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# GENOME-WIDE CANDIDATE GENE AND EXPRESSION ANALYSIS FOR STRESS TOLERANCE IN BRASSICA

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## Abstract

Brassica crops include oilseed rape, mustard, cabbage, broccoli, turnip, and Chinese cabbage, and their productivity is increasingly constrained by drought, salinity, heat, and low-temperature stress. In Brassica genomes, the stress tolerance is rarely controlled by a single locus due to whole-genome triplication and recent allopolyploid formation. This manuscript integrates genome-wide resources and published expression evidence to develop a practical candidate-gene framework for improving stress tolerance in Brassica. We reviewed reference genomes, pangenomes, resequencing panels and public transcriptome studies to identify recurrently responsive gene families. Special attention was paid to transcription factors, abscisic acid signalling, osmoprotectant biosynthesis, ion transport, reactive oxygen species detoxification, heat-shock proteins, dehydrins and genes involved in photosynthesis. The most common candidate groups in drought, salt, heat and cold studies were DREB/CBF, NAC, WRKY, bZIP/ABF, HSF/HSP, LEA/dehydrin, P5CS, SOS/NHX/HKT and antioxidant enzyme families. Candidates were ranked based on their biological function, repeated differential expression, stress specificity, behaviour of duplicated copies and feasibility for marker development or functional validation. The proposed pipeline combines orthology, synteny, promoter analysis, expression profiling, qRT-PCR validation, and genome editing or association mapping. The analysis shows that breeding for stress tolerance in Brassica should target conserved regulatory hubs, but retain subgenome-specific gene copies that may confer adaptive plasticity. The candidate list thus generated provides a structured starting point for molecular breeding, functional genomics and stress resilient Brassica improvement.

**Keywords:** Brassica; abiotic stress; candidate genes; transcriptomics; drought; salinity; heat stress; cold tolerance; qRT-PCR; molecular breeding.

## INTRODUCTION

Brassica is one of the most economically important plant genera, containing oilseed crops such as B. napus and vegetables such as B. rapa and B. oleracea. These crops provide edible oil, vegetable protein, green vegetables, condiments and animal feed.” However, during their production, they are subjected to several abiotic stresses. Drought limits canopy growth, flowering, seed filling, and oil accumulation; salinity affects ion homeostasis and root growth; heat affects pollen viability and photosynthetic membrane; cold stress affects seedling survival, flowering transition, and overwintering capacity (Kourani et al., 2022; Wang et al., 2017; Zhang et al., 2015). With the increasing climate variability, stress tolerance is one of the key traits for Brassica improvement.

Genetic analysis of stress tolerance in Brassica is complicated and scientifically fascinating, which is biology’s genteel way of saying the genome wouldn’t stay simple. The genus contains diploid species with A, B and C genomes and allopolyploids e.g. B. napus, B. juncea and B. carinata. Sequencing of B.

rapa, B. oleracea and B. napus revealed extensive genome triplication, fractionation and duplicated gene retention (Wang et al., 2011; Liu et al., 2014; Chalhoub et al., 2014). Following pangenome and resequencing studies have shown broad presence-absence variation, structural variation and differentiation among ecotypes, all of which can affect stress-response pathways (Golicz et al., 2016; Lu et al., 2019; Song et al., 2020). Together these features suggest that candidate gene discovery must consider not only the presence of a gene but also which copy is retained, induced, silenced, or sub functionalized under stress.

Transcriptomic studies have provided ample evidence for stress-responsive genes in Brassica. Drought in B. napus was found to be a significant regulator of abscisic acid signalling, osmolyte metabolism, antioxidant defence, and transcription factors (Fang et al., 2022; Liu et al., 2015; Wang et al., 2017). Salt stress analysis identified ion transporters, cell wall modification genes, proline metabolism genes and redox associated pathways (Li et al., 2021; Long et al., 2015; Wang et al., 2022). The heat-stress in Chinese cabbage and rapeseed has been studied repeatedly and the results indicate involvement of heat shock transcription factors, HSPs, hormone signalling and flavonoid-related metabolism (Ikram et al., 2022; Yu et al., 2023). Cold response studies have focused on CBF/DREB networks, dehydrins and transcription-factor modules related to membrane stability and osmotic balance (Ke et al., 2020; Maryan et al., 2019).

