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MOLECULAR PERSPECTIVE ON THE MECHANISMS REGULATING LEAF SENESCENCE IN PLANTS UNDER WATER STRESS

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ABSTRACT

Leaf senescence is an irreversible growth process that determines plant productivity and survival, especially under environmental stress. Among water stresses, drought and submergence significantly influence senescence pathways through distinct molecular mechanisms. Drought stress accelerates leaf senescence by impairing photosynthesis, reducing leaf expansion, and disrupting water balance, with transcription factors such as NAC, WRKY, and AP2/ERF playing critical roles in its regulation. In particular, the NAC transcription factor family modulates key senescence-associated genes, while WRKY and AP2/ERF members coordinate stress responses through ABA-dependent and independent pathways. Submergence, on the other hand, induces ethylene-mediated senescence, primarily through hypoxia-induced metabolic shifts and light deprivation. ERF transcription factors, particularly ERFVII, regulate hypoxia-responsive genes, whereas bHLH and WRKY transcription factors contribute to ethylene-induced senescence. Furthermore, NAC family regulators, along with EIN3, modulate dark-induced senescence under submergence, revealing mechanistic overlap with natural senescence processes. Recent advances further reveal that epigenetic modifications dynamically alter chromatin accessibility, activating or suppressing senescence. Moreover, posttranslational regulation through ubiquitin-proteasome degradation and autophagy modulates senescence, with the proteasome accelerating it and autophagy delaying it through selective protein turnover. This review comprehensively explores the transcriptional regulation of leaf senescence under drought and submergence stresses, along with epigenetic and posttranslational regulation, and emphasizes the role of key transcription factor families. Understanding the molecular and physiological mechanisms regulating leaf senescence under these contrasting water stresses is critical for developing stress-resilient crops and enhancing agricultural sustainability in the face of climate change.

Key words: drought stress, epigenetic regulation, ethylene signaling, posttranslational regulation, submergence stress, transcription factor

INTRODUCTION

Leaf senescence is an essential aspect of the plant developmental program, a natural and irreversible progression that leads plants to the final stage of their life cycle (Popov et al. 2022). It is a type of programmed cell death in higher plants, which can be triggered by internal and environmental factors. Drought, submergence, light, heat, nutrient stress, pathogen infection, etc., are environmental factors that lead to early leaf senescence. Endogenous factors, including various plant hormones,

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developmental age, and signals related to reproductive development, initiate the same process (Zhao et al. 2022). Essential nutrients are then transferred from the senescing leaf to other actively growing sites. The change in leaf color from green to yellow, caused by chlorophyll degradation, is the earliest visible symptom of leaf senescence. Furthermore, the degradation of lipids, proteins, and RNA, along with the observed increase in ethylene synthesis, are among the various cellular transformations that occur during leaf senescence (Guo et al. 2021). Reports have shown that adjustments in the activity levels of various antioxidative enzymes were observed in various plant species, including an increase in peroxidase (POD) and a decrease in superoxidase dismutase (SOD) (Omidi et al. 2022). Altered gene expression has also been reported, marked by a reduction in photosynthesis-associated transcripts and an increase in senescence-associated gene (SAG) transcripts (Tan et al. 2023).

As sessile plants, they often encounter a variety of environmental stresses that can alter or degrade their biochemical, physiological, morphological, anatomical, and molecular attributes (dos Santos et al. 2022). Nearly 50% crop loss has been reported due to various environmental stresses (Oyebamiji et al. 2024). Among them, two extreme water stresses that significantly affect plant physiology, especially leaf senescence, are drought and submergence stress (Cabusora 2024, Kalairaj et al. 2024). Drought stress is an environmental constraint that plants face throughout their life cycles, hindering overall productivity, reproductive success and survival, and significantly influencing global agriculture, thereby affecting the food supply for a growing population around the world (Wahab et al. 2022). Erratic precipitation often leads to drought, adversely affecting plant survival. Limiting cell growth and enlargement are the physiological effects of drought stress, which directly affect the proper development and functioning of leaves. Reduced leaf expansion reduces the total photosynthetic area under stress conditions, thereby leading to premature leaf senescence (Guo et al. 2021). Several families of transcription factors (TFs) such as NAC (*NAM*, *ATAF1/2*, and *CUC2*), WRKY, ABI3/VP1 (Abscisic Acid Insensitive3/Viviparous1), CBF/DREB (C-repeat Binding Factor/Dehydration-Responsive Element Binding Protein), MYB (Myeloblastosis), AP2/ERF (APETALA2/Ethylene Responsive Factor), etc., play a crucial role in regulating senescence under drought stress (Jan et al. 2019). Each of these TF families contributes uniquely to the regulation of senescence in various crop species. In horticultural crops, they act as central molecular regulators, integrating hormonal, developmental, and stress signals to coordinate the initiation and progression of leaf senescence (Table 1).

