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A REVIEW OF CRISPR-CAS APPLICATIONS IN ENHANCING ABIOTIC STRESS TOLERANCE IN CROP PLANTS

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Abstract

Abiotic stresses such as drought, salinity, heat, cold, oxidative damage and heavy-metal toxicity reduce crop productivity by disturbing water relations, ion homeostasis, membrane stability, photosynthesis and reproductive development. Conventional breeding has led to the development of important stress tolerant cultivars but many adaptive traits are polygenic, environmentally dependent and linked to yield penalties. CRISPR-Cas genome editing provides an alternative route as it can modify specific genes, promoters, alleles or regulatory elements while maintaining the elite varietal backgrounds. Here we review the current applications of CRISPR-Cas systems for improving crop plant tolerance to abiotic stresses and focus on Cas9 knockouts, Cas12a editing, base and prime editing, promoter engineering and DNA-free delivery of ribonucleoproteins. Data from rice, maize, wheat, tomato and other crops indicate that editing of negative regulators, stress-signaling components, ion transporters and developmental genes can enhance salinity tolerance, drought resilience, heavy-metal management and heat or cold adaptation. But stress tolerance is not a single laboratory phenotype. Useful edited cultivars need to combine stress survival with yield stability, quality, low off-target risk, predictable inheritance, and regulatory acceptability. The most promising future strategy is therefore not indiscriminate gene knockout, but integrated trait design combining genomics, phenomics, transcriptomics, precise editing, multi-location validation and pre-breeding pipelines. Careful target selection, transparent biosafety assessment and realistic field evaluation of CRISPR-Cas tools are likely to accelerate climate-resilient crop improvement.

Keywords Crispr-Cas9; Genome Editing; Abiotic Stress; Drought Tolerance; Salinity Tolerance; Crop Improvement; Climate-Resilient Agriculture; Plant Biotechnology.

INTRODUCTION

LITERATURE SEARCH APPROACH

This paper manuscript was prepared as a narrative review and not as a formal systematic review. The source base consisted of peer-reviewed studies and reviews on CRISPR-Cas genome editing in crops, abiotic stress physiology, plant transformation, DNA-free delivery, base editing, and prime editing. We included papers reporting edited plant lines, experimentally validated stress phenotypes, or practical constraints on cultivar deployment. The reviewed literature covers the period from the seminal discovery of CRISPR-Cas and the first demonstrations of plant genome editing through to recent studies of crops published up to 2026. The field is moving quickly and thus the manuscript focuses on reproducible principles rather than on transferability of any particular target. Evidence from controlled environments is interpreted conservatively and differentiated from validated field performance, where possible.

MECHANISTIC BASIS OF EDITED ABIOTIC STRESS TOLERANCE

Networks confer abiotic stress tolerance, not single heroic genes. Drought necessitates coordinated root foraging, stomatal regulation, hydraulic conductance, accumulation of osmolytes, antioxidant defence and reproductive timing. Thus, editing

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can operate in two different ways. One strategy is to change a regulator of multiple downstream responses, as seen in allelic manipulation of drought-responsive growth regulators. The other is to change a particular process, such as root architecture or ABA sensitivity, while maintaining normal growth. The second approach is often safer, as it reduces broad developmental side effects, but may require stacking multiple edits to produce a visible field phenotype.

The most useful targets under salinity are generally those that affect sodium exclusion, potassium retention, vacuolar compartmentalisation, osmotic adjustment and damage repair. Although editing a negative regulator like OsRR22 can lead to significant salt tolerance, care is needed when manipulating ion homeostasis genes, as over-restricting transport could upset nutrient balance. Timing also influences tolerance to heat and cold. A heat-stress edit that enhances protein protection during grain filling might be useful, whereas constitutive expression of the same pathway might drain resources under normal temperatures. This makes promoter editing, cis-regulatory tuning and inducible expression more attractive. Heavy-metal tolerance adds another layer of complexity: not just survival in contaminated soil, but in edible organs as well.

