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REVIEW

CRISPR-Cas genome editing for climate-resilient crop development: Recent advances, emerging strategies, and future prospects

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ABSTRACT

Food security in the 21st century has an opponent that does not respect season or geography – a rapidly destabilising climate. Rising temperatures are increasing the geographic range of crop pathogens and exposing crops to salinity, drought and heat stress faster than conventional breeding can respond. This capability gap between breeders and farmers is widening. CRISPR-Cas genome editing has altered this calculation. After the first demonstration of targeted modifications in a crop plant, this technology progressed very rapidly from proof-of-concept to field-applicable tool. Being able to make precise, often DNA-free modifications to endogenous plant genomes circumvents the regulatory and public acceptance issues typically associated with transgenesis. The review synthesizes recent advances of CRISPR-Cas applications for abiotic stress tolerance – drought, heat, cold, salinity, and biotic resistance to bacterial, fungal, and viral pathogens in major food crops along with the implications for Indian agriculture and soybean improvement. We look at the enhanced editing toolkit (base editing and prime editing) available for crop improvement as well as delivery platforms (from

Agrobacterium transformation to ribonucleoprotein-based DNA-free) and evolving regulatory regimes in India, Japan, and beyond. Alongside the considerable promise, we also address persistent challenges: off-target activity in polyploid genomes, recalcitrance in transformation-resistant crops, and the still-limited translation of laboratory gains to farmer-facing varieties. The integration of CRISPR with multi-omics, artificial intelligence, and speed breeding is discussed as the most likely route to realizing the technology's full potential. Throughout, we assess not only what has been achieved, but what remains unresolved, underexplored, or contested in the literature.

KEYWORDS

CRISPR-Cas9; Climate-resilient crops; Soybean improvement; Drought tolerance; Heat stress

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Introduction

There is something deeply unsettling about where we are now. Surface temperatures globally are set to rise 1.5 to 4 degrees Celsius [1]. Agricultural systems are already facing the impacts, not as projections, but as real losses in yield and quality and harm to farmers' livelihoods. In 2011, Lobell and colleagues recorded a decrease in the global yields of the major crops due to climate change, between 1980 and 2008 [2]. Similarly, Zhao et al. found that the global yield of wheat, rice, maize and soybean fall by 6.0, 3.2, 7.4 and 3.1 percent respectively for each degree Celsius rise in temperature [3]. As global population trends demonstrate 10 billion by 2050, these are numbers that require a serious technological response [4]. To be honest, conventional plant breeding has served us well, but we are coming up against its limitations. Crop adaptation proved to be architecturally ill-suited for the sort of stresses imposed by climate change because of slow selection cycles, reliance on available genetic variation and generation time constraints of most major crops [5]. Transgenic approaches, for all their molecular precision, carry regulatory and public acceptance burdens that have significantly curtailed their reach, especially in South Asia and Europe. CRISPR-Cas genome editing entered this space not simply as a faster version of the same thing, but as something qualitatively different: a tool capable of making precise, heritable, often foreign-DNA-free modifications to endogenous crop genomes, with a turnaround time measured in months rather than decades [6,7]. The significance of that distinction, from both scientific and regulatory standpoints, is hard to overstate.

In 2013, Shan et al. were the first to achieve targeted genome modification in cereal crops including rice and wheat using CRISPR-Cas9 [7]. In the subsequent decade, applications have extended to dozens of crop species and ever-more-diverse trait categories. The base editor is a tool which allows for editing of single nucleotide bases without causing double strand breaks. Nucleotide alterations, known as point mutations, can be introduced in DNA sequences. The CRISPR/Cas system from the bacterium Streptococcus pyogenes comprises 69 nucleotides and its key enzyme is Cas9. Cas9 works like restriction enzymes. The methodological innovation rate has made it difficult, at times, for the application community to keep up.

This evaluation is offered from a perspective that takes Indian agriculture seriously as both a context and a driver of research priorities. Despite being one of the largest producers of rice, wheat, sugarcane, cotton, and soybean among other commodities in the world, India carries one of the largest climate-related agricultural risk burdens. The soybean, specifically, shows the problem well. Indian soybean is primarily cultivated as a rainfed kharif crop in Madhya Pradesh, Maharashtra and Rajasthan, and is being managed institutionally through the ICAR-Indian Institute of Soybean Research (ICAR-IISR, Indore). Indian soybean production suffers from chronic vulnerability to erratic onset of monsoon, mid-season drought during pod filling, Mungbean yellow mosaic India virus (MYMIV), and charcoal rot caused by Macrophomina phaseolina. Although this species is vulnerable, the genetic base of cultivated Indian soybean remains narrow, which can limit what conventional breeding can accomplish alone [8]. CRISPR allows work to be done more successfully within that narrow base. We explicitly drawing out the intersection's relevance throughout the rest of this article.

The scale of this vulnerability is not abstract. India cultivates soybean on approximately 12.3 million hectares and produces close to 13.0 million tonnes annually, accounting for roughly 42 percent of the country's total oilseed area [9]. Despite this scale, the national average yield has remained largely static at around 1,000–1,250 kg/ha for well over a decade [9,10], well below the yield levels realized under

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optimal management in multi-location AICRP trials. This stagnation is not a single-cause problem: erratic monsoon onset, mid-season moisture deficit during pod-filling, and recurrent MYMIV epidemics each erode realized yield independently, and often in combination within a single season. MYMIV alone can cause yield losses ranging from 5 to 100 percent depending on the crop stage at infection, and regional annual losses across MYMIV-susceptible legume crops, soybean included, have been estimated at over US$300 million [11]. Conventional breeding has made only incremental progress against this constraint, constrained by a narrow donor base for MYMIV resistance and by the multi-year timelines inherent to backcross introgression programs [8]. It is this specific combination, stagnant on-farm yield, a narrow cultivated gene pool, and a fast-moving biotic and abiotic stress complex that gives CRISPR-based intervention its urgency for Indian soybean specifically.

We proceed section by section through the major stress categories where CRISPR has made demonstrable progress, assess the delivery and regulatory landscape, and close with a frank assessment of where the gaps remain technically, institutionally, and in terms of translational readiness. Our aim is not to produce an exhaustive catalog of every editing study published, but to critically evaluate what has been proven, what has been shown only under controlled conditions, and where the genuinely important work still needs to happen.

