

Molecular, Biochemical and Physiological Mechanisms Underlying Plant Adaptation to Environmental Stress: A Synthesis of Recent Evidence

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Abstract: Seldom do plants growing in their natural habitat encounter a single, isolated stress. The transcriptome, metabolome, and, eventually, plant shape are all marked differently by drought, waterlogging, high soil iron, canopy shade, and changing microbial alliances, all of which frequently coexist across time. These signatures have been broken down over the past few years by a surge of meta-analyses and machine-learning-assisted research, which has revealed both stress-specific reactions and a smaller, recurrent “core” of genes and pathways that plants appear to target regardless of the insult. Nine recent studies covering drought stress in tomatoes, flooding tolerance strategies across species, iron toxicity in rice grown on acidic soils, high-throughput enzyme phenotyping, a genome-wide functional annotation of maize under combined biotic and abiotic stress, transcription-factor cross-talk in the shade-avoidance response, an ethylene-centered meta-analysis of *Arabidopsis* stress transcriptomes, nanoparticle-mediated amelioration of drought stress, and the rhizosphere carbon economy that connects microbial support are synthesized here. When taken as a whole, these studies support a multifaceted theory of adaptation in which hormone signaling, microbial recruitment, antioxidant and osmotic adjustment, and morphological remodeling are all manifestations of a shared regulatory logic rather than distinct tactics. We discuss the implications for stress-resilient crop breeding and the areas where gaps still remain.

Keywords: DELLA proteins; transcription factors, enzyme phenomics, rhizosphere microbiome, carbon catabolite repression, QTL mapping; gene expression profiling, crop resilience breeding, cross-stress signaling convergence

1. INTRODUCTION

Figure 1. Layered Model of Plant Stress Adaptation

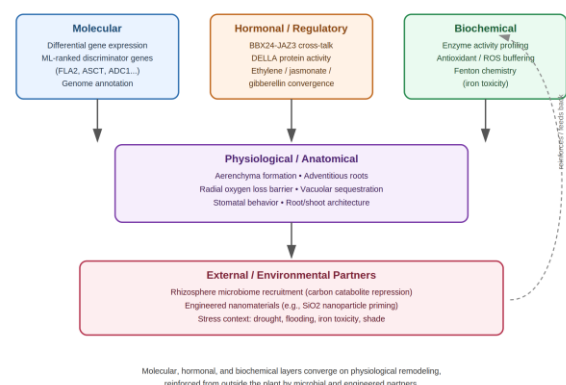


Fig -1: Layered model of plant stress adaptation across molecular, hormonal, biochemical, physiological, and external levels.

It has long been at the nexus of physiology, biochemistry, and, more recently, genetics to

understand how plants perceive and react to a hostile environment. The resolution at which we may pose the question has changed, not the question itself. Thousands of differentially expressed genes can now be routinely cataloged in a single experiment thanks to RNA-sequencing, and machine learning has made it possible for researchers to sort through that massive amount of data to find the few genes, transcription factors, or enzymes that are most important. However, traditional morphological and physiological observations — such as the elongation of a shaded stem, the shutting of a stoma under water deficit, and the swelling of aerenchyma in a wet root — remain the phenotypic anchor that any molecular explanation must ultimately explain.

Table -1: Levels of plant stress adaptation and associated regulatory components

Level	Key Mechanisms/ Processes	Associated Genes/Regulators	Stress Context	Source Study
Molecular	Differential gene expression; ML-ranked discriminator genes; genome annotation	FLA2, ASCT, ADC1, NPF7.3, BAG5, DCL2b; ethylene-core gene set	Drought; multiple abiotic stresses	Chowdhury et al. (2023); Sanchez-Munoz et al. (2025); Hayford et al. (2024)
Hormonal/Regulatory	Transcription-factor cross-talk; hormone signaling convergence	BBX24-JAZ3 interaction; DELLA proteins; ethylene, jasmonate, gibberellin	Shade avoidance; cross-stress hormonal hub	Saura-Sanchez et al. (2023); Sanchez-Munoz et al. (2025)
Biochemical	Enzyme activity profiling; antioxidant buffering; Fenton chemistry management	Carbon/nitrogen/antioxidant metabolism enzymes; ROS-scavenging systems	General stress phenomics; iron toxicity	Jammer et al. (2022); Gupta, Panda & Bauer (2025)
Physiological /Anatomical	Aerenchyma formation; adventitious roots; radial oxygen loss	Programmed cortical cell death; root architecture genes	Flooding; iron toxicity	Jia et al. (2021); Gupta, Panda & Bauer

