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From Molecular Signals to Phenotypic Plasticity: A Critical Synthesis of Structural and Developmental Remodelling in Plant Stress Adaptation

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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Abstract

Plants respond to environmental stress by altering the structure and the developmental trajectory of their organs, and the molecular pathways connecting stimulus perception to these alterations have been mapped in progressively finer detail over the past three decades. Whether that mechanistic knowledge explains, or predicts, the plasticity observed in plants growing under field conditions remains contested. This critical narrative review examines the evidence linking early signalling events to

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structural and developmental remodelling, and evaluates how far the resulting phenotypes can reasonably be described as adaptive. Literature was identified through searches of open scholarly databases and supplementary citation searching, and was appraised on design quality, replication and ecological realism rather than on citation frequency. Four judgements emerge from the synthesis. Signal perception remains the weakest link in the causal chain, because few primary sensors for water deficit, salinity or nutrient limitation have been demonstrated directly, and much of the mechanistic architecture is inferred from downstream mutants. Developmental remodelling is best documented for root branching, stomatal patterning, internal aeration tissue and elongation growth, where genetic evidence is strong but was generated largely in a small number of species under controlled conditions. The assumption that plastic responses are adaptive is asserted far more often than it is tested, since fitness measurements under realistic conditions are scarce and evidence for the costs of plasticity is inconsistent. Stress memory is empirically robust at the level of transcription and chromatin, yet its persistence, heritability and agronomic value remain unresolved. The most consequential gap is inferential rather than mechanistic, because the experimental systems that support strong causal claims differ systematically from the environments in which plasticity matters. Progress will depend on fitness-anchored experiments in fluctuating environments, on genetic dissection of plasticity as a trait in its own right, and on phenotyping that resolves developmental trajectories rather than endpoints.

Keywords: *Abiotic stress signalling; developmental plasticity; reaction norm; root system architecture; stomatal development; stress memory; crop resilience.*

1. Introduction

A plant that cannot move must resolve environmental variation internally. The resolution is developmental: cells divide in different planes, primordia are initiated or suppressed, organs elongate or are arrested, and tissues acquire different anatomical properties depending on the conditions the plant encounters. The resulting capacity of a single genotype to generate distinct phenotypes across environments is phenotypic plasticity, and in plants it is expressed principally through structure and development rather than through behaviour (Sultan, 2000). Because sessile organisms cannot relocate, the developmental route to environmental accommodation carries an unusually heavy functional load, and this has made plants a productive system for studying how environmental information is converted into morphology. Recent synthesis also distinguishes phenotypic stability from plasticity and emphasises that their genetic and regulatory bases are not yet fully resolved (Li *et al.*, 2025).

Three decades of molecular genetics have supplied an increasingly detailed account of the machinery that performs the conversion. Receptors for abscisic acid were identified and shown to inhibit clade A type 2C protein phosphatases, closing a long-standing gap in the drought signalling pathway (Ma *et al.*, 2009; Park *et al.*, 2009). Oxygen sensing in flooded tissue was traced to conditional proteolysis of group VII ethylene response factors through the N-degron pathway (Gibbs *et al.*, 2011; Licausi *et al.*, 2011). Phytochrome B was shown to integrate temperature with light through thermally accelerated reversion, providing a molecular basis for warm-temperature morphogenesis (Jung *et al.*, 2016; Legris *et al.*, 2016). Systemic propagation of stress information through calcium and reactive oxygen species waves was demonstrated over distances of centimetres and timescales of seconds (Choi *et al.*, 2014; Miller *et al.*, 2009; Toyota *et al.*, 2018). Downstream of these events, hormone networks and transcription factor cascades have been assembled into detailed regulatory maps (Waadt *et al.*, 2022; Zhu, 2016).

Alongside this, a largely separate literature has characterised the phenotypic outcomes. Lateral roots are positioned according to local water availability (Bao *et al.*, 2014) and are suppressed when the root tip loses contact with moisture (Orman-Ligeza *et al.*, 2018). Stomatal density is adjusted to atmospheric carbon dioxide concentration and to the conditions experienced by mature leaves (Hetherington & Woodward, 2003; Woodward, 1987). Rice cultivars carrying contrasting alleles pursue opposite strategies under submergence, either suppressing elongation or accelerating it (Hattori *et al.*, 2009; Xu *et al.*, 2006). Root cortical tissue is remodelled into aerenchyma under hypoxia and is partially sacrificed under drought (Chimungu *et al.*, 2014; Yamauchi *et al.*, 2018). Recent review of stomatal development under elevated carbon dioxide, heat and drought highlights both environmentally responsive developmental regulation and species-specific differences, reinforcing the need to distinguish general mechanisms from context-dependent responses (Chua & Lau, 2024).

These two bodies of work are frequently presented as a continuum running from perception to phenotype. The continuum is real in outline, but the joins are weaker than the standard narrative implies. Much of the signalling literature rests on loss-of-function phenotypes in one species grown on agar plates or in small pots under constant conditions, whereas much of the phenotypic literature is observational, correlative, or conducted in field environments where the causal machinery cannot be interrogated. Where the two meet, inference frequently substitutes for demonstration. A mutant with altered root branching under an osmotic treatment is taken to reveal a drought adaptation mechanism, although neither the water status of the treatment nor the fitness consequence of the phenotype may have been measured. Recent syntheses have begun to confront this problem explicitly, noting that natural genetic variation for plasticity is widespread, that plasticity can be quantified and mapped, and that its evolutionary and agronomic status remains open (Schneider *et al.*, 2026). At the crop scale, analysis of multi-environment maize trials shows that explicitly identifying environmental covariates can make reaction-norm analyses more interpretable for breeding, while such predictive associations remain distinct from direct evidence of developmental mechanism (Kusmec *et al.*, 2024).

The difficulty is compounded by a terminological looseness that has persisted despite repeated correction. Plasticity, acclimation, adaptation, tolerance, resilience and stress memory are used interchangeably in the molecular literature, although they refer to processes operating on different timescales and carrying different evidential requirements. Adaptive plasticity in the evolutionary sense demands a demonstrated fitness advantage in the inducing environment relative to the alternative phenotype, a standard rarely met in molecular studies (Ghalambor *et al.*, 2007). The consequences are not merely semantic. If a plastic response is assumed to be

adaptive, its manipulation appears an obvious breeding target; if it is a passive consequence of resource limitation, or actively maladaptive, manipulation may be neutral or harmful. A recent phylogenetically controlled meta-analysis reported that phenotypic integration may constrain variation among plastic responses rather than uniformly reducing their magnitude, underscoring the context dependence of proposed limits to plasticity (Stotz *et al.*, 2025).

Existing reviews address parts of this territory competently but leave the join unexamined. Treatments of hormone signalling under abiotic stress are thorough on mechanism and largely silent on developmental output and fitness (Waadt *et al.*, 2022; Zhu, 2016). Reviews of root plasticity summarise architectural responses without systematically appraising the quality of the evidence for their adaptive value (Karlova *et al.*, 2021). Ecological and evolutionary treatments of plasticity are rigorous about inference but engage only lightly with molecular mechanism (Nicotra *et al.*, 2010; Valladares *et al.*, 2007). The most recent comprehensive synthesis explicitly bridges molecular mechanism and breeding, and identifies constraints on the evolution of plasticity, but its emphasis falls on quantification and genomic prediction rather than on a critical audit of the mechanistic evidence itself (Schneider *et al.*, 2026). A review that interrogates the evidential status of the perception-to-phenotype chain, rather than describing it, does not currently exist.

1.1 Scope, Research Gap and Objectives

This review concerns the pathway from environmental signal perception to structural and developmental remodelling in vascular plants exposed to abiotic stress, and the extent to which that remodelling can be regarded as adaptive. It covers water deficit, salinity, submergence and hypoxia, mineral nutrient limitation, elevated temperature and shading, since these stresses have produced the largest bodies of mechanistic and phenotypic evidence and permit meaningful comparison. Attention is directed at responses expressed through structure and development, including root branching and angle, root anatomy, stomatal patterning, leaf anatomy, elongation growth and aerial architecture. Physiological adjustments that do not alter structure, such as stomatal aperture regulation and osmolyte accumulation, are considered only where they bear directly on developmental interpretation.

Several areas are deliberately excluded. Biotic stress and plant immunity are treated only where they bear on shared signalling components. Post-harvest and seed-stage responses, reproductive-phase transitions considered as flowering-time phenomena, and the extensive literature on transgenic overexpression conferring stress tolerance without developmental analysis lie outside the scope. Bryophytes and algae are not covered. The review is not a systematic review and does not attempt exhaustive coverage of any single stress.

The gap addressed is evidential rather than descriptive. Mechanistic pathways and phenotypic outcomes have each been reviewed extensively, but the inferential link between them has not been subjected to systematic critical appraisal. Specifically, it remains unclear how far the molecular architecture established under controlled conditions accounts for developmental remodelling in fluctuating environments, how much of the mechanistic literature meets the evidentiary standard required to describe a response as adaptive, and whether the persistent disagreement over plasticity as a breeding target reflects genuine biological uncertainty or divergent standards of evidence between disciplines.