CRISPR-Cas Systems in Plant Biology: What the Toolkit Now Offers

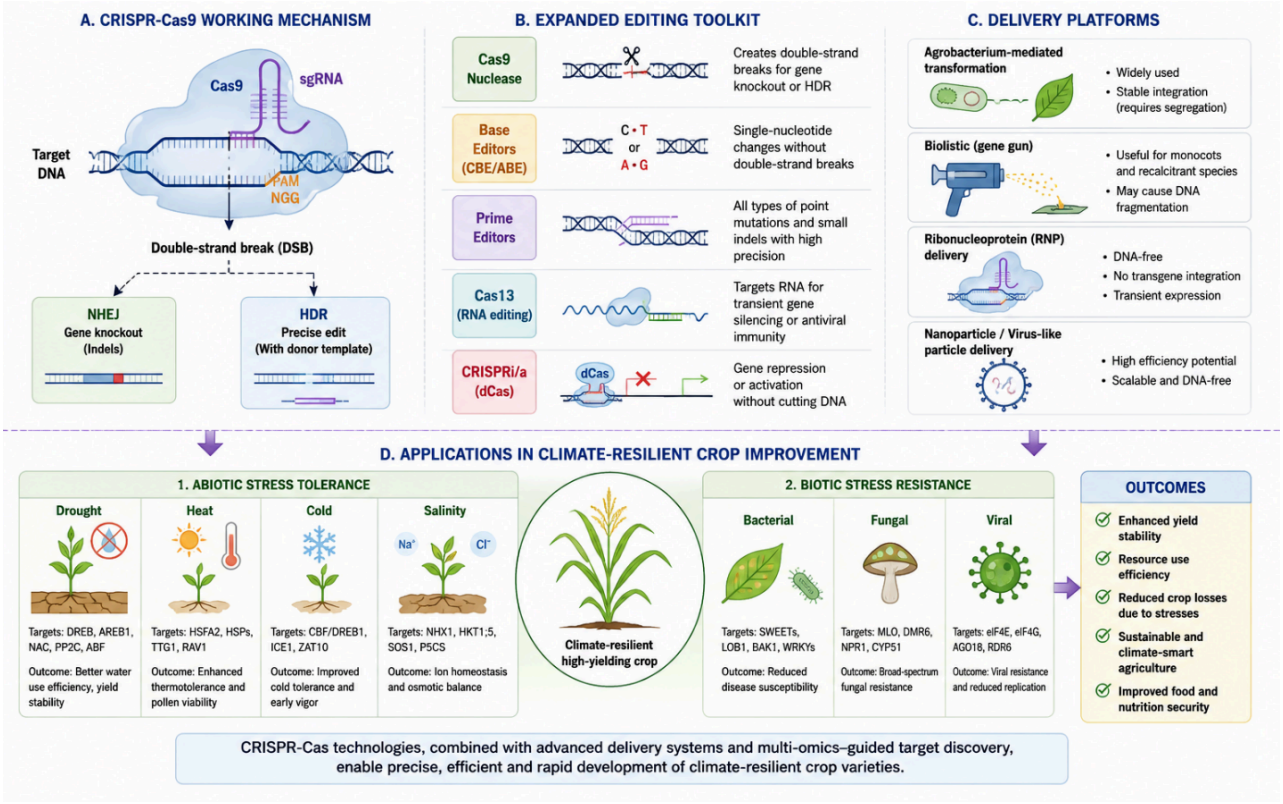

Figure 1. Overview of CRISPR-Cas technologies and their applications in climate-resilient crop improvement. Panel A illustrates the CRISPR-Cas9 working mechanism, in which a single guide RNA (sgRNA) directs Cas9 to a target genomic locus adjacent to a PAM sequence, generating a double-strand break that is repaired through Non-Homologous End Joining (NHEJ) or Homology-Directed Repair (HDR). Panel B summarizes the expanded genome-editing toolkit, including Cas9 nucleases, cytosine and adenine base editors (CBE/ABE), prime editors, Cas13-based RNA editing systems, and CRISPR interference/activation (CRISPRi/a). Panel C presents major delivery platforms used for plant genome editing, including Agrobacterium-mediated transformation, biolistic delivery, ribonucleoprotein (RNP) complexes, and nanoparticle-based systems. Panel D highlights representative applications of CRISPR technologies for enhancing abiotic stress tolerance, biotic stress resistance, and overall climate resilience in crop plants, leading to improved productivity, resource-use efficiency, and food security.

It is easy to forget, given how rapidly the CRISPR field has moved, that the prokaryotic immune function at its core was only fully characterized in 2007 [12]. Jinek et al. provided the biochemical reconstitution that transformed CRISPR from an interesting bacterial phenomenon into a programmable genome editing instrument: The Streptococcus pyogenes Cas9 nuclease, guided by a synthetic single guide RNA (sgRNA), introduces double-strand breaks at any genomic locus adjacent to a suitable Protospacer Adjacent Motif (PAM) [6]. Elegant in concept; transformative in practice.

In the plant biology context, Wang et al. demonstrated something that went beyond model-system proof-of-concept: Simultaneous editing of all three TaMLO homoeoalleles in hexaploid wheat [13]. That achievement was significant precisely because it showed CRISPR could handle polyploid genome complexity - a barrier that had frustrated gene targeting in wheat for years. The resulting powdery mildew-resistant plants were heritable and contained no exogenous DNA, placing them in a regulatory grey zone that, as we discuss later, has since been resolved in India's favor. Subsequent years brought diversification of the Cas protein family (Cas12a, Cas13, CasΦ) and, more practically important for crop improvement, the development of base editors and prime editors. Komor et al. showed that fusing cytidine deaminase to a catalytically impaired Cas9 allowed C-to-T conversions within a defined editing window - no double-strand break, no reliance on homology-directed repair machinery that operates at frustratingly low efficiency in plant cells [14]. The adenine

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base editor followed, covering A-to-G transitions. Anzalone et al. extended the concept further still with prime editing, which uses a reverse transcriptase fused to Cas9 nickase and a prime editing guide RNA (pegRNA) to install any point mutation plus small insertions or deletions [15]. In principle, prime editing covers all twelve possible point mutation types.

It would be an oversimplification, on the other hand, to claim that this set of tools is fully mature and completely reliable. Several caveats should be mentioned in this regard. Base editors show a certain level of context dependence in terms of efficiency, which depends on the editing window and is affected both by the nucleotide sequence surrounding the target site as well as unintended deamination events at off-target cytosines within the same or a different window. The efficiencies of prime editing in plants, though being considerably improved lately, continue to lag behind the corresponding parameters for mammals due to pegRNA degradation and differences in DNA repair pathways between plants and animals. They are no reason to stop using these tools, yet they should be considered in the interpretation of early studies on crops. What works well for Arabidopsis or protoplasts does not necessarily work in a transgenic line of hexaploid wheat or rain-fed soybean. The main base editing tools and their distinctive features are shown in Figure 1 [16].

In the case of soybean, Jacobs et al. applied CRISPR-Cas9 to induce mutations at the DD20 and DD43 loci, providing an initial proof-of-concept for this important agricultural crop [17]. In a further demonstration of the power of genome editing in soybean, Du et al. showed that TALENs and CRISPR/Cas9 could be used for multiplex gene editing of genes involved in fatty acid biosynthesis, with practical results for oil quality [18]. Previous work in this area had been done by Haun et al., who had used targeted mutagenesis of the GmFAD2-1A and GmFAD2-1B genes to improve the oleic acid content in soybeans [19]. Thus, soybeans have proven susceptible to genome editing, although due to their difficult transformation biology and tetraploid nature, homozygous edits may not be as straightforward to generate as in crops such as rice or tomato.