Reactive oxygen species are a common stress node in drought, salinity, heat, chilling and metal toxicity. CRISPR-Cas can alter antioxidant enzymes, redox regulators or transcription factors that orchestrate ROS scavenging. However, excessive suppression of ROS signalling may be detrimental, because ROS are also signalling molecules. Thus, the most rational trait designs are to tune stress responses rather than to maximise them because over-activation of stress pathways can reduce growth, fertility, or grain quality under non-stress conditions.

INTRODUCTION

Crop plants are increasingly exposed to drought, soil salinity, heat waves, chilling episodes, oxidative stress and toxic metal accumulation. These stresses influence plant performance through the common mechanisms like reduction in water uptake, ionic imbalance, buildup of reactive oxygen species, changed hormone signalling, impaired photosynthesis and reproductive failure. Salinity is a good example of this complexity since it involves both an immediate osmotic phase and a slower ionic phase and plants must coordinate root uptake, xylem loading, tissue tolerance and growth regulation in order to survive without sacrificing yield (Munns & Tester, 2008). These stresses are increasingly encountered in combination and hence single-stress tolerance is an incomplete breeding objective.

This is because tolerance is often quantitative and environment-specific, so traditional breeding is still required. But it can be slow when beneficial alleles are rare, obscured by genetic background, or linked to undesirable traits. Genome editing changes the game. The programmable RNA-guided DNA cleavage described by Jinek et al. (2012), and later popularised as a general genome-engineering platform by Doudna and Charpentier (2014), enables researchers to modify a chosen locus rather than to blindly reshuffle whole genomes. Early demonstrations in rice, wheat, Arabidopsis, Nicotiana, and other species showed that CRISPR-Cas systems could make heritable edits in plant genomes (Li et al., 2013; Shan et al., 2013; Zhang et al., 2014) in crops.

CRISPR-Cas is best seen as an accelerator of trait validation and allele development for abiotic stress tolerance. It can knock out negative regulators, change promoters to fine-tune gene expression, edit transporter specificity, or introduce beneficial natural alleles to elite backgrounds. The review summarises the main CRISPR-Cas systems, reported abiotic stress applications, delivery methods, challenges, and future prospects for developing climate-resilient crop varieties for use in genetics and molecular biology research.

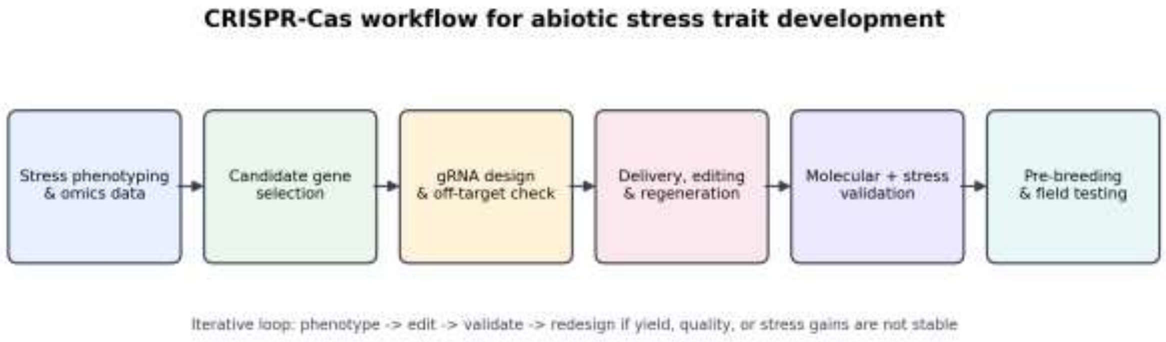

Figure 1. Proposed CRISPR-Cas workflow for developing abiotic stress-tolerant crop lines. Original schematic prepared for this manuscript.

CRISPR-CAS PLATFORMS FOR CROP STRESS IMPROVEMENT

The commonly used CRISPR-Cas9 system produces site-specific double-strand breaks guided by a single-guide RNA. Cas9 is especially useful for knocking out susceptibility genes or negative regulators of stress tolerance because repair of plant DNA via non-homologous end joining often results in insertions or deletions. Early crop studies showed the efficiency of Cas9 to edit crop genomes such as wheat and rice, and multiplex systems increased the power to target multiple loci in monocot and dicot species (Ma et al., 2015; Zhang et al., 2014). Multiplex editing is important in complex traits such as drought tolerance, because single-gene edits can be too weak, unstable or biologically costly.

