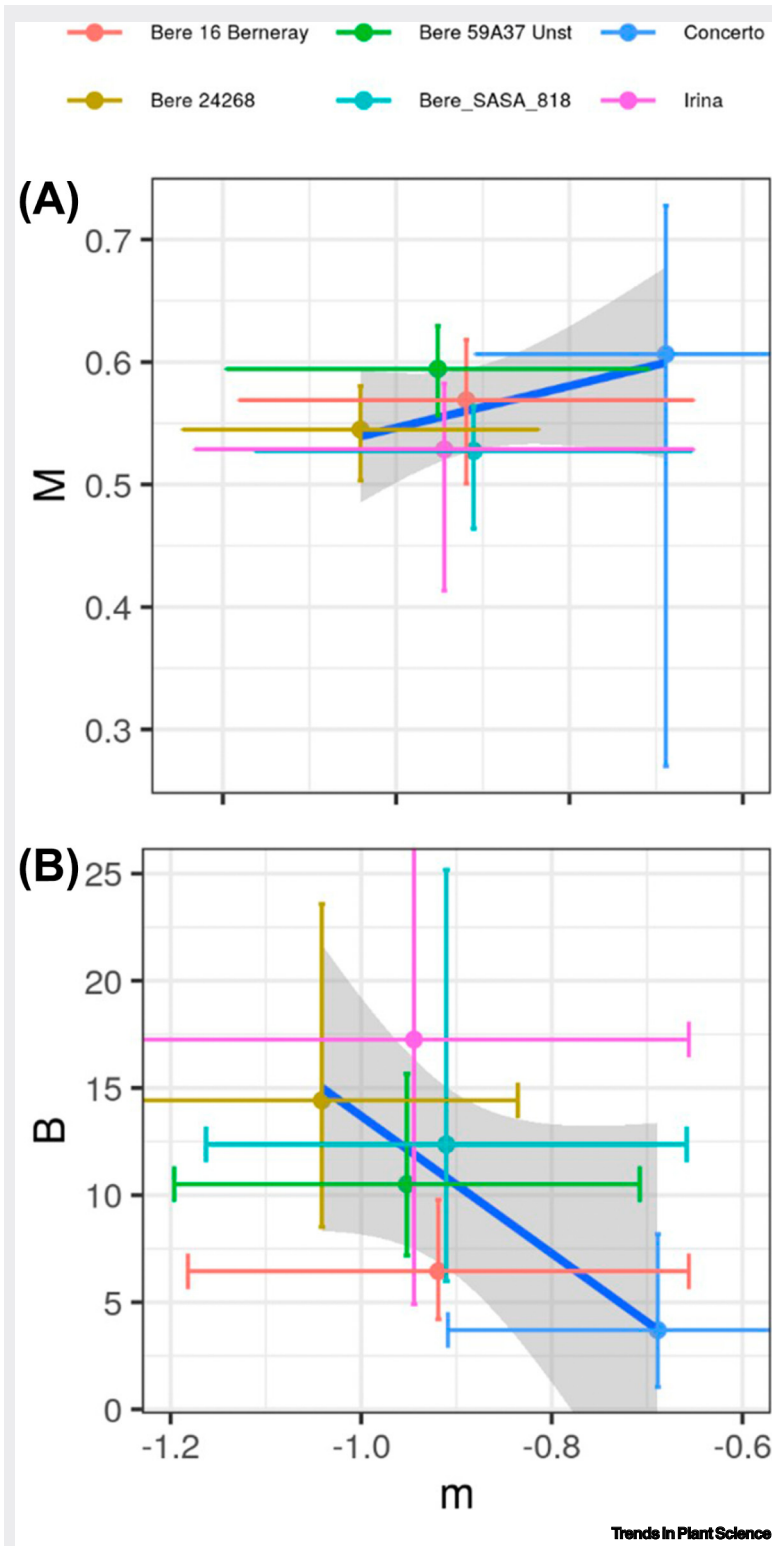
Figure I. Results of sigmoid logistic measure of success modelling across a drought gradient. (A) Maintenance of peak production (M) and (B) the collapse rate (B) from sigmoid logistic measure of success modelling of biomass across a drought gradient versus m the slope of linear response norm modelling of root:shoot ratio across the drought gradient. Error bars: 95% confidence intervals on measure of success and response norm model fit parameters; blue line with grey ribbon: best fit linear model with 95% confidence level interval for predictions.

and relates to the trade-offs and interdependencies linked to developmental progression (see, e.g., [66]). There is inevitably also some association between activation of epigenetic control mechanisms and responses to environmental change, with epigenetic responses to stress exposure including responses to soil salinity [67] and relative humidity [48]. Most involve changes in DNA methylation profile (e.g., [68,69]) or modifications to histone tail configuration [70,71], but post-transcriptional systems of epigenetic regulation may also be recruited (for review, see [72]). Linking epigenetic responses to changes in gene expression and alterations in phenotype/development must represent the long-term aspiration in this arena. As stated by Bradshaw [3], 'Genes must exist not only to determine character means, but also to determine character response, which adds interesting complexity to our ideas about evolution.'

Finally, account should be taken of the fact that a single driver, such as temperature, can have multiple impacts on plant physiological processes that affect responses to other environmental stresses (e.g., drought, nutrient deficiency, and salt toxicity). Certainly, the transcriptional, metabolomic, and epigenetic responses of a plant to multiple stresses can vary from that caused by a single stressor ([73] and references therein). Modifications of single field conditions are relatively easy (e.g., undersoil heating or rain exclusion), but interpretation of effect needs care.