Table 1. Regulation of leaf senescence in horticultural plants associated with transcription factor/promoter

Plant	Transcription factor/promoter	Chlorophyll	Yield/biomass	References
Tomato	SAG12/SAG13	advanced flowering	increased fruit weight	Swartzberg et al. 2006
Tomato	AGPaseS1	nd	nd	Luo et al. 2005
Tomato	SlNAP2	reduced chlorophyll accumulation	reduced yield	Ma et al. 2018
Tomato	SlERF.F5	reduced chlorophyll accumulation	nd	Chen et al. 2022
Tomato	SlERF36	reduced chlorophyll accumulation	no adverse effect on yield	Upadhyay et al. 2014; Garg et al. 2024
Eggplant	SAG12	higher chlorophyll content	increased yield	Xiao et al. 2017
Cucumber	SAG12	higher chlorophyll content	increased yield	Liu et al. 2022
Gerbera	SAG12/SAG13	nd	extended lifespan	Huang et al. 2021
Canola	AtMYB32	higher chlorophyll content	increased production	Kant et al. 2015

nd – not determined

On the other hand, submergence stress resulting from excessive water availability presents a completely different challenge. Particularly in areas prone to flooding, submergence stress is a serious environmental problem for many plants. While submerged, plants experience numerous stresses that interfere with normal physiological functions. Submerged plants experience hypoxia or anoxia, which leads to a shift from aerobic to less efficient anaerobic metabolic processes and to complete darkness (Yuan et al. 2023). Although direct studies on submersion-induced leaf senescence are limited, the effects of hypoxia, low light, or complete darkness under submerged conditions may offer important insights. Water prevents the exchange of light and gases necessary for respiration and photosynthesis, leading to senescence (Krieger-Liszkay et al. 2019). Therefore, stress symptoms such as early leaf senescence are common in submerged plants. It is a plant survival strategy to allocate resources to vital parts more rapidly (Guo et al. 2021). When leaves are submerged, a complex regulatory environment is created that accelerates senescence due to hypoxia and low light or darkness (Dalle Carbonare et al. 2023, Tan et al. 2023). Submergence stress often leads to elevated ethylene levels in plants because it is a key signaling molecule responsive to flooding conditions, playing a significant role in regulating senescence via various TF families (Koyama 2014).

Understanding how plants regulate leaf senescence in response to these contrasting stresses is important because it demonstrates the adaptability and flexibility of plant systems, highlighting the intricate interactions between transcription factors and signaling pathways. A better understanding of the regulatory mechanism might help researchers grow plants with higher quality, productivity, and tolerance to environmental challenges, ensuring food security and sustainable agriculture. Therefore, this review aims to explore the mechanisms regulating leaf senescence, particularly under drought and submergence stresses, mainly focusing on different TFs.

REGULATION OF LEAF SENESCENCE INDUCED BY DROUGHT

Responses to drought stress can be very diverse, from alterations in gene expression patterns to changes in plant metabolism and growth. Drought accelerates leaf senescence by maintaining the overall water balance of the plant while redistributing nutrients from senescing or source leaves to other absorbent organs or younger leaves. Loss of photosynthesis and reductions in yield and canopy size are the results of drought-induced senescence (Guo et al. 2021). Various TFs were found to be associated with senescence under drought stress (Table 2). TFs control gene expression to help plants adapt to drought conditions, often accelerating senescence to conserve resources (Abdelrahman et al. 2017; Jan et al. 2019). A better understanding of their functions can help develop drought-resistant crops and shed light on the molecular processes underlying drought-induced senescence.

Genome-wide analyses of *Arabidopsis* plants have revealed that senescence-related genes are active in multiple phases of senescence, including macromolecule disintegration, remobilization, and transit, as well as distinct stress responses (Asim et al. 2023). Molecular research has identified and examined key genes in the model plant *Arabidopsis* involved in senescence. These include: NAC124 with Transmembrane Motif1 like 4 (*NTL4*), *WRKY53*, *ORESARA9* (ORE9), senescence-associated gene 101 (*SAG101*), Lipoxygenase 1 (*LOX1*), *Arabidopsis* NAC-like, activated by *APETALA3/PISTILLATA* (*ANAC029*, *AtNAP*), and *ORESARA1* (*ORE1*, *ANAC092*; *AtNAC2*) (Li et al. 2012; Rauf et al. 2013; Fan et al. 2023). Among the numerous TFs induced during senescence, the NAC and WRKY families play crucial roles in the regulation of senescence (Chen et al. 2017; Mao et al. 2017; Cao et al. 2023).

Table 2. Main genes and transcription factors associated with regulation of drought-induced leaf senescence and their functions

Number	Gene/transcription factor	Function	References
1	NTL4	Promotes ROS accumulation in distal leaf areas during drought stress, accelerating leaf senescence and programmed cell death	Arce et al. 2022
2	ATAF1	Directly interacts with genes involved in ABA biosynthesis (*NCED3*, *ABCG40*), increasing ABA levels and promoting senescence in response to drought	Jan et al. 2019
3	ORE1	Positive regulator of leaf senescence; overexpression speeds up senescence, and its deletion delays it	Rauf et al. 2013
4	JUB1	Negative regulator of senescence; reduces ROS accumulation and delays senescence under drought conditions	Fuertes-Aguilar & Matilla 2024
5	ORS1	Positive regulator of drought-induced leaf senescence; overexpression accelerates senescence, deletion delays it; linked to hydrogen peroxide and salt stress responses	Chen et al. 2023
6	VNI2	Negative regulator of leaf senescence, suppresses senescence in response to drought stress	Cao et al. 2023
7	WRKY53	Positive regulator of leaf senescence in Arabidopsis, involved in stress-related gene expression during drought	Miao & Zentgraf 2007
8	WRKY22	Positive regulator of leaf senescence, particularly in response to darkness, also relevant to drought conditions	Zhou et al. 2011
9	WRKY6	Promotes the expression of senescence-associated genes (SAGs); overexpression accelerates senescence, knockout delays it	Miao et al. 2004
10	WRKY54, WRKY70	Redundant roles in promoting leaf senescence, double mutants show early senescence phenotypes under stress conditions	Besseau et al. 2012
11	WRKY30	Mediator of positive and negative senescence transcription factors, involved in ROS signaling during drought stress	Scarpeci et al. 2013
12	PIF3, PIF4, PIF5	Phytochrome-interacting factors regulating dark- and drought-induced senescence; control chlorophyll degradation and ROS production	Cao et al. 2023
13	ARF2	Optimizes stress response by regulating genes associated with senescence, balances growth and survival under drought	Lim et al. 2010
14	SR1	Regulates ethylene signaling to balance senescence and growth during drought stress, controls ethylene-induced senescence	Sarwat 2017
15	RCD1	Interacts with DREB2A, linking drought stress to senescence by heat and drought response regulation	Sato et al. 2024