Core stress-responsive gene families: An integrative overview

Before turning to individual stresses, it is worth noting that the CRISPR-editable gene space for abiotic stress tolerance is more interconnected than a stress-by-stress narrative might suggest. Three gene families recur across the drought, heat, cold, and salinity discussions below and are introduced here once to avoid repetition later. The DREB/CBF family regulates ABA-independent stress-responsive transcription and underlies both drought and cold acclimation responses; the HSF (Heat Shock Factor) family governs the heat-shock transcriptional cascade relevant to heat stress; and the FAD (Fatty Acid Desaturase) family controls membrane lipid unsaturation, relevant to both cold tolerance and oil quality [19-22]. Table 1 summarizes these families so that the sections that follow can focus on stress-specific signalling detail and crop-level case studies.

Table 1. Core stress-responsive gene families.

Gene family	Primary function	Stress domain (s)	Key reference
DREB/CBF	ABA-independent transcriptional activation of cold- and dehydration-responsive genes	Drought, Cold	[20]
HSF (HSFA/HSP)	Heat-shock transcription factor network; thermotolerance signalling	Heat	[23]
FAD (FAD2/FAD 3)	Fatty-acid desaturation; membrane fluidity and oil quality	Cold, Oil quality	[19,22]
GmERF / aerenchyma genes	Ethylene-response signalling; adventitious root and aerenchyma formation	Waterlogging	[24]

Engineering Drought Tolerance: Progress and Persistent Gaps

The most economically damaging abiotic stress in agriculture worldwide is drought. Drought accounts for a yield loss of between 20-40% for crops grown in regions affected by drought. For example, drought during the pod-filling stage can lead to yield failure for rainfed soybeans in India's rain-fed soybean belt, particularly in Madhya Pradesh and Vidarbha [8,25]. The molecular basis for the various responses to drought have been classified into ABA dependent (abscisic acid) and ABA independent signalling pathways, which converge onto stomatal regulation, osmotic adjustment, and management of reactive oxygen species.However, there remains a gap with respect to successfully converting this molecular understanding into durable field phenotypes using precision editing (e.g., CRISPR/Cas9).

One of the most compelling examples of CRISPR for drought tolerance in maize was achieved by the team's substitution of the native promotor of ARGOS8 (a negative regulatory gene for ethylene response) with the constitutive GOS2 promoter, creating a gain-of-function effect without the introduction of foreign DNA, and resulting in significantly greater yields for the edited lines compared with the control lines under induced drought stress in numerous field environments, without the yield drag that typically occurs when transgenic drought tolerance constructs are used under optimal conditions [25]. This is genuinely important: most earlier attempts at engineering drought tolerance in maize, whether through transcription factor overexpression or stress-responsive pathway manipulation, sacrificed yield potential under non-stress conditions. The promoter-swap strategy offers a way around that trade-off, and its applicability to analogous regulators in soybean - including members of the GmERF and GmARF families - warrants systematic investigation.

Root architecture is arguably the most underexplored avenue in the CRISPR-drought space, despite being one of the most promising. Deeper roots with greater lateral branching can access subsoil water reserves that become critical when surface layers dry. Uga et al. demonstrated that loci controlling root angle, particularly DRO1, can substantially improve water acquisition and drought adaptation in rice [24]. For Indian soybean, analogous work targeting GmPIN auxin efflux carriers or GmDREB1 transcription factors involved in root growth could be particularly valuable, yet to our knowledge no such study has been published for Indian genotypes. Scheben et al. emphasized that the integration of CRISPR with high-resolution 3D root phenotyping platforms is essential for systematic target identification a pipeline that ICAR-IISR and allied institutions are well-positioned to develop [26]. In wheat, Molla et al. demonstrated that base editors can introduce drought-relevant modifications in both diploid and polyploid backgrounds, which broadens the toolkit beyond knockout strategies and deserves further exploration in Indian wheats where point allele variants often explain significant phenotypic variation [16].

Heat Stress Tolerance: Gains at the Reproductive Stage Matter Most

1. Heat stress during anthesis and grain filling is uniquely damaging because it strikes at the reproductive bottleneck - pollen viability, fertilization success, and assimilate supply to the developing grain. The IPCC projects that temperatures currently considered extreme will become the statistical norm across major cereal belts within decades [1]. For Indian soybean, flowering and early pod-set stages in July to August already coincide with heat episodes in the central Indian plateau, and this overlap is expected to intensify. The question for CRISPR applications is whether the molecular targets that confer

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thermotolerance in model systems translate to meaningful reproductive buffering in field conditions.

Tran et al. provided some of the clearest evidence to date with their SlHyPRP1 knockout in tomato [23]. The gene encodes a hybrid proline-rich protein that acts as a negative regulator of heat shock signalling, and its disruption produced plants maintaining commercial fruit yields at 38°C - conditions under which unedited controls showed near-total reproductive failure. The mechanistic logic is sound: removing a brake on the Heat Shock Transcription Factor (HSF) network allows the cell to deploy its thermal protection machinery more aggressively. Whether equivalent negative regulators in soybean or wheat can be targeted with similar outcomes is a legitimate and answerable research question that, to date, remains unanswered in the published literature. The soybean GmHSP and GmHSFA families have been characterized transcriptionally, but CRISPR-based functional editing of their regulatory architecture has not been reported for Indian cultivar backgrounds.

The angle of photorespiration as presented by Zhang et al. should get more consideration regarding the effects of heat stress [21]. C3 plants are very carbon-intensive; heat increases the rate of use of this carbon. Therefore, photorespiration is both indicative of heat stress and a contributor to heat stress in C3 plants. Suppressing photorespiration using CRISPR provides an avenue to improve photosynthesis efficiency without having to introduce foreign photorespiratory pathway alternatives; these types of genetic modification are of interest among people looking for transgenic opportunities due to regulatory challenges. The use of endogenous gene editing is a cleaner approach. However, testing of the disruption of photorespiration must be thorough before deployment under field conditions, which vary widely in temperature, CO2 and/or sunlight. CRISPRa provides a conceptually attractive option for enhancing gene expression without permanently altering gene sequence or function. The disadvantage of using CRISPRa is that expression induced by dCas9-activator will likely not be stably transmitted by self-pollinated crops such as soybean and wheat if there is not ongoing expression of dCas9-activator.