	barrier; vacuolar sequestration			(2025)
External/Environmental	Root exudate-driven microbial recruitment; nanoparticle priming	Carbon catabolite repression circuits; engineered nanomaterials	Rhizosphere ecology; drought amelioration	Franzino et al. (2021); Haider et al. (2025)

This review compiles a number of recent studies that, while focusing on quite different stresses and species on their own, together paint a clear picture of how plants deal with hardship at three interconnected levels: the molecular (gene expression, transcription factors, signaling networks), the biochemical (enzyme activities, antioxidant systems, hormone and metabolite pools), and the physiological (root and shoot architecture, stomatal behavior, whole-plant water and nutrient relations). The rhizosphere microbiome, whose carbon economy is shaped by root exudates, and engineered nanomaterials, which are increasingly used to prime or reinforce a plant's own stress machinery, are two “external” contributors to adaptation that are easy to ignore in a purely plant-centric account.

2. MOLECULAR SIGNATURES OF STRESS: LESSONS FROM TRANSCRIPTOMIC META-ANALYSIS

Recent research has consistently shown that no single experiment, no matter how well-designed, can fully capture the range of a plant's transcriptional response to stress; instead, the response relies on genotype, tissue, developmental stage, and the exact timing of sampling. As a result, meta-analysis — combining numerous independently produced datasets and reanalyzing them under a common framework — has emerged as a crucial technique for distinguishing experiment-specific noise from long-lasting, biologically significant signal.

This method is demonstrated in tomatoes (*Solanum lycopersicum*) by Chowdhury et al. [1]. The authors classified the response into early, medium, and late stages by collecting RNA-seq data across multiple genotypes, tissue types, and six time points of progressive drought (3 to 120 h). They discovered that the number of upregulated genes increased steadily with the duration of stress, peaking at 120 h, while a smaller set of genes was induced early and remained active into the later stages. This pattern is consistent with an initial, rapid signaling wave giving way to a sustained acclimation program. The scientists constructed a gradient-boosting classifier (XGBoost) using normalized expression values to rank genes according to their contribution to differentiating watered from water-deficit samples, as opposed to merely listing differentially expressed genes. The cell-surface protein FLA2 (fasciclin-like arabinogalactan protein 2) had the highest importance score among the six genes shown to be the strongest discriminators: FLA2, ASCT, ADC1, NPF7.3, BAG5, and DCL2b. The physical mapping of three of these genes — FLA2, ASCT, and NPF7.3 — to chromosomal regions that overlap previously identified drought-related QTLs for traits like fruit weight, soluble solid content, and time-to-ripening supports the idea that the genes identified by the model are likely functional candidates for breeding programs rather than statistical artifacts.

The meta-analysis by Sanchez-Munoz et al. [9] on *Arabidopsis thaliana* follows a similar reasoning, albeit on a much bigger scale. Rather than concentrating on a single stress, the scientists asked whether several abiotic stresses converge on a common molecular core by combining an unsupervised machine-learning method with a sizable collection of publicly accessible stress-related transcriptomes. They demonstrate that a small core of stress-responsive genes, centered on ethylene production and signaling components, is consistently active in both shoots and roots during both an early window (1–6 h) and a later window (12–24 h) of exposure. The conclusion is significant: plants seem

to route a significant portion of their response through a common hormonal hub, with ethylene serving as an integrator that downstream, stress-specific branches subsequently build upon, rather than each stress triggering a unique transcriptional program.