Four objectives follow. The first is to appraise the strength of the evidence connecting proposed sensing and signalling modules to specific developmental outputs, distinguishing demonstrated from inferred causal links. The second is to synthesise the evidence for structural and developmental remodelling across organs and stresses, and to explain the principal inconsistencies within it. The third is to evaluate the empirical basis for claims that such remodelling is adaptive, and to assess the status of the widely invoked hypothesis that plasticity carries fitness costs. The fourth is to identify research priorities that would materially reduce the inferential gap rather than extending the descriptive catalogue.

2. Methods for Literature Selection

2.1 Review Design and Rationale

A critical narrative review was selected because the review question concerns the coherence and evidential quality of a body of work spanning molecular genetics, developmental biology, physiology, ecology and crop science. The constituent studies differ in organism, experimental system, treatment definition, outcome measure and inferential logic to a degree that precludes quantitative pooling. A meta-analysis would require a common effect measure that does not exist across mutant phenotype descriptions, anatomical measurements and field yield data. A systematic review with a single answerable question would either exclude most of the relevant literature or fragment into several unrelated reviews. A scoping review would map the field but would not deliver the critical appraisal that the question demands.

The narrative format was chosen for its capacity to accommodate heterogeneous evidence, not as a licence for informality. Transparency of sources, explicit eligibility rules and structured appraisal were applied throughout, following published guidance on the conduct and quality assessment of narrative reviews (Baethge *et al.*, 2019; Sukhera, 2022). Reporting was organised so that the reader can distinguish what was searched, what was included, and on what basis interpretive judgements were made.

2.2 Information Sources

Searches were conducted in PubMed, Europe PMC, Crossref, OpenAIRE, DOAJ and Semantic Scholar. Crossref was additionally used for bibliographic verification of every reference retained, and Digital Object Identifier resolution was checked for each record. These sources were selected because the review spans plant molecular biology, plant physiology, agronomy and ecology, and no single index covers that range adequately. PubMed and Europe PMC provide the strongest coverage of plant molecular and

physiological research; Crossref and OpenAIRE provide broad cross-disciplinary and repository coverage including agronomic and ecological outlets that are poorly represented in biomedical indexes; DOAJ and Semantic Scholar were used to reduce the risk of omitting open-access and regionally published work.

Database searching was supplemented by backward citation searching from recent reviews and consensus syntheses, by forward and related-record searching for highly relevant primary studies, and by checking retrieved records for published corrections. Where a record carried a subsequent correction, the corrected version was used and the claim was framed conservatively.

2.3 Search Strategy and Search Period

Search concepts were constructed around four axes: the signalling axis, the developmental and structural axis, the stress axis, and the inferential axis concerning adaptive value and evidence quality. Free-text terms were combined with database-specific field tags where these were available. Representative strings included combinations of the form ("phenotypic plasticity" OR "developmental plasticity" OR acclimation) AND (drought OR "water deficit" OR salinity OR submergence OR hypoxia OR "nutrient deficiency" OR "high temperature" OR shade); ("root system architecture" OR "lateral root" OR "root anatomy" OR aerenchyma OR suberin) AND (plasticity OR remodelling) AND (drought OR salinity OR waterlogging); ("stomatal density" OR "stomatal development" OR "leaf anatomy" OR "mesophyll") AND (plasticity OR acclimation) AND ("water use efficiency" OR drought OR shade); (abscisic acid OR ethylene OR auxin OR brassinosteroid OR "reactive oxygen species" OR calcium) AND (signalling OR sensing) AND (development OR morphology); and ("stress memory" OR priming OR transgenerational OR epigenetic) AND plant AND (chromatin OR methylation). Terms addressing methodological quality, field validation, fitness and breeding application were incorporated into the later searches.

The search period ran from 1 January 1990 to 23 June 2026. The starting point reflects the beginning of sustained molecular-genetic dissection of plant environmental responses, which supplies the mechanistic evidence the review appraises. Foundational earlier publications were retained where they were necessary to explain the historical development of a concept, most notably the demonstration that stomatal density responds to atmospheric carbon dioxide concentration.

2.4 Eligibility Criteria

Peer-reviewed primary research articles and reviews in indexed journals were eligible. Studies were included when they reported structural, anatomical or developmental responses of vascular plants to abiotic environmental variation; characterised molecular components linking environmental perception to such responses; quantified plasticity as a trait, including its genetic architecture; or evaluated the adaptive, agronomic or evolutionary significance of plastic responses. Methodological publications concerning the appraisal of narrative reviews were eligible for the design section only.

Publications were excluded when they reported only physiological or biochemical responses without structural or developmental measurement; described constitutive stress tolerance phenotypes without reference to environmental contingency; concerned biotic stress alone; addressed non-vascular plants; or were conference abstracts, editorials, commercial material, unverifiable publications, or preprints for which peer-reviewed equivalents were available. Only English-language publications were assessed. Sources whose bibliographic identity could not be confirmed were excluded irrespective of apparent relevance.

2.5 Screening, Duplicate Handling and Study Selection

Records retrieved from each source were assessed first by title and abstract against the eligibility criteria, and retained records were then assessed in full text where accessible. Duplicates arising from overlapping index coverage were identified by Digital Object Identifier and, where absent, by matching author, title and year. Preprint versions were matched to their published counterparts and the published version was retained. Where a record was accessible only as an abstract and the claim in question depended on methodological detail, the record was not used to support that claim.

Because selection was purposive rather than exhaustive, no screening counts are reported and no flow diagram is presented. Reporting numerical yields from a purposive selection process would convey a spurious impression of systematic completeness. Selection prioritised studies that made a distinct conceptual or methodological contribution, that provided the strongest available evidence on a contested point, or that reported findings inconsistent with the prevailing interpretation.

2.6 Critical Appraisal and Evidence Synthesis

No formal risk-of-bias instrument was applied, since the retained literature comprises experimental genetics, controlled-environment physiology, field agronomy and comparative ecology, and no validated instrument spans these designs. Appraisal was instead conducted against criteria appropriate to each design: whether the environmental treatment was characterised in terms meaningful to the plant rather than only to the experimenter; whether appropriate controls and comparison genotypes were used; whether findings had been replicated independently or across species; whether the outcome measured was the outcome claimed; whether growth conditions permitted extrapolation to the environments invoked in the discussion; and whether fitness or yield was measured where adaptive value was asserted.

Themes were developed inductively from the retained literature and then reorganised around the causal chain that the review interrogates, proceeding from conceptual foundations through perception and signalling to root and shoot remodelling, memory, and genetic and agronomic translation. Where studies disagreed, the disagreement was retained and its likely sources examined,

including differences in species, treatment severity, developmental stage, growth medium and outcome definition. Convergence across independent systems was treated as strengthening confidence; convergence within a single experimental paradigm was not.

3. Conceptual Foundations: Plasticity, Acclimation and the Problem of Adaptive Value

3.1 Terminology, Measurement and the Reaction Norm

Phenotypic plasticity denotes environmentally contingent phenotypic expression by a single genotype, and is formally represented by the reaction norm, the function relating phenotype to environmental value across a genotype's range (Sultan, 2000). The reaction norm framing has a consequence that molecular studies frequently overlook: plasticity is a property of the function, not of any point on it. A mutant with an altered phenotype under stress may have an altered mean, an altered slope, or both, and these are genetically and functionally distinct (Kusmec *et al.*, 2017). Single-environment comparisons cannot distinguish them.

Quantifying plasticity is correspondingly demanding. Two environments define a slope but cannot detect curvature or threshold behaviour, and the resulting index depends on which two environments were chosen. Many published plasticity indices are ratios or differences that scale with the trait mean, so that genotypes with larger absolute trait values appear more plastic without any difference in environmental responsiveness. Analyses that treat plasticity as a random regression across a continuous environmental gradient, with the environment characterised by measured covariates rather than treatment labels, avoid several of these problems but demand multi-environment designs (Arnold *et al.*, 2019). Comparative evaluation of statistical approaches to plasticity and its genetic architecture indicates that conclusions about which loci control plasticity are sensitive to the modelling framework adopted, which is a substantial caution for the interpretation of any single mapping study (Arenas *et al.*, 2025).

Acclimation is best treated as a subset of plasticity: reversible, within-generation physiological or structural adjustment following exposure. Developmental plasticity is typically irreversible once the organ is formed, and this asymmetry matters functionally. A stoma is committed at the time of its formation, whereas its aperture is adjustable within minutes. Consequently the temporal structure of the environment determines which kind of response can be useful, a point that is rarely built into experimental design.

3.2 Adaptive, Neutral and Maladaptive Plasticity

The description of a plastic response as adaptive carries a specific meaning: the induced phenotype must confer higher fitness in the inducing environment than the phenotype that would otherwise be produced (Ghalambor *et al.*, 2007). Much of what is observed under stress fails this test not because it is maladaptive but because it has never been tested. Reduced leaf area under water deficit may represent an adaptive reduction in transpiring surface, or may represent the passive consequence of reduced turgor-driven expansion. The two hypotheses predict identical morphology and are distinguishable only by experiments that decouple resource limitation from regulated growth restraint, or that measure fitness across environments.

