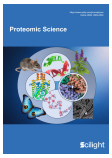
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Review

Heat and Cold Stress in Plants: Comparative Proteomic Insights into Stress Responses and Tolerance

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Abstract: Heat and cold stress are major abiotic constraints on plant growth, development, reproduction, and crop productivity. Recent advances in mass spectrometry have expanded plant thermal-stress proteomics from gel-based protein profiling to multiplexed tandem mass tag (TMT), data-independent acquisition (DIA), and post-translational modification (PTM)-resolved approaches. Studies across model plants and crops reveal both shared responses, including proteostasis, reactive oxygen species (ROS) management, metabolic adjustment, and maintenance of photosynthetic function, and stress-specific responses involving heat shock protein networks, membrane remodeling, phosphorylation, and cold-acclimation processes. However, differential protein abundance or modification is not equivalent to functional importance. This review therefore distinguishes three levels of evidence: stress-associated proteins identified through differential abundance or modification, candidate biomarkers that reproducibly distinguish contrasting phenotypes, and functional determinants supported by genetic, biochemical, or transgenic evidence. We first compare heat- and cold-responsive proteomes across species, tissues, developmental stages, and stress combinations, and then examine the transition from discovery proteomics to functional characterization. Particular attention is given to temperature sensing, proteostasis, photosynthetic protein turnover, and PTM-dependent regulation. Finally, we discuss proteomics-assisted breeding, technical and conceptual limitations, and emerging directions including PTM-resolved, single-cell and spatial proteomics and multi-omics integration. The central challenge is to move from increasingly comprehensive lists of responsive proteins toward experimentally validated mechanisms and deployable strategies for improving crop resilience under realistic thermal stress.

Keywords: heat stress; cold stress; plant proteomics; mass spectrometry; crop breeding; abiotic stress tolerance

1. Introduction

Temperature extremes are important constraints on plant growth and productivity, and their effects are becoming increasingly relevant to crop production under climate variability. Heat and cold cause partly overlapping but physiologically distinct disturbances. Heat stress can destabilize proteins, impair photosynthesis, alter membrane properties, and disrupt cellular metabolism, whereas cold stress reduces membrane fluidity, affects enzyme activity and water relations, and perturbs cellular homeostasis. Both stresses can increase oxidative pressure and require coordinated adjustment of metabolism, signaling, and protein quality control [1,2].

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Proteomics provides a direct view of these responses at the protein level and can therefore complement transcriptomic measurements. Recent studies have reported changes in proteins associated with photosynthesis, chaperone activity, ROS metabolism, carbohydrate and amino-acid metabolism, protein turnover, and stress signaling across diverse plant systems. Comparative experiments between tolerant and sensitive genotypes are particularly useful for identifying proteins associated with contrasting phenotypes, while time-resolved studies can distinguish early regulatory events from later metabolic adjustment [3–6]. Importantly, these observations are strongly influenced by tissue, developmental stage, stress intensity, duration, and recovery conditions [6–8].

Quantitative mass spectrometry has expanded the scale and depth of thermal-stress proteomics. TMT and related isobaric-labeling strategies support multiplexed comparisons, whereas DIA-based workflows provide reproducible label-free quantification [9]. Increasingly, proteomic studies also measure PTMs rather than total protein abundance alone. For example, DIA-based phosphoproteomics in tomato fruit detected extensive phosphorylation changes after a short cold shock without corresponding changes in total protein abundance, illustrating how early signaling can be missed by conventional abundance profiling [10]. Similarly, maize phosphoproteomics identified 1594 phosphopeptides assigned to 875 proteins during heat stress, with changes linked to translation, protein turnover, chaperone interactions, and MAPK-associated signaling [11].

Despite these advances, the evidentiary strength of thermal-stress proteomics varies considerably. A protein that changes in abundance under stress is stress-associated, but this alone does not establish that it contributes to tolerance. A protein that repeatedly discriminates tolerant and sensitive genotypes may be considered a candidate biomarker, but it still requires independent validation. Functional determinants require stronger evidence, such as gain- or loss-of-function experiments, biochemical validation, or consistent genetic evidence. Throughout this review, these categories are kept distinct to avoid equating proteomic association with causality

This mini-review focuses mainly on recent literature from 2021–2026 and follows a comparative framework: first, what proteins and pathways change under heat and cold stress; second, which candidates have been functionally characterized; and third, how proteomic information can be translated into breeding and biotechnology. The review also considers technical limitations and emerging approaches that may improve spatial, temporal, and regulatory resolution.