Hayford et al. [5] addressed a different but related issue by working at the genome scale in a crop species: a large portion of the maize (*Zea mays*) genome is still functionally unannotated, which restricts what a transcriptomic experiment can truly inform a researcher. After mapping RNA-seq readings from 24 publicly accessible datasets — seven biotic and seventeen abiotic stress studies — onto the B73 reference genome (B73v5), the authors used the resulting expression patterns to give hitherto unannotated maize gene models stress-related functional annotations. This type of resource significantly expands the pool of candidate genes available to researchers studying maize responses to combined biotic and abiotic pressure, and it demonstrates how meta-analysis can serve an annotation function as much as a discovery function. However, it does not, by itself, identify a new regulatory mechanism.

3. TRANSCRIPTION FACTORS AND HORMONAL CROSS-TALK: THE CASE OF SHADE AVOIDANCE

Figure 2. BBX24-JAZ3-DELLA Node in Shade Avoidance

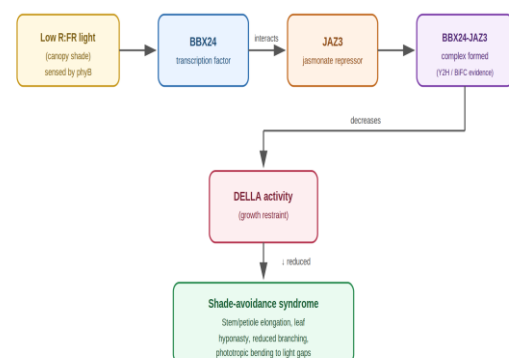


Fig -2: BBX24-JAZ3-DELLA regulatory node underlying shade avoidance.

The shade-avoidance syndrome (SAS), which includes stem and petiole elongation, leaf hyponasty, reduced branching, and phototropic bending toward gaps in the canopy, is one of the best-studied examples of a plastic developmental response to a purely informational signal (the ratio of red to far-red light, sensed primarily by phytochrome B). However, competition for light itself is a powerful environmental cue. The interaction between two regulatory proteins, JAZ3 and BBX24, to regulate this response in *Arabidopsis* was studied by Saura-Sánchez et al. [8]. They showed a direct physical contact between BBX24 and the jasmonate-signaling repressor JAZ3 using yeast two-hybrid and bimolecular fluorescence complementation experiments. They also showed that this association increases growth by decreasing DELLA protein activity. DELLA proteins are well known as growth-restraining hubs that integrate gibberellin, light, and other hormonal signals. By demonstrating that a B-box transcription factor can modulate DELLA function through a jasmonate-pathway component, this study adds a concrete molecular link between light signaling, jasmonate signaling, and the classical gibberellin-DELLA growth module. It serves as a helpful reminder that “adaptation” in plants is not limited to abiotic stress tolerance in the strict sense; the same transcription-factor logic that protects a plant from drought or flooding also controls how its leaves and stems are positioned in relation to their neighbors.

4. BIOCHEMICAL AND ENZYMATIC DIMENSIONS OF STRESS RESPONSE

Figure 4. Iron Toxicity and Tolerance Mechanisms in Rice Roots

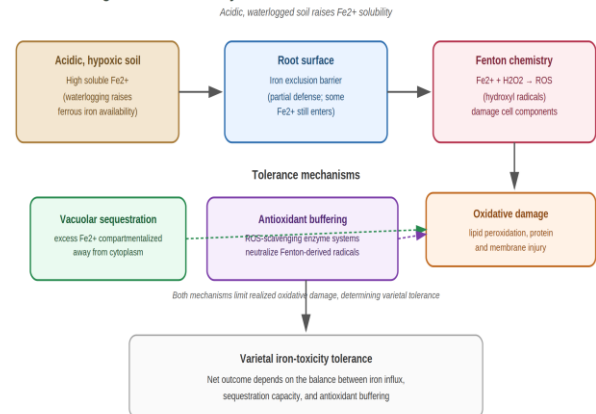


Fig -3: Iron toxicity and tolerance mechanisms (Fenton chemistry, vacuolar sequestration, antioxidant buffering) in rice roots.