Cas12a has a different protospacer-adjacent motif, makes staggered cuts, and can enable multiplex guide processing, expanding the toolbox. However, temperature-sensitive performance must be considered in plants where tissue culture and growing conditions vary. Malzahn et al. (2019) showed that temperature can enhance Cas12a editing in rice, maize and Arabidopsis suggesting the importance of enzyme selection, tissue-culture conditions and species-specific optimisation.

Base editors and prime editors are particularly attractive for improving abiotic stress because many beneficial alleles differ by small sequence changes, rather than complete loss of function. Base editors comprising cytosine and adenine can introduce precise nucleotide substitutions without inducing double-strand breaks (Komor et al., 2016). Prime editing is a more advanced search-and-replace system by employing a Cas9 nickase fused with reverse transcriptase, which could enable the insertion of alleles without donor DNA (Anzalone et al., 2019). In crops, these approaches may allow tuning of promoters, modification of transporters or reintroduction of favourable natural variants with minimal pleiotropic damage.

Table 1. CRISPR-Cas platforms relevant to abiotic stress improvement in crops

Platform	Edit type	Main advantage	Abiotic stress use	Key considerations
Cas9 nuclease	Indels by NHEJ	Efficient knockout and multiplex editing	Remove negative regulators of drought or salt response	May create pleiotropy if target has broad developmental roles
Cas12a	Staggered DSBs; alternative PAM	Useful for multiplexing and loci inaccessible to Cas9	Potential editing of stress regulators and promoters	Temperature and species-dependent efficiency
Base editing	Single-base conversion	Precise allele engineering without DSBs	Modify transporter, promoter, or enzyme alleles	Editing window and bystander edits require testing
Prime editing	Small substitutions, insertions, deletions	Flexible allele installation without donor DNA	Recreate beneficial natural alleles	Efficiency and regeneration still crop-dependent
RNP delivery	Transient Cas protein + guide RNA	DNA-free edited plants possible	Useful for regulatory-sensitive breeding pipelines	Delivery and regeneration are major bottlenecks

Note. DSB = double-strand break; NHEJ = non-homologous end joining; RNP = ribonucleoprotein complex.

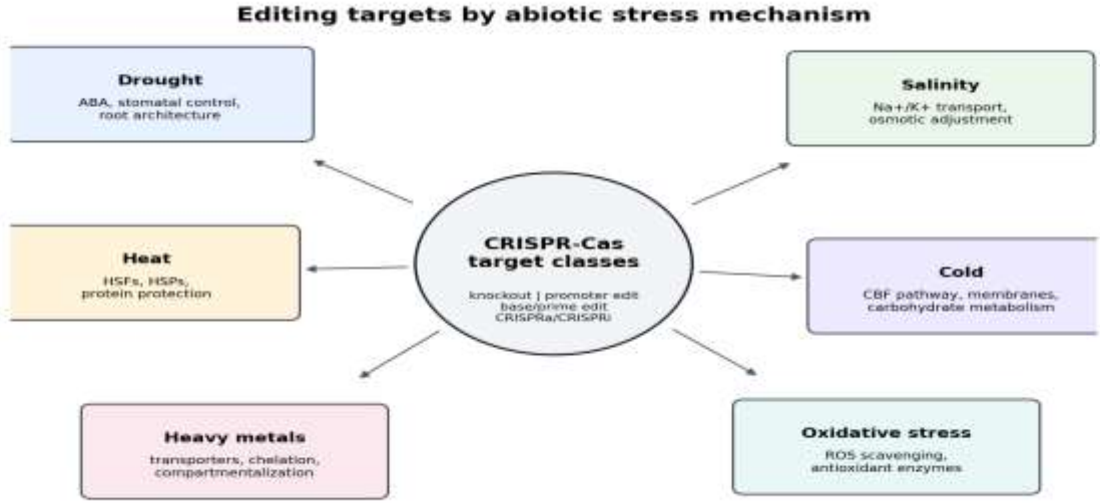

Figure 2. Major abiotic stress mechanisms and candidate CRISPR-Cas target classes. Original schematic prepared for this manuscript.