Cold and Frost Tolerance: A Secondary Priority with Regional Significance

The differential significance of cold stress within Indian agricultural production is variable and exists mainly in distinct areas of production. Cold stress limits yields and cropping calendars for upland rice in Jharkhand and Uttarakhand, rabi soybean growing trials conducted in part of Punjab and Haryana, and for highland horticulture throughout northeast India. Compared with the eastern portions of Asia and temperate rice producing areas across the globe, cold stress is a more significant issue. Cold stress has a molecular basis related to the CBF (C-Repeat Binding Factor) cold-responsive regulon proposed by Gupta et al. Gupta et al. reviewed the functionality of this network and identified potential candidates for the exploitation of their regulatory targets [20]. CBF overexpression continuously limits plant growth at typical temperatures, thereby creating a challenge to the continued advancement of transgenic cold tolerance programs through two different means: 1) through CRISPR-mediated editing technologies that allow the cold-inducible or tissue-specific activation of CBF targets instead of simply constitutive expression; and 2) through base editing of regulatory regions that control the expression of stress-responsive cis-elements. One of these two approaches has yet to be demonstrably practical on a significant crop.

The membrane lipid angle is arguably more tractable. Zhang et al. demonstrated that modification of fatty acid desaturation pathways increased membrane lipid unsaturation and significantly improved tolerance to low-temperature stress [22]. These findings suggest that modern CRISPR-based editing of FAD2 homologs could provide a precise strategy for enhancing cold tolerance in crop plants. This is mechanistically well-grounded: Membrane fluidity at low temperature is a direct physical function of lipid unsaturation degree. For soybean, which already has an active fatty acid editing research agenda, Haun et al. demonstrated targeted GmFAD2-1A/1B editing for oil quality, the same FAD gene family could be explored for cold tolerance outcomes, potentially achieving multiple trait improvements from overlapping targets [19]. Soyk et al. provided an instructive example of how CRISPR editing of photoperiod response genes (sp5g) in tomato could indirectly expand the cultivable temperature window by shortening the time to reproductive onset, allowing crops to mature before terminal cold [27]. Whether analogous adaptation logic can be applied to Indian soybean varieties that are day-length sensitive and which suffer from late-maturing phenotypes under shifting day-length regimes deserves investigation. Mahmood et al. made the reasonable argument that multi-omics integration will be necessary to identify the less obvious cold tolerance targets beyond the CBF pathway - a recommendation we endorse, particularly for crops where the stress tolerance gene regulatory network has not been fully characterized [28].

Disease and Pest Resistance: Susceptibility Gene Editing as a Durable Strategy

The ecological relationship between climate change and plant disease is bidirectional and, from an agricultural standpoint, worrying. Warmer winters allow pathogen overwintering in regions previously too cold to support them; altered precipitation patterns promote foliar disease in some crops while triggering soil-borne epidemics in others; and geographic range shifts in insect vectors are bringing viruses to crops with no evolutionary history of exposure to them. Strange and Scott estimated pre-climate-change annual losses to crop diseases at 20 to 40 percent of production - a figure that is certainly not improving [29]. Two broad CRISPR-based resistance strategies have emerged: Disrupting host susceptibility (S) genes that pathogens require for infection and directly targeting pathogen genomes in planta. Both have demonstrated results, though the maturity and field applicability of these approaches differ considerably.

The S-gene approach received its most convincing validation in Oliva et al., who edited the promoter regions of SWEET11, SWEET13, and SWEET14 in rice - three sucrose transporter genes whose promoters are hijacked by *Xanthomonas oryzae pv. oryzae* (Xoo) to facilitate nutrient theft during bacterial blight infection [30]. By disrupting the Xoo-specific promoter binding sites without disabling gene expression in non-pathogen contexts, the authors obtained broad-spectrum resistance to multiple blight strains across field sites in Asia and Africa, without yield penalties. This is precisely the kind of outcome that makes S-gene editing strategically attractive: resistance that is not race-specific, because it targets the host rather than the pathogen. For Indian soybean, the equivalent high-priority target is Mungbean yellow mosaic India virus (MYMIV), a begomovirus transmitted by Bemisia tabaci whitefly that causes yellow mosaic disease - the single most damaging biotic constraint on soybean in peninsular India. Ali et al. demonstrated that CRISPR-Cas9 could directly degrade geminivirus genomes in planta; since MYMIV is itself a geminivirus, the conceptual framework is directly applicable [31]. No published study has yet applied this specifically to MYMIV-resistant soybean editing, representing a notable gap in the Indian CRISPR-crop improvement agenda.

Wang et al. accomplished the triple-allele TaMLO knockout in hexaploid wheat that conferred heritable powdery mildew resistance, and Nekrasov et al. reinforced the finding through a rapid, transgene-free protocol producing plants with no detectable foreign DNA [32,33]. These studies are well cited, and rightly so. What is less often discussed is the specificity of MLO loss-of-function resistance. Commercially, barley has had MLO resistance applied for numerous years and has displayed a large degree of effectiveness against Blumeria graminis, a unique example of pathogen durability due to the fact that a host's cell membrane protein necessary for normal cellular processes presents major challenges for pathogens to adapt around. However, whether TaMLO-edited wheat will maintain equivalent durability in a range of growing conditions over many seasons is an empirical question that requires long-term field studies (not just verification of initial resistance).

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The work of Chandrasekaran et al. regarding virus resistance in cucumber provides a valuable architectural as well as agronomic model [34]. By simultaneously disrupting three different eIF4E family members (the expression of which are important for potyviral infection but not for the normal growth of plants), it was possible to produce resistance against CVYV, ZYMV and PRSV-W as a result of only a single editing process. A logical corollary for Indian soy is the potential to create resistance against Soybean Mosaic Virus (SMV) and Bean Pod Mottle Virus (BPMV) through the control of the eIF4E/eIF(iso)4E interactions. While the connections have been made within the literature, a CRISPR editing project involving Indian-specific germplasm has yet to be initiated [35]. Thus, it can be stated that there exists an established scientific basis to realize this goal. Furthermore, the barriers to realizing this goal lie within institutions' ability to develop capacities and provide resources to fund research for these beneficiaries.

Salinity and Waterlogging: Two Sides of India's Monsoon Problem

Salt-affected soils occupy roughly 20 percent of irrigated agricultural land worldwide, with a particularly heavy concentration in the Indo-Gangetic plains, Rajasthan, and coastal areas of Odisha and Andhra Pradesh [36]. The problem is compounding: Secondary salinization from irrigated agriculture is advancing faster than reclamation efforts. For soybean, salinity during emergence and early vegetative stages is especially damaging, and Indian soybean cultivars have generally not been selected for salinity tolerance because the crop is grown rain-fed in environments where salinity was historically not the primary constraint. As cropping patterns shift and irrigation expands, that calculus is changing.

