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Mini Reveiw

Advances in understanding plant senescence regulation using CRISPR/Cas technology

Jyothish Madambikattil Sasi[1] & Biju Dharmapalan[1]*

[1]Garden City University, Bangalore, Karnataka 560049, India

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Leaf senescence marks the final stage of leaf development, and is governed by a genetically controlled process that is crucial for nutrient recycling and overall plant health. However, the premature onset of this process can negatively affect crop yield and produce quality. This study explores the critical role of CRISPR -Cas genome editing in understanding the complex regulatory pathways that control plant senescence. CRISPR-based studies have enabled profound functional insights into the main senescence-associated genes (SAGs), including transcription factors, elements of hormone signalling pathways (ethylene, jasmonate, and abscisic acid) and genes that interact with chlorophyll catabolism, autophagy and nutrient remobilisation. CRISPR has, therefore, become valuable for breeding crop species. Moreover, applications of CRISPR have revealed an array of regulatory pathways, highlighting the role of nuclear architecture proteins, peptide signalling pathways and epigenetic regulators in senescence regulation. This review compiles the studies that used CRISPR technology to understand the regulation of plant senescence. The study also opens new paths for gene manipulation, including precise promoter editing methods, multiplexed gene targeting and the incorporation of multi-omics technologies that could outperform the traditional methods.

Keywords: CRISPR-Cas, crop improvement, genome editing, nutrient remobilization, plant senescence, stress resilience

Introduction

Plant senescence is a genetically programmed process that marks the final phase of a plant's life cycle. During this stage, nutrients are systematically transferred from the older tissues to the developing organs or seeds. The significance of this phase is paramount because it plays a vital role in plant fitness, optimising yield, and enhancing stress resilience[1,2]. Although it supports nutrient recycling, particularly nitrogen, which enhances grain filling during stress premature senescence can significantly reduce the yield and adversely affect the postharvest quality of leafy vegetables and fruits, leading to a shorter shelf life and a decline in nutritional value[3-5]. Environmental stresses such as drought and heat can hasten senescence and reduce photosynthetic efficiency and biomass production, thereby jeopardising global food security[6,7]. Several approaches that are aimed at delaying Senescence, including autoregulatory inhibition and transgenic techniques, have shown increases in drought resistance and yield stability[8,9]. A prudent balance of the senescence process is an essential factor in the effective remobilization of nutrients[10,11]. CRISPR-Cas technology is a potent genome-editing system that uses a guide RNA to locate and precisely modify genetic targets by using Cas9[12]. CRISPR-Cas constructs used to knock out or activate major regulatory genes provide scientists with the opportunity to regulate the dynamics and timing of leaf senescence, to stimulate nutrient cycling, photosynthetic performance, and plant adaptation to heterogeneous environments[13-15]. These applications are of special interest to agronomy, where the optimization of senescence pathways can be used to increase crop production and enhance stress resistance in the area of environmental stressors. Published articles in the past 5-6 years that addressed the mechanism of senescence in plants with the help of CRISPR-Cas technology have been included in the present review. Gene Functional characterization studies using CRISPR-Cas technology were taken into account as a selection criterion for the present review irrespective of the senescence system.

CRISPR systems

CRISPR-Cas system represents a third-generation gene editing technique, distinguished by its superior efficiency, precision, simplicity, cost-effectiveness, and

*Correspondence:
E-mail: bijudharmapalan@gmail.com

multifunctionality compared to earlier methods[16]. The mechanism of action of this system commences with a single-guide RNA (sgRNA) that guides the Cas protein to a specific complementary DNA sequence. The Cas protein cleaves double-stranded DNA upon binding, resulting in a double-stranded break (DSB) through its HNH and RuvC nuclease domains. The break activates the cell's inherent repair mechanisms: the error-prone Non-Homologous End-Joining (NHEJ), which frequently leads to gene knockout, or the accurate Homology-Directed Repair (HDR), which facilitates the insertion of a new DNA sequence, thus allowing for potent and precise genetic alterations[16,17]. CRISPR-Cas technology relies on RNA-guided genetic editing, such as gene knockout, gene knock-in, base editing, transcriptional regulation, and epigenetic editing[18] (Fig. 1). With gene knockout, the double-kin event creates a small insertion or deletion at the site of the double-strand break (DSB) that disrupts gene activity through error-prone non-homologous end-joining. Gene knock-in is the process by which a target gene is provided via a donor DNA template, on which a new genetic sequence is introduced via homology-directed repair. Base editing enables the accurate editing of specific nucleotides without introducing any double-strand breaks, whereas prime editing enables specific insertion, deletions, and potential permutations of bases[19].

CRISPR-Cas offers numerous advantages over conventional breeding methods. The current review thoroughly examines recent cases of using CRISPR-Cas technology in gene control and the ensuing phenotypes of senescence. The emphasis is made on

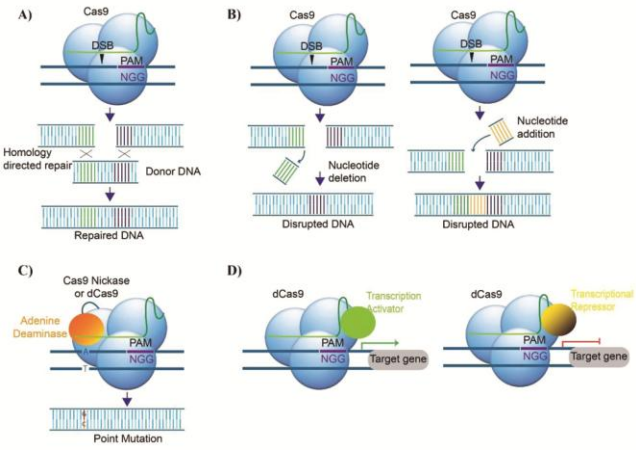

Fig. 1 — Application of CRISPR/Cas9 Technology, (a) Knock-in; (b) Knock-out; (c) Base editing; (d) Transcriptional regulation, DSB: double-stranded break, PAM: protospacer adjacent motif, dCas9: dead Cas9.

the senescence-related genes that affect vital agronomic characteristics such as biomass gain and stress resistance based on recent empirical evidence. The in-depth study enhances the insight into the senescence processes and provides an excellent genetic pool to breed with the precise breeding goal to create a high-yielding cultivar with excellent senescence characteristics. Its high level of precision allows highly specific alterations with low off-target effects, most recently including prime editing[19]. The system supports multiplexing and therefore allows simultaneous control of multiple gene loci using a variety of sgRNAs[20,21]. The aspect is particularly beneficial when it comes to combat multifaceted traits that are based on polygenic networks. CRISPR-Cas is a groundbreaking technology in the field of crop improvement because of its ease, efficiency, and flexibility. It is more effective in producing plants with superior qualities like disease resistance, stress tolerance, and high nutritional value[22].