2. Proteomic Responses and Identification of Heat- and Cold-Responsive Proteins in Plants

2.1. Heat-Responsive Proteomes across Species and Tissues

Heat-responsive proteomes have been characterized in *Arabidopsis*, rice, maize, wheat, and other plant systems. In *Arabidopsis thaliana* seedlings, ^{15}N metabolic labeling combined with protein-turnover analysis showed that elevated temperature altered the turnover dynamics of hundreds of proteins and that the magnitude of the response differed between shoots and roots, emphasizing that thermal proteostasis is organ-specific [3]. This type of experiment extends conventional differential-abundance analysis by considering protein replacement and stability rather than abundance alone.

Reproductive tissues provide another important perspective because heat stress can strongly affect fertility. In rice anthers, comparative proteomics of Moroberekan, IR64, and Nagina22 under short- and long-term heat treatments associated the thermotolerant Nagina22 genotype with stronger responses in unfolded-protein binding, amino-acid metabolism, vitamin E biosynthesis, and cellular homeostasis [4]. A separate comparison of Huang Huazhan and Yang Dao6 at flowering identified differences in antioxidant, hormone-associated, protein-processing, and carbohydrate-metabolism responses [7]. These studies support the view that reproductive thermotolerance depends on coordinated proteome remodeling rather than a single universal heat-responsive protein.

Heat effects on reproductive tissues can also involve membrane and surface-associated processes. Combined lipidomic and physiological analysis in wheat has linked heat stress with changes in lipid composition and membrane-associated processes in anthers, highlighting the importance of membrane remodeling alongside protein-level responses [12]. More broadly, TMT-based proteomic and transcriptomic analysis of heat-stressed systems has shown that proteomic responses can capture coordinated changes in protein folding, metabolism, and stress defense that are not fully represented by transcript abundance alone.

2.2. Cold-Responsive Proteomes across Species and Tissues

Cold responses also involve extensive proteome remodeling, but the timing and regulatory level of the response depend strongly on the stress regime. In the alpine plant *Chorispora bungeana*, quantitative proteomics under freezing conditions identified 302 differentially accumulated proteins. Early responses were associated with signaling and stress protection, whereas prolonged exposure involved broader changes in RNA-related processes and metabolism [8]. In winter rapeseed (*Brassica napus*), comparative proteomics between cold-tolerant and cold-

sensitive cultivars identified extensive differences in proteins associated with ROS scavenging and secondary metabolism, providing candidate pathways associated with enhanced cold tolerance [5].

Recent multi-omics studies further demonstrate that phosphorylation can dominate early cold responses. In tobacco seedlings exposed to 4 °C for 24 h, proteomics identified 153 and 212 differentially accumulated proteins in shoots and roots, respectively, whereas hundreds of differential phosphopeptides were detected in both tissues. The results implicated phosphorylation of kinases and transcription factors in chilling signaling and showed that shoots and roots differed in their downstream responses [6]. These findings are consistent with the broader principle that early cold signaling can occur through PTM changes before substantial remodeling of total protein abundance.

Tomato fruit provides a particularly clear example of this distinction. DIA-based proteome and phosphoproteome profiling after a 30-min cold shock detected more than 11,000 proteins and more than 24,000 high-confidence phosphosites; approximately 10% of quantified phosphopeptides changed significantly, while no corresponding global changes in protein abundance were observed [10]. Together, these studies indicate that cold stress should not be viewed solely as a differential-abundance problem. The timing of sampling and the inclusion of PTM measurements can substantially alter the biological conclusions.

2.3. Proteomic Responses under Combined Stress

Combined stress experiments are important because field environments rarely expose crops to a single stress in isolation. A 2025 study screened 45 maize inbred lines under combined drought and heat stress and then compared the leaf proteomes of contrasting lines. The identified proteins were associated with defense, metabolism, photosynthesis, and structural functions, illustrating that combined stress can generate proteomic patterns that are not readily inferred from single-stress experiments [13]. These findings are relevant to field conditions, but they should not be interpreted as evidence that every responsive protein specifically confers tolerance: some changes may reflect injury or general stress exposure, whereas others may distinguish more tolerant genotypes. Disentangling these possibilities requires comparisons with matched control, heat-only, and drought-only treatments, alongside combined-stress treatments and physiological measurements. Such factorial designs help determine whether the combined response is additive or differs from the responses to individual stresses. The current evidence base represented here is limited, however, and further comparative proteomic studies across crops, genotypes, stress intensities, and sampling times are needed before general mechanisms of combined-stress tolerance can be established [13–15].