TRANSCRIPTION FACTOR-ASSOCIATED REGULATION UNDER DROUGHT STRESS

Regulatory role of the NAC transcription factor family

The NAC TF family is divided into three main superfamilies: no apical domain (*NAM*), *Arabidopsis* transcription activation factor (*ATAF*), and cup-shaped cotyledon (*CUC*) based on similarities of their DNA-binding domains (Fuertes-Aguilar & Matilla 2024). NAC TFs contain a highly conserved N-terminal DNA-binding NAC domain and a variable C-terminal transcriptional regulatory region, allowing diverse roles in development and stress responses. A considerable number of NAC genes have been recognized due to the accessibility of whole genome sequences for various plants, including 117 in *Arabidopsis thaliana*, 151 in *Oryza sativa*, 79 in *Vitis vinifera*, 152 in *Glycine max*, and 163 in *Populus* spp. (Li et al. 2022; Xu et al. 2024).

NAC TFs play diverse roles in regulating developmental processes and responses to various abiotic and biotic stressors (Fuertes-Aguilar & Matilla 2024, Liu et al. 2024). During leaf senescence in *Arabidopsis*, approximately 30 NAC genes have been shown to be highly elevated by global transcriptome profiling, underscoring their significance in senescence regulation (Lindemose et al. 2014; Fuertes-Aguilar & Matilla 2024). Several NAC TFs are important senescence regulators in *Arabidopsis*, such as NTL4, ORS1, VNI2, ATAF1, ANAC016, AtNAP, and ORE1 (AtNAC2) (Zentgraf 2007; Rauf et al. 2013; Fan et al. 2023). A positive regulatory function in leaf senescence is supported by the finding that silencing of the *ATAF1*, *ORS1*, *AtNAP*, *ORE1*, and *ANAC016* genes delays senescence, while overexpression of these genes accelerates it (Chen et al. 2023). In turn, leaf senescence is suppressed by *VNI2* and *JUB1* (Cao et al. 2023). Further evidence for their important role in senescence-associated regulatory networks comes from the senescence-induced expression patterns of homologs of these TFs, including *RD26* (*ANAC072*), *ANAC019*, and *ANAC055* (Ramaswamy et al. 2017). Several observations on drought-induced leaf senescence have highlighted the physiological significance of *NTL4*. Mutants deficient in *NTL4* exhibit traits such as delayed leaf senescence, reduced ROS levels, confirming the interrelation between leaf senescence and ROS accumulation under drought conditions, and improved drought resistance (Balazadeh et al. 2010; Tan et al. 2023). Despite of the high expression of *NTL4* in senescing leaves and its induction mainly in leaves during drought, the precise physiological significance of NAC TFs in drought-induced leaf senescence is not fully understood. The researchers found that while *ntl4* mutants exhibit increased stress tolerance (Rajani et al. 2018), mutants with the gene for these proteins knockout exhibit stress-susceptible phenotypes. In turn, transgenic plants overexpressing other membrane-bound NAC proteins, such as *NTL9* and *NTL6*, demonstrate increased resistance to stress (Shu et al. 2024). The distinct function of *NTL4* in ROS generation helps to reconcile these seemingly contradictory data. ROS levels increase in specific parts of the plant, rather than the entire plant, when it is subjected to biotic and abiotic challenges (Mittler et al. 2022). According to recent research, plants must accumulate reactive oxygen species (ROS) locally in specific tissues or cells to respond to drought stress (Nadarajah 2020; Szechyńska-Hebda et al. 2022; Wang et al. 2024). Evidence shows that drought induces ROS accumulation as well as programmed cell death in root tips (Huang et al. 2022a). Similarly, the hypersensitive response in infected plants, drought-induced leaf senescence, allows them to survive drought by limiting the spread of damage to the other parts of the plant by relocating nutrients and reducing water loss (Mathibela 2021). Several factors, including metabolic regulators, hormone receptors, TFs, and environmental stress signaling components, control senescence. The RADICAL-INDUCED CELL DEATH1 (RCD1) protein interacts with the transcription factor DREB2A, which is known to regulate the responses of heat stress and drought (Sato et al. 2024). This finding suggests an interrelationship between leaf senescence and drought stress. However, the precise biochemical mechanisms behind drought-induced leaf senescence are poorly understood. According to Lee et al. (2012), *NTL4* gene expression increases rapidly in leaves during drought stress but is low in aerial plant components during vegetative phases (Han et al. 2023). This induction is particularly noticeable in the distal leaf regions, where senescence begins during drought. These distal regions are also where ROS accumulation and cell death begin in senescent leaves during drought (Lee et al. 2012; Arce et al. 2022). These results clearly show that NTL4 is necessary for ROS accumulation in the distal leaf areas.