CRISPR/Cas editing of senescence-associated gene classes in plants

The CRISPR-Cas technology has brought a revolution in plant genome editing because it offers a very specific path through which genes can be modified, including those that lead to plant senescence. Various studies based on CRISPR-Cas have contributed to the field of senescence biology (Table 1). In addition to conventional research, the CRISPR-Cas technology has made it possible to spot various groups of genes, such as transcription factors (TFs), kinases and proteases, which are involved in the regulation of plant senescence (Fig. 2). Below is a compilation of some senescence-associated gene classes tarsgeted by CRISPR-Cas technology.

Transcription factors

Plant senescence, an intricate developmental phase marked by substantial reprogramming of gene expression, is primarily regulated by transcription factors (TFs). A wide range of transcription factors, such as WRKY, NAC, and AP2/ERF, have been recognised as essential regulators of senescence-associated genes (SAGs) and pathways[23-25]. WRKY transcription factors comprise a significant group of transcriptional regulators found exclusively in plants, and are essential for numerous physiological processes and stress responses. WRKY transcription factors are characterized by their distinctive WRKY domain, a conserved sequence of approximately

Table 1 — Senescence-Related Phenotypes associated with CRISPR/Cas9 Gene Manipulation (DS: Delayed senescence; AS: Accelerated senescence)

Plant	Genes Targeted	Gene Class	Senescence Phenotype Associated with the knock-out	Reference
Alfalfa	*FLOWERING LOCUS Ta1*	phosphatidylethanolamine-binding protein	DS	45
Apple	*MdWRKY70L*	transcription factor	DS	32
	WRKY28	transcription factor	DS	33
	SGR1	chloroplast degradation	AS	69
	CLAVATA3/ESR-RELATED 14	signal peptide	AS	86
Arabidopsis	*SCOOP12*	signal peptide	AS	87
	KAKU4	nuclear envelope protein	AS	103
	Fibrillin2	structural protein	AS	72
	CLE42	signal peptide	AS	86
Brassica	*NPC4/PLDZ2*	pPhospholipase	DS	94
Campanula	*CpEil1*	lipoprotein	DS	52
Japanese gentians	*EPH1L*	transcription factor	DS	42
Maize	*ZmSAG39*	protease	DS	97
	NtCCD8	Carotenoid Cleavage	AS	59
Nicotiana	*NtNAC028/NtNAC080*	transcription factor	DS	43
	NtNAC028	transcription factor	DS	41
Petunia	*PhATG6*	Autophagy	AS	93
	PhACO1	ethylene biosynthesis	DS	47
Potato	*StDND1*	RNA-binding protein	AS	100
	PSL50	Ubiquitin-like protein	AS	99
	PLS2	glycosyltransferase	DS	96
	OsCPK12	kinase	AS	67
	Leaf senescence 1	transcription factor	AS	102
	SnRK1α	kinase	AS	66
	PWL1	kinase	AS	63
	BBS1/RLCK109	*kinase*	*AS*	*64*
	HXK1	kinase	DS	65
Rice	*S40*	transcription factor	DS	47
	NCED5	chloroplast degradation	DS	60
	CAO1	chlorophyll biosynthesis	AS	70
	WRKY93	transcription factor	AS	29
	Ghd2	transcription factor	DS	46
	NAC103	transcription factor	DS	40
	ACA9	transport proteins	AS	98
	CKX11	cytokinin oxidase	DS	95
	AGO2	RNA-binding protein	AS	81
Sorghum	*SbWRKY50*	transcription factor	AS	31
Soybean	*GmCRY1*	photoreceptor	AS	76
	SlJAZ10/ SlJAZ11	jasmonic acid signaling	AS	56
	Chloroplast Vesiculation	chloroplast degradation	DS	73
	SlYTHDF2	RNA-binding protein	AS	82
Tomato	*SBPase*	photosynthesis	AS	74
	SGR1	chloroplast degradation	DS	55
	SAE1	SUMOylation protein	DS	88
	SlWRKY37	transcription factor	DS	30
	Sal1	transcription factor	DS	101
Wheat	*TaARE1*	nitrogen assimilation	DS	95
	ARF15	transcription factor	AS	57
Zoysia	*ZmNYC1*	chloroplast degradation	DS	71

60 amino acids that enables them to bind specifically to W-box elements located in the promoter regions of target genes[26].

Transcription factors play a crucial role in shaping plant responses to various stresses, including biotic challenges such as pathogen attacks, and abiotic factors

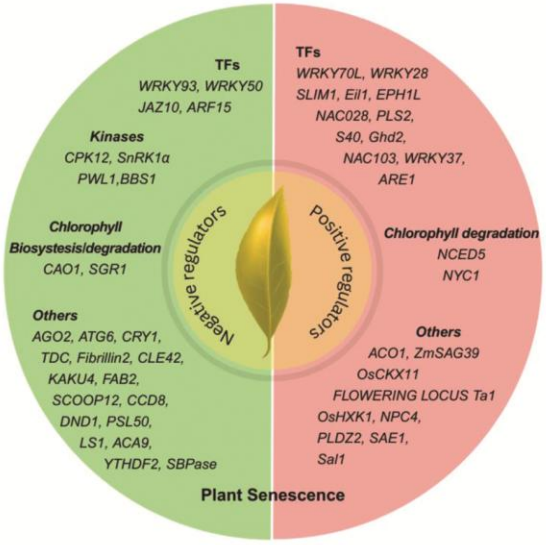

Fig. 2 — Plant senescence-associated genes investigated through CRISPR/Cas9 gene editing technology.