Proteomic responses under combined stress should therefore be interpreted in relation to the experimental design, genotype, tissue, and sampling time. Integration with physiological phenotyping and other omics layers may help distinguish general stress responses from candidate mechanisms of tolerance [13–15].

2.4. Evolution of Proteomic Strategies

Proteomic workflows have progressed from two-dimensional gel electrophoresis and spot-based identification toward high-resolution, gel-free mass spectrometry. TMT and related multiplexed methods facilitate controlled comparisons among genotypes and treatments, while DIA improves measurement consistency and can provide deep proteome coverage [9]. These advances have increased the number of proteins that can be quantified, but greater coverage does not by itself increase causal evidence.

PTM-resolved proteomics has added an important regulatory dimension. Maize phosphoproteomics identified 1594 phosphopeptides assigned to 875 proteins during heat stress, with enrichment in translational and post-translational regulation, protein turnover, and MAPK-associated processes [11]. In rice, integrated proteome and ubiquitylome profiling of cold tolerance associated with the rice growth-regulating factor 4 gene (*OsGRF4*) quantified thousands of proteins and ubiquitination sites, providing evidence that cold responses can involve extensive regulation at both abundance and ubiquitination levels [16]. The broader implication is that the appropriate analytical level depends on the biological question: total proteomics is well suited to metabolic and structural remodeling, whereas phosphoproteomics and other PTM workflows are particularly informative for rapid signaling. Table 1 summarizes representative recent proteomic studies of heat and cold stress, highlighting the plant system, tissue or developmental stage, proteomic strategy, and major biological responses identified. Together, these studies illustrate both the common proteomic features of thermal stress and the substantial variation among experimental systems.

Table 1. Recent proteomic studies revealing heat- and cold-responsive proteins and pathways in plants.

Stress	Plant Species	Tissue/Stage	Proteomic Strategy	Main Response	References
Heat	*Arabidopsis thaliana*	Seedlings	^{15}N metabolic labeling + turnover analysis	Heat altered protein-turnover dynamics and showed organ-specific responses	[3]
Heat	Rice: Moroberekan, IR64, Nagina22	Anthers	LC-MS/MS proteomics	Nagina22 showed responses involving proteostasis, amino-acid metabolism and vitamin E biosynthesis	[4]
Heat	Rice: Huang Huazhan and Yang Dao6	Anthers at flowering	TMT proteomics + physiology/transcripts	Contrasting genotypes differed in antioxidant, hormone-associated and protein-processing responses	[7]
Heat + drought	Maize inbred lines	Leaves, early vegetative stage	Quantitative proteomics	Contrasting lines differed in defense, photosynthesis and metabolic responses under combined stress	[13]
Heat	Maize	Leaves/seedlings	iTRAQ phosphoproteomics	1594 phosphopeptides mapped to 875 proteins; signaling, translation and protein turnover were prominent	[11]
Cold/freezing	*Chorispora bungeana*	Seedlings	TMT quantitative proteomics	302 differential proteins indicated early signaling/protection followed by metabolic adjustment	[8]
Cold	Tobacco	Shoots and roots	Proteome + phosphoproteome	Phosphorylation changes exceeded total-protein changes and differed between organs.	[6]
Cold	Tomato	Red-ripe fruit	DIA proteome + phosphoproteome	Rapid phosphoproteome remodeling occurred without detectable global protein-abundance change	[10]
Cold	Rice	Seedlings	Proteomics + ubiquitylome + PRM	*OsGRF4*-associated cold tolerance involved coordinated protein-abundance and ubiquitination changes	[16]

3. Functional Characterization and Proteomics-Assisted Improvement of Thermal Tolerance

3.1. Heat- and Cold-Stress Sensing and Signaling

Proteomic surveys identify candidate signaling proteins, but the strongest evidence for sensing and signaling comes from experiments that directly manipulate the candidate. Heat shock transcription factors and heat shock proteins form a well-established heat-response network, with HsfA1-family factors functioning upstream of many heat-responsive genes. Recent work has also identified TWA1 as a temperature-sensing transcriptional co-regulator in *Arabidopsis thaliana*. TWA1 changes its conformation at elevated temperature, accumulates in nuclear subdomains, and is required for induction of *HSFA2* (heat shock transcription factor A2) and heat shock proteins (HSPs) for basal and acquired thermotolerance [17]. This provides direct functional evidence for a temperature-sensing component rather than a proteomic association only.