TARGETS AND APPLICATIONS IN ABIOTIC STRESS TOLERANCE

A good example of the good and the bad of CRISPR-based gene engineering is drought tolerance. For example, editing ARGOS8 alleles in maize increases grain production in dry fields. This demonstrates that engineering the promoter or allele can have a real-world effect on agriculture, not just keeping seedlings green in a grow room (Shi et al., 2017). Tobacco work has demonstrated this even more vividly, although in some cases the changes have brought less tolerance, not more. The decrease in drought tolerance after the modification of SlMAPK3 and SlNPR1 with CRISPR-Cas9 indicates that they are involved in the drought response of the plants and should not be targeted for deletion (Li et al., 2019; Wang et al., 2017). Even bad results are useful for science, because they stop breeding programs from going down expensive dead ends, and make it easier to choose targets in future editing programs.

The salinity tolerance is of great interest to many since ion toxicity and osmotic stress have a large impact on yield. Generation of rice OsRR22 mutant. Homozygous mutant lines generated by CRISPR-Cas9 showed increased salt tolerance at the seedling stage with no significant negative effects on crop yields under normal field conditions (Zhang et al., 2019). RNA regulators, ion transporters, osmoprotectant pathways, and ABA-related signalling genes appear to be good targets for editing rice under salt stress (Farhat et al., 2019; Shelake et al., 2022). However, salt tolerance has to be shown at different growth stages and salt levels.

Heat and cold stresses are influenced by more factors than just temperature and time. These include proteostasis, membrane fluidity, blooming time, reproductive development and grain filling. Changes to heat shock factors, heat shock proteins, membrane-related enzymes, or chilling regulators can help cells better respond to stress, but these genes also control how cells grow normally. The conditional expression, and the promoter might be safer than a full knock out some people think. Much research is on-going on heat, cold, drought, salinity, oxidative stress and heavy metals mainly in rice, wheat and maize as recently summarised in reviews of CRISPR in core crops (Chen et al., 2024; Kumar et al., 2023; Yadav et al., 2022).

Another important new field of research is heavy metal stress affecting food quality and crop yield. 2024; Xu et al. The CRISPR-Cas was employed to alter the silicon transporter genes of rice so as to diminish the quantity of arsenic absorbed by the rice. This indicates that CRISPR-Cas can be used for more than just stress tolerance. It can also be used to remove contaminants. That is important because we need tough plants that can grow in tough conditions and give us better parts to eat. Pressures target most strongly groups of negative regulators, transporters, ABA and ROS signalling genes, root architecture genes and stress protective transcription factors.

Table 2. Representative CRISPR-Cas applications and target evidence for abiotic stress traits

Stress	Crop	Target/edit	Editing strategy	Reported relevance	Reference
Drought	Maize	ARGOS8 variants	CRISPR-Cas9 allele/promoter engineering	Improved grain yield under field drought stress	Shi et al., 2017
Drought	Tomato	SlMAPK3	CRISPR-Cas9 knockout	Reduced tolerance; validates SlMAPK3 as a positive drought-response regulator	Wang et al., 2017
Drought	Tomato	SlNPR1	CRISPR-Cas9 knockout	Reduced tolerance; links defense regulator to drought response	Li et al., 2019
Salinity	Rice	OsRR22	CRISPR-Cas9 targeted mutagenesis	Enhanced salinity tolerance in homozygous mutant lines	Zhang et al., 2019
Salinity	Rice	Multiple salt-response genes	CRISPR-Cas9 target discovery and engineering	Framework for improving ion balance and stress signaling	Farhat et al., 2019