such as temperature, drought and salinity[27,28]. They function as either transcriptional activators or repressors, and are influenced by biological context and their specific interactions with other protein complexes. WRKY transcription factors are critical not only in stress responses, but also in plant growth and development processes of plants[28]. Many of the studies have indicated that WRKY family members contribute to plant senescence particularly when genome-editing technologies are used on various plant species. Li *et al.* (2021) investigated the presence of *OsWRKY* genes in senescence of rice leaf and their vulnerability to biotic stress. The paper focused on *OsWRKY93*, in which researchers used CRISPR/Cas9 to create knockout mutants. Unlike the wild-type plants, the *oswrky93-1* CRISPR mutant had a faster development of leaf senescence in the dark-induced environment. On the other hand, plants that showed enhanced *OsWRKY93* expression showed a delay in senescence of the leaves under the same condition. These findings indicate that OsWRKY93 plays a vital role in regulating leaf senescence and defence responses against *Magnaporthe oryzae* in rice[29]. In another experiment with tomato WRKY37 (SlWRKY37), a WRKY transcription factor belonging to group IIe, *slwrky37* mutant exhibited a mutant phenotype characterized by delayed symptoms related to leaf-senescence under the influence of either the jasmonic acid (JA) or darkness, in comparison with wild type plant[30]. Conversely, lines overexpressing *SlWRKY37* experienced accelerated senescence. This study revealed a regulatory framework in which SlWRKY37 operates downstream of SlMYC2, directly activating *SlWRKY53* and *SlSGR1* to promote leaf senescence[30]. In sorghum, CRISPR knockout mutants of *SbWRKY50* exhibited an accelerated senescence phenotype, characterised by notable chloroplast loss and heightened leaf senescence compared to wild-type plants subjected to darkness and ethylene[31]. These findings indicated that SbWRKY50 is an inhibitor of the leaf senescence. Another study by Wang et al. on apple fruit senescence highlights the significance of WRKY transcription factor MdWRKY70L in the progression of senescence in the fruits[32]. MdWRKY70L CRISPR -knockout lines of *MdWRKY70L* in Orin exhibited a retarded senescence phenotype with much lower reactive oxygen species (ROS)-levels than wild -type calli. These results demonstrate that MdWRKY70L interacts with, and is phosphorylated by MdMPK6/02G to increase its stability, and induce senescence. FAR-RED ELONGATED HYPOCOTYL3 (FHY3) is a transposase-based transcription factor that, in Arabidopsis, was reported to play a negative role in the age- and light-regulated leaf senescence by negatively regulating *WRKY28* expression[33]. In this study CRISPR -Cas9 technology was used to establish *wrky28* null alleles in the wild-type No 0 and an *fhy3 -4* background. These CRISPR generated mutants were observed to have senescence traits, whereby the transition of leaf senescence in the CRISPR mutated mutants of the *wrky28* gene was delayed compared to wild-type plants. FHY3-WRKY28 transcriptional module is intensely required to combine signals with respect to both age and light that influences leaf senescence establishment and onset, particularly when red to far red light ratios are high[33].

The NAC transcription factor family, which includes NAM, ATAF, and CUC, is recognized as one of the largest gene families exclusive to plants and is distinguished by its diverse roles in plant growth, development, and stress responses. This group includes many representatives spread throughout the majority of the higher plant taxa, and it is useful in the regulation process(s), especially in relation to plant immunity and stress adaptability[34,35]. NAC transcription factors have a strongly conserved N -terminal DNA-binding domain, which is balanced by the C -terminal domain that facilitates protein-protein interactions. NAC proteins possess an inherent connection to their functional repertoire primarily determined by the conformational structure that allows them to be involved in a variety of

signaling and regulatory pathways[36]. Transcriptional reprogramming produces a strong effect on structural versatility concerned with plant responses to stress[37]. Specific NAC transcription factors have been reported to suppress or induce senescence via a number of signaling pathways[38,39]. The discovery of rice NAC103 (OsNAC103) has been emphasized in recent studies as playing a central role in leaf senescence and plant development[40]. The CRISPR mutant *osnac103* showed a delayed onset of senescence compared to wild-type plants. OsNAC103 serves as a key positive regulator of leaf senescence in rice by coordinating a complex network of genetic, hormonal, and environmental responses. The main process involves direct stimulation of transcription of senescence-associated genes (SAGs) including those fundamentally associated with chlorophyll catabolism (OsSGR, OsNYC1, OsNOL, OsNYC3, OsPAO and OsRCCR) and additional interesting regulators including OsSAG12 and OsNAP. Also, OsNAC103 combines and magnifies the effects of senescence by engaging in interactions with important phytohormone pathways. It supplements abscisic acid (ABA) signalling through up-regulation of OsABI5 and OsbZIP23 as well as increases JA biosynthesis and signal[40]. In tobacco, NtNAC028 has been recognized as a positive regulator of natural leaf senescence while simultaneously serving as a negative regulator of stress tolerance[41]. The generated loss-of-function mutant, *ntnac028*, exhibited a delay in leaf senescence and improved drought and salt stress tolerance compared to wild-type plants.

Takahashi *et al.* (2022) investigated the involvement of EPHEMERAL1 LIKE (EPH1L) gene family, which is the part of NAC family, in *Japanese gentians* and found that these genes contribute the process of floral senescence acceleration. The report concentrated on the isolation of *EPH1L* genes and the generation of *ePh1l*-knock out mutants by CRISPR/Cas9 technique. The mutants exhibited delayed senescence phenotype, suppression of senescence-linked gene SAG12, and a diminished genomic DNA deterioration[42]. Also, the investigation of CRISPR knockouts of *NtNAC028* and *NtNAC080* in tobacco has confirmed the positive effect of these genes on the process of senescence regulation[43]. The examined mutants showed a delay in leaf senescence traits both in natural settings and under stress conditions. These findings elucidate the molecular mechanisms governing leaf senescence in tobacco and suggest prospective avenues for enhancing the crop quality[43].