According to prior studies and Lee et al. (2012), *NTL4* can increase ROS in leaves, thereby triggering programmed cell death and leaf senescence under drought stress (Jan et al. 2019; Latif et al. 2020). Furthermore, the interaction of NAC TFs and ABA is crucial as it controls how the plant responds to drought. For example, the ATAF1 TF was found to directly interact with genes involved in ABA biosynthesis, such as *ABCG40* and the ABA transporter, and with the *NCED3*, which increases ABA levels in response to drought (Jan et al. 2019). By enhancing ABA-mediated signaling pathways, this interaction not only promotes senescence but also enhances the plant response to drought stress. Moreover, the regulation of senescence under drought stress is also associated with other NAC TFs, including ORS1. While deletion of *ORS1* slows senescence, overexpression of the protein accelerates it (Balazadeh et al. 2011; Huang et al. 2022b). According to Baker et al. (2023), hydrogen peroxide (H_2O_2) treatment and salt stress upregulate *ORS1*-regulated genes that are associated with plant behavior in response to drought stress. By lowering cellular H_2O_2 levels, the NAC TF, JUB1, acts as a negative regulator of leaf senescence, providing further evidence for the involvement of ROS in drought-induced senescence (Aloryi et al. 2023; Cao et al. 2023). JUB1 highlights the intricate interactions between NAC TFs, ROS, and ABA signaling in controlling senescence under drought conditions by reducing ROS accumulation and delaying senescence under drought stress (Fuertes-Aguilar & Matilla 2024) (Fig. 1). It can therefore be concluded that NAC TFs optimize plant life under water stress by integrating drought stress signals through interactions with ROS generation pathways and ABA signaling, thereby modulating leaf senescence. Furthermore, in tomato, SlNAP2, a NAC TF, has been identified as a positive regulator of leaf senescence, which directly binds to the promoters of several SAGs, such as *SlPAO*, *SlSGR1*, and *SlSAG113*, and activates their expression (Ma et al. 2018).

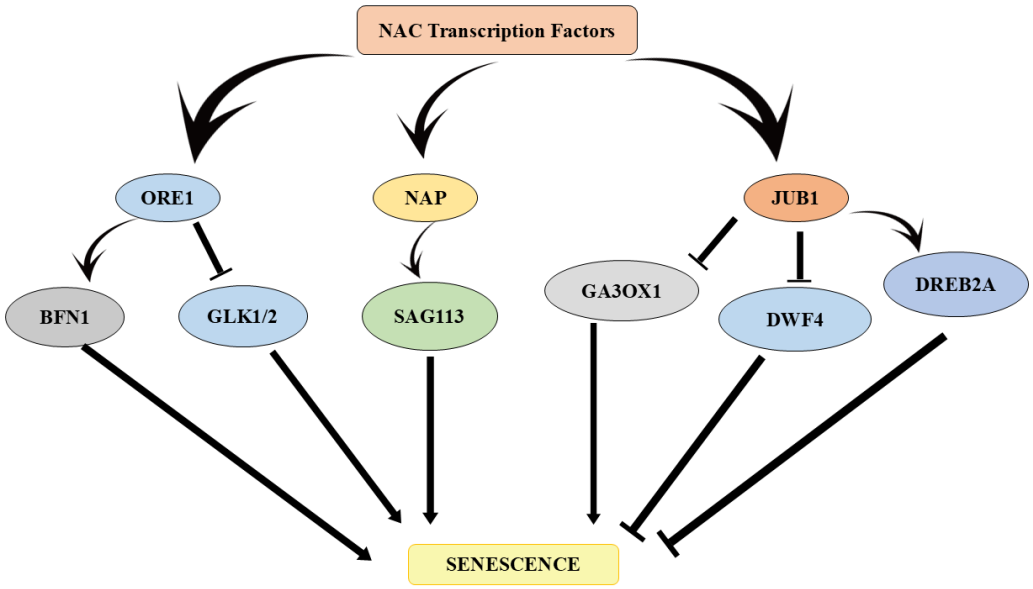

Figure 1. The NAC transcription factor regulating senescence: ORE1 acts as a key transcriptional regulator, directly targeting BFN1 to promote nucleic acid degradation during programmed cell death while suppressing GLK1/2, which impairs chloroplast maintenance; AtNAP activates senescence by inducing SAG113, a negative regulator of ABA-mediated stomatal closure; JUB1 delays senescence by stimulating DREB2A expression while suppressing *GA3ox1* and *DWF4*, which are essential genes in the brassinosteroid (BR) and gibberellin (GA) biosynthetic pathway