Cold sensing and signaling are similarly distributed across membrane-associated and intracellular pathways. Calcium-permeable channels, protein kinases, and transcription factors can undergo rapid phosphorylation changes during chilling. In *Arabidopsis thaliana*, differential phosphorylation of cyclic nucleotide-gated channel 20 (*CNGC20*) was shown to modulate calcium-mediated freezing tolerance, illustrating how PTM analysis can connect a candidate signaling protein to a measurable tolerance phenotype [18]. Tobacco phosphoproteomics further identified calcium-dependent protein kinases (CDPKs), receptor-like kinases, and several transcription factors among chilling-responsive phosphoproteins [6]. These studies support a model in which early thermal signaling is often encoded in protein modification and activity rather than abundance alone.

3.2. Genetic and Transgenic Validation of Candidate Tolerance Genes

Genetic and transgenic experiments provide a stronger basis for functional interpretation than differential abundance alone. Overexpression of the wheat salt stress root protein gene (*TaSSRP*) in tobacco increased several physiological indicators of heat tolerance, supporting a functional role for this candidate in heat response [19]. Likewise, a thermostable Rubisco activase variant from *Oryza australiensis* improved growth and seed production of transgenic rice under severe heat, providing direct evidence that protein thermostability can limit photosynthetic performance under heat stress [20].

Cold-tolerance studies provide additional examples. Overexpression of the voltage-dependent anion-selective channel gene (*MsVDAC*) from *Medicago sativa* in tobacco increased cold and drought tolerance and

altered ROS and osmolyte responses [21]. In *Medicago falcata*, overexpression of the eukaryotic elongation factor 2 gene (*MfEF2*) increased cold tolerance and was accompanied by broad proteome changes, including 336 differentially accumulated proteins, linking translation machinery to cold-response reprogramming [22]. These studies illustrate how proteomics can be used after genetic validation to determine downstream mechanisms rather than being treated as proof of function by itself.

OsGRF4 provides a more recent example of PTM-resolved functional proteomics. Genetic manipulation of *OsGRF4* altered cold tolerance, while integrated proteome and ubiquitylome analyses revealed extensive changes in protein abundance and ubiquitination [16]. Similarly, the rice component of oligomeric Golgi complex 3 gene (*COG3*) was investigated using QTL mapping, loss- and gain-of-function experiments, and molecular analysis. The results showed that *COG3* positively regulates chilling tolerance through interaction with OsFtsH2 and maintenance of D1 turnover in chloroplasts [23]. These examples illustrate the higher evidentiary value of integrating proteomic observations with genetic perturbation.

3.3. Photosynthetic Apparatus as a Shared Functional Target

Photosynthetic machinery is a recurrent target of both heat and cold stress, but the mechanisms differ. Under heat stress, Rubisco activase can become a limitation to Rubisco activation and photosynthetic recovery because its thermal stability is lower than that of Rubisco itself [20,24]. Under chilling, damage to photosystem II requires efficient turnover of the D1 reaction-center protein. The *COG3*-OsFtsH2 module provides direct evidence that regulation of chloroplast proteolysis is required to maintain D1 turnover and chilling tolerance in rice [23]. Thus, protein quality control is a common functional theme even though the affected targets and regulatory mechanisms differ between temperature extremes.

Proteostasis and redox control are additional points of convergence. Heat strongly activates chaperone networks that limit protein aggregation, whereas cold responses frequently involve antioxidant systems, membrane protection, and metabolic adjustment. Phosphoproteomic studies indicate that these responses can be initiated rapidly through signaling events before large changes in protein abundance become detectable [6,10]. Accordingly, proteomic interpretation should consider the temporal sequence from sensing and PTM regulation to protein abundance, metabolism, and physiological phenotype. Proteomic profiling is primarily a discovery tool and does not, by itself, establish that a stress-responsive protein contributes directly to tolerance. Table 2, therefore summarizes representative proteins and regulatory modules for which proteomic observations have been complemented by genetic, transgenic, biochemical, or molecular evidence. These examples illustrate the transition from identifying stress-associated proteins to establishing functional roles in heat or cold tolerance and provide a basis for evaluating the translational potential of proteomics-assisted candidate discovery.

Table 2. Functionally characterized proteins and regulatory modules associated with heat and cold tolerance.