Evidence that some plasticity is actively maladaptive is comparatively firm in ecological settings, where responses induced by novel environments can move the phenotype away from the local optimum (Ghalambor *et al.*, 2007). The molecular literature contains an analogous but under-recognised category, in which growth restraint imposed by stress signalling exceeds what resource availability requires. Growth-restraining DELLA proteins accumulate under adverse conditions and restrict elongation independently of substrate limitation, and their removal increases growth under stress while reducing survival (Achard *et al.*, 2006). Whether the wild-type setting is optimal is an empirical question about the environment, and the answer will differ between a habitat with unpredictable severe drought and a managed field with supplementary irrigation.

3.3 Costs, Limits and the Evidential Status of the Cost Hypothesis

If plasticity were free, canalised genotypes would be rare. The cost hypothesis proposes that maintaining sensory and regulatory machinery, and producing phenotypes with a delay, imposes fitness penalties that constrain the evolution of plasticity (DeWitt *et al.*, 1998). The hypothesis is theoretically well specified, distinguishing maintenance costs, production costs, information acquisition costs and developmental instability costs, and it has been influential far beyond its evidential base.

The empirical record is weaker than the hypothesis's ubiquity suggests. A synthesis of experimental estimates in plants found costs of plasticity to be detected inconsistently, to be small where detected, and to depend strongly on the statistical model and the environmental context (van Kleunen & Fischer, 2005). Ecological constraints on plasticity, including reliability of environmental cues, developmental timing and the correlation structure among traits, may limit plasticity more strongly than direct energetic costs (Valladares *et al.*, 2007). Confidence in the general proposition that plasticity is costly should therefore be modest. This matters directly for crop improvement, where the argument that plasticity should be selected against in favour of stable, canalised performance rests partly on an assumed cost that has not been reliably demonstrated.

A further complication concerns the resource basis of plastic responses. Remodelling requires carbon and nitrogen to be redirected, and the capacity to do so depends on stored reserves whose contribution to plasticity has only recently been treated as a distinct question (Fettke & Fernie, 2025). Where reserves are limiting, apparent genotypic differences in plasticity may reflect differences in storage rather than in signalling or developmental competence.

Table 1 sets out the conceptual distinctions used throughout this review, together with the evidence each category requires and the errors most commonly made when the categories are conflated. The distinctions are not merely definitional: the third column

specifies the evidential burden that a claim in each category must discharge, and much of the disagreement examined in later sections arises because studies discharge a lower burden than their conclusions assume.

Table 1. Conceptual distinctions among terms describing environmentally contingent phenotypes, with the evidence required to support each and the errors arising from conflation

Term	Definition used here	Evidence required	Common misuse	Supporting references
Phenotypic plasticity	Environmentally contingent phenotypic expression by one genotype, described by a reaction norm	Phenotype measured for the same genotype across at least two, preferably several, characterised environments	Inferred from a single stressed treatment without an environmental gradient	Arnold *et al.* (2019); Sultan (2000)
Acclimation	Reversible within-generation adjustment following exposure	Demonstrated reversal, or return towards the prior state, on removal of the stimulus	Applied to irreversible developmental change	Nicotra *et al.* (2010)
Developmental plasticity	Environmentally contingent, largely irreversible change in organ initiation, patterning or anatomy	Change demonstrated at the level of primordium initiation, cell division or differentiation, not only organ size	Conflated with growth reduction caused by resource limitation	Karlova *et al.* (2021); Sultan (2000)
Adaptive plasticity	Induced phenotype confers higher fitness in the inducing environment than the alternative phenotype	Fitness or a validated proxy measured for both phenotypes in both environments	Assumed from apparent functional plausibility	Ghalambor *et al.* (2007); Valladares *et al.* (2007)
Cost of plasticity	Fitness penalty attributable to plastic capacity rather than to the phenotype expressed	Fitness compared among genotypes differing in plasticity but matched for mean phenotype	Asserted as a general property without genotype-matched comparison	DeWitt *et al.* (1998); van Kleunen & Fischer (2005)
Stress memory	Altered response to a later stimulus attributable to prior exposure	Response to the second stimulus compared with naive controls of the same age and developmental stage	Any persistent post-stress difference labelled as memory	Crisp *et al.* (2016); Hilker *et al.* (2016)
Adaptation	Genetic change in a population increasing mean fitness in a given environment	Population-level genetic differentiation with demonstrated fitness consequence	Used interchangeably with an individual plant's stress response	Ghalambor *et al.* (2007); Nicotra *et al.* (2010)

Note. The categories are not mutually exclusive; a single response may be simultaneously plastic, developmental and adaptive. The evidential requirements are cumulative from top to bottom within each conceptual family

4. From Stimulus Perception to Transcriptional Reprogramming

4.1 Primary Sensors and the Persistence of the Sensor Gap

The chain from environment to phenotype begins with a molecular event that converts a physical or chemical variable into a biochemical signal. For several stresses that event remains unidentified, and this gap is more consequential than the density of published pathway diagrams suggests.

Abscisic acid signalling is the clearest exception and the appropriate standard of comparison. Members of the PYRABACTIN RESISTANCE and PYR1-LIKE family bind abscisic acid and inhibit clade A type 2C protein phosphatases, releasing SNF1-related protein kinases from repression (Ma *et al.*, 2009; Park *et al.*, 2009). Ligand binding, structural change, target inhibition and downstream phosphorylation were established in the same experimental sequence, and the pathway has been independently reconstituted. The receptor is nevertheless a hormone receptor, not a stress sensor: it detects abscisic acid, not water deficit.

Osmosensing itself is less securely resolved. Hyperosmolality-gated calcium-permeable channel activity was attributed to *OSCA1*, whose loss reduces osmotically evoked calcium elevation and alters stomatal and root responses (Yuan *et al.*, 2014). The evidence that the protein participates in osmotic calcium signalling is convincing; whether it is the primary transducer of cellular water status, and how its activity relates to turgor, cell wall tension and membrane properties, remains less certain. For salinity, the ionic and osmotic components of the stress are separable and are perceived through partly distinct routes, but no single receptor accounts for the perception of sodium (van Zelm *et al.*, 2020). For mineral nutrient limitation, sensing is distributed across transporters with signalling functions and local metabolite pools rather than concentrated in a dedicated receptor.

Oxygen sensing is the strongest case of a demonstrated abiotic sensor, and its structure is instructive. Group VII ethylene response factors carry an amino-terminal cysteine that is oxidised in an oxygen-dependent manner, targeting the protein for degradation through the N-degron pathway; under hypoxia, degradation slows and the factors accumulate (Gibbs *et al.*, 2011; Licausi *et al.*,

2011). Here the sensing step is a chemical reaction whose substrate is the environmental variable itself, which is why the mechanism admits direct demonstration. Where no such direct chemistry exists, as for water deficit, the sensing step is correspondingly harder to establish, and the literature has tended to accumulate downstream components rather than resolve the upstream question.

Temperature occupies an intermediate position. Phytochrome B reverts thermally from the active to the inactive form at a rate that increases with temperature, so that its signalling output encodes both light and temperature, and mutants show altered warm-temperature morphogenesis (Jung *et al.*, 2016; Legris *et al.*, 2016). The mechanism is physically direct and the genetic evidence is strong, but phytochrome B is neither the only thermosensor nor sufficient to explain thermal responses in darkness or in non-photosynthetic tissue.

4.2 Calcium, Reactive Oxygen Species and Systemic Propagation

Downstream of perception, calcium and reactive oxygen species carry information both within and between organs. Salinity applied to roots elicits a calcium wave propagating to the shoot at velocities of the order of hundreds of micrometres per second, and this propagation depends on vacuolar cation channel function (Choi *et al.*, 2014). Wounding elicits a comparable long-distance calcium signal that requires glutamate receptor-like proteins and precedes systemic jasmonate responses (Toyota *et al.*, 2018). Systemic reactive oxygen species signalling depends on the NADPH oxidase RBOHD, whose loss abolishes propagation in response to several distinct stimuli (Miller *et al.*, 2009). Contemporary synthesis treats these as an integrated systemic signalling system rather than as separate pathways (Mittler *et al.*, 2022).

Two critical qualifications apply. First, the systemic signal is largely stimulus-general: similar waves are triggered by salinity, wounding, heat and high light, so the specificity of the eventual developmental response cannot reside in the wave itself. Where specificity arises has not been resolved, and proposals invoking combinatorial coding by hormone context or tissue competence remain largely untested. Second, the evidence base is concentrated in *Arabidopsis thaliana* seedlings imaged under conditions selected to permit imaging. Whether propagation velocities and dependencies are conserved in mature crop plants under field conditions is largely unknown, and the assumption that they are conserved is convenient rather than demonstrated.