Xu et al. demonstrated multiplex CRISPR-Cas9 editing of negative regulators within the rice salt-stress signaling network, producing lines with improved K+/Na+ ratios and maintained growth at 150 mM NaCl [37]. The approach is methodologically sound, and the simultaneous disruption of multiple pathway repressors produced a cumulative effect greater than any single-gene edit alone - an important practical lesson. The limitation, as with much of the salinity tolerance literature, is that experiments were conducted hydroponically or in controlled root-zone conditions that differ substantially from heterogeneous, salt-crusted field soils where spatial variation in NaCl concentration, soil pH, and other ion interactions all modify plant response. Zhao et al. introduced an interesting variant using CRISPR-Cas13a for RNA-level knockdown of negative regulators, allowing temporal modulation of stress responses without permanent genomic alteration - a creative approach that could be particularly useful where permanent loss of a pleiotropic gene would be costly [38].

Waterlogging is best read alongside the drought, since both represent opposite extremes of a single water-availability axis and their editable gene targets are frequently co-located in the same mapping populations. Waterlogging presents the mirror-image problem. When the Indian monsoon delivers excess rainfall - a pattern becoming more common with increasing climate variability - soybean fields in Madhya Pradesh and central Maharashtra experience transient anaerobic root zone conditions that can cause yield losses of 30 to 50 percent within 48 hours of flooding during early vegetative stages. The submergence tolerance CRISPR work by Uga et al. in rice addressed both the flooding phase and the recovery phase after drainage - an important distinction because cellular damage during re-aeration can equal or exceed the anoxic injury itself [24]. For soybean, the equivalent genetic system involves GmERF transcription factors and aerenchyma formation genes, but targeted CRISPR editing for waterlogging tolerance in Indian soybean germplasm has not been reported. Singh et al. noted that QTL-to-editing pipelines - where loci identified in mapping populations are then fine-mapped and CRISPR-targeted in elite backgrounds - represent a practically efficient strategy for stacking multiple stress tolerance traits, and this is precisely the kind of structured research agenda that Indian national programs need to formalize for soybean [39].

Nutritional Quality and Biofortification: CRISPR as a Regulatory Shortcut

One of the most underappreciated arguments for CRISPR in the nutritional improvement space is regulatory, not just scientific. Transgenic biofortification approaches - Golden Rice being the canonical example - have spent decades navigating regulatory processes in countries where the need is greatest. CRISPR-mediated editing of endogenous biosynthesis genes, producing modifications indistinguishable from natural allelic variation, offers a path through that regulatory landscape that transgenics cannot take. This matters enormously for India, where the regulatory reforms of 2022 now explicitly exempt SDN-1 edited crops from biosafety oversight, and where nutritional deficiencies in zinc, iron, and provitamin A remain widespread.

One of the most amazing discoveries in the history of nutritional editing has been the ability to delete several alpha-gliadin genes from wheat at the same time using CRISPR-Cas9 and reduce the immunogenicity of gluten by 85 percent while maintaining an acceptable baking quality [40]. The technical obstacles in achieving this target were substantial since it involved performing such coordinated editing across a multigene family that contains many copies of genes within a hexaploid wheat plant, so it is remarkable that these authors accomplished so with successful agronomic performance. It will be important to determine whether the same level of reduction can be accomplished in different environments and under different processing methods, considering that gluten's make-up in wheat grains can vary based upon differences in the nitrogen nutrition of the plant, as well as other environmental parameters such as temperature and soil moisture during the filling period of the grain. The research by Xu et al. used a much more targeted approach to achieve the same goal in rice [41]. The authors used cytosine base editing to change the Wx gene so that rice could be produced with a continuous range of amylose contents from waxy to high amylose, all generated from the same crop. The elegance of their technology is noteworthy, as are the potential health implications of producing rice with high amylose starches and decreased glycemic index foods.

The potential for nutritional editing through soybean cultivation in India is not only broad but also considerably under-utilized. Haun et al. provided early proof-of-concept for creating high oleic soybean oil via molecular targeting of the GmFAD2-1A/1B loci, which have commercial ramifications for the Indian market [19]. With respect to soybean oil (high-volume edible oil consumed in India) and its several oxidative stability features being foremost priorities for commercial use, a growing body of evidence supports that application of multiplex editing techniques throughout the fatty acid pathway gene are viable using CRISPR. Another specific benefit of performing nutritional edits to soybean could include the targeted elimination of the trypsin inhibitor activity present in the KTi1 and KTi3 genes, which affect the digestibility of soybean protein consumed by the general population of India. Current research institutions in India have not sufficiently researched the societal benefits offered by this option (e.g., trypsin inhibition inactivity). Moreover, Dong and Ronald documented that CRISPR-mediated transcriptional activation of natural beta-carotene genes found in rice provides a good alternative to Golden Rice-style transgenic regulation for fortification programs targeting soy-based diets among certain groups of people in India [42]. An option based on this same CRISPR approach, utilizing existing carotenoid chemical pathway structures within soybean, could provide another means of creating fortification programs targeting these same soy-consuming groups.

Delivery Platforms: The Regulatory Value of DNA-Free Editing

Before comparing delivery platforms, it is useful to fix three terms used throughout this review. “Transgene-free” describes the final plant genotype: no foreign DNA is stably integrated, regardless of delivery method. “DNA-free” is narrower and describes the delivery method itself: the editing reagents (typically a Cas9-sgRNA

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ribonucleoprotein, RNP) are never encoded in DNA at any stage, which is one route - though not the only route - to a transgene-free outcome. "SDN-1" (Site-Directed Nuclease-1) is the regulatory classification used in India's 2022 genome-editing guidelines for edits consisting of small insertions or deletions with no exogenous DNA integrated, irrespective of the delivery method used to achieve them. In short: DNA-free is a method, transgene-free is an outcome, and SDN-1 is a regulatory category built on that outcome.

Deciding how to deliver CRISPR to a cell is more than a technological choice, as it will be increasingly determined by regulatory and commercial consideration. The delivery of CRISPR/Cas9 plasmids that integrate into the genome, though may only for short time may differ, from the delivery of Cas9/gRNA RNP complexes in that the latter degrade within days of delivery to the cell and do not leave a lasting foreign sequence; in many parts of the world including India, only the use of the former is classified as transgenic, while the latter is generally considered unregulated. As this distinction continues to shape how research is being conducted in the field, it is likely to have profound implications for how the research will continue to develop and move forward [43].

Agrobacterium tumefaciens-based transformation and biolistic-based delivery are the primary delivery mechanism for stable CRISPR delivery in 90% or more of crop species. Svitashev et al. recently obtained high frequencies of editing (integration) of RNPs into maize via biolistics; thus, while historically RNPs have been delivered via either method of transformation, their research indicates that both methods can be used in combination [44]. Malnoy et al. provides further support for the use of biolistics as a means to deliver Cas9/gRNA complexes directly to protoplasts derived from grapevine and apple, producing heritable mutations with no foreign DNA detectable using any standard molecular assay [45]. This approach is important not just in principle but in practice: the edited grapevine plants fell outside the EU's GMO definition as it was then interpreted, a precedent with significant implications for Indian researchers seeking to deploy edited soybean varieties under the post-2022 SDN-1 framework. Zhang et al. extended RNP-biolistic delivery to wheat and barley, achieving comparable editing efficiencies to plasmid-based systems while producing transgene-free lines in the T0 generation [21].