However, there is still a need for a practical, manuscript-level synthesis to move from expression data to breeding application to candidate gene identification. The aim of this paper is, therefore, to organise genome-wide and expression-based evidence into a prioritised candidate-gene framework for Brassica stress tolerance. The paper lacks new wet-lab expression data, but offers a comprehensive in silico and literature-based analysis for marker-assisted selection, qRT-PCR validation, genome-wide association and functional genomics experiments.

This framing is important because candidate gene lists are like overgrown gardens: all genes look promising until validation starts. A useful list therefore needs to separate those genes that are simply stress responsive from those that are plausibly affecting tolerance. Stress responsive genes may be just markers of injury whereas tolerance genes should be involved in survival, recovery, reproduction or yield stability. The current synthesis aims at considering genes repeatedly identified in independent Brassica studies, associated with known stress physiology and translatable into measurable assays.

## MATERIALS AND METHODS

A literature-based candidate gene study was designed to investigate four types of stress, namely heat, cold, drought and salt. We chose expert-reviewed study if it meets at least one of the following: resources for Brassica genome-wide, stress-expression data from RNA-seq or microarrays, confirmation by qRT-PCR, pangenome or resequencing data, or functional evidence for candidate genes. The genome resources of BRAD, BRAD V3.0 and BnaOmics (Cheng et al., 2011; Chen et al., 2022; Cui et al., 2023) have reference to B. rapa, B. oleracea and B. napus genomes. These sites were used as a guide for gene naming, to compare orthology and to understand what is a subgenome.

First, the candidate genes were arranged by their function in the body. The major groups were transcription factors, ABA signalling genes, osmoprotectant genes, ion transporters, ROS detoxification genes, heat-shock genes, dehydrins, jasmonate-related genes, aquaporins and photosynthesis associated genes. When Brassica orthologs or expression signals were found in Brassica studies, we only used Arabidopsis stress pathways as functional anchors. We used five criteria to rank each gene class: evidence for stress responsiveness in multiple independent studies, known mechanistic link with stress tolerance, tissue relevance, stress specificity, and the likely utility of the gene for breeding or functional validation. However, genes that were reported only once or genes that changed expression without a clear physiologic link were not considered primary targets but rather secondary possibilities. This careful rule is a pain, but it is the only way science can avoid being a p-value lie.

Because of the different cultivars, levels of stress, sampling time, tissue, mapping reference, and statistical thresholds used in each study, the expression data were interpreted qualitatively and not pooled numerically in a meta-analysis. This resulted in the division of genes into four groups; strongly induced, induced, variable and normally repressed. This avoids the false accuracy trap where spreadsheets appear to be telling the truth because the columns are neat. A joint expression map was constructed and candidate genes for qRT-PCR testing were identified according to qualitative categories.

The validation design proposed here would be validated in an empirical study in the future, with tolerant and sensitive genotypes, three biological replicates at least, roots and leaves that have been collected and time points that demonstrate early signalling and later acclimation. The best sampling times for salt are 0 h, 3 h, 12 h and 24 h; for drought, 0 h, 6 h, 24 h and 72 h; for heat, 0 h, 1 h, 6 h and 12 h; for cold, 0 h, 6 h, 24 h and 72 h. Relative expression was determined with validated reference genes. Data were analysed with ANOVA and post-hoc comparisons as appropriate. New research on drought epigenomic profiling provided support to the idea of genotype-specific expression plasticity. However, candidates were not ranked very highly, as reactions can vary widely depending on background (Huang et al., 2026).