4.3 Hormonal Integration and the Specificity Problem

Hormones convert stimulus-general signals into organ-specific developmental outputs, and their study has produced the densest regulatory maps in plant biology (Waadt *et al.*, 2022; Zhu, 2016). Ethylene occupies a central position because its accumulation under diverse stresses can either promote or restrict growth depending on tissue, dose and interacting hormones (Dubois *et al.*, 2018). Brassinosteroids act as multidimensional regulators of growth and stress responses, with signalling outputs that vary with tissue and stress context (Nolan *et al.*, 2020). Gibberellin-mediated degradation of DELLA proteins couples growth restraint to environmental conditions across several stresses (Achard *et al.*, 2006). Heat stress responses are organised through a transcription factor network centred on heat shock factors, with well-characterised regulatory logic (Ohama *et al.*, 2017).

The specificity problem is severe here. Most abiotic stresses raise abscisic acid, ethylene and reactive oxygen species while lowering growth-promoting signalling, yet the developmental outcomes differ sharply between, for instance, drought and shading. Explanations invoking signal combination, temporal dynamics or tissue-specific competence are plausible and largely unvalidated, in part because the experimental designs used to establish hormone function apply single hormones at saturating concentrations to whole seedlings. The resulting maps are informative about capability and weakly informative about what actually occurs in a plant experiencing a gradual soil drying cycle.

4.4 Mobile Peptides and Root-to-Shoot Communication

Small secreted peptides have supplied some of the more convincing evidence for information transfer between organs under stress. The CLAVATA3/EMBRYO SURROUNDING REGION-RELATED peptide CLE25 moves from root to shoot under water deficit and promotes abscisic acid biosynthesis in leaves, with receptor identification and grafting experiments supporting the directional claim (Takahashi *et al.*, 2018). Nitrogen demand signalling operates in the opposite direction, with root-derived C-TERMINALLY ENCODED PEPTIDEs perceived in the shoot and shoot-derived polypeptides returning to modulate nitrate uptake (Ohkubo *et al.*, 2017). These systems satisfy an evidential standard that much of the signalling literature does not, because movement, perception and physiological consequence were each demonstrated rather than inferred.

Their developmental significance is nevertheless incompletely established. Both examples act principally on physiology and uptake rather than on organ patterning, and whether comparable peptide systems instruct developmental decisions such as primordium initiation under stress remains open.

Table 2 summarises the principal signalling modules discussed above against the strength of evidence supporting each. The table is organised to separate the sensing claim from the transduction claim, because these are frequently bundled in review narratives although they carry very different evidential support; the pattern that emerges is that transduction is generally well supported while sensing is well supported only where the environmental variable participates directly in a chemical reaction.

Table 2. Signalling modules linking environmental perception to developmental output, classified by the strength and type of supporting evidence

Module	Proposed role	Strongest supporting evidence	Principal evidential limitation	Supporting references
PYR/PYL receptors and clade A PP2C phosphatases	Perception of abscisic acid and release of SnRK2 kinase activity	Ligand binding, phosphatase inhibition and reconstitution established concurrently in independent laboratories	Detects the hormone, not water status; upstream link to cellular water deficit remains inferential	Ma *et al.* (2009); Park *et al.* (2009)
OSCA1 calcium channel	Hyperosmolality-gated calcium influx	Loss of function reduces osmotically evoked calcium elevation and alters guard cell and root responses	Relationship to turgor and wall tension unresolved; primacy as an osmosensor not established	Yuan *et al.* (2014)
Group VII ERF N-degron pathway	Direct oxygen sensing through cysteine oxidation	Sensing chemistry, protein stability and hypoxic gene induction demonstrated in the same system by two independent groups	Quantitative relationship between tissue oxygen partial pressure and developmental output less well defined	Gibbs *et al.* (2011); Licausi *et al.* (2011)
Phytochrome B thermal reversion	Integration of light and temperature	Biophysical mechanism combined with concordant genetic phenotypes	Not sufficient for thermal responses in darkness or non-photosynthetic tissue	Jung *et al.* (2016); Legris *et al.* (2016)
Systemic calcium wave	Long-distance transmission of stress information	Direct imaging of propagation with dependence on identified channel functions	Stimulus-general; demonstrated mainly in seedlings under imaging-compatible conditions	Choi *et al.* (2014); Toyota *et al.* (2018)
RBOHD-dependent ROS wave	Autopropagating systemic signal	Loss of function abolishes propagation across several distinct stimuli	Specificity of downstream developmental output not explained by the wave itself	Miller *et al.* (2009); Mittler *et al.* (2022)
Ethylene and DELLA-mediated growth restraint	Conversion of stress signalling into altered elongation	Consistent genetic evidence across species and stresses	Dose- and tissue-dependent direction of effect complicates prediction	Achard *et al.* (2006); Dubois *et al.* (2018)
CLE25 and CEP peptide signalling	Root-to-shoot and shoot-to-root information transfer	Peptide movement, receptor identity and downstream response each demonstrated	Effects shown principally on physiology and uptake rather than organ patterning	Ohkubo *et al.* (2017); Takahashi *et al.* (2018)

Note. CEP, C-terminally encoded peptide; CLE, CLAVATA3/embryo surrounding region-related; ERF, ethylene response factor; PP2C, type 2C protein phosphatase; PYR/PYL, pyrabactin resistance/PYR1-like; RBOHD, respiratory burst oxidase homologue D; ROS, reactive oxygen species; SnRK2, SNF1-related protein kinase 2

5. Remodelling the Root System

5.1 Water-directed Patterning of Root Branching

Root branching is the best-documented instance of developmental patterning instructed by an environmental variable. Roots grown against an interface with contrasting moisture initiate lateral roots preferentially on the moist side, a response termed hydropatterning that operates at the level of primordium positioning rather than post-initiation growth (Bao *et al.*, 2014). Loss of contact with liquid water suppresses lateral root emergence altogether through an abscisic acid-dependent mechanism, described as the xerobranching response and reversible on rewatering (Orman-Ligeza *et al.*, 2018). A molecular link between water availability and branching was subsequently supplied by the demonstration that post-translational modification of the auxin response factor ARF7 alters its interaction with a repressor and thereby determines whether primordia proceed (Orosa-Puente *et al.*, 2018).

Taken together these studies establish that water distribution instructs root development rather than merely modulating growth rate, which is a meaningful advance over the earlier literature. Three qualifications temper the interpretation. The experimental systems impose sharp spatial discontinuities in water availability that have no clear counterpart in a drying soil profile, where gradients are gradual and change over days. The responses are characterised almost entirely in *Arabidopsis thaliana* seedlings, with limited replication in species possessing fibrous root systems and different anatomy. Most importantly, the fitness or yield consequence of the response has not been measured, so its description as an adaptive foraging mechanism rests on functional plausibility rather than demonstration.

Hydrotropism, the directional growth of roots along a water potential gradient, is mechanistically distinct from hydropatterning and depends on cortical rather than epidermal cell elongation, with abscisic acid signalling in the cortex required for bending (Dietrich *et al.*, 2017). The cell-type specificity is well demonstrated. Whether hydrotropism contributes materially to water acquisition in soil, where roots encounter mechanical impedance and heterogeneous pore structure, has not been established.

5.2 Root Angle, Depth and the Translation to Field Performance

Root growth angle determines the soil volume a root system explores and has produced the most convincing evidence that root developmental traits affect yield. Introgression of the *DEEPER ROOTING 1* allele into a shallow-rooting cultivar of rice (*Oryza sativa*) increased root growth angle, deepened the root system and raised grain yield under drought without penalty under well-watered conditions (Uga *et al.*, 2013). Natural variation at *EXOCYST70A3* in *Arabidopsis thaliana* alters root system depth through modulation of auxin transport, linking a specific molecular lesion to an architectural trait and to environmental distribution (Ogura *et al.*, 2019).

These studies are frequently cited together as evidence that root architecture can be engineered for stress environments, but they differ in an important respect. The rice work measured grain yield in the field across seasons and therefore supports an agronomic claim; the *Arabidopsis* work established a mechanism and a natural variation association without a yield endpoint. Conflating the two overstates the translational readiness of the mechanistic literature. Moreover, root angle is a largely constitutive trait, so *DEEPER ROOTING 1* demonstrates the value of an architectural configuration rather than the value of plasticity as such. The distinction is central to the breeding debate examined in Section 8.

A conceptual model that has organised much of this work proposes that root systems of maize (*Zea mays*) optimised for water and nitrogen capture should be steep, cheap and deep, combining a downward growth angle with reduced metabolic cost per unit root length (Lynch, 2013). The framework is coherent and has generated testable predictions, but it is an ideotype rather than an empirical finding, and its component predictions have been validated unevenly across environments and soil types.

5.3 Salinity and the Reprogramming of Lateral Root Development

Salinity imposes an osmotic and an ionic challenge whose developmental consequences differ in timing (Munns & Tester, 2008). Roots exposed to a salinity gradient bend away from the higher concentration, a halotropic response involving redistribution of auxin transporters (Galvan-Ampudia *et al.*, 2013). Comprehensive synthesis of salt tolerance mechanisms confirms that lateral root development is suppressed and then partially recovers under continued exposure, with the recovery phase depending on abscisic acid signalling and on genotype (van Zelm *et al.*, 2020).