Li *et al.* (2023) examined the involvement of the auxin response factor transcription factor TaARF15 - A1 in senescence of hexaploid wheat (*Triticum aestivum* L.). They generated *TaARF15* knockout mutants in the Kenong199 (KN199) cultivar and found that lines with loss-of-functions had strong senescence phenotypic characteristics, such as premature yellowing of leaves and rapid grain-ripening, in the natural field as well as when subjected to the dark-induced senescence[44]. The latest improvements in CRISPR/Cas9 genome editing have provided the opportunity of precise alteration of flowering-time genes, therefore, enhancing agronomic characteristics in forage crops is of great importance. Wolabu *et al.* (2023) demonstrated this method by focusing on *MsFTa1*, an essential floral integrator gene in lucerne (*Medicago sativa*) that results in delayed flowering and extended vegetative growth. The research brought up tetra allelic *MsFTa1* knockout mutants which additionally showed a significant delay in flowering, of up to 21 days, and a conspicuous senescence delay in comparison to their wild type. This delay in senescence was greatly associated with a massive increment in biomass yield up to 78 per cent fresh weight and 76 per cent dry weight[45]. Furthermore, it improved the forage quality as indicated by the decreased lignin content and the decreased fibre components together with an increase in crude protein and mineral levels. These results highlight the critical role of MsFTa1 in flowering and regulating the development of senescence in lucerne[45]. Liu et al. (2016) conducted another study examining the role of *Ghd2*, a CONSTANS-like gene featuring CCT and B-box domains, in regulating drought response and leaf senescence in rice using CRISPR/Cas9 genome editing. The team has found that the development of *Ghd2* knockout mutants resulted in significant delays in the leaf senescence characteristics during drought, such as the extension of leaf greenness and the inhibition of leaf rolling, as compared to the wild-type plants. *Ghd2*-CRISPR lines demonstrated improved drought tolerance, as indicated by elevated relative spikelet fertility and reduced expression of *SAG*s under stress conditions. The delayed senescence observed in knockout mutants suggests that Ghd2 promotes leaf senescence, making it a potential target for creating drought-resistant rice varieties that maintain longer

photosynthetic activity[46]. Xu *et al.* (2021) examined the OsS40 gene family in rice, and made knockout mutants of each of the 13 members of the broth containing the *DUF584* gene. Their broad CRISPR screen has helped to recognize five individual *OsS40* genes (*OsS40 1, 7, 12, 13, 14*) the disruption in which resulted in a unique stay-green phenotype during natural senescence and dark-induced senescence. One of the studies revealed that the five nuclear-localized proteins have little transcriptional activation activity, which implies that they might be senescence-regulating transcription factors that target senescence-associated gene networks[47].

Transcription factors like WRKY, NAC, ARF and CONSTANS-like proteins have been consistently identified as regulators of senescence in a broad range of plant species, through regulation of senescence associated genes, chlorophyll degradation, of hormone signaling and stress responses[23-47]. Strong causal evidence for the effects of disrupting positive regulators came from the CRISPR/Cas9 knockout studies, which showed that disruption of the positive regulators delayed senescence. Loss of negative regulators accelerated the aging phenotypes. Several responses, however, were environment-dependent, and their sensitivity to dark, drought, ethylene, jasmonic acid and light quality differed. These results indicate that the function of transcription factors in plant senescence is conserved across different species, but differs in specific conditions, and also reveal the potential of genome editing for enhancing crop stress tolerance, biomass and yield.

Genes involved in hormone signalling

In plant senescence, hormone signalling is a critical process. The different hormones affect the pace or avoidance of senescence by diverse pathways which often interrelate with each other. Ethylene, abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), and strigolactones (SLs) are known to contribute to the promotion of senescence. Hormones achieve this through various signalling pathways, often involving chlorophyll degradation, macromolecule breakdown, and the redistribution of nutrients from older tissues to new growth areas[48]. Cytokinins (CKs) are known for their ability to postpone senescence by promoting cell division and expansion, which helps reduce the effects of aging. Hormone regulation is woven into a broader genetic network that is influenced by various internal and external factors, including aging and stress responses[49]. The incorporation of hormonal signals is a complex process with multiple levels of regulation with the interaction of various hierarchies of hormonal signalings. To counter stress, the pathways often experience changes that may affect senescence[50]. The interaction between hormone signaling and plant senescence in crosstalk indicates that there is indeed a complex web of interplay both between developmental steps of the plant and external environment influences[51]. In the following discussion, studies which use CRISPR/Cas9 technology to study senescence phenotypes will be discussed with references to plant hormone signaling.

Ethylene pathway

Ethylene is one of the crucial phytohormone that regulate plant senescence. In a study carried out by Holme *et al.* (2024), CRISPR/Cas9 in *Campanula portenschlagiana* was used to examine the function of ethylene signalling through the EIN3/EIL transcription factors, CpEil1a and CpEil1b[52]. Their allelic series approach revealed a notable gene dosage effect; plants with quadruple knockouts showed complete ethylene insensitivity in flowers, whereas partial mutants exhibited intermediate phenotypes. These mutations specifically blocked responses to external ethylene but did not affect the natural process of senescence. Based on this fundamental research, other experiments by Xu *et al*. elaborated on this literature by designing an overall genetic approach to flower senescence delay in petunia by attacking the ethylene generation pathway[53,54]. They reported that in their 2019 study, knock-out of the *PhACO1* gene lowered the production of ethylene and increased longevity of flowers, hence, a causal relationship between this pathway and ageing was established. A separate study conducted by the same group has revealed that the targeting of two additional important genes, *PhACO3* and *PhACO4*, using CRISPR/Cas9 was more effective[53]. These genes were concurrently mutated to cause a higher level of ethylene reduction, achieved senescence assayed by ethylene and a significant improvement in the lifetime of the florals.

Jasmonate pathway

Kim *et al.* (2022) used CRISPR/Cas9 to disrupt Fibrillin2 (FBN2) which is a key and structural protein in chloroplast plastoglobules critically involved in photoprotection in Arabidopsis. The presence of *fbn2* knockout mutants in high-light stress and methyl jasmonate (MeJA) conditions resulted in faster leaf senescence in the mutants and loss of

chlorophyll with subsequent oxidative injury percentages. These findings demonstrate the exclusive biologic ability of FBN2 in the inhibition of senescence associated with jasmonate, unlike other fibrillin family members[55]. In a related study, Tang *et al*. (2022) investigated SlJAZ10 and SlJAZ11, key repressors of jasmonate signalling in tomatoes. Knockout lines (*sljaz10* and *sljaz11*) exhibited yellowing similar to the wild-type during dark-induced senescence, whereas overexpression lines, especially *SlJAZ11-OE*, showed a delay in chlorosis, indicating greater resistance to senescence. The difference between the knockout and overexpression phenotypes highlights the function of JAZ proteins as negative regulators of senescence operating downstream of jasmonate perception[56].