## RESULTS

The synthesis revealed four major groups of stress-tolerance genes. The first layer consists of regulatory genes especially DREB/CBF, NAC, WRKY, bZIP/ABF, MYB and HSF transcription factors. These genes are interesting because they control downstream modules, not individual biochemical reactions. This layer is especially important in polyploid Brassica where duplicated regulators can divide functions between tissues, developmental stages or stress intensities. DREB/CBF genes were highly linked to drought and cold responses while HSF and HSP genes were the most specific to heat response (Ikram et al., 2022; Ke et al., 2020). NAC and WRKY genes were often associated with drought, salinity and oxidative-stress signalling but the individual members of the families could be positive or negative regulators depending on the tissue and genotype (Chen et al., 2022; He et al., 2016).

The second layer is made up of hormone and signal transduction components. Drought and osmotic responses involve genes such as PYR/PYL receptors, PP2C phosphatases, SnRK2 kinases, ABF transcription factors and ABI5-like bZIP genes involved in ABA signalling. Their significance is supported by transcriptomic drought studies in B. napus and seed-germination studies that associated ABA-related loci with drought response (Fang et al., 2022; Wang et al., 2017). Furthermore, the DELLAs genes, especially BnaA6.RGA, are also relevant because drought and ABA can induce their expression and change the balance of growth-defense (Wu et al., 2020).

The third layer is protection and homeostasis genes. P5CS and Other Proline Biosynthesis Genes Contribute to Osmotic Adjustment Under Drought and Salinity Under salt stress, SOS1, NHX, HKT and other transporter families provide sodium exclusion, vacuolar sequestration and potassium-sodium balance (Li et al., 2021; Long et al., 2015; Wang et al., 2022). Secondary oxidative stress is a frequent consequence of drought, salt, heat and cold. Therefore, genes involved in ROS-scavenging such as SOD, CAT, APX, glutathione related enzymes and peroxidases are repeatedly involved. LEA proteins and dehydrins are particularly important for drought and cold tolerance as they help to stabilise proteins, membranes and cellular structures during dehydration or chilling (Maryan et al., 2019).

Genes related to photosynthesis, cell-wall and development form the fourth layer. In fact, photosynthesis associated genes are often downregulated under drought, salinity and heat especially in sensitive genotypes indicating that maintenance rather than simple induction is the desired tolerance phenotype. For example, XTHs genes related to cell wall formation may affect the root growth under salt stress. Aquaporins may mediate the water movement and hydraulic adjustment. These genes may not be sexy enough for conference posters, but plants depend on them inconveniently for survival.

One useful observation from the studies reviewed is that early signalling genes and late protection genes should not be lumped together. We expect early genes such as DREB/CBF, WRKY, HSF, ABF and some copies of NAC to change within hours after perception of stress. Late-response genes may be more strongly induced after accumulation of injury signals including LEA/dehydrins, antioxidant enzymes and osmolyte genes. Validation is all about timing. Sampling too late may obscure early regulators; sampling too early may mean that protective genes are not yet visible. A candidate gene paper that ignores the biology of the time course is asking the plant to confess on command, which plants do not do, unsurprisingly.

The gene classes prioritised are shown in Tables 1 and 2. The best candidates to validate in the near term are generally DREB/CBF, NAC, WRKY, ABF/ABI5, HSF/HSP, LEA/dehydrin, P5CS, SOS/NHX/HKT, SOD/APX/CAT and aquaporin families. Table 3 shows a phased validation design. Figures 1-3 show the analysis workflow, Brassica genome context and consensus expression direction under stresses.