Heavy metals	Rice	Silicon transporter genes	Targeted genome editing	Reduced arsenic accumulation in rice	Xu et al., 2024
Drought/salinity pipeline	Multiple crops	Regulators, transporters, ABA/ROS pathways	Target selection review	Defines target classes and practical bottlenecks	Shelake et al., 2022
Delivery-sensitive stress breeding	Wheat/maize	DNA-free edited lines	RNP-mediated editing	Reduced transgene concerns and supports breeding deployment	Liang et al., 2017; Svitashev et al., 2016

DELIVERY, REGENERATION, AND VALIDATION

If you cant change the genotype of the crop or grow it again, your editing plan won't matter. Agrobacterium mediated transformation, particle bombardment, protoplast transfection, viral vectors, nanoparticles and ribonucleoprotein transport are all important, but depend on genotype, tissue, cost and regulations. DNA-free ribonucleoprotein editing is very attractive for plants as it can allow transgene insertion and subsequent segregation of proteins. In maize and wheat, ribonucleoprotein-mediated editing has been demonstrated to produce edited lines without stable integration of foreign DNA (Liang et al., 2017; Svitashev et al., 2016). (Kocsisova and Coneva, 2023) genotype independent regeneration is one of the major bottlenecks in real world crop transformation.

Sequencing the target site alone is not evidence that it is valid. A full pipeline would check for types of editing, number of zygotes, inheritance, absent or low enough frequency of the target off-target events, expression shifts, signs of physiological stress, yield components, grain quality and real-life field conditions. Many studies on CRISPR-Cas have discussed its applications and the need to integrate it with phenomics, multi-environment trials and breeding (Li et al., 2022; Shelake et al., 2022). So, the field experiment still holds water. A seedling that can tolerate salt in a controlled test may not be able to maintain its yield in the field when exposed to heat, pests, different types of soil and different watering schedules.

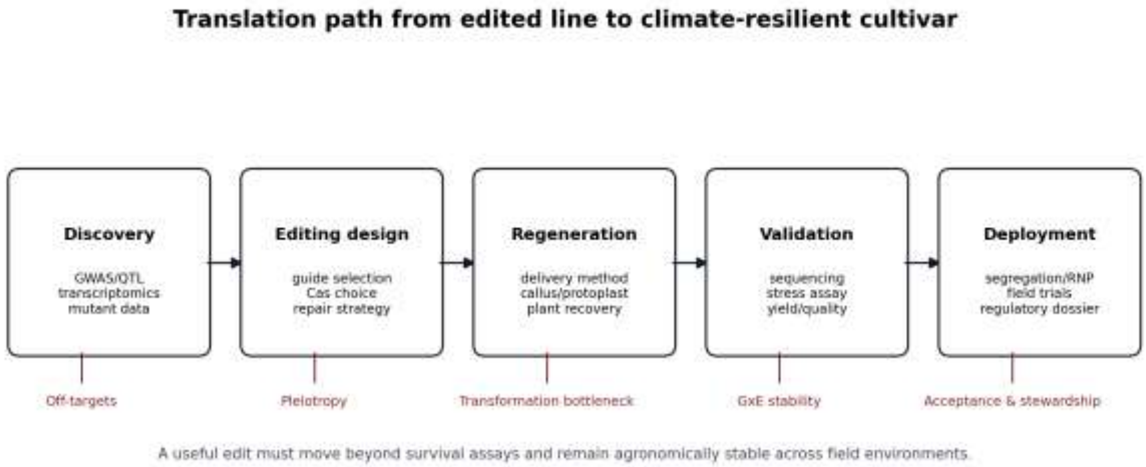

Figure 3. Translation pipeline and risk points for moving edited stress-tolerance traits from laboratory discovery to cultivar development. Original schematic prepared for this manuscript.

INTEGRATION WITH BREEDING AND FIELD DEPLOYMENT

CRISPR-Cas should not be seen as a substitute for breeding programs. Its greatest application lies in the deployment of validated alleles into elite backgrounds, speeding functional testing and shortening the path from gene discovery to pre-breeding material. Recovery of edited plants when DNA vectors are used still requires segregation of transgenic components, background recovery, seed multiplication and comparison to elite checks. CRISPR-Cas can be integrated with marker-assisted selection, genomic selection and speed breeding to combine edited loci with naturally favourable haplotypes from landraces, wild relatives or established tolerant cultivars.