Stress	Plant/System	Protein/Gene	Functional Evidence	Proteomic Evidence	Significance	References
Heat	Arabidopsis	TWA1	Mutant and ectopic-expression analyses established a role in basal and acquired thermotolerance.	Molecular expression and functional analyses.	Direct evidence for a temperature-sensing regulator	[17]
Heat	Wheat → tobacco	TaSSRP	Heterologous overexpression improved physiological performance under heat	No direct discovery-proteomics component	Functional validation of a candidate stress-response protein	[19]
Heat	Rice	Rca-Oa	Thermostable Rubisco activase improved growth and seed production under severe heat	Protein abundance of recombinant Rca was quantified	Links protein thermostability to heat tolerance	[20]
Cold	*Arabidopsis*	*CNGC20*	Differential phosphorylation affected calcium-mediated freezing tolerance.	Phosphoproteomic/molecular evidence.	Connects PTM-dependent channel regulation with freezing tolerance.	[18]

Table 2. *Cont.*

Stress	Plant/System	Protein/Gene	Functional Evidence	Proteomic Evidence	Significance	References
Cold	Rice	*COG3*-OsFtsH2-D1	QTL, mutants, overexpression and interaction assays linked *COG3* to chilling tolerance and D1 turnover	Molecular protein-turnover analysis	Strong genetic evidence for chloroplast proteostasis in chilling tolerance	[23]
Cold	Rice	*OsGRF4*	Genetic manipulation altered cold tolerance	Proteome + ubiquitylome + PRM	Links a regulatory protein with PTM-resolved cold-response remodeling	[16]
Cold	*Medicago falcata* → tobacco	*MfEF2*	Overexpression increased cold tolerance	iTRAQ identified 336 differential proteins	Links translation machinery with downstream proteome remodeling	[22]
Cold	*Medicago sativa* → tobacco	*MsVDAC*	Overexpression improved cold and drought tolerance	Physiological and molecular validation	Supports a mitochondrial contribution to cold tolerance	[21]

3.4. Proteomics-Guided Strategies for Improving Tolerance

Proteomics can contribute to tolerance improvement through four complementary strategies. First, comparative proteomics can prioritize candidate genes or proteins for genetic testing, especially when candidates are reproducible across independent tolerant-versus-sensitive comparisons. Second, PTM-resolved proteomics can identify regulatory switches that are not apparent from total protein abundance, as shown by cold-responsive phosphoproteomes and the *OsGRF4* ubiquitylome [16,18]. Third, pathway-level analysis can prioritize coordinated biological processes rather than isolated proteins. This is particularly relevant for ROS scavenging, proteostasis, photosynthetic maintenance, and membrane remodeling, where tolerance is likely to depend on multiple interacting components. Fourth, combined proteomic and lipidomic profiling can identify protein targets associated with membrane and cuticular remodeling under heat stress [12]. These approaches are best regarded as candidate-generation and prioritization frameworks until validated by genetic, biochemical, and physiological experiments.

4. Applications in Plant Breeding, Limitations, and Emerging Directions

4.1. Applications in Plant Breeding

Proteomics can support breeding through biomarker discovery, candidate-gene prioritization, QTL refinement, and integration with genomic and phenotypic information. Proteins that reproducibly distinguish tolerant and sensitive genotypes may provide screening markers, but their use should be separated from claims about mechanism. Combining proteomic data with known QTLs can reduce the candidate space and provide genetic context for subsequent functional testing. Proteomics can also complement phenotyping approaches such as pollen-viability based heat susceptibility indices, which provide relatively rapid measurements of reproductive heat response in wheat [25].

Multi-omics integration provides a broader route toward breeding applications. Proteomic measurements can be combined with genomic, transcriptomic, metabolomic, and phenomic data to prioritize candidates and identify coordinated tolerance signatures [14,15]. Machine-learning approaches may assist this integration, but their predictive performance depends on the quality, scale, independence, and field relevance of the training data. Consequently, model-based prioritization should complement, rather than replace, biological validation.

4.2. Technical and Conceptual Limitations

Plant proteomics remains technically challenging because plant tissues contain abundant proteins, rigid cell walls, secondary metabolites, and highly variable protein abundance. These factors can complicate extraction, digestion, peptide recovery, and mass-spectrometric detection. The challenges become more pronounced in low-input and single-cell workflows, where sample loss and limited material can constrain coverage [9,26].