Changes in gene expression are only useful when they result in modifications to metabolite flux, enzyme activity, and ultimately physiology. In their analysis of high-throughput enzyme activity profiling as a functional phenomics method, Jammer et al. [6] make this point clear. They contend that a layer of regulation — post-translational modification, allosteric control, substrate availability — that transcript abundance alone cannot reveal is captured by profiling the activities of important enzymes involved in carbon, nitrogen, and antioxidant metabolism, and that this layer is frequently what actually restricts growth or survival under stress. The practical challenge they identify is more about analyzing and visualizing the resulting datasets so that the functional information on plant development, stress response, and pathogen defense is not lost in the volume of numbers produced than it is about generating the data, since enzyme assays can now be run at a scale approaching that of transcriptomics.

One example of how a single nutrient can change from being a biochemical necessity to a source of biochemical damage is iron homeostasis. The genetics and mechanisms of iron excess tolerance in rice (*Oryza sativa*) grown on acidic soils — where

waterlogging-induced hypoxia raises the solubility and availability of ferrous iron (Fe^{2+}) to a hazardous level — were reviewed by Gupta, Panda, and Bauer [3]. Iron toxicity is a significant barrier to rice production in the areas where rice is most essential for food security, since acidic, iron-rich soils are prevalent over much of South America, Africa, and Asia. The authors compile the genes and physiological processes that collectively determine varietal tolerance, such as vacuolar sequestration, iron exclusion at the root surface, and antioxidant buffering of the reactive oxygen species that excess iron generates through Fenton chemistry. They present this as a meta-analytic synthesis of what is otherwise a fragmented literature spread across breeding programs in various countries.

5. PHYSIOLOGICAL AND ANATOMICAL STRATEGIES: FLOODING AS A CASE STUDY

Figure 3. Anatomical Adaptation of Roots to Flooding

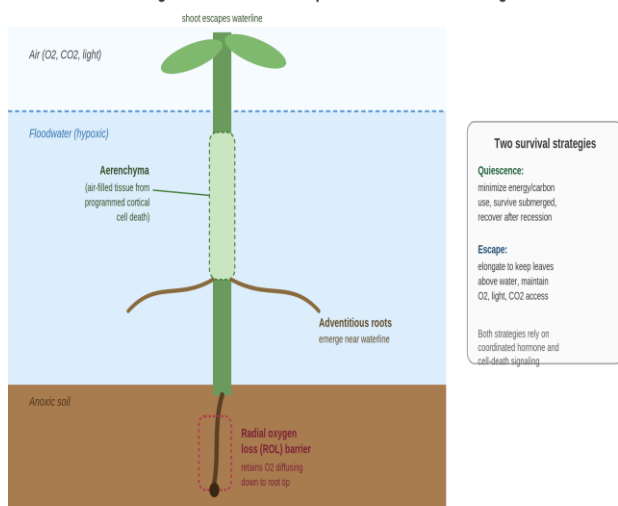


Fig -4: Anatomical adaptation of rice roots to flooding, showing aerenchyma, adventitious roots, and the radial oxygen loss barrier.

Anatomical remodeling is frequently the visible result of a plant's internal stress sensing and buffering processes, which are explained by molecular and biochemical mechanisms. Few

stresses better demonstrate this than flooding. The low-oxygen quiescence syndrome, in which plants minimize energy and carbon expenditure to prolong survival underwater and recover quickly once floodwater recedes, and the low-oxygen escape syndrome, in which plants instead elongate to keep their upper leaves above the waterline and maintain access to oxygen, light, and carbon dioxide, are the two broad strategies described in the literature reviewed by Jia et al. [4]. The development of adventitious roots, the formation of aerenchyma (air-filled tissue that promotes internal oxygen diffusion), and the induction of a radial oxygen loss barrier — which stops oxygen carried down to the root tip from leaking out into the anoxic soil before it can be used — are all described by the authors at the anatomical level. This physiological explanation is linked to the molecular and biochemical mechanisms previously discussed, because these structures are constructed through coordinated changes in cell division, cell death (in the case of aerenchyma, which frequently forms through programmed lysis of cortical cells), and hormone signaling.