Regulatory role of the WRKY transcription factor family

WRKY TFs are characterized by a conserved WRKYGQK motif in the DNA-binding domain and a zinc finger structure that enables specific binding to W-box elements in the promoters of target genes. Numerous investigations of the functions of WRKY TFs indicate that they play an important role both in the regulation of leaf senescence and in the response of plants to various abiotic factors, including drought (Ge et al. 2024). Studies on *Arabidopsis thaliana*, and in particular on the *AtWRKY6* gene, were the first to provide evidence for the role of WRKY TFs in leaf senescence (Besseau et al. 2012). This phase has been shown to significantly stimulate the expression of genes relevant for senescence. These genes were more highly expressed when *WRKY6* was overexpressed, but knockout mutants showed noticeably lower amounts (Ciolkowski et al. 2008). Furthermore, WRKY53 was found to play a positive role in regulating leaf senescence, focusing on several TFs, senescence-associated genes (SAGs), and stress-related genes (Rinerson et al. 2015; Tan et al. 2023). However, EPITHIOSPECIFYING SENESCENCE REGULATOR (ESR) limits its function by preventing WRKY53 from binding to DNA, which inhibits senescence (Miao & Zentgraf 2007; Wang et al. 2023). Further investigation revealed that WRKY70 and WRKY54 also exhibit functional redundancy in the leaf senescence regulation, as evidenced by different senescence phenotypes in single and double mutants, as well as a more noticeable early senescence phenotype in the latter two. While the *wrky70* single mutant showed only mild, premature senescence, the *wrky54wrky70* double mutant exhibited a pronounced early senescence phenotype (Besseau et al. 2012). WRKY30 also participates in reactive oxygen species (ROS) signaling. It is a critical mediator influencing the regulation of TFs both positively and negatively during senescence, as demonstrated by its interaction with WRKY70, WRKY53, and WRKY54 (Scarpeci et al. 2013). Furthermore, *WRKY22* has been shown to act as a positive regulator of leaf senescence, especially in response to darkness. Overexpression of this gene accelerates senescence, while its knocking out slows it down (Zhou et al. 2011). Additionally, in *Arabidopsis*, the wheat (*Triticum aestivum* L.) gene database identified 116 WRKY TFs (Zhang et al. 2016), including 13 TaWRKYs, which are known to be senescence-associated genes (SAGs). TaWRKY7 was the most studied of the 13 *TaWRKY*s and its expression was shown to be triggered during leaf senescence. Similarly, Fan et al. (2017) showed that WRKY65 interacts with critical senescence-associated gene promoters during postharvest senescence in a commercial leafy crop, *Brassica rapa*. Collectively, the results of these investigations emphasize the critical role of WRKY TFs in regulating complex transcriptional networks during leaf senescence in a variety of plant species, including both model organisms and commercial crops.

Regulatory role of other transcription factor families

Other TFs, besides the well-researched WRKY and NAC TFs, also influence the regulation of leaf senescence. For example, the *Arabidopsis* B3-domain type TF, which is related to *ABA-INSENSITIVE3* (*ABI3*)/VIVIPAROUS1 (*AtRAV1*), induces leaf senescence (Woo et al. 2010). In contrast, *C-REPEAT/DEHYDRATION-RESPONSIVE ELEMENT BINDING FACTOR 2* (*CBF2*) plays a negative role in regulating this process (Sharabi-Schwager et al. 2010). Furthermore, *MYBL*, a RR-type MYB family TF in *Arabidopsis*, has been found to act as a positive regulator of leaf senescence (Zhang et al. 2011). For example, phytochrome-interacting factors (PIFs), particularly PIF4, have been shown to regulate ROS production and chlorophyll degradation – two processes essential for both senescence and the regulation of oxidative stress in drought-affected environments (Song et al. 2014). Similarly, Lim et al. (2010) found that plant response to drought is linked to *AUXIN RESPONSE FACTOR-2* (*ARF2*), which is well known for its role in auxin-mediated leaf senescence. Ethylene levels typically increase

during drought. A positive regulator of the ethylene signaling pathway, the *ETHYLENE-INSENSITIVE3* (*EIN3*) promoter, is directly linked to the calmodulin-binding TF SIGNAL RESPONSIVE1 (SR1), which regulates ethylene-induced leaf senescence (Sarwat 2017). Together, these TFs link drought stress responses to senescence, enabling plants to adapt physiological processes in real time to environmental challenges and ensuring their survival. Because of their complex interactions, identifying the specific effectors of these TFs responsible for metabolic and cellular regulation during senescence is crucial.

REGULATION OF LEAF SENESCENCE INDUCED BY SUBMERGENCE

When plants are submerged in water for prolonged periods, oxygen availability decreases, leading to hypoxia. For plants to maintain cellular respiration and enable a variety of biochemical processes, oxygen molecules are essential for proper cellular activity (Mandal et al. 2022). As water levels rise, soil oxygen concentration decreases, depriving plant roots of the oxygen necessary for proper cellular respiration. However, prolonged hypoxia can accelerate leaf senescence, ultimately reducing plant growth and productivity. Ethylene response factor group VII (ERFVII) TFs play a key role in this process, stabilizing in hypoxic environments and triggering gene expression, helping plants adapt to low oxygen levels (Giuntoli & Perata 2018; Loreti et al. 2018). For example, in *Oryza sativa* (rice), *SUBMERGENCE1A* (*SUB1A*), an ERFVII TF that reduces leaf senescence with prolonged submergence, is essential for submergence tolerance (Table 3). In various plant species, including rice, *Arabidopsis*, and poplar (*Populus* spp.), a collection of 49 genes has been identified that are persistently active under hypoxic or submerged conditions, leading to their classification as core hypoxia-responsive genes (HRGs) (Basit et al. 2024). These HRGs encode enzymes involved in critical metabolic processes, such as reactive oxygen species (ROS) regulation, sucrose breakdown, anaerobic fermentation (e.g., pyruvate decarboxylase and alcohol dehydrogenase), and transcriptional regulation, as well as proteins with unclear functions (van Veen et al. 2025). In addition to hypoxia, plants often experience darkness due to the shading effect of the water surface. Light is crucial for plant growth and development, significantly affecting leaf morphology and function. Plants undergo leaf senescence when exposed to prolonged shade or complete darkness (Li et al. 2023). This process is controlled by light signaling pathways mediated by phytochromes, particularly phytochrome B (phyB) and phytochrome A (phyA), which play an important role in delaying the initiation of leaf senescence (Liebsch & Keech 2016; Li et al. 2023). Transcriptome investigations suggest that darkness-induced changes in gene expression are similar to those observed during natural senescence. In fact, during senescence, more than half of the genes whose expression is upregulated also exhibit higher expression in the dark. In *Arabidopsis,* a key TF in the ethylene signaling pathway is *EIN3*, which is positively regulated during leaf senescence (Peerzada & Iqbal 2021). Rice NAC TFs, including *OsNAC2*, *OsNAC054*, and *OsNAC096*, positively influence the expression levels of senescence-associated genes (SAGs) under dark-induced senescence (Li et al. 2024). DNA binding with one finger (DOF) TFs act as negative regulators of both dark-induced and age-dependent senescence in plants. Overexpression of DOF TFs has been shown to increase chlorophyll content, indicative of delayed senescence. It is associated with significant downregulation of chlorophyll-degrading genes (*CDG*s), such as *NYC1* (*NON-YELLOW COLORING 1*), *NYC3*, and *SGR* (*STAY-GREEN*), whose expression is typically upregulated during senescence (Gad et al. 2021). These stress conditions, often occurring in flood-prone or aquatic environments, trigger a cascade of molecular and physiological responses, including changes in gene expression and TF activity, to adapt to low-oxygen, low-light environments.