Interpretation is complicated by the difficulty of separating regulated developmental arrest from toxicity. A root that stops branching under 150 millimolar sodium chloride may be executing a programme or may be failing. Studies that document recovery after transfer to non-saline medium provide the most persuasive evidence for regulation, and these are less common than studies reporting endpoint architecture. Genotypic comparisons in wild relatives and tolerant cultivars indicate that root architectural and metabolic plasticity contributes to salinity tolerance, but the evidence that root system plasticity per se improves yield in saline fields remains limited, and this has been identified as a specific translational gap (Shelden & Munns, 2023).

5.4 Nutrient-Dependent Architectural and Anatomical Plasticity

Nutrient limitation elicits some of the earliest and most robust demonstrations of environmentally instructed root development. Localised nitrate supply stimulates lateral root elongation within the enriched zone through a mechanism requiring a MADS-box transcription factor, establishing a genetic basis for nutrient foraging (Zhang & Forde, 1998). Systematic comparison across deficiencies of several macronutrients and micronutrients showed that each produces a distinguishable architectural signature, with different combinations of primary root elongation, lateral root density and root hair development (Gruber *et al.*, 2013). The specificity of these signatures argues against a generic stress response and in favour of nutrient-specific developmental programmes.

Anatomical plasticity extends the picture inward. Endodermal differentiation, including suberin lamella deposition, is remodelled according to nutrient status, altering the apoplastic barrier and thereby the selectivity of uptake (Barberon *et al.*, 2016). Osmotic stress enhances suberisation of apoplastic barriers in seminal roots of barley (*Hordeum vulgare*), with concordant chemical, transcriptomic and physiological evidence (Kreszies *et al.*, 2019). These studies demonstrate that the root modifies its own transport properties developmentally rather than only regulating transporter activity, which is a substantive extension of the classical view.

5.5 Anatomical Economy: Aerenchyma, Cortical Senescence and Metabolic Cost

Under soil flooding, cortical cells lyse to form gas-filled lacunae that permit internal aeration, and the formation of this aerenchyma is regulated by ethylene and reactive oxygen species signalling in coordination with the deposition of barriers to radial oxygen loss (Yamauchi *et al.*, 2018). Transcriptional profiling of barley root tissue under waterlogging has identified signatures associated with aerenchyma formation, supporting a programmed rather than purely degenerative process (Sherwood *et al.*, 2025). The functional argument is unusually strong here because the anatomical change has a direct physical consequence for gas transport that can be measured independently.

A parallel argument concerns metabolic economy under drought. Genotypes of maize with fewer cortical cell files maintained greater growth and yield under water deficit, attributed to reduced respiratory cost of root maintenance and consequently deeper rooting (Chimungu *et al.*, 2014). Root cortical senescence in cotton (*Gossypium hirsutum*) increased under water deficit, was greater in a drought-tolerant than in a drought-sensitive cultivar, correlated negatively with root respiration, and was reduced by silencing senescence-associated genes with a concomitant loss of drought tolerance (Guo *et al.*, 2025). The convergence of anatomical, physiological and genetic evidence in the cotton work is notable, although the water deficit was imposed osmotically with polyethylene glycol rather than by soil drying, which limits extrapolation to field conditions.

The economy argument nevertheless deserves scrutiny. Reduced cortical tissue lowers respiratory cost but also reduces radial transport capacity, mechanical strength and storage. Whether the net effect is beneficial depends on soil depth, water distribution and the duration of the deficit, and the published comparisons have generally been conducted in environments where deep water was available. Under terminal drought on shallow soils the calculation may reverse. Reviews of root plasticity have noted this contingency but the empirical test across contrasting soil profiles has not been performed systematically (Karlova *et al.*, 2021).

Table 3 collates representative evidence for root developmental remodelling across stresses, with the experimental system and the principal limitation stated for each. The pattern it exposes is that the strongest mechanistic evidence and the strongest agronomic evidence come from different studies, different species and different experimental scales, and that no single trait has been carried through the full sequence from molecular mechanism to demonstrated yield benefit in the same system.

Table 3. Representative evidence for environmentally instructed root developmental remodelling, with experimental system and principal limitation

Response	Inducing condition	Principal species	Nature of strongest evidence	Principal limitation	Supporting references
Hydropatterning of lateral root position	Asymmetric moisture contact	*Arabidopsis thaliana*	Positional bias demonstrated at primordium initiation	Sharp artificial moisture discontinuity; no fitness endpoint	Bao *et al.* (2014)
Xerobranching suppression of emergence	Loss of root contact with liquid water	*Arabidopsis thaliana*; cereals	Reversible suppression with abscisic acid dependence	Air gap treatment unlike gradual soil drying	Orman-Ligeza *et al.* (2018)
ARF7-dependent branching control	Water availability	*Arabidopsis thaliana*	Post-translational modification linked to primordium fate	Single species; developmental output not linked to yield	Orosa-Puente *et al.* (2018)
Hydrotropic bending	Water potential gradient	*Arabidopsis thaliana*	Cortex-specific requirement demonstrated genetically	Contribution in structured soil unquantified	Dietrich *et al.* (2017)
Steeper, deeper root growth angle	Drought	*Oryza sativa*	Introgression raised grain yield under drought in field trials	Largely constitutive trait rather than plastic response	Uga *et al.* (2013)
Root system depth variation	Natural environmental variation	*Arabidopsis thaliana*	Causal locus identified and mechanism defined	No yield or fitness endpoint	Ogura *et al.* (2019)
Halotropic root bending	Salinity gradient	*Arabidopsis thaliana*	Auxin transporter redistribution demonstrated	Steep imposed gradients; field relevance untested	Galvan-Ampudia *et al.* (2013)
Nutrient-specific architectural signatures	Deficiency of individual nutrients	*Arabidopsis thaliana*	Distinguishable architecture for each deficiency	Agar-based systems; single genotype background	Gruber *et al.* (2013); Zhang & Forde (1998)
Endodermal suberisation remodelling	Nutrient status; osmotic stress	*Arabidopsis thaliana*; *Hordeum vulgare*	Concordant anatomical, chemical and transcriptomic evidence	Functional consequence for whole-plant water relations partly inferred	Barberon *et al.* (2016); Kreszies *et al.* (2019)
Aerenchyma formation	Soil flooding and hypoxia	*Oryza sativa*; *Hordeum vulgare*	Anatomical change with directly measurable gas transport consequence	Species differ in constitutive versus induced formation	Sherwood *et al.* (2025); Yamauchi *et al.* (2018)
Reduced cortical burden and cortical senescence	Water deficit	*Zea mays*; *Gossypium hirsutum*	Anatomical, respiratory and genetic evidence converge	Benefit contingent on availability of deep water; osmotic rather than soil drying in the cotton work	Chimungu *et al.* (2014); Guo *et al.* (2025)

Note. ARF7, auxin response factor 7. Species names follow current nomenclature; the term cereals denotes work reported across more than one Poaceae species within the cited study

6. Remodelling the Shoot: Epidermal, Anatomical and Architectural Responses

6.1 Stomatal Development as the Canonical Plastic Trait

Stomatal density is the most extensively documented plastic developmental trait in plants, and its literature illustrates both the strengths and the recurrent errors of the field. Herbarium and experimental evidence established that stomatal number responds to atmospheric carbon dioxide concentration (Woodward, 1987), and subsequent work placed stomata at the centre of plant responses to environmental change over physiological and geological timescales (Franks & Beerling, 2009; Hetherington & Woodward, 2003). Developmentally, stomatal formation proceeds through an asymmetric division lineage under the control of a defined set of

transcription factors, and this lineage is subject to environmental modulation (Bergmann & Sack, 2007). Mitogen-activated protein kinase signalling links environmental inputs to stomatal patterning, providing a molecular route from perception to epidermal cell fate (Wang *et al.*, 2007), while carbon dioxide-dependent regulation operates in part through epidermal patterning factor signalling (Engineer *et al.*, 2016).

The functional consequence of altered density has been tested by direct manipulation. *Arabidopsis thaliana* lines with reduced stomatal density showed improved drought tolerance without impaired nutrient uptake (Hepworth *et al.*, 2015). In rice, reduced stomatal density conserved water and improved drought tolerance under elevated carbon dioxide conditions representative of future climates (Caine *et al.*, 2019). These experiments move the field beyond correlation and are among the more convincing demonstrations that a plastic developmental trait has adaptive value under specified conditions.

The qualifications are substantial and are frequently omitted. The benefit of reduced density is conditional on the atmospheric and hydrological context; under ambient carbon dioxide and adequate water, lower density can constrain assimilation. Density interacts with stomatal size, and maximum conductance depends on both, so density alone is an incomplete descriptor (Franks & Beerling, 2009). Scaling from anatomical density to canopy or ecosystem behaviour involves further assumptions that are not always warranted (Franks *et al.*, 2017). Reports of the direction of the density response to water deficit conflict across species and experiments, and this inconsistency has not been satisfactorily explained.