**Table 1. Main Brassica candidate gene classes for abiotic stress tolerance**

| Gene class | Representative genes/families | Main stress relevance | Common expression pattern | Breeding value |
|---|---|---|---|---|
| Regulatory transcription factors | DREB/CBF, NAC, WRKY, MYB, bZIP/ABF, HSF | Drought, salt, heat, cold | Often induced rapidly; copy-specific behavior in polyploids | High-value regulatory markers and editing targets |
| ABA signaling | PYR/PYL, PP2C, SnRK2, ABF, ABI5 | Drought and osmotic stress | Induced or pathway-rebalanced in tolerant genotypes | Useful for seedling survival and stomatal control |
| Osmoprotectant metabolism | P5CS, ProDH, LEA, dehydrins | Drought, salt, cold | P5CS and LEA/DHN commonly induced under dehydration | Direct stress-protection targets |
| Ion transport and homeostasis | SOS1, NHX, HKT, AKT, CLC | Salt stress | Transporter expression varies by tissue and genotype | Markers for sodium exclusion and K/Na stability |
| ROS detoxification | SOD, CAT, APX, GPX, GST, peroxidases | All major abiotic stresses | Generally induced where oxidative stress is controlled | Physiological and molecular co-selection targets |
| Heat protection | HSF, HSP70, HSP90, small HSPs | Heat stress | Strong and early heat induction | Targets for reproductive heat resilience |
| Water transport and cell wall | Aquaporins, XTH, expansins | Drought and salt | Variable; often tissue-specific | Useful when combined with root traits |

| | | | | |
|---|---|---|---|---|
| Photosynthesis and chloroplast genes | LHCB, photosystem genes, Calvin-cycle genes | Drought, salt, heat | Frequently repressed under severe stress | Tolerance may involve maintaining expression/function |

**Table 2. Prioritized candidate targets for validation in Brassica stress-tolerance studies**

| Priority | Candidate target | Suggested stress assay | Rationale | Validation readout |
|---|---|---|---|---|
| 1 | DREB/CBF copies | Drought and cold | Conserved regulators of dehydration and cold-responsive genes | Early induction; downstream COR/LEA activation |
| 2 | NAC TFs | Drought and salt | Regulate senescence, root growth, and stress defense | Genotype-specific induction and root/shoot response |
| 3 | WRKY TFs | Salt, drought, oxidative stress | Large Brassica family with multiple stress-responsive copies | Copy-specific qRT-PCR and promoter stress elements |
| 4 | ABF/ABI5/bZIP genes | Drought/ABA seedling assay | Central to ABA-mediated osmotic response | ABA sensitivity, germination, stomatal response |
| 5 | HSF/HSP modules | Heat shock and recovery | Heat-response core and protein-stability protection | Rapid HSP induction and recovery survival |
| 6 | LEA/dehydrin genes | Drought and cold | Cellular stabilization under dehydration/chilling | Sustained induction during stress and recovery |
| 7 | P5CS/ProDH balance | Drought and salt | Controls proline accumulation and osmotic adjustment | Proline content plus transcript ratio |
| 8 | SOS1/NHX/HKT transporters | Salt stress | Maintain Na+ exclusion/sequestration and K+/Na+ balance | Ion content, root length, transporter expression |
| 9 | SOD/APX/CAT network | All stresses | ROS detoxification is a shared tolerance mechanism | Enzyme activity, MDA, electrolyte leakage |

| | | | | |
|---|---|---|---|---|
| 10 | Aquaporins and XTHs | Drought/salt root assay | Water transport and cell-wall adjustment | Root hydraulic traits and root elongation |