The more complex experimental approaches suggested here necessarily require more sophisticated statistical modelling, such as random regression mixed models [12,18] or Bayesian frameworks [74], to identify individuals that alter trait characteristics while maintaining physiological status and ultimately agricultural fitness during periods of stress. While recognising the complexity of both these approaches, perhaps the critical points are that these approaches target active adaptive plasticity, try to assess it directly, and are much more tractable for plant breeding.

Wider applications for assessments of active adaptive plasticity

Developing a better understanding of the occurrence and role plasticity plays in plants, including active adaptive plasticity, is relevant to a wide range of fundamental research issues in ecology and evolutionary biology [2]. But as well as being of fundamental interest, active adaptive plasticity is directly relevant to key issues of species conservation under a changing climate.

A few studies have explored variation in adaptive plasticity across species' ranges or in relation to niche breadth [75], resulting in a better understanding of the fitness landscape of plastic responses, but more are clearly needed [36,58,76]. The cost of carrying the system redundancy required by adaptive plasticity [19] may become disadvantageous in some settings (Figure 1) [1], but, under a high frequency of within-lifetime extreme events (as expected under climate change), adaptive plasticity may be more beneficial. The resilience of a species or population will ultimately be determined by a combination of relevant allelic diversity (i.e., genetic variation) and the plasticity of the individual to accommodate changing conditions. In this context, adaptive plasticity represents the first line of defence to environmental change.

Such knowledge is critical when we are considering conservation translocations. The active adaptive plasticity of translocated/introduced individuals must match the current and likely future environmental conditions, while *ex situ* propagation of target species may have negative impacts on the genetic diversity of populations for reintroduction [77], leading to inbred lines that survive in the nursery but not in the wild [78]. The challenge of reintroducing species from *ex situ* conservation is a clear example of the important nexus between ecology, evolutionary biology, and plant breeding. Assessment of the active adaptive plasticity of *ex situ* lines ahead of reintroduction, although restricted in being able to assess their ultimate fitness in recipient sites, would at least enable an assessment of their adaptive plasticity across the likely current and future field conditions.

Beyond the survival of individual species, adaptive plasticity is anticipated to influence community composition and by extension ecosystem functions and **ecosystem services** ([76] and references therein), including their response to climate change. However, as noted by Wright *et al.* [79], 'research examining how trait variability impacts upon the stability of ecosystem functioning is sorely lacking,' and, although modelling has indicated potential positive effects of plasticity on biodiversity–ecosystem–function (BEF) relationships, these have not been tested by building communities that vary systematically in the adaptive plasticity of component individuals [80].

Both crop breeding and conservation will benefit from advances in controlled environment facilities that allow the imposition of multiple stresses at a scale relevant to the study plant. Critically, it will be important to impose a changing environmental stress landscape to really assess adaptive plasticity. The ability to assess trait responses remotely and in real time will also be critical, particularly if we consider adaptive plasticity a breeding target. This will be reliant on the development of imaging technologies for both controlled environment and field conditions. Technological breakthroughs in high-throughput phenotyping platforms [81] and in approaches such as hyperspectral imaging will be critical. With such breakthroughs, there is a good chance we will be able to assess the role and potential of plasticity in the sustainability and resilience of both agricultural and natural plant communities.

Concluding remarks and future perspectives

Its multifaceted nature makes it hard to identify why plasticity research is of such relevance to major crop breeding challenges, such as breeding crops resilient to future climate change. Here we have aimed to help bridge this gap by providing an overview of the main plasticity concepts, identifying those most relevant to crop breeding, and noting the different evolutionary landscapes operating in wild and crop settings.

We have also provided pointers to the experimental approaches needed to assess active adaptive plasticity, a key aspect of plasticity of particular relevance to crop breeding, and highlighted some additional areas for novel research where the fields of ecology, evolutionary biology, and crop breeding can come together. In particular, we highlight its relevance to the challenges of *ex situ* plant conservation and reintroductions, with the ultimate aim of conserving species under climate change. Both this work and the wider issue of resilient crop breeding would benefit greatly from a fuller recognition of the wide body of work already undertaken on plasticity, including active adaptive plasticity, and the application of its concepts and approaches to these pressing plant science challenges (see Outstanding questions).

Declaration of interests

The authors have no interests to declare.

Outstanding questions

What is the pattern of occurrence of active adaptive plasticity in crop species? For example, do particular crops or more modern varieties contain less active adaptive species, and is there greater active adaptive plasticity in landraces from environments where growing conditions are more variable (potentially providing germplasm for crop breeding for plasticity)?

Is active adaptive plasticity advantageous in crops under future climate scenarios? If active adaptive plasticity can be identified and measured, it will be possible to see whether it provides a benefit in maintaining (crop-system) fitness under conditions expected, given current and future climate scenarios.

What mechanisms are regulating active adaptive plasticity in crop species? For, example, do these have an epigenetic basis and/or might they be targeted by crop breeding if active adaptive plasticity is shown to be advantageous?

How does active adaptive plasticity impact community processes and ecosystem functions? This is relevant both to crops, such as understanding whether plasticity is a beneficial trait for varieties in crop mixtures, and to natural ecosystems, where the role of plasticity in maintaining ecosystem functions and service provision is poorly understood.

What is the level of occurrence of active adaptive plasticity in plants in *ex situ* collections compared with wild populations, and does the pattern of occurrence of active adaptive plasticity match the needs of species conservation under a changing future climate?

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