ABA, Auxin, Cytokinin and Strigolactone Pathways

Li *et al.* (2023) studied TaARF15-A1, an auxin response factor, in hexaploid wheat. The *taarf15* knockout lines exhibited accelerated senescence traits, marked by early leaf yellowing and swift grain maturation under both natural and dark-induced conditions. These findings further support the fact that TaARF15-A1 is a negative regulator of senescence pathway in the auxin pathway[57]. In an another study, Zhang *et al.* (2021) examined OsCKX11 in rice which is a cytokinin oxidase/dehydrogenase that facilitates the catabolism of cytokins. *Osckx11* knockout mutants produced by CRISPR did not age their leaves soon, and even had higher chlorophyll levels and augmented photosynthetic efficiency compared to wild-type vegetation[58]. This study revealed that OsCKX11 is a crucial negative regulator of leaf longevity, connecting cytokinin homeostasis to the inhibition of senescence and an increase in grain yield. The prolonged photosynthetic activity observed in the mutants suggests that careful regulation of cytokinin degradation through gene editing may enhance source-sink dynamics in cereal crops[58].

Gao *et al.* (2018) utilised CRISPR/Cas9-mediated targeted mutagenesis to silence the genes *NtCCD8A* and *NtCCD8B* in *Nicotiana tabacum* and revealed the role of the strigolactone biosynthetic pathway in leaf senescence. The resultant *NtCCD8* intact mutants exhibited the anticipated architectural modifications, along with heightened branching and decreased internode expansion together with a strong accelerated senescence phenotype as manifested by early-stage leaf chlorosis and reduction in chlorophyll content[59]. Another study, Huang *et al*. (2019) used the 9-cis-epoxycarotenoid dioxygenase dioxinase 5 gene - OsNCED5- to study the role of this gene in *Oryza sativa*. A knockout of *OsNCED5* with CRISPR/Cas9 resulted in rice lines with a delayed senescence phenotype and an increased sensitivity to abiotic stresses, but the opposite with overexpression lines which had an enhanced senescence and better resistance to stress through the capacity to survive abiotic stressors. The given results highlight the central role of the intensity of regulation of abscisic acid biosynthesis, facilitated by the OsNCED5, in a stress-based senescence pathway[60].

Studies with CRISPR/Cas9 in various plant species have found hormone signaling pathways to be key regulators of plant senescence, such as ethylene, jasmonate, auxin, cytokinin, ABA and strigolactones[48-60]. Reduced ethylene, ABA and strigolactone signalling tends to delay senescence, whereas increased cytokinin signalling tends to extend the life of the leaf and increase photosynthetic activity, according to conserved findings. Several effects were, however, condition-dependent and changed under stress, dark, high light or hormone induced conditions. The precise manipulation of hormone-related genes in knockout and overexpression studies gave direct causal evidence: the ability to change the rate of chlorophyll degradation, stress responses and progression of senescence was observed beyond the earlier correlative observations.

Kinases

Protein kinases play a crucial role in plant senescence and are vital mediators in the signal transduction pathways that regulate this complex process[61]. They govern signal transduction processes that enable responses to developmental signals and environmental stress, thereby ensuring optimal adaptation and survival[61,62]. Recent studies using CRISPR/Cas9 have deepened our understanding of the genetic regulation of leaf senescence, revealing a complex network that encompasses receptor kinases, metabolic enzymes, and signalling components. Xu *et al.* (2023) demonstrated that knocking out the lectin receptor-like kinase *PWL1* results in premature senescence and seedling lethality, underscoring its role in maintaining ROS homeostasis and chloroplast activity[63]. Zeng *et al.* (2018) conducted a separate study using CRISPR to verify that

OsBBS1/OsRLCK109 play a role in regulating margin-specific leaf senescence[64]. Zheng et al. (2021) highlighted the significance of metabolic regulation, demonstrating that the hexokinase OsHXK1 promotes senescence by inducing ROS accumulation through glucose metabolism[65]. Moreover, Pathak *et al.* (2022) analyzed the maladaptations of the editing of key metabolic regulators, including OsTOR and OsSnRK1a with loss-of-function mutations often initiating premature senescence or sterility[66]. Wang *et al.* (2019) took advantage of using CRISPR/Cas9 and revealed that the calcium-dependent protein kinase OsCPK12 mediated chlorophyll catabolism and photosynthetic efficiency since the edited rice lines displayed early senescence phenotypes[67]. Together, these studies support the fact that CRISPR/Cas9 can be useful to study senescence pathways, describe positive and negative regulators (e.g., OsHXK1/2/3, OsCPK12, PWL1, OsBBS1/2/3), elucidating the nexus between senescence and stress responses, and demonstrate how essential genes impact the decision-making of the leaf. The studies using CRISPR/Cas9 consistently demonstrate that protein kinases and signalling regulators play critical roles in regulating plant senescence by maintaining ROS homeostasis, chlorophyll and stress response pathways[61-67]. Key regulators, like PWL1, OsCPK12 and OsBBS1/ OsRLCK109, are frequently disrupted, resulting in premature senescence and reduced photosynthetic activity, as revealed by conserved findings.

Genes associated with chloroplasts and photosynthesis

Photosynthetic related chloroplasts and genes play complex and multifaceted roles in plant senescence. Being one of the most vital organelles, chloroplasts perform photosynthesis thus providing the energy that plants need in their growth and a very strong effect on senescence control by various means, among which are different molecular pathways[68]. Current research in different crop species has highlighted the role played by chlorophyll metabolism in the senescence regulation. Xue *et al*. (2022) utilised CRISPR-Cas9 to generate an *sgr1-101* knockout allele, thereby effectively mitigating the early senescence observed in the *abs3-1D* mutant during carbon deprivation[69]. This study has highlighted the vitality of the senescence-associated gene of the chlorophyll catabolic pathway, likeness to that of SGR1. The study by Jung *et al.* (2021) has shown that an OsCAO1, which is an encoder of the chlorophyllide oxygenase required to synthesize chlorophyll b, when knocked out, gave rise to a senescence-like phenotype with the characteristics of pale green foliage, low chlorophyll content, and poor chloroplast development. These mutants exhibit notable declines in photosynthetic efficiency, biomass, and grain yield, underscoring OsCAO1's dual function in chlorophyll biosynthesis and degradation[70]. Ng *et al.* (2024) investigated the relationship between chlorophyll breakdown and stay-green traits in *Zoysia matrella* in greater detail. Simultaneously impairing all four alleles of ZmNYC1 that encode chlorophyll b reductase using the CRISPR/Cas9 system resulted in reducing chlorophyll degradation and retaining color in plants of *Zea mays* plants throughout winter. This study confirmed the role of a chlorophyll-catabolic enzyme and demonstrated the application of the NYC1 gene in gene-editing methods for turfgrass cultivation to enhance its aesthetic value[71]. Investigations with the use of the Arabidopsis species have provided insights into the role of the plastoglobule-related proteins in the regulation of senescence[72]. The loss-of-function mutants of *FBN2* possessed were characterized by accelerated leaf senescence and chlorophyll catabolism under high-light conditions and the presence of the methyl jasmonate, which would confirm the essential nature of FBN2 loss-of-function in photoprotection and in reducing the senescence state in the presence of methyl jasmonate. This study highlighted FBN2's unique function in the stress response and the regulation of senescence, setting it apart from other members of the fibrillin family[72]. Empirical observations have shown that, CV-deficient plants have retained photosynthetic competence during water deficit and salinity, hence delaying senescence and having a better yield[73]. Ding *et al*. (2018) also analysed tomato lines with knockouts of *SBPase* that disrupt Calvin Benson cycle; these lines exhibited an accelerated senescence phenotype, with lower chlorophyll levels and decreased photosynthetic efficiency when subjected to methyl jasmonate and long-term darkness[74]. Furthermore, the adaptability of CRISPR was demonstrated through the development of *SGR1* knockout lines, which exhibited delayed fruit senescence, along with modified chlorophyll degradation and carotenoid profiles during the ripening process[75]. Recent developments feature Li *et al*. (2024), who developed *Gmcry1abcd* quadruple mutants in soybean that exhibited early senescence, whereas *GmWRKY100* knockouts demonstrated