Field deployment also requires phenotype design appropriate to the target environment. A drought-tolerance edit selected under severe terminal stress may not be useful under intermittent drought, and a salinity edit screened at seedling stage may not perform during reproductive development. Thus, multi-location trials need to assess survival, yield, harvest index, flowering behaviour, grain quality, nutrient accumulation and recovery from stress. Different countries have different regulatory treatment of transgene-free edits versus SDN-1 knockouts, base-edited alleles and edits using repair templates and so regulatory strategy should be planned early. Documentation of guide design, target rationale, off-target assessment, and molecular characterisation can support subsequent regulatory review and confidence in edited crop products.

CHALLENGES AND FUTURE PERSPECTIVES

The first one, is biological complexity. Tolerance to abiotic stress is generally quantitative, stage specific and the result of genotype-by-environment interaction. A knockout that adds tolerance in one context could reduce vigour or delay flowering, or mess with grain quality in another. Hence, future editing should focus on allele design, cis-regulatory tuning and multiplex combinations supported by systems biology rather than on one-gene miracle stories. Base and prime editing can help, as they allow subtle sequence changes, but plant efficiency, editing window, by-products, and delivery remain active concerns.

The second problem is governance. Regulations vary from country to country on genome-edited crops, and especially when the final line has no foreign DNA. This inconsistency impacts international breeding pipelines, seed movement and commercialisation. Transparent documentation of the design of edits, molecular characterisation, phenotypic effects, and stewardship will be required for public and regulatory confidence. The third challenge is equity: climate-resilient editing should not be restricted to a few highly transformable crops and private pipelines. Whether CRISPR-Cas becomes a widespread agricultural tool or just another costly badge of biotechnology will be decided by public-sector platforms for rice, wheat, maize, sorghum, pulses, vegetables and orphan crops.

Future developments will probably include a combination of pangenomes, alleles from wild relatives, guide design with machine learning, high-throughput phenotyping and speed breeding. A better question is not can CRISPR make stress tolerance, but rather what edits give stable performance with no yield or quality trade-offs. This question is key to practical crop improvement, as farmers and breeders ultimately need stable performance, not proof-of-concept edits in isolation.

Trait stacking with measurable decision rules is another future priority. For example, an edited line may require a root architecture allele, a salinity transporter allele, and a heat-protective promoter variant to survive combined drought-salt-heat episodes. Such combinations should be built up stepwise, testing each edit individually and in combination, as epistasis can change the expected trait outcomes. Public databases linking edited loci, guide sequences, genetic backgrounds, stress protocols and field outcomes would increase the re-use potential of the field and reduce dependence on isolated success stories.

The best papers for genetics and molecular biology journals will connect phenotype to mechanism. Thus, edited plants should be supported by expression data, metabolite or ion measurements, stress physiology, inheritance analysis and yield-related phenotyping rather than visual scoring alone. Such evidence is required to link genotype, mechanism and agronomic value.

CONCLUSION

CRISPR-Cas technology has evolved from a gene disruption tool to a versatile tool for crop trait engineering. In rice, maize, wheat, tomato and other species, targeted editing has provided evidence of enhanced or elucidated drought, salinity, heat, cold, oxidative and heavy-metal stress responses. Its greatest value is in the accurate validation of candidate genes and rapid generation of elite background alleles. However, the abiotic stress tolerance has to be stable, heritable, safe and compatible with yield and quality for agronomically utility. Therefore, the next phase of CRISPR-Cas crop improvement should focus on carefully selected targets, accurate editing formats, DNA-free delivery whenever possible, thorough off-target assessment and field-level validation. Edited lines must also be assessed in terms of priorities of local farmers, seed system capacity and specific stress profiles of the target production zones. With responsible use, CRISPR-Cas can be a key technology to develop climate-resilient crop varieties in an increasingly volatile production environment.

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