**Figure 1. Workflow for genome-wide candidate gene identification and expression-based prioritization in Brassica**

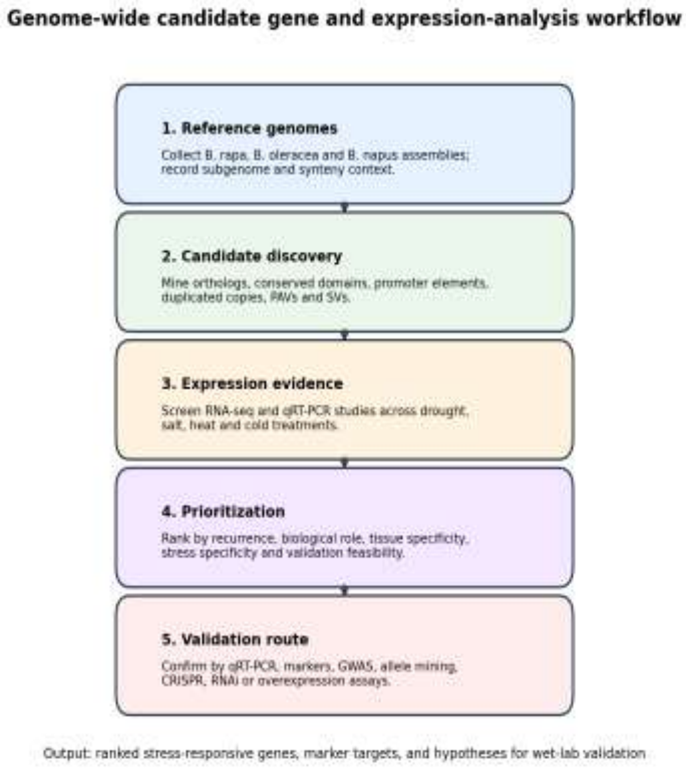
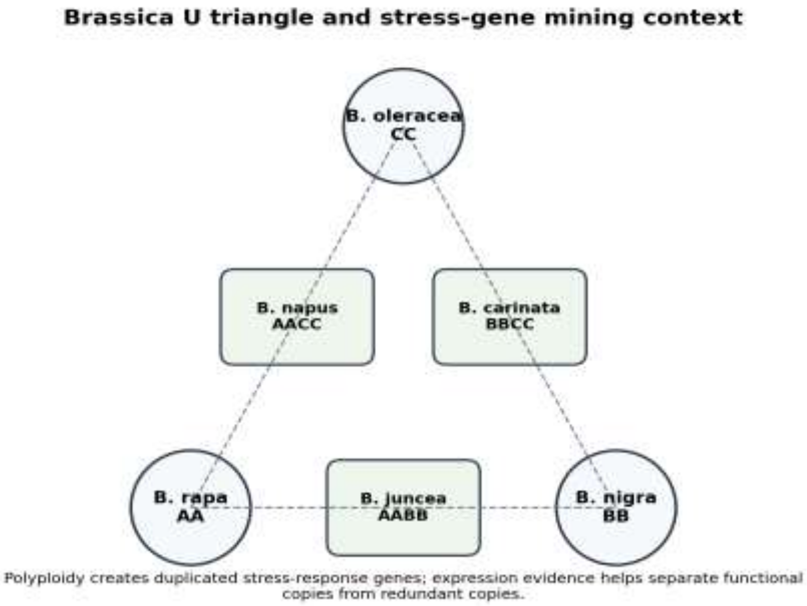
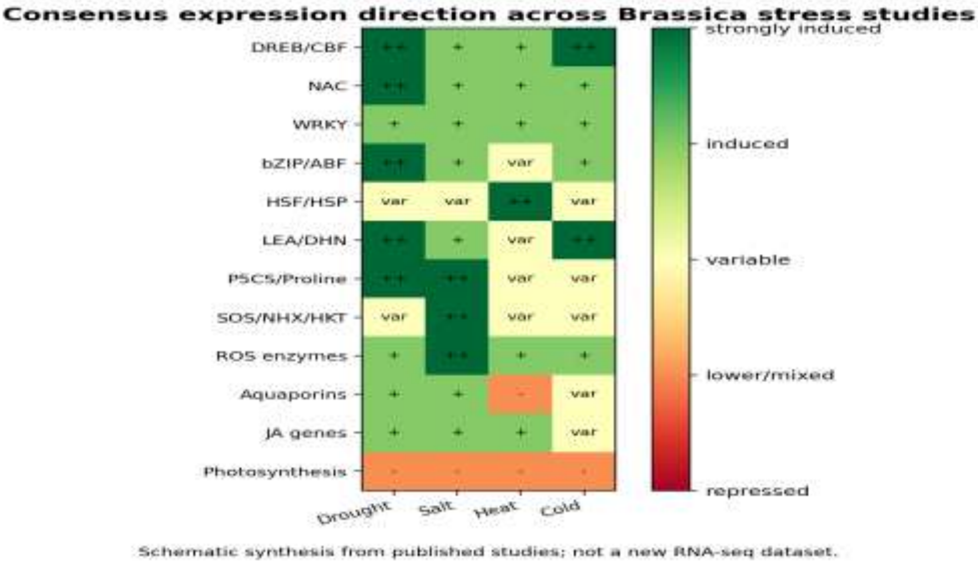