The regeneration bottleneck is the harder problem. Lowe et al. demonstrated that co-expression of the morphogenic regulators Baby Boom and Wuschel dramatically improved callus formation and plant regeneration efficiency in recalcitrant maize genotypes, and the principle has since been applied to other monocots [46]. For soybean, which is notoriously difficult to regenerate from protoplasts and shows strong genotype dependence in Agrobacterium-based systems, this is arguably the most important technical bottleneck in the CRISPR pipeline. Most published soybean editing studies use a small number of highly transformable elite North American genotypes - Williams 82 appears in most of them - which are agronomically irrelevant to the Indian subcontinent. Adapting efficient transformation and regeneration protocols specifically for Indian soybean varieties such as JS 335, NRC 37, and MAUS 71 is a foundational need that Indian institutions like ICAR-IISR, the National Research Centre for Soybean, and state agricultural universities are best placed to address. Without this, the translation gap between published CRISPR achievements and cultivar development will remain very wide. On the horizon, nanoparticle-mediated delivery - including carbon nanotube and mesoporous silica nanoparticle approaches - offers the prospect of organ-targeted, protoplast-free CRISPR delivery to intact tissues, though current efficiencies are not yet competitive with established methods in most crop systems [38].

Summary of Representative CRISPR-Cas Applications in Climate-Resilient Crops

Table 2 provides a consolidated reference of the representative CRISPR-Cas editing studies discussed in this review. The entries are organized to reflect the breadth of crops, stress categories, and editing modalities covered, and are intended as a quick reference for readers seeking to compare methodological approaches or identify analogous targets in crops not yet addressed. Notably, the table reveals a concentration of published work in rice, wheat, tomato, and cucumber - and a corresponding gap in published CRISPR editing studies for soybean varieties adapted to the South Asian production environment. This imbalance is not a reflection of biological intractability; it reflects funding priorities and institutional capacity, both of which are within our collective power to reorient.

The Regulatory Landscape: India at an Inflection Point

Regulatory frameworks for genome-edited crops have been in flux globally since the mid-2010s, and the trajectory matters enormously for determining how quickly CRISPR-based crop improvements reach farmers. The contrast between jurisdictions is stark. Waltz highlighted the early US regulatory response to the CRISPR-edited browning-resistant mushroom - essentially, no oversight because no foreign DNA was present - which set a precedent that has been incrementally expanded [35]. The European Union, by contrast, applied its process-based GMO framework to rule that organisms produced by new mutagenesis techniques, including CRISPR, are subject to full GMO regulation, a decision handed down by the Court of Justice of the EU in 2018 and widely criticized by the scientific community as scientifically inconsistent. That position is now under legislative review, but the regulatory uncertainty it created cost European plant breeding programs years.

India has moved more pragmatically. The 2022 guidelines issued by the Department of Biotechnology, developed through extensive consultations involving ICAR institutes, state agricultural universities, and the Review Committee on Genetic Manipulation, clarified that SDN-1 edited organisms - those carrying only small insertions or deletions at a targeted site with no foreign genetic material - are exempt from biosafety regulations under the Environment Protection Act, 1986, and Rules, 1989. This regulatory clarification is, in practical terms, a significant enabling act for India's public crop improvement programs, including soybean [47]. It means that an ICAR team that uses RNP-delivered CRISPR to knockout a susceptibility gene in JS 335 soybean can, in principle, advance its edited lines through variety release trials without engaging the biosafety review process applicable to transgenic crops - a reduction of years, potentially, in the path to farmer access. Whether this regulatory clarity is being translated into funded research programs at an adequate scale is a separate and more uncomfortable question.

Japan's experience is instructive as a model of what regulatory clarity can enable in practice. The 2021 commercial release of a CRISPR-edited high-GABA tomato - developed by Sanatech Seed and grown by farmers under a voluntary notification system - demonstrated that edited crops can reach consumers with proportionate regulatory scrutiny and without the years of mandatory containment trials required of transgenic crops. Hamazaki and Iwata observed that consumer acceptance in Japan, while initially cautious, has improved with transparent communication about the specificity of the modification [48]. This is an important behavioral science data point: public attitudes to genome-edited crops are malleable and respond to evidence-based communication in ways that public responses to transgenics often did not. The Indian scientific and institutional community has an opportunity to get this communication right from the beginning, particularly with respect to soybean - a crop whose genetic improvement by any means is relatively uncontroversial to Indian consumers compared with food staples like rice or wheat.

Challenges, Unresolved Questions, and Where the Work Needs to Go

The CRISPR-in-crops literature has a characteristic profile of strengths and gaps that it is worth being honest about. The strengths are genuine and impressive: molecular proof of concept is well established across diverse targets and species, the editing toolkit is

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Table 2. Representative CRISPR-Cas applications in climate-resilient crop development reviewed in this article. The inclusion of both international and Indian-relevant soybean entries reflects the review's analytical focus. Gene names are italicized per standard nomenclature. Abbreviations: CBE, Cytosine Base Editor; RNP, Ribonucleoprotein; RT, Reverse Transcriptase; CVYV, Cucumber vein yellowing virus; ZYMV, Zucchini yellow mosaic virus; PRSV-W, Papaya ring spot mosaic virus-Watermelon strain; Xoo; ABA, abscisic acid; WUE, water use efficiency; FAD.