Submergence increases ethylene signaling in plant tissues because it is poorly soluble in water and diffuses slowly. Ethylene is a crucial plant regulator that adapts to flooding, and its endogenous concentrations increase in response to various abiotic stresses due to enhanced biosynthesis (Argueso et al. 2007). It is a key positive regulator of leaf senescence (Graham et al. 2012), and its accumulation during submergence accelerates leaf senescence, particularly in accessions of flood-sensitive plants. For instance, sensitive genotypes of maize, rice, *Arabidopsis*, and *Lotus japonicus* exhibit more pronounced leaf senescence during and after flooding than tolerant genotypes (Buraschi et al. 2020). Ethylene-induced senescence is enhanced in mature leaves, whereas young leaves are protected by specific regulatory mechanisms (Muzzaffar et al. 2022).

Table 3. Main genes and transcription factors associated with submersion-induced regulation of leaf senescence and their functions

Number	Gene/transcription factor	Function	References
1	ORE1 (ANAC092)	Positive regulator of leaf senescence; induces NAC genes, nucleases, sugar transporters, and senescence-associated genes (SAGs); interacts with GLK2 to inhibit chloroplast maintenance	Rauf et al. 2013
2	ANAC019, ANAC055	Upregulated via EIN2-dependent signaling; likely controlled by CBFs and other TFs during stress and senescence	Kim et al. 2014
3	AtNAP	Directly regulated by EIN3; promotes senescence and ABA signaling	Kim et al. 2014
4	OsNAP1 (rice homolog of AtNAP)	Positive regulator of leaf senescence; targets genes involved in ABA biosynthesis	Liang et al. 2014
5	AUX/IAA	Negative regulator; inhibits auxin responses, delaying senescence	Koyama et al. 2013
6	SUB1A (rice)	Negative regulator; inhibits senescence	Fukao et al. 2012
7	CRF6	Negative regulator of senescence	Zwack et al. 2013
8	WRKY53	Positive regulator; enhances senescence by activating SAGs	Miao & Zentgraf 2007
9	WRKY6, WRKY54, WRKY57, WRKY75	Involved in senescence regulation; *WRKY53* and *WRKY6* upregulate WRKY genes, forming a feedback loop	Besseau et al. 2012
10	WRKY33	Induces ethylene biosynthesis genes, promoting senescence	Breeze et al. 2011
11	WRKY75	Functions in ethylene-dependent defense signaling	Chen et al. 2013
12	*ETR1*	Ethylene receptor; acts as a repressor of ethylene signaling, delaying senescence	Wang et al. 2013
13	*EIN2*	Positive regulator; transduces ethylene signal by relocating EIN2-C to the nucleus, promoting senescence	Potuschak et al. 2003
14	*EIN3*	Transcription factor; stabilizes in response to ethylene, inducing senescence-related gene expression	Peerzada & Iqbal 2021
15	*EILs*	Functionally similar to EIN3; regulates senescence genes	Potuschak et al. 2003

TFs – transcription factors

ETHYLENE-INDUCED SENESCENCE REGULATION DURING SUBMERGENCE

Understanding the ethylene signaling pathway is essential to identifying the gene regulatory networks that initiate leaf senescence. The endoplasmic reticulum (ER) membrane contains ethylene receptors, which are responsible for detecting the presence of ethylene (Chien & Yoon 2024). These receptors negatively regulate downstream components of the signaling cascade in the absence of ethylene, but they reverse this suppression, initiating the signaling cascade. A protein complex consisting of the ER membrane protein ETHYLENE INSENSITIVE2 (*EIN2*) and the Raf-like serine/threonine kinase CONSTITUTIVE TRIPLE RESPONSE1 (CTR1) receives the ethylene signal (Ju et al. 2012; Wang 2024). In the absence of ethylene, the cytosolic C-terminal domain (EIN2-C) of *EIN2* is phosphorylated by CTR1. However, this phosphorylation is inhibited in the presence of ethylene, resulting in cleavage and translocation of EIN2-C to the nucleus, where it activates the TFs EIN3-LIKE (EIL) and EIN3. Once EIN3 and EIL are stabilized, which are typically transient without ethylene signaling (Potuschak et al. 2003), ethylene signaling triggers numerous physiological processes, including the initiation of leaf senescence. The timing of leaf senescence is altered by mutations in ethylene signaling components, suggesting their involvement in its regulation. Ethylene receptors, such as ETHYLENE RESISTANT1 (*ETR1*), generally act as repressors in the signaling pathway. Mutations that produce dominant-negative versions of these receptors, such as the *etr1* mutation, have been shown to delay senescence in petunia and *Arabidopsis* (Wang et al. 2013). Analysis of genetic loci revealed a key role for *EIN2* in the positive regulation of leaf senescence and senescence initiation in *Arabidopsis* (Kim et al. 2009). *EIN3* also positively influences the initiation of leaf senescence (Fig. 2), as observed in mutants lacking *EIN3*, which exhibit delayed senescence, whereas its overexpression accelerates this process (Kim et al. 2014). On the other hand, *ctr1* mutants do not exhibit early senescence, and the role of *ctr1* in regulating leaf senescence remains unclear (Jing et al. 2005).