**Figure 2. Brassica U triangle showing diploid and allopolyploid genome relationships relevant to candidate gene copy analysis**



Polyploidy creates duplicated stress-response genes; expression evidence helps separate functional copies from redundant copies.

**Figure 3. Literature-supported consensus expression direction of major stress-related gene classes. The heatmap is a schematic synthesis, not a newly generated RNA-seq matrix**



| | Drought | Salt | Heat | Cold |
|---|---|---|---|---|
| DREB/CBF | ++ | + | + | ++ |
| NAC | ++ | + | + | + |
| WRKY | + | + | + | + |
| bZIP/ABF | ++ | + | var | + |
| HSF/HSP | var | var | ++ | var |
| LEA/DHN | ++ | + | var | ++ |
| P5C5/Proline | ++ | ++ | var | var |
| SOS/NHX/HKT | var | ++ | var | var |
| ROS enzymes | + | ++ | + | + |
| Aquaporins | + | + | - | var |
| JA genes | + | + | + | var |
| Photosynthesis | - | - | - | - |

Schematic synthesis from published studies; not a new RNA-seq dataset.

## DISCUSSION

The analysis is consistent with a model in which stress tolerance in Brassica is dependent on coordinated regulation rather than the action of single genes. This is expected as drought, salinity, heat and cold all have several common downstream effects such as osmotic imbalance, accumulation of reactive oxygen species (ROS), membrane injury and inhibition of growth. A practical breeding strategy should integrate regulatory and protective genes. For example, DREB/CBF, NAC, WRKY and ABF genes can activate transcriptional reprogramming, while P5CS, LEA/dehydrin, ROS-scavenging enzymes and ion transporters perform cellular protection.

Polyploidy is a challenge and an opportunity. B. napus has A and C subgenomes, and duplicated genes may show unequal expression, nonfunctionalization or stress-specific subfunctionalization. Hence, a single Arabidopsis-like annotation is not enough. Candidate genes should be followed as copy specific Brassica loci, ideally using synteny and subgenome information from BRAD, BnaOmics and reference genomes (Chen et al., 2022; Cui et al., 2023). The best candidate might not be the most conserved copy but the copy induced in the right tissue at the right stress stage. Plants also appear to believe in timing, because even chloroplasts have more discipline than some project timelines.

Expression evidence also indicates that tolerance may be related to avoidance of excessive repression of photosynthesis. The lower expression of genes involved in photosynthesis has been reported in many studies on stress, especially under severe stress or in sensitive genotypes. Therefore, breeding should not only select for induced defence genes, but also test if tolerant genotypes maintain chlorophyll content, photosynthetic efficiency and reproductive performance. This becomes especially important in conditions of heat stress, where the sensitivity of flowers and pollen can lead to a decrease in yield, even if the vegetative tissues exhibit moderate tolerance (Kourani et al., 2022; Lohani et al., 2021).