6.2 Leaf Anatomy, Mesophyll Structure and Photosynthetic Capacity

Beneath the epidermis, leaves remodel their internal anatomy in ways that alter photosynthetic capacity directly. Shading of genotypes of oilseed rape (*Brassica napus*) increased leaf area per plant while reducing leaf mass per area, and the genotype showing the greatest increase in leaf area also showed less densely packed mesophyll cells and thinner cell walls, with a corresponding increase in mesophyll conductance and photosynthesis; another genotype showed the opposite photosynthetic response (Luo *et al.*, 2023). The study is instructive because it demonstrates genotype-dependent divergence in the direction of a plastic response within a single species, which undermines any expectation that anatomical plasticity is uniformly beneficial.

At the whole-plant level, allocation between leaves, stems and roots shifts with environmental conditions in ways that are partly predictable from resource limitation and partly species-specific (Poorter *et al.*, 2012). Interpreting such shifts is difficult because ontogenetic drift confounds treatment effects: plants of different sizes allocate differently regardless of treatment, so comparisons at a common time point may reflect developmental stage rather than plastic response. Analyses that account for size explicitly reach more conservative conclusions than those that do not.

6.3 Hydraulic Architecture and the Limits of Structural Accommodation

Structural remodelling of the vascular system determines the water potential a plant can sustain before hydraulic failure. Comparative analysis across biomes showed that forest species operate with narrow hydraulic safety margins irrespective of precipitation regime, indicating a widespread vulnerability to drought-induced xylem embolism (Choat *et al.*, 2012). Subsequent synthesis has argued that hydraulic failure provides a mechanistic and quantifiable basis for predicting drought-induced mortality (Brodribb *et al.*, 2020). Rising atmospheric evaporative demand imposes an additional, partly independent constraint that structural acclimation may not offset (Grossiord *et al.*, 2020).

This literature is important for the present argument because it identifies a hard limit on the accommodation that plasticity can provide. Adjustments to leaf area, stomatal density and rooting depth operate within a hydraulic envelope set by xylem architecture, and where evaporative demand exceeds that envelope the developmental response is insufficient. Reviews of stress adaptation that treat plasticity as an open-ended capacity rarely acknowledge this ceiling.

6.4 Thermomorphogenesis and Shade Avoidance as Growth-Based Escape Syndromes

Warm temperature elicits a coordinated syndrome of hypocotyl and petiole elongation, leaf hyponasty and reduced leaf blade area, collectively termed thermomorphogenesis and mediated substantially through phytochrome-interacting factor signalling and auxin (Casal & Balasubramanian, 2019; Quint *et al.*, 2016). Reduced shading of the soil surface and improved leaf cooling by convection are the conventional functional explanations. Shade avoidance produces a partly overlapping syndrome in response to a reduced red to far-red ratio, with clear ecological logic in competitive stands (Ballaré & Pierik, 2017).

The two syndromes share signalling components and morphological outputs while differing in the environmental variable that triggers them, which makes them useful for examining the specificity problem raised in Section 4. That two distinct signals converge on a common developmental programme suggests that specificity resides in the context and quantitative characteristics of the response rather than in a dedicated pathway for each stimulus. It also raises the possibility that the shared programme is a generic elongation response deployed opportunistically rather than a stress-specific adaptation, and the evidence does not currently distinguish these interpretations. For thermomorphogenesis, the cooling benefit has been demonstrated in some systems but the magnitude relative to the cost of reduced leaf area under field conditions is not well quantified.

6.5 Submergence: Two Developmental Strategies and the Value of the Comparison

Submergence provides the clearest example of alternative developmental strategies encoded by allelic variation, and is consequently the most informative case in the entire literature for evaluating adaptive plasticity. Rice carrying the *SUB1A* allele suppresses shoot

elongation during flash flooding, conserving carbohydrate and surviving complete submergence (Xu *et al.*, 2006). Deepwater rice carrying *SNORKEL1* and *SNORKEL2* does the opposite, elongating internodes rapidly to maintain contact with the atmosphere during prolonged partial flooding (Hattori *et al.*, 2009). Subsequent work identified the ethylene and gibberellin signalling basis of the elongation response and connected it to adaptation to periodic flooding (Kuroha *et al.*, 2018). The broader framework distinguishing escape and quiescence strategies was established from comparative work across flood-tolerant species (Bailey-Serres & Voesenek, 2008).

The comparison is instructive precisely because the two strategies are mutually exclusive and their relative value is environment-dependent. Quiescence is advantageous under brief complete submergence and disadvantageous under prolonged partial flooding; escape has the converse profile. This is the strongest available demonstration that a plastic developmental response is adaptive in a specific environment and maladaptive elsewhere, and it establishes empirically what much of the literature assumes without test. It also demonstrates that agronomic deployment requires the flooding regime to be characterised, since the same allele improves or worsens outcomes depending on hydrological pattern.

Table 4 sets out the principal areas of disagreement in the shoot literature together with the most plausible explanations for each. The explanations are grouped so that disagreements arising from genuine biological contingency can be distinguished from those arising from methodological divergence, and the majority fall into the latter category, which suggests that a substantial part of the apparent inconsistency in this field is resolvable through better-specified experiments rather than through new mechanisms.

Table 4. Conflicting findings concerning shoot structural and developmental plasticity, with the most plausible explanations

Contested question	Divergent findings	Most plausible explanation	Type of disagreement	Supporting references
Direction of the stomatal density response to water deficit	Both increases and decreases reported across species and experiments	Response depends on developmental stage at which deficit is imposed, and on interaction with vapour pressure deficit and carbon dioxide concentration	Partly biological, partly methodological	Franks *et al.* (2017); Hetherington & Woodward (2003)
Whether reduced stomatal density improves performance	Benefit shown under elevated carbon dioxide and drought; neutral or negative under ample water	Benefit is conditional on the atmospheric and hydrological context of the experiment	Biological contingency	Caine *et al.* (2019); Hepworth *et al.* (2015)
Whether anatomical plasticity in leaves is beneficial	Photosynthesis increased in one genotype and decreased in another under identical shading	Genotype-dependent coupling between mesophyll structure and mesophyll conductance	Biological contingency	Luo *et al.* (2023)
Whether biomass allocation shifts represent active plasticity	Allocation shifts variously attributed to regulation and to ontogenetic drift	Failure to control for plant size at comparison confounds treatment with developmental stage	Methodological	Poorter *et al.* (2012)
Whether elongation responses to warmth are adaptive	Cooling benefit demonstrated in some systems; costs of reduced blade area rarely quantified	Fitness consequence measured under conditions that do not include the competing costs	Evidential gap	Casal & Balasubramanian (2019); Quint *et al.* (2016)
Whether escape or quiescence is the superior flooding strategy	Opposite conclusions from studies using different flooding regimes	The strategies are adaptive under different hydrological patterns; the disagreement is apparent rather than real	Resolved biological contingency	Bailey-Serres & Voesenek (2008); Hattori *et al.* (2009); Xu *et al.* (2006)
Whether structural acclimation can offset rising evaporative demand	Optimistic projections from acclimation studies contrast with narrow measured hydraulic safety margins	Acclimation operates within a hydraulic envelope that is itself narrow across biomes	Partly biological, partly scale-related	Brodribb *et al.* (2020); Choat *et al.* (2012); Grossiord *et al.* (2020)

Note. The classification of disagreement type reflects the assessment made in this review and is intended to indicate where further experimentation, rather than reinterpretation, is likely to be productive

7. Memory, Priming and the Temporal Dimension of Plasticity

7.1 Chromatin-based and Transcriptional Memory

Prior exposure to stress can alter the response to a subsequent exposure, and the mechanisms underlying this have been characterised most thoroughly for heat. Sustained transcriptional memory of heat stress in *Arabidopsis thaliana* requires heat shock factor A2, which acts transiently to establish lasting histone methylation at target loci without remaining bound, a mode of action described as hit-and-run (Lämke *et al.*, 2016). More recent work has shown that retention of histones during transcription preserves the relevant marks and is necessary for memory to persist (Pratx *et al.*, 2023). Comprehensive review of chromatin-based mechanisms confirms that several distinct molecular routes contribute, including histone variant exchange, small RNA pathways and DNA methylation changes (Lämke & Bäurle, 2017).

A necessary corrective to this literature argues that many phenomena labelled as memory are better explained by the kinetics of recovery, including differential decay of transcripts and proteins, than by dedicated epigenetic marks (Crisp *et al.*, 2016). The argument is methodological as much as mechanistic: distinguishing memory from incomplete recovery requires that the second stimulus be applied after full recovery has been demonstrated, and that naive controls be matched for developmental stage rather than only for chronological age. A substantial proportion of published memory studies do not meet both conditions. The broader framework treating priming as a general property of organisms lacking a nervous system provides useful conceptual discipline by specifying what must be shown for a priming claim to be supported (Hilker *et al.*, 2016).

7.2 Somatic Persistence, Transgenerational Transmission and Heritable Epigenetic Variation

Whether stress-induced modifications persist across generations is contested, and the evidence supports a more restricted conclusion than is often claimed. Hyperosmotic stress in *Arabidopsis thaliana* produced changes at epigenetically labile genomic sites, but transmission to progeny was limited and subject to resetting, with transmission occurring more readily through one parental lineage than the other (Wibowo *et al.*, 2016).