6. BEYOND THE PLANT: MICROBIOME AND ENGINEERED MATERIALS AS ADAPTIVE PARTNERS

The ability of a plant to adapt to its surroundings is influenced by factors other than its genome. Franzino et al. [2] examined how the ecology of the rhizosphere, the small area of soil directly impacted by root exudates, is shaped by carbon catabolite repression, the regulatory mechanism by which bacteria prioritize which carbon sources to consume first. The order in which rhizosphere bacteria ingest the complex mixture of sugars, organic acids, and amino acids released by roots — which is controlled by catabolite repression circuits — determines which microbial populations flourish near the root.

This carbon economy is essentially an indirect but consequential layer of the plant's adaptive strategy,

because many of these bacteria go on to support the plant through nutrient solubilization, pathogen suppression, or hormone production. A genotype that exudes a specific carbon profile may recruit a microbial community better suited to the local stress, even without any change in the plant's own stress-response genes. Since it is an externally applied, manufactured intervention rather than an internal plant mechanism, the nanoparticle work of Haider et al. [7], which was previously reviewed from a biochemical perspective, belongs equally in this section. When combined with the literature on the rhizosphere, it implies that “adaptation” in an applied, agronomic sense is becoming more and more of a hybrid result: a combination of plant genetics, microbiome assembly, and possibly intentional material science intervention.

7. AN INTEGRATIVE VIEW

Taken individually, these nine studies might read as a disconnected sampling of plant science: a machine-learning analysis of tomato drought genes, a review of flooding anatomy, a rice iron-toxicity synthesis, a phenomics methods paper, a maize genome annotation effort, a shade-avoidance signalling study, an ethylene-centred Arabidopsis meta-analysis, a nanoparticle drought trial, and a rhizosphere carbon-cycling review. Read together, however, a pattern develops that is worth explaining simply.

First, the molecular response to practically any stress addressed here is not monolithic; it breaks between an early, often shared signalling phase and a later, more stress-specific acclimation phase, a divergence seen both in the tomato time-series data and in the Arabidopsis ethylene-core study. Second, hormone signaling — ethylene, jasmonate, gibberellin, and their distinct points of contact with DELLA proteins — recurs as a convergence point across conditions that would otherwise appear to be quite different, such as drought, shade, and (by extension, given

known cross-talk) flooding. Third, rather than being separate adaptations, the morphological and physiological outcomes of stress tolerance — such as aerenchyma development, iron sequestration, or a stomatal response aided by nanoparticles — are best viewed as results of these upstream regulatory choices. Fourth, and perhaps most practically, the move in almost all of these studies toward large-scale meta-analysis and machine learning reflects a methodological convergence in the field: models trained across multiple datasets are increasingly nominating candidate genes and pathways instead of relying solely on single-experiment differential expression, which is altering what constitutes strong evidence for a gene's significance.

8. CONCLUSIONS

A layered model of plant adaptation is supported by the studies reviewed here, wherein molecular signaling, biochemical buffering, and physiological remodeling function on distinct but overlapping timescales, reinforced from outside the plant by microbial partners and, increasingly, by engineered materials. The candidate genes, QTL overlaps, and regulatory nodes that this synthesis reveals — such as FLA2 and its co-identified partners in tomato, the ethylene core in Arabidopsis, the iron-tolerance loci in rice, and the BBX24-JAZ3-DELLA node in shade signaling — offer a practical starting point for marker-assisted selection or targeted gene editing.

However, a number of gaps remain. It is challenging to determine whether the molecular “core” found by meta-analysis truly predicts the physiological outcome in a particular genotype, since very few studies have integrated transcriptomic, enzymatic, and anatomical data from the same experimental material. Similarly, despite the fact that both are shown here to affect the same phenotypic endpoints, the rhizosphere and nanomaterial literatures are still

mainly distinct from the plant-genetics literature. For a field that has become very adept at producing data over the past few years and is now being asked to turn that data into resilient crops, bridging these threads — ideally through experiments specifically designed to sample molecular, biochemical, and physiological layers together, across a shared time course, and in field-relevant soil conditions — is probably the most fruitful next step.

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