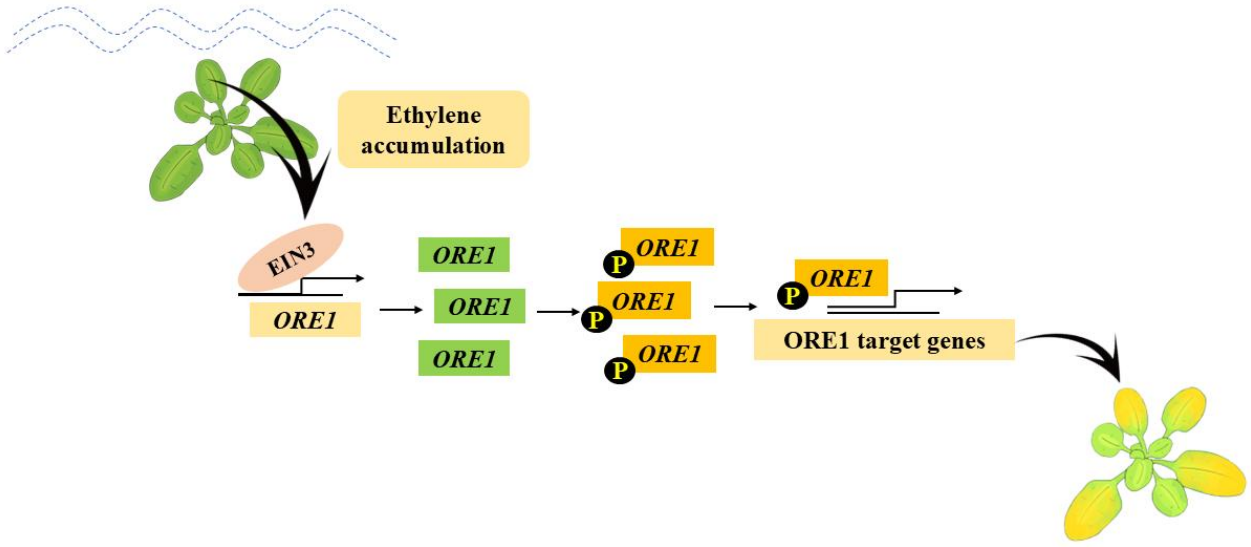

Figure 2. Model of ethylene-regulated leaf senescence in submerged plants: ethylene rapidly accumulates throughout the plant and stabilizes *EIN3*, leading to increased *ORE1* expression; *ORE1* is then activated by age-dependent phosphorylation, which induces senescence in older leaves before younger ones, ensuring the remobilization of nutrients from older tissues while younger leaves and meristems remain functional

TRANSCRIPTION FACTOR ASSOCIATED REGULATION UNDER SUBMERGENCE STRESS

Regulatory role of NAC transcription factor family

Several studies have explored the role of ethylene signaling pathway in modulating NAC TFs during leaf senescence (Kim et al. 2014). The NAC TF family in *Arabidopsis* comprises 105 members that play significant roles in developmental processes and stress responses (Mitsuda & Ohme-Takagi 2009). Amongst the NAC genes activated during leaf senescence, six specific genes are upregulated via the *EIN2*-dependent signaling pathway, such as *ANAC019*, *ANAC055*, *ANAC047*, *ORE1 (ANAC092)*, *ORS1 (ANAC059),* and *AtNAP* (*NAC*-like activated by AP3) (Kim et al. 2014). The TF *ORE1* plays a positive role in regulating leaf senescence and induces its own expression, as well as that of other NAC genes, nucleases, and different senescence-associated genes (SAGs) (Rauf et al. 2013). It also associates with a GARP family TF, namely GOLDEN-LIKE2 (*GLK2*), which is essential for chloroplast development and inhibits *GLK2* activity, potentially halting chloroplast maintenance (Rauf et al. 2013). The microRNA *miR164* targets *ORE1* mRNA, and its decrease during leaf aging, primarily driven by the *EIN2* gene, results in the *ORE1* mRNA accumulation in older leaves (Kim et al. 2014). Notably, *EIN3* also suppresses the expression of three *miR164* precursor genes, playing a dual role in *ORE1*'s direct and indirect regulation (Li et al. 2013). Supporting these molecular findings, *ORE1* expression is reduced in *ein3* mutants during leaf senescence, suggesting a regulatory network involving *EIN3*, *miR164*, and *ORE1* that operates downstream of the ethylene signaling pathway. *AtNAP*, among other NAC genes downstream of *EIN2*, is directly regulated by *EIN3*, while *ORS1*, *ANAC055*, *ANAC047*, and *ANAC019* are activated independently of *EIN3* (Kim et al. 2014). *AtNAP* is a positive regulator of leaf senescence and induces the abscisic acid (ABA) signaling pathway that contributes to stress responses and senescence (Zhang & Gan 2012). Similarly, *OsNAP1*, rice homolog, plays a positive role, directly targeting a gene involved in ABA biosynthesis (Liang et al. 2014).