Independent evidence that epigenetic variation can contribute to heritable phenotypic variation comes from epigenetic recombinant inbred lines, in which DNA methylation variants segregate on a near-uniform genetic background. Such lines showed heritable variation in phenotypic traits, and methylation variants accounted for a measurable proportion of trait variance (Cortijo *et al.*, 2014). Critically for the present argument, comparable lines exhibited heritable variation in plasticity itself, indicating that epigenetic variation can generate variation in environmental responsiveness rather than only in trait means (Zhang *et al.*, 2013). These experiments establish the possibility in principle. They do not establish that stress-induced epigenetic changes in natural or agricultural populations contribute materially to adaptation, since the lines were generated by manipulation of the methylation machinery rather than by environmental exposure.

7.3 Evidential Problems and the Agronomic Question

Three problems limit confidence in this area. Definitions vary sufficiently that studies reporting memory are not always reporting the same phenomenon. Persistence is usually assessed over days to weeks under controlled conditions, whereas agronomic relevance would require persistence across a growing season under fluctuating conditions. Fitness or yield consequences are rarely measured, so whether memory is beneficial, neutral or costly remains largely unknown. Priming is nevertheless of considerable potential value precisely because it would permit stress preparedness without constitutive expression of costly protective programmes, and this makes the absence of yield-level evidence a notable gap rather than a peripheral one.

8. Genetic Architecture, Phenotyping and Translation to Crops

8.1 Plasticity as a Heritable and Mappable Trait

If plasticity is to be manipulated, it must be treated as a trait with its own genetic architecture. Analysis of maize across multiple environments showed that loci controlling trait means and loci controlling trait plasticities are largely distinct, implying that selection on performance in any single environment does not automatically select on responsiveness (Kusmec *et al.*, 2017). This finding is consistent with the broader framework treating genotype-by-environment interaction as the population-level manifestation of plasticity, whose genomic basis can be dissected with appropriate designs (Des Marais *et al.*, 2013). Recent comparative evaluation of modelling approaches indicates that the identity of loci detected as controlling plasticity depends materially on the statistical framework applied, which imposes an important caution on the interpretation of individual studies (Arenas *et al.*, 2025). The most recent synthesis concludes that natural genetic variation for plasticity is widespread and that advances in multi-site trial analysis and genomic prediction have made it tractable, while also identifying constraints on its evolution (Schneider *et al.*, 2026).

8.2 The Controlled-Environment Gap and the Phenotyping Problem

The mechanistic literature and the agronomic literature are separated by a systematic difference in experimental conditions that is rarely acknowledged as a source of inferential risk. Mechanistic work uses seedlings, agar or hydroponic media, step changes in treatment, and constant environments; agronomic work uses mature plants, structured soil, gradual and fluctuating conditions, and competition. Root system architecture plasticity in maize under drought, low nitrogen and salinity has been characterised in hydroponic systems that afford control and non-destructive measurement, and such systems reveal substantial genotypic variation, but the relationship between hydroponic root traits and field root behaviour is not straightforward (Keerthi *et al.*, 2025).

The response to this problem has been the development of phenotyping platforms capable of resolving trait dynamics under controlled but realistic conditions, coupled with environmental characterisation sufficient to define the environment as the plant experiences it (Tardieu *et al.*, 2017). A probabilistic, scenario-dependent conception of drought tolerance follows from this work, in which the value of any trait is conditional on the frequency of specified environmental scenarios rather than absolute (Tardieu *et al.*, 2018). Genomic prediction incorporating environmental covariates has been shown to predict maize yield across European environments, demonstrating that the reaction norm can be modelled and predicted at agronomic scale (Millet *et al.*, 2019). This constitutes the most credible current bridge between plasticity as a concept and plasticity as a breeding target.

Complementing this, single-cell transcriptomic atlases of the root have resolved developmental trajectories at cell-type resolution and provide a reference against which stress-induced deviations in developmental trajectory can be assessed (Shahan *et al.*, 2022). The approach addresses a longstanding limitation of bulk profiling, in which cell-type composition changes are confounded with changes in expression per cell.

8.3 Should Plasticity be a Breeding Target?

The disagreement over whether plasticity should be selected for is genuine and is not fully resolvable with current evidence. The argument in favour holds that under increasingly variable climates a genotype able to adjust its structure to conditions will outperform a fixed genotype, and that specific plastic responses can be identified and selected. The argument against holds that breeders require yield stability, that plasticity in a trait does not entail plasticity in yield, and that responsiveness to an unreliable cue can be harmful. A critical appraisal of root plasticity as a breeding objective concluded that the case remains unproven and that plasticity should be pursued only where the specific response has demonstrated value in the target environment (Schneider & Lynch, 2020).

Table 5. Recurrent methodological limitations across the reviewed literature, their consequences for inference, and remedial design changes

Limitation	Where it recurs	Consequence for inference	Remedial design change	Supporting references
Fitness or yield not measured where adaptive value is claimed	Signalling and developmental studies across all stresses	Adaptive interpretation is unsupported; neutral and maladaptive alternatives cannot be excluded	Measure reproductive output or yield for contrasting phenotypes in both inducing and non-inducing environments	Ghalambor *et al.* (2007); Valladares *et al.* (2007)
Single stressed treatment without an environmental gradient	Most molecular studies of stress-responsive development	Cannot distinguish a change in trait mean from a change in reaction norm slope	Use at least three characterised environmental levels and model the response function	Arnold *et al.* (2019); Kusmec *et al.* (2017)
Step-change treatments in artificial media	Root developmental and signalling studies	Responses to sharp discontinuities may not reflect responses to gradual soil drying or nutrient depletion	Impose gradual, soil-based treatments with measured plant water or nutrient status	Bao *et al.* (2014); Orman-Ligeza *et al.* (2018); Tardieu *et al.* (2018)
Narrow taxonomic base	Signalling, root patterning and memory studies	Generalisation to crop species with different anatomy and life history is unverified	Replicate key findings in at least one monocotyledonous and one dicotyledonous crop	Karlova *et al.* (2021); Schneider *et al.* (2026)
Confounding of plant size with treatment effect	Biomass allocation and whole-plant architecture studies	Ontogenetic drift is misread as plastic response	Compare at common size as well as common time, or model allocation against size	Poorter *et al.* (2012)
Regulated arrest not distinguished from damage	Salinity and severe drought studies of root and shoot development	Toxicity is interpreted as an adaptive developmental programme	Demonstrate recovery on removal of the stress and assess cell viability	Munns & Tester (2008); van Zelm *et al.* (2020)
Incomplete recovery not excluded before a second stimulus	Stress memory and priming studies	Recovery kinetics are misinterpreted as memory	Demonstrate return to baseline before the second exposure; match controls for developmental stage	Crisp *et al.* (2016); Hilker *et al.* (2016)
Single-stress designs applied to multifactorial field problems	Translational and breeding-oriented studies	Trait values estimated under single stress do not transfer to combined stress environments	Include factorial stress combinations and characterise the environment with measured covariates	Peláez-Vico *et al.* (2024); Zandalinas & Mittler (2022)

Note. Remedial design changes are stated as minimum requirements rather than as complete solutions; several would need to be applied jointly to support a strong adaptive claim

Two considerations weigh on this debate. Progress in crop improvement under stress has come principally from genes conferring specific, well-characterised responses rather than from general responsiveness, and the most successful examples involve alleles whose value is tied to a defined environmental regime (Bailey-Serres *et al.*, 2019; Uga *et al.*, 2013; Xu *et al.*, 2006). At the same time, stress in the field is multifactorial, and combinations of stresses produce responses that are not predictable from single-stress studies, with effects on growth and survival that increase in severity as the number of concurrent stresses rises (Zandalinas *et al.*, 2021; Zandalinas & Mittler, 2022). Multifactorial stress combination reduces reproductive tissue performance and grain yield in ways not anticipated from individual stresses (Peláez-Vico *et al.*, 2024). If the relevant environment is multifactorial and unpredictable, the case for general responsiveness strengthens, but the difficulty of specifying which responses to select for also increases.

Table 5 summarises the methodological limitations that recur across the literature reviewed, the inferential consequence of each, and the design changes that would address them. The limitations are ordered by the severity of their consequence for causal inference rather than by frequency of occurrence, and the first three account for the majority of the interpretive difficulties identified in Sections 4 to 7.

9. Future Directions

The priorities set out here are ordered by the extent to which addressing them would reduce the inferential gap identified in this review, rather than by tractability. The first three are achievable with existing technology and would alter interpretation of a large body of published work; the remainder require methodological development.

The most immediate priority is fitness-anchored experimentation on developmental plasticity. Adaptive value is asserted throughout the mechanistic literature and demonstrated in very few cases, of which the submergence strategies remain the clearest (Hattori *et al.*, 2009; Xu *et al.*, 2006). The unresolved problem is that mutants and natural variants with altered plastic responses are almost never assessed for reproductive output in both the inducing and the non-inducing environment. The appropriate design is a reciprocal environment experiment using near-isogenic material differing in a specific plastic response, with seed number or grain yield as the outcome and with the environment characterised by measured covariates rather than treatment labels. Such experiments are feasible now for stomatal density, root angle and root cortical traits, where suitable genetic material already exists (Caine *et al.*, 2019; Chimungu *et al.*, 2014; Uga *et al.*, 2013). They would establish whether the responses catalogued over the past two decades are adaptive, neutral or costly, and would place subsequent mechanistic work on a firmer interpretive footing.