Comparability across studies is also limited by differences in temperature intensity, treatment duration, recovery conditions, tissue, developmental stage, genotype, extraction procedures, statistical thresholds, and

proteomic platform [3–9,12]. A list of 1000 differential proteins from a deep DIA experiment should therefore not be interpreted as directly equivalent to a list of several dozen spots from a gel-based study, because differences in analytical coverage and quantification methods affect the number and type of proteins detected [9]. Time resolution is another important limitation because rapid PTM changes may precede changes in total protein abundance, whereas late sampling may primarily capture downstream metabolic adjustment [6,10,11].

Most importantly, many thermal-stress proteomic studies remain associative. Differential abundance, pathway enrichment, or correlation with tolerance can generate biologically useful hypotheses but cannot establish that a protein is required for tolerance [4–6,13,16]. Stronger causal inference requires gain- or loss-of-function experiments, allelic validation, biochemical assays, or convergent genetic and physiological evidence [17–23]. Field conditions add another layer of complexity because heat and cold frequently occur together with drought, high light, nutrient limitation, or pathogen pressure [1,2,14,15].

4.3. Emerging Directions

Single-cell and spatial proteomics offer an emerging route to resolving cell-type-specific responses that are obscured by whole-organ averaging. Early plant studies demonstrate the feasibility of single-cell proteomic measurements, although sensitivity, throughput, sample preparation, and spatial preservation remain important limitations [26]. These approaches may become particularly useful for comparing vascular, epidermal, mesophyll, reproductive, and meristematic responses to thermal stress.

PTM-resolved proteomics is likely to remain central to mechanistic studies. Phosphorylation, ubiquitination, SUMOylation, and acetylation can alter protein activity, localization, stability, or interactions without changing total protein abundance. The rapid phosphoproteomic responses observed in tomato, tobacco, and maize demonstrate the value of time-resolved PTM measurements for identifying early signaling events [6,10,11].

Greater integration of proteomics with genomics, transcriptomics, metabolomics, phenomics, and environmental measurements should also improve interpretation of thermal tolerance. The most useful future datasets will connect molecular responses to quantitative phenotypes across genotypes and environments rather than generating isolated lists of differentially abundant proteins. Finally, functional validation should be incorporated earlier in the workflow, with candidate selection followed by gene editing, transgenic analysis, biochemical testing, and field or near-field multi-stress evaluation.

5. Conclusions and Perspectives

Proteomic studies have expanded the understanding of plant responses to heat and cold across species, tissues, and developmental stages. Several response themes recur across temperature extremes, including proteostasis, ROS management, metabolic adjustment, membrane protection, and maintenance of photosynthetic function. At the same time, heat and cold produce distinct regulatory signatures, particularly in heat shock protein networks, membrane remodeling, and PTM-dependent signaling.

The strength of evidence varies substantially among studies. Most comparative proteomic surveys identify stress-associated proteins or candidate biomarkers, whereas a smaller number of studies combine proteomics with genetic or transgenic experiments that support a functional role. Examples such as TWA1, thermostable Rubisco activase, *CNGC20*, *COG3*, *OsGRF4*, *MsVDAC*, and *MfEF2* illustrate how proteomics can be connected to functional evidence and physiological outcomes.

Future progress will depend on resolving thermal responses across time, cell type, and regulatory level. PTM-resolved, single-cell and spatial proteomics, together with multi-omics and quantitative phenotyping, can improve mechanistic resolution. However, translation into crop improvement will require reproducible candidates, genetic validation, realistic multi-stress testing, and evaluation under field-relevant conditions. The key opportunity is therefore to move from cataloguing responsive proteins toward integrating proteomic association with functional evidence and deployable breeding or biotechnology strategies.

Author Contributions

Conceptualization, S.B.M.; formal analysis, S.B.M. and P.Y. writing—original draft, S.B.M.; writing—review and editing, S.B.M., Y.G. and P.Y.; visualization, S.B.M.; investigation, S.B.M.; supervision, P.Y.; project administration, Y.G. and P.Y. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

No data was generated in this work.

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Conflicts of Interest

Given the role as an Editorial Board Member of Proteomic Science, Pingfang Yang had no involvement in the peer review of this paper and had no access to information regarding its peer-review process. Full responsibility for the editorial process of this paper was delegated to another editor of the journal.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the author(s) used OpenAI ChatGPT (GPT-4) in order to improve the readability and English grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Abbreviations

DEP—differentially expressed protein; DIA—data-independent acquisition; TMT—tandem mass tag; PTM—post-translational modification; MS—mass spectrometry; QTL—quantitative trait locus; HSP—heat shock protein; ROS—reactive oxygen species; CDPK—calcium-dependent protein kinase.

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