A reasonable next step journal submission would be to couple the candidate framework to a small but clean expression experiment. A feasible design would test 10–12 prioritised genes in two genotypes under two stresses, with three biological replicates and two tissues. That design wouldn't answer every question because biology loves to keep receipts, but it would provide enough primary evidence to rank candidates. Physiological characters such as root length, relative water content, chlorophyll fluorescence, proline content, malondialdehyde and electrolyte leakage should also be added, so that expression changes can be interpreted in the light of stress injury, rather than decorative molecular noise.

One of the limitations of this synthesis is the heterogeneity of published datasets. There is a great variation in cultivars, tissues, developmental stages, stress intensity, sampling time and reference genomes. As such, the candidate-gene list should be viewed as a ranked set of hypotheses, rather than a definitive causal map. We recommend that researchers include an empirical component (RNA-seq reanalysis, qRT-PCR validation, GWAS, functional testing) before submitting their work as a full original article to a journal. The best design would include contrasting tolerant and sensitive genotypes, standardised stress treatments, biological replication, and measurements of recovery from stress. Otherwise, the work is more suitable as a review, short communication or in silico hypothesis article.

Candidate genes can be used in applied breeding in 3 ways. First, copy-specific markers can be developed around validated stress-responsive loci. Second, gene expression markers can be combined with traits that are physiologically screened such as root to shoot ratio, electrolyte leakage, proline content, sodium potassium ratio and chlorophyll fluorescence. Third, genome editing can be used to test negative regulators, or to make duplicates of uncertain function. In Brassica, where redundancy often obscures phenotypes, multiplex editing or allele mining across pangenome panels may be more effective than testing single genes.

The last priority should consider target environment as well. Drought-responsive root architecture, ABA signalling and osmotic adjustment are likely to be most valuable in rainfed production systems. In saline soils, ion transporters and ROS defence genes should be paid more attention. In the tropics or with late sowing, heat-stable reproductive development and protein protection via HSPs may be more important than seedling survival. Cold responsive TFs and dehydrins might be crucial for winter rapeseed. Ranking this to a particular environment avoids the common mistake of treating stress tolerance as a single universal trait, as if plants were politely facing only one problem at a time.

**Table 3. Suggested experimental validation plan for candidate gene confirmation.**

| **Step** | **Recommended design** | **Why it matters** |
|---|---|---|
| Genotype selection | Use tolerant and sensitive Brassica genotypes from the same species/ecotype | Reduces false expression differences caused by unrelated background variation |
| Stress treatments | Drought: PEG or soil drying; salt: 150-200 mM NaCl; heat: 38-42 C; cold: 4 C | Standardized treatments make candidate ranking defensible |
| Tissue sampling | Collect roots and leaves; add flower buds for heat stress if yield is the target | Stress responses are strongly tissue-specific |
| Time points | Early and late sampling: 0, 3/6, 12/24, 72 h depending on stress | Separates signaling genes from acclimation genes |
| Expression analysis | qRT-PCR with validated reference genes; RNA-seq for discovery if budget allows | Confirms copy-specific expression |
| Statistics | Use biological replicates, ANOVA/Tukey or suitable non-parametric tests, and report SE/SD | Prevents reviewers from asking the obvious, which they will |
| Functional follow-up | GWAS, allele mining, overexpression, RNAi, CRISPR, or marker-assisted selection | Moves candidate genes from correlation to breeding utility |

## CONCLUSION

Genome-wide resources and expression studies provide a firm basis for the identification of stress-tolerance candidate genes in Brassica. Among the most consistent targets are transcriptional regulators, ABA pathway genes, osmoprotectants, ion transporters, ROS detoxification genes, heat shock genes and LEA/dehydrin genes. The combination of these targets bridges early stress perception, cellular protection and recovery, which is precisely the link breeding programs require. Reliable interpretation and selection require copy-specific analysis of duplicated and structurally variable Brassica genomes. The candidate pipeline shown here can be used for the robust qRT-PCR validation, association mapping, marker assisted selection, prioritisation and genome editing experiments for developing stress resilient Brassica cultivars.

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