delayed senescence. This study uncovered a new blue light signalling pathway that influences chloroplast function[76]. Collectively, these studies demonstrate the impressive precision of CRISPR/Cas9 technology in investigating the roles of genes associated with chloroplasts and photosynthesis in the regulation of senescence. In various plant species, the study of CRISPR/Cas9 has consistently identified chloroplast- and photosynthesis-related genes as key regulators of senescence, encompassing chlorophyll metabolism, photoprotection, and efficiency of photosynthesis[68-76]. Conserved findings suggest that disruptions in the genes that regulate chlorophyll degradation tend to delay senescence and favor stay-green, while impairment of photosynthesis-related genes tend to cause senescence to progress more quickly and to reduce growth and yield.

Epigenetic & post-transcriptional regulator

Epigenetic mechanisms include modifications in chromatin structure, DNA methylation, and histone alterations, all of which can influence the activity of transcription factors crucial for regulating genes associated with plant senescence. However, these alterations did not modify the genetic code. Rather, they influence the processing of genetic information, which is essential for gene expression and critical for regulating the expression dynamics of senescence-related genes[77,78]. Similarly, post-transcriptional regulation is essential for plant senescence. This involves processes that include RNA alterations modifying the mRNA stability and translation efficiency and hence, refining gene expression. Small RNAs, in particular, microRNAs (miRNAs) and small interfering RNAs (siRNAs) are the incredibly important post-transcriptional regulators[79]. In a recent study, it was found that epigenetic editing was capable of delivering heritable alterations in changes of methylation patterns in spontaneously occurring epialleles, which affected the phenotypes of plants in the subsequent generations. This was demonstrated in a targeted DNA demethylation investigation of a spontaneous epiallele in Arabidopsis using CRISPR/dCas9-TET1cd technology[80]. This investigation focused on NMR19-4, a naturally occurring methylation region within the *PPH* promoter. *PPH* encodes an enzyme involved in the degradation of chlorophyll and in the process of leaf aging. By effectively demethylating NMR19-4, they observed an increase in *PPH* expression and quicker onset of leaf senescence in modified plants. A study of rice *Osago2* mutants demonstrated that the ARGONAUTE protein OsAGO2, an integral part of the RNA-induced silencing complex (RISC), regulates senescence by influencing *OsNAC300* expression via DNA methylation. This finding connects small RNA-mediated post-transcriptional silencing with the epigenetic control of transcription factors associated with senescence[81]. Similarly, Chen *et al*. (2024) utilized CRISPR/Cas9 to knockout *SlYTHDF2* in tomatoes, an m6A-binding protein that influences mRNA stability and translation. A lack of this protein accelerated dark-induced senescence by disrupting chloroplast function through its interaction with the photosynthetic protein SlRBCS3 and heightened ABA sensitivity[82]. In conclusion, epigenetic and post-transcriptional regulators play important roles in modulating plant senescence via DNA methylation, RNA silencing, and mRNA stability pathways, as revealed by the studies on the three species, Arabidopsis, rice and tomato.

Peptide signalling and cell wall modifiers

Recent studies have recognized the role of peptide signaling molecules as a critical controller of leaf senescence[83]. These peptides act via their effects on membrane receptor kinases and are inherent members of more comprehensive networks of signaling that have been previously believed to be primitively controlled by canonical phytohormones[84]. Another important finding, the involvement of Cell-wall remodelling in plant senescence, provides a recent update on plant senescence. Cell-wall remodelling is a dynamic process which is mediated by many factors which include the signaling pathways due to stress. The production of reactive oxygen species (ROS) through abiotic stress leads to the realization of the subsequent adjustments in the cell wall which consequently prompts further resilience and defensive capacity of the plant[85]. The CLE peptide family has become one of the master regulators of the leaf senescence in Arabidopsis. The small genomic loci of the genes of the CLE family were overcome by the CRISPR/Cas9 tool enabling Zhang *et al.* (2022) to design loss-of-function mutants of the gene *CLE42*. *CLE42* loss increased senescence, but increase in its expression slowed and prevent leaf senescence with age and darkness. Further investigations revealed that CLE42 inhibits senescence by negatively regulating ethylene biosynthesis and signalling pathways, particularly affecting the ACS-EBF-EIN 3 cascade[86]. Studies have shown that knocking out *CLE 14*, led to