Crop species	Target Gene / Locus	Stress / Trait type	CRISPR tool	Key phenotypic outcome	Reference
Maize (*Zea mays*)	ARGOS8 (promoter replacement)	Drought	CRISPR-Cas9	Improved grain yield under multi-environment field drought; no yield penalty under optimal conditions	[25]
Wheat (*Triticum aestivum*)	TaGW2 (all homoeoalleles)	Drought / Yield	CRISPR-Cas9	Increased grain weight; tolerance improvement under moderate water deficit	[21]
Tomato (*Solanum lycopersicum*)	SlHyPRP1	Heat stress	CRISPR-Cas9	Improved pollen viability and fruit set at 38 °C; commercial yield maintained under sustained heat	[23]
Tomato (*Solanum lycopersicum*)	sp5g	Climate adaptation / Photoperiod	CRISPR-Cas9	Day-neutral flowering; adaptation to short-season, cool environments without fruit quality loss	[27]
Rice (*Oryza sativa*)	SWEET11, SWEET13, SWEET14 (promoter regions)	Bacterial blight (Xoo)	Multiplex CRISPR-Cas9	Broad-spectrum Xoo resistance across multiple strains; stable across multi-location field trials in Asia and Africa	[30]
Cucumber (*Cucumis sativus*)	eIF4E gene family (3 members)	Viral resistance	CRISPR-Cas9	Simultaneous resistance to CVYV, ZYMV, PRSV-W; no significant agronomic penalty observed	[35]
Wheat (*Triticum aestivum*)	TaMLO-A1/B1/D1 (all homoeoalleles)	Powdery mildew	CRISPR-Cas9	Heritable, transgene-free, broad-spectrum powdery mildew resistance confirmed across backgrounds	[32]
Soybean (*Glycine max*)	GmFAD2-1A / GmFAD2-1B	Oil quality / Oxidative stress	Targeted mutagenesis / CRISPR	High-oleic acid phenotype; improved oxidative stability relevant to edible oil markets	[19]
Soybean (*Glycine max*)	DD20, DD43 (proof-of-concept loci)	General / Trait editing	CRISPR-Cas9	First demonstration of targeted CRISPR mutagenesis in soybean; foundational for trait editing programs	[17]
Rice (*Oryza sativa*)	Multiple salt-stress regulatory loci	Salinity	Multiplex CRISPR-Cas9	Improved K+/Na+ homeostasis; maintained growth under 150 mM NaCl; cumulative multiplex effect demonstrated	[37]
Wheat (*Triticum aestivum*)	Alpha-gliadin gene family	Nutritional quality	CRISPR-Cas9	85% reduction in gluten immunoreactivity in celiac patient assays; baking quality retained	[40]
Rice (*Oryza sativa*)	Wx gene	Grain starch quality	Cytosine base editor (CBE)	Continuous spectrum of amylose modification from waxy to high-amylose profiles via single precise edit	[41]
Multiple crops	Any target locus	Universal platform	Prime editing (pegRNA + RT)	All 12-point mutation classes achievable; small indels; substantially lower off-target frequency vs Cas9	[15]

expanding rapidly, delivery methods are improving, and the regulatory environment in key countries is becoming more enabling. The gaps are also real, and they compound each other in ways that slow translation to the field.

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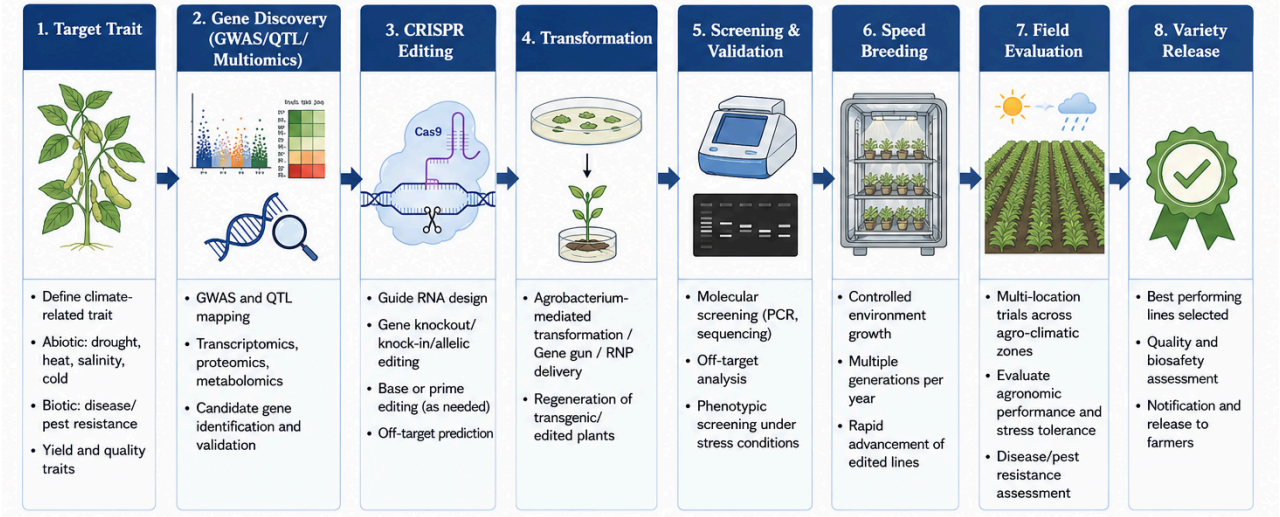

Figure 2. CRISPR-based strategy pipeline for developing climate-resilient soybean varieties in India. The pipeline begins with identification of priority climate-resilience traits, followed by gene discovery through GWAS, QTL mapping, and multi-omics approaches. Candidate genes are edited using CRISPR-based technologies, regenerated through suitable transformation systems, screened for editing accuracy and stress-response phenotypes, accelerated through speed breeding, validated across diverse agro-climatic environments, and ultimately advanced toward varietal release. The framework highlights the integration of modern genomics, genome editing, and breeding technologies for rapid soybean improvement under changing climatic conditions. Source: Prepared by the authors based on concepts synthesized from Watson et al., Mahmood et al, Hamazaki and Iwata, and Xu et al. [24,37,48,50].

Off-target editing remains a concern, particularly in polyploid crop genomes where guide RNA sequences encounter multiple paralogous targets. Scheben et al. drew early attention to this problem in the plant CRISPR context, and it has not been fully resolved despite improved high-fidelity Cas9 variants and better guide RNA design algorithms [49]. Whole-genome sequencing of edited lines - which is now technically feasible and increasingly affordable - provides the necessary quality assurance but adds both cost and time that many national programs, including those in India, cannot absorb at scale. This creates a two-tier system in the literature: well-resourced international programs publish fully sequenced, carefully characterized edited lines, while resource-constrained programs may not, creating interpretive uncertainty about the clean- ness of reported phenotypes. This is worth acknowledging rather than papering over.

The regeneration and transformation bottleneck are, in our assessment, the single most limiting technical barrier for translating CRISPR to Indian crops. As noted earlier, many soybean editing studies have used Williams 82 - a North American genotype with high transformation competence that is agronomically irrelevant in India. Lowe et al. demonstrated that morphogenic regulators Baby Boom and Wuschel can substantially improve transformation efficiency in recalcitrant maize; extending this approach to Indian soybean and other legumes is a concrete, fundable research priority [46]. Without genotype-specific transformation protocols for JS 335, NRC 37, MAUS 71, and the new ICAR-IISR varieties, the CRISPR toolbox remains inaccessible for Indian soybean improvement in any practical sense. This is the kind of enabling infrastructure investment that national funding agencies need to prioritize.