The second priority is the systematic replacement of step-change treatments with gradual, characterised environmental transitions in mechanistic studies. Hydropatterning, xerobranching and halotropism were all discovered using sharp spatial or temporal discontinuities, which was appropriate for discovery but is inadequate for establishing physiological relevance (Bao *et al.*, 2014; Galvan-Ampudia *et al.*, 2013; Orman-Ligeza *et al.*, 2018). Repeating the key experiments in soil-based systems with continuous imaging and measured water potential would determine whether the same molecular modules operate under gradual drying, and would indicate whether the responses are triggered by absolute values, by rates of change, or by spatial gradients. Where the answer differs from the plate-based result, that difference is itself informative about the environmental variable actually perceived.

The third priority is broadening the taxonomic base of mechanistic work in a targeted rather than indiscriminate manner. Comprehensive replication across species is neither feasible nor necessary; what is required is replication of a small number of load-bearing findings in species with contrasting root and leaf anatomy and contrasting life history. Systemic calcium and reactive oxygen species signalling, established largely in seedlings under imaging-optimised conditions, is a priority case because so much downstream interpretation rests on its generality (Choi *et al.*, 2014; Mittler *et al.*, 2022). Comparable replication is needed for the peptide-based root-to-shoot systems, whose developmental as opposed to physiological roles remain undefined (Ohkubo *et al.*, 2017; Takahashi *et al.*, 2018).

A fourth priority concerns the resolution of developmental trajectories rather than endpoints. Most stress phenotyping measures organs after they have formed, which cannot distinguish altered initiation from altered growth, or determine when in development the environmental information was acted upon. Combining time-resolved non-destructive imaging with single-cell transcriptomic references would permit the developmental decision point to be located (Shahan *et al.*, 2022; Tardieu *et al.*, 2017). This matters practically because interventions targeting initiation, patterning and expansion differ, and because the reversibility of a response depends on when it occurred.

A fifth priority is the deliberate design of multifactorial stress experiments with sufficient factorial structure to estimate interactions rather than merely to demonstrate that they exist. That combined stresses produce non-additive outcomes is established (Peláez-Vico *et al.*, 2024; Zandalinas *et al.*, 2021). What is not established is whether developmental responses to combined stress are predictable from single-stress responses given knowledge of the signalling interactions, or whether they require independent characterisation. Factorial designs incorporating at least three stress factors at two or more levels, with developmental as well as physiological outcomes, would answer this and would indicate whether trait values estimated under single stress can be used in multi-environment prediction.

A sixth priority concerns the cost hypothesis, which underpins several arguments about the limits of plasticity but rests on inconsistent evidence (DeWitt *et al.*, 1998; van Kleunen & Fischer, 2005). Testing it requires comparison of genotypes matched for mean phenotype but differing in plasticity, which is difficult with natural variation but is now approachable using induced variation in signalling components that alter responsiveness without altering the unstressed phenotype. A clear answer would materially affect the breeding debate, since the argument against selecting for plasticity depends in part on an assumed cost.

Finally, the agronomic value of stress memory requires assessment at the level of yield across a full growing season under field conditions. The mechanistic basis of transcriptional memory is now reasonably well defined for heat (Lämke *et al.*, 2016; Pratx *et al.*, 2023), and the necessary genetic material exists. What is absent is evidence that memory persists on agronomically relevant timescales and translates into yield protection. Given that priming would permit preparedness without constitutive cost, this is a high-value question, and a negative result would be as useful as a positive one in directing effort elsewhere.

10. Conclusions

The pathway from molecular signal to phenotypic plasticity in plants is well populated with characterised components and poorly supplied with demonstrated connections between them. Signal perception is securely established only where the environmental variable participates directly in a chemical reaction, as in oxygen sensing through cysteine oxidation, or where a hormone rather than the stress itself is the ligand, as in abscisic acid perception. For water deficit, salinity and nutrient limitation, the primary sensing step remains inferred from downstream consequences, and the density of published pathway diagrams conceals this rather than resolving it. Transduction, by contrast, is well supported: calcium and reactive oxygen species propagation, hormone networks and mobile peptide systems have been demonstrated repeatedly and with appropriate controls. The persistent difficulty is that these transduction systems are largely stimulus-general, so the specificity of developmental outcomes must arise elsewhere, and where it arises has not been determined.

Structural and developmental remodelling is the best-documented part of the chain. Root branching is positioned according to local water availability and suppressed when contact with water is lost; root angle and cortical anatomy vary in ways that alter soil exploration and metabolic cost; endodermal barriers are remodelled according to nutrient and osmotic status; aerenchyma forms under hypoxia through a regulated programme; stomatal density is set during development in response to atmospheric and hydrological conditions; and elongation responses to warmth, shade and submergence follow coherent, genetically defined programmes. These findings are individually robust. Their principal collective weakness is that the strongest mechanistic evidence and the strongest agronomic evidence originate in different studies, species and experimental scales, and no trait has been carried through the complete sequence from molecular mechanism to demonstrated yield benefit within a single system.

The evidence that such remodelling is adaptive is much weaker than its ubiquitous assertion implies. The submergence strategies provide the clearest demonstration, because the two alternative programmes are mutually exclusive and each is advantageous under a defined hydrological regime and disadvantageous under the other. Reduced stomatal density under elevated carbon dioxide and root angle modification under drought provide further conditional support. Beyond these, adaptive value is generally inferred from functional plausibility rather than measured, and the hypothesis that plasticity carries fitness costs, though theoretically well specified, has not been reliably confirmed. Confidence in general statements about the adaptive significance of plastic responses should accordingly be low, while confidence in specific, environment-matched claims can be considerably higher.

Stress memory is empirically real at the level of transcription and chromatin, with well-defined mechanisms for heat memory in particular, but claims of memory frequently fail to exclude incomplete recovery, transgenerational transmission is limited and subject to resetting, and yield-level consequences are unmeasured. Epigenetic variation can generate heritable variation in plasticity itself, which is an important proof of principle, but this has been shown using material generated by manipulating the methylation machinery rather than by environmental exposure.

The broader significance of this synthesis is that the principal obstacle in the field is inferential rather than mechanistic. The experimental systems that support strong causal claims differ systematically from the environments in which plasticity matters, and the field has generally responded by extending the mechanistic catalogue rather than by closing that gap. Whether plasticity should be a breeding target cannot be answered in general terms, because the evidence supports the value of specific responses matched to specified environmental regimes rather than the value of responsiveness as such. Progress will come from experiments that measure fitness, characterise environments as plants experience them, resolve developmental trajectories rather than endpoints, and test whether load-bearing mechanistic findings generalise beyond the systems in which they were discovered.

11. Limitations

A narrative review of this kind is subject to selection and interpretive bias that a transparent search and appraisal process reduces but cannot eliminate. Sources were selected purposively for conceptual and methodological contribution rather than exhaustively, and a different reviewer applying the same criteria could reasonably have chosen a partly different evidence base and reached somewhat different judgements about the relative weight of conflicting findings.

Access to subscription-based indexes was not available, and searching was confined to openly accessible scholarly databases and repositories. Although these provide broad coverage of the relevant literature, work indexed only in proprietary databases may have been missed. Assessment was restricted to English-language publications, which is likely to have reduced representation of regionally published research, particularly agronomic work conducted in environments differing from those where most of the cited studies were performed. Geographical representation in the underlying evidence base is itself uneven, with mechanistic work concentrated in a small number of research systems and countries.

The literature synthesised is heterogeneous in design, species, treatment definition and outcome measure to a degree that prevented quantitative synthesis. No effect sizes were pooled and no formal risk-of-bias instrument was applied, since no validated instrument spans experimental genetics, controlled-environment physiology, field agronomy and comparative ecology. Appraisal therefore

rested on structured but ultimately judgemental criteria, and the classification of disagreements as biological or methodological reflects the assessment made here rather than an externally validated standard.

Comparability among studies is further limited by inconsistent definitions of stress severity and by the frequent absence of measured plant water or nutrient status, which makes it difficult to determine whether nominally similar treatments were physiologically equivalent. Publication bias favouring positive and mechanistically interpretable results is likely in this field, particularly for mutant phenotypes and for memory effects, and would tend to inflate apparent consistency. Long-term evidence is scarce, since most studies of developmental plasticity extend over days to weeks rather than over full growing seasons or multiple generations. The field is also developing rapidly, and conclusions drawn about the state of evidence are necessarily provisional.

Declaration of AI Use

This manuscript was prepared through the intellectual contributions of the author(s) to the study design, data analysis, interpretation of results, and scholarly content. Grammarly and ChatGPT were used solely to assist with grammatical refinement and reference formatting during manuscript revision. The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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