accelerated senescence. The peptide that is examined in this study acts as a negative regulator that promotes JUB1-mediated reactive oxygen species (ROS) scavenging[86]. In another extension of these results, Zhang et al. (2024) studying the role of serine-rich endogenous peptides (SCOOPs) and their association with the receptor-like kinase MIK2 in senescence regulation in Arabidopsis. When they induced *prosocop12* mutant using CRISPR-Cas9, they had observed phenotypes associated with premature senescence. It was found that there is a subtle competitive binding process in which the activity of the two SCOOP10 and SCOOP12 peptides has an opposing effect on the progression of senescence due to the activity of MIK2 within subfamily XI, a leucine repeat receptor-like kinase (LRR-RLK)[87]. This piece of work demonstrates that phytocytokine signalling is vital in the regulation of senescence in leaves of the Brassicaceae. Simultaneously, the studies used CRISPR/Cas9 editing on tomatoes to examine how cell-wall associated proteins regulate senescence by interrogating their roles. Lu *et al.* (2023) generated knockout lines of *SAE1* (*SENESCENCE-ASSOCIATED EXTENSIN 1*) and also reported this delay in leaf senescence in response to natural ageing and dark induction. SAE1, which had been proven to be a classical extensin protein of the hydroxyproline equipped glycoprotein one, was shown to positively affect the leaf senescence through a pathway involving ubiquitin-ligase SINA4 and also ubiquitin-proteasome system[88]. This study revealed a new connection of cell-wall structure and senescence. Jeong *et al.* (2024) recently produced *fab2* null mutants in tomato to highlight the contextuality of cell-wall alteration in the regulation of senescence. Arabinosyl transferase *FAB2* mutants exhibited augmented senescence and sterility as a result. Transcriptomic data showed that FAB2 helps in the promotion of leaf longevity by silencing activity of genes normally up-regulated in mature leaves. The past decade has revealed that peptide signalling molecules and cell-wall modifiers play significant roles in regulating senescence in Arabidopsis and tomato via ROS homeostasis, ethylene signaling and cell-wall remodeling pathways[83-88]. The precise modification of peptide and cell-wall associated genes in a CRISPR-based knockout study directly demonstrated causal evidence, as this alteration was shown to directly affect senescence phenotypes, stress responses and developmental stability.

Autophagy and nutrient remobilization

Autophagy, which allows the degradation and recycling of cell components, is essential for plant senescence. This process helps to redistribute essential nutrients from aging tissues, such as leaves, to developing or storage organs, such as seeds[89,90]. Moreover, literature has also found that autophagy serves a central role in carbon, nitrogen and redox homeostasis and as such affects both metabolomic and transcriptomic landscapes. The autophagy deficits cause significant faults, such as the reduction of antioxidant concentrations and the inappropriate distribution of metabolic resources[91,92]. In Petunia, Lin and Jones (2022) utilized CRISPR/Cas9 to generate knockout mutants of the crucial autophagy gene *PhATG6*. The *PhATG6-KO* lines exhibited significantly accelerated corolla senescence, resulting in flowers with shorter lifespans than the wild-type controls. Early ethylene production and enhanced expression of senescence-related genes are associated with the premature senescence phenotype, suggesting that autophagy typically modulates hormonal and transcriptional processes to delay petal senescence[93]. This study emphasized that PhATG6-mediated autophagy plays a crucial role in effective phosphorus remobilization during petal senescence. This was evidenced by impaired phosphorus transport to seeds in knockout plants, resulting in a reduced seed yield[93]. Nutrient mobilization plays a crucial role in plant senescence and enhances the overall fitness of plants. Research in Brassica revealed that knockout mutants of *NPC4* (a nonspecific phospholipase C) and *PLDZ2* (a phospholipase D), enzymes that hydrolyze membrane phospholipids during senescence, showed delayed leaf senescence phenotypes, whereas overexpression lines demonstrated accelerated senescence. These findings indicate that these phospholipases play a crucial role in promoting senescence. This study offers insights into the role of membrane lipid degradation in phosphorus recycling from ageing leaves to growing tissues, highlighting the importance of phospholipid catabolism in nutrient remobilisation during senescence[94]. Additionally, Zhang *et al.* (2021) used CRISPR/Cas9 to modify TaARE1, a negative regulator of nitrogen assimilation in wheat. The researchers successfully created transgene-free mutant lines featuring either partial or complete knockouts of *TaARE1* homologs[95]. Under nitrogen-limited and ideal field conditions, the gene-edited lines showed improved nitrogen use efficiency

(NUE), delayed senescence, and higher grain production. Research has shown that TaARE1 generally promotes senescence when nitrogen is limited, and its disruption enables extended photosynthetic activity and improved nitrogen distribution in grains[95]. Similarly, a study of knockout lines of a glycosyltransferase gene *PLS2* which is linked with the metabolism of sucrose revealed a senescent early leafless phenotype and less height of plant. These findings highlight the relationship between senescence regulation and sugar metabolism. Further analysis revealed that *PLS2* mutation led to sucrose accumulation and reduced the expression of genes involved in sucrose metabolism, indicating that appropriate sugar partitioning is crucial for normal leaf senescence progression[96]. The importance of the autophagy and nutrient remobilization pathways in controlling senescence, nutrient recycling and productivity has been consistently demonstrated in crop plants, such as petunia, Brassica, wheat, and others. Dysfunction of genes involved in autophagy, phospholipid degradation, or sugar metabolism typically promote senescence and inhibit nutrient remobilization, but on the contrary, increased nitrogen assimilation causes a delay in senescence and boosts yield, as seen in conserved findings. The importance of the autophagy and nutrient remobilization pathways in controlling senescence, nutrient recycling and productivity has been consistently demonstrated in crop plants, such as petunia, Brassica, wheat, and others[89-96]. Dysfunction of genes involved in autophagy, phospholipid degradation, or sugar metabolism typically promote senescence and inhibit nutrient remobilization, but on the contrary, increased nitrogen assimilation causes a delay in senescence and boosts yield, as seen in conserved findings.

Stress responsive genes

The stress-responsive genes create a fine balance between survivals and ageing, which helps the plants to cope with the ever-changing environment and to regulate processes that are important in development. Wang *et al.* (2022) showed the use of CRISPR-Cas9 in maize to silence *ZmSAG39* which is a recently identified senescence-specific gene. The resultant knockout lines were more tolerant to dark and drought conditions, had high rates of seed germination, increased seedling survival, and an increase in chlorophyll concentrations. Furthermore, these lines exhibit reduced concentrations of reactive oxygen species and malondialdehyde (MDA) compared to wild-type plants[97]. This study demonstrates that ZmSAG39 typically functions as a negative regulator of stress tolerance. Its knockout was found to delay stress-induced senescence, indicating its potential as a target for creating drought-resistant maize varieties[97]. Two large-scale studies on rice have demonstrated a complex association between stress responses and the regulation of senescence. Wang *et al.* (2024) generated *OsACA9* knockout mutants using CRISPR/ Cas9, that exhibited enhanced resistance to bacterial diseases. However, these mutants unexpectedly exhibited early leaf senescence, characterised by leaf yellowing, a decline in the photosynthetic rate, and reduced chlorophyll content[98]. This finding suggests that the calcium transporter OsACA9, a member of the P-type IIB Ca2+-ATPase family, plays a dual role in regulating calcium homeostasis and balancing disease resistance with senescence progression of senescence[98]. PSL50 proved to be one of the main regulators of heat stress and senescence, identified by He *et al.* (2021), in sl50 mutants, early senescence of leaves and an increase in their sensitivity in the face of heat stress was observed, which could be explained by membrane damage and cell death by H_2O_2.