Looking forward, several convergences seem particularly promising. The integration of CRISPR with AI-assisted target identification has moved from conceptual proposal to early implementation: Hamazaki and Iwata showed how simulation-based AI optimization of mating and selection strategies can amplify genetic gains when combined with precision editing, and Mahmood et al. demonstrated that multi-omics data integration can surface regulatory gene targets that would not be identified by single-platform analyses [28,48]. Both approaches are relevant to Indian soybean, where the population structure and environmental adaptation of germplasm are now well enough characterized to support GWAS and transcriptome-based target discovery. Speed breeding, which Watson et al. showed can reduce soybean generation time from 20 weeks in field conditions to 8 to 10 weeks under controlled lighting and extended photoperiod, addresses the other major time constraint in moving from edited T0 lines to homozygous field-ready material [50]. Combining speed breeding with RNP-mediated editing and efficient screening for biallelic events could compress the timeline from editing event to agronomic evaluation from 3 to 4 years under conventional conditions to perhaps 18 months. That is the kind of acceleration that would genuinely change what is possible for Indian breeders working on kharif season crops. The translation of CRISPR-mediated discoveries into farmer-ready climate-resilient soybean cultivars requires a coordinated pipeline integrating target trait prioritization, multi-omics-assisted gene discovery, genome editing, transformation, rapid generation advancement, and multi-location field validation. A conceptual framework for this process in the Indian soybean improvement context is presented in Figure 2.

Multiplex editing - targeting several loci simultaneously - aligns well with the biological reality that climate resilience in the field is a multi-trait phenotype. Xu et al. showed that up to eight targets could be edited simultaneously in rice without major efficiency losses, and the soybean tetraploid genome, where functional redundancy between paralogous gene pairs is common, may benefit from multiplex approaches that are necessary to produce a clean phenotypic outcome [37]. Raza et al. made the argument, with which we concur, that climate-smart crop improvement must be designed as a multi-stress, multi-trait strategy from the outset - the practice of engineering single traits under single controlled stress conditions and extrapolating to complex field environments is a persistent misalignment between what the laboratory produces and what the farmer faces. CRISPR's multiplexing capability is one of its most practically important features, and it is one that the Indian soybean improvement community should be designing around from the start rather than bolting on as an afterthought.

Limiting Factors Restricting the Translation of Laboratory-Edited Traits to Field Production

This translational gap is, on reflection, the single most consequential

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limitation of the evidence base reviewed here. With the partial exception of the ARGOS8 promoter-swap in maize, validated across multiple field environments under genuine drought stress, nearly every other CRISPR abiotic-stress result discussed above - the rice salinity multiplex edits of Xu et al., the Cas13a-based salinity knockdown of Zhao et al., the SlHyPRP1 heat-tolerance knockout of Tran et al. , and the FAD-based cold tolerance work of Zhang et al. was generated and evaluated under hydroponic, greenhouse, or single-location controlled conditions [23]. Three specific gaps follow. First, trait trade-offs under co-occurring stresses are essentially unstudied for CRISPR-edited lines: A soybean line edited for salinity tolerance has no published data on its performance under the simultaneous drought that frequently accompanies salinity stress in Indo-Gangetic and Rajasthan production zones. Second, the field stability of homozygous edited alleles across seasons in polyploid and tetraploid backgrounds - tetraploid soybean among them - has not been systematically tracked. Third, adaptability to smallholder, rain-fed farming systems, the dominant production context for Indian soybean, is essentially absent from the CRISPR literature reviewed here; none of the cited field trials, including ARGOS8, report performance under the combination of rain-fed moisture variability, limited fertilizer access, and simultaneous pest-and-pathogen pressure characteristic of smallholder soybean cultivation in Madhya Pradesh and Maharashtra. Closing this gap requires multi-location, multi-year field trials under combined-stress conditions and explicit testing under representative smallholder input regimes, built into CRISPR soybean improvement programs from the outset rather than added after single-stress proof-of-concept. Table 3 summarizes where each stress category reviewed in this manuscript currently sits on this laboratory-to-field spectrum [23,25,37,38].

Table 3. Laboratory-to-field validation status of the CRISPR abiotic and biotic stress-tolerance studies reviewed in this article.

Stress category	Best available validation stage	Field/smallholder data available?	Key reference
Drought	Multi-location field trials (maize)	Yes - maize only; not soybean	[25]
Heat	Controlled growth-chamber (38°C)	No	[23]
Cold	Greenhouse / lab	No	[22]
Salinity	Hydroponic / controlled root-zone	No	[37,38]
Waterlogging	Lab-based submergence assay	No	[24]
Disease (bacterial blight)	Multi-country field sites (rice)	Yes - rice only; not soybean	[30]
Disease (MYMIV, soybean)	No CRISPR study yet published	No	[31]

Conclusion and Research Priorities

CRISPR-Cas genome editing has earned its place at the center of the climate-resilient crop improvement agenda. The evidence base reviewed here - spanning drought tolerance in maize and rice, heat stress resistance in tomato, viral resistance in cucumber, bacterial blight resistance in rice, gluten reduction in wheat, and fatty acid quality improvement in soybean - collectively demonstrates that precision endogenous editing is a practically viable route to traits that conventional breeding cannot access at the same speed or specificity. The technology is not hypothetical; it is already producing edited varieties that are entering regulatory review and, in some cases, commercial cultivation.

What this review has also tried to make clear is that the gap between published results and farmer impact remains wide, and that closing it requires attention to things that rarely appear in methodology sections: genotype-specific transformation protocols, multi-season field validation, off-target characterization at whole-genome resolution, regulatory engagement, and institutional capacity building in the countries where the need is greatest. For India specifically, the 2022 SDN-1 regulatory clarification has removed a major barrier, but the research pipeline has not yet responded at a scale commensurate with the opportunity - particularly for soybean, where MYMIV resistance, drought tolerance during pod-filling, and high-oleic oil quality represent three well-defined, high-impact targets that are technically tractable through existing CRISPR approaches.

Several specific priorities emerge from this synthesis. First, investment in genotype-specific transformation and regeneration protocols for Indian soybean varieties is foundational and should be treated as infrastructure, not optional. Second, CRISPR-based MYMIV resistance - building on the gemini virus interference work of Ali et al. represents the most urgent biotic stress target for Indian soybean and deserves a coordinated national editing program. Third, the multiplexing approach demonstrated by Xu et al. in rice should be adapted for simultaneous drought and salinity tolerance engineering in soybean, given that these stresses co-occur in many Indian production environments. Fourth, speed breeding integration with CRISPR pipelines, following Watson et al., could bring these gains to farmers within realistic timelines rather than theoretical ones. The sequential integration of these activities into a unified soybean improvement pipeline is illustrated in Figure 2. Finally, the scientific community and Indian regulatory agencies need to work together on communication strategies that build public understanding and acceptance of SDN-1 edited soybean varieties, taking lessons from the Japanese GABA tomato experience rather than repeating the communication failures that characterized the early transgenic era.

The tools are better than they have ever been. The regulatory environment in India is, for the first time, genuinely enabling. What is now needed is the disciplined, funded, institutional commitment to turn CRISPR's scientific promise into the crop varieties that Indian farmers and food systems need. That translation - from laboratory discovery to varietal release to farmer adoption - is never automatic, but it is achievable. The present moment, perhaps uniquely, offers the conditions to make it happen.

Disclosure Statement

No potential conflict of interest was reported by the author.

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