PSL50 encodes a subunit of a clathrin-associated adaptor protein complex that plays a role in vesicular trafficking, connecting intracellular transport to the stress response and regulation of senescence[99]. The study conducted by Kieu *et al.* (2021) also examined the resistance of potato against late blight by targeting the genes that are connected to defense against pathogens using CRISPR/Cas9. According to their data, when StDND1, the protein of a population representing a cyclic nucleotide-gated ion channel involved in Ca^{2+} conductance, is knocked out, it does not only increase the disease resistance but also initiates a senescence-like phenomenon with necrotic lesions observed in the leaves[100]. Results of these studies indicate that StDND1 can be involved in various physiological processes that combine the pathogen defence system and the process of senescence. Mohr *et al.* (2022) utilized CRISPR-Cas9 in wheat to disrupt all *Sal1* genes responsible for encoding plastid-localized oxidative stress sensors. This led to the creation of mutants that exhibited delayed senescence under water-limiting conditions, although no improvement in yield was observed[101]. These findings point to the possibility that under drought conditions, Sal1 normally facilitates senescence, possibly as has been proposed in a drought-sensing system. Based on these findings,

Zhang *et al.* (2022) have shown that CRISPR/Cas9 - mediated knockout of *LS1* in rice triggers premature senescence of the leaf, which is characterized by the depletion of chlorophyll content and an increase in ROS buildup, thus, establishing LS1 as a positive controller of the leaf longevity in rice[102]. The results of such findings give a basis for selective breeding and biotechnological intervention aimed at optimization of senescence timing and thus enhance stress resistance of crops. They further bring up the need to trade-off between stress resistance and yield potential because senescence mutation can result in trade-offs in plant performance[101].

The relationship between stress tolerance, ROS homeostasis, senescence progression and the role of stress responsive genes has been consistently demonstrated in maize, rice, potato and wheat using CRISPR/Cas9 system[97-101]. Conserved results show that disruption of multiple genes involved in stress response results in changes in the stability of chlorophyll, build-up of ROS, and longer leaf lifespan, with an increased tolerance often observed for drought, heat, or pathogens. The direct causal evidence was provided by the CRISPR-based knockout studies, which directly demonstrated that the modification of one of the genes involved in stress responses directly impacted senescence timing, stress adaptation and other physiological trade-offs.

Regulators of Nuclear Architecture

Recent advancements in CRISPR/Cas9 genome editing have underscored the role of nuclear architecture in leaf senescence, as shown by Cao *et al.* (2024) in their study of the nuclear lamina component KAKU4 in Arabidopsis. The researchers generated three unique mutant alleles (*kaku4-03Cas9*, *kaku4-04Cas9*, and *kaku4-05Cas9*) contain specific alterations in the *KAKU4* gene, which encodes an essential nuclear lamina protein that plays a crucial role in regulating nuclear shape and chromatin organization[103]. All CRISPR-generated mutants showed consistent and accelerated leaf senescence traits in both the cotyledons and rosette leaves of mature plants, reinforcing the senescence characteristics seen in traditional T-DNA insertion lines. This study enhances our understanding of the role of nuclear architecture in plant aging, demonstrating that KAKU4 is a negative regulator of age-related leaf senescence, possibly affecting H3K27me3 deposition patterns throughout the genome[103].

Conclusion and Future Prospects

Plant senescence is a normal developmental process that combines genetic program and environmental cues to facilitate nutrients recycles, stress adaptive and reproduction success. With the introduction of CRISPR-Cas genome editing, the ability to study and control complex biological systems has been transformed, and important regulatory networks in transcription factors, hormone signal transduction, chloroplast regulation, autophagy, and epigenetic control can now be precisely characterised. Besides confirming current senescence pathways, CRISPR has also uncovered new regulatory elements, such as nuclear architecture proteins and peptide signalling. In addition, it has important agronomic benefits, including extension of senescence to increase photosynthetic effectiveness, ability to remobilise nutrients and increase stress resistance in major crops. Manipulation of senescence-associated genes has shown considerable agronomic benefits such as increase in biomass, grain yield, stress tolerance, increased longevity, and enhancing stress-related postharvest quality traits like delaying flower and leaf senescence. However, studies demonstrated that improving disease resistance or stress adaptation comes with trade-offs such as accelerated senescence, decreased fertility, and growth penalties were found to be associated with senescence pathway enhancements, highlighting the importance of balancing senescence pathway improvements in crop improvement.

The integration of CRISPR with senescence-inducible promoters and cis-regulatory element (CRE) editing is a powerful method for precisely adjusting senescence dynamics to improve yield. Targeting the promoter regions of senescence-associated genes enables spatiotemporal modulation of expression, which is achieved through either developmental stage-specific or stress-responsive induction. This strategy could be used to protect the coding sequences and avoid genetic instability as well as to enhance agronomic value. The next-generation CRISPR technologies, which include base and prime editors, along with CRISPRa/i, will enhance the accuracy of the modulation of senescence dynamics and coordinate the prolonged photosynthetic action and the optimum distribution of nutrients in crops. By combining these methods with multi-omics data, the interactomes that regulate senescence, especially the interaction between phytohormones and the environment, will be made clear. It is imperative to

note that field trials in translational programs can be used to evaluate CRISPR-edited senescence mutations in real-world environments and explore whether they have pleiotropic consequences on plant structure, resistance to disease, and ecosystem interactions. The intersection of accurate genome editing, controllable promoter technology, and CRE development allows fresh chances to create weatherproof crops that can regulate senescence adaptively and thus increase yield, nutritional value and sustainability to meet worldwide agricultural problems.

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Conflict of interest

The authors confirm that no financial, professional, or personal conflicts of interest could influence the research, analysis, or conclusions presented in this manuscript.

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