Regulatory role of ERF transcription factor family

Ethylene plays a crucial role in activating several AP2/ERF genes, some of which affect the initiation of leaf senescence. In *Arabidopsis,* the AP2/ERF TF family consists of 146 members, including both transcriptional repressors and activators (Mitsuda & Ohme-Takagi 2009). Several repressors possessing the ERF-associated repression (EAR) motif, such as *AtERF8*, *NtERF3* and *AtERF4*, are found to play a positive role in leaf senescence initiation (Koyama et al. 2013). The proteins AtERF8 and AtERF4 are usually degraded via a proteasome-dependent pathway; however, their accumulation increases with the plant ages (Koyama et al. 2013). They directly inhibit the expression of *EPITHIOSPECIFIER PROTEIN/EPITHIOSPECIFYING SENESCENCE REGULATOR* (*ESP/ESR*), known to act as an opposing player in leaf senescence initiation. *ESP/ESR* mRNA levels are high in younger leaves but diminish with age (Koyama et al. 2013). It suppresses WRKY53, which plays a positive role in leaf senescence (Miao & Zentgraf 2007). It suggests that AtERF8 and AtERF4 may activate WRKY53 by alleviating the repression exerted by *ESP/ESR* (Koyama et al. 2013). Moreover, AtERF8 and AtERF4 downregulate the expression of the gene AUXIN/INDOLE-3-ACETIC ACID (*AUX/IAA*), which typically act as inhibitors of auxin responses, including those that promote leaf senescence. Therefore, *AUX/IAA* suppression by AtERF8 and AtERF4 likely enhances auxin activity, thereby accelerating leaf senescence. Additionally, in tomato plants, overexpression of the *AtERF4* homolog, *SlERF36*, was shown to accelerate leaf senescence (Upadhyay et al. 2013). Conversely, TFs such as *GmRAV1* and *RAV1*, which harbor distinct repression domains, function as negative regulators of leaf senescence. Ethylene induces the expression of these RAV TFs (Alonso et al. 2003). In *Arabidopsis*, overexpression of *RAV1* genes delays senescence (Woo et al. 2010). Therefore, within the ethylene signaling pathway, the balance between positive and negative regulators appears to modulate the progression and timing of leaf senescence.

Specific ERF TF activators also play roles in leaf senescence regulation. For instance, *SUBMERGENCE1A* (*SUB1A*) in rice inhibits leaf senescence (Fukao et al. 2012), at the same time, *CYTOKININ RESPONSE FACTOR6* (*CRF6*) similarly responds as a negative regulator of senescence (Zwack et al. 2013). In *Arabidopsis*, overexpression of the *CBF3* and *CBF2* genes delays leaf senescence (Sharabi-Schwager et al. 2010). These CBF TFs likely influence leaf senescence via downstream targets such as *COR15* and *RD29* genes, and may also regulate *ANAC055* and *ANAC019* (Hickman et al. 2013). However, there is no conclusive evidence linking ethylene to these ERF TFs activators, suggesting a complex and multifaceted control mechanism in leaf senescence.

Regulatory role of WRKY transcription factor family

Jasmonic acid (JA) is an essential regulator in leaf senescence initiation. Evidence shows that mutants deficient in JA biosynthesis display delayed leaf senescence, whereas JA application to the leaves promotes senescence (Seltmann et al. 2010). It usually works synergistically with the ethylene to drive various physiological processes (Zhu et al. 2011). JA, along with plant aging, induces the expression of numerous WRKY TF genes (Lin & Wu 2004). Among these, *WRKY53* plays a positive role in leaf senescence, with its function being altered by *ESP/ESR* during transcriptional and translational stages (Miao & Zentgraf 2007). Moreover, *ESP/ESR* directly interacts with *WRKY53* transcripts, likely inhibiting its DNA-binding activity and reducing its level in leaves (Besseau et al. 2012). Given that *WRKY6* and *WRKY53* can increase the expression of various WRKY genes, as well as senescence-associated genes (SAGs), there may be a self-reinforcing mechanism that enhances WRKY activity, contributing to robust regulation leaf senescence (Robatzek & Somssich 2002; Miao et al. 2004). Several pieces of evidence highlight the interactions between the ethylene signaling pathway and WRKY TFs. For example, the expression of *WRKY53* induced by nematode infection requires a functional *EIN2* gene (Murray et al. 2007). Additionally, *WRKY75* has been implicated in the ethylene-dependent defense signaling cascade (Chen et al. 2013). Expression of *WRKY33* increases significantly during leaf senescence, inducing genes involved in ethylene biosynthesis, thereby contributing to ethylene production (Breeze et al. 2011). Therefore, the regulation of leaf senescence by WRKY TFs may affect the combined effects of ethylene and JA signaling pathways. Further regulatory mechanisms include the involvement of the histone methyltransferase and the single-stranded DNA-binding protein WHIRLY1A, which target *WRKY53* gene in *Arabidopsis* plants (Miao et al. 2013). In soybean, a basic helix-loop-helix (bHLH) TF triggers the activation of *WRKY53*, positively influencing the initiation of leaf senescence (Meng et al. 2013). Additionally, in tomato, *SlWRKY37* acts as a downstream effector of *SlMYC2* within the jasmonic acid (JA) signaling pathway and regulates the expression of *SlSGR1* and *SlWRKY53*. This TF promotes both JA-mediated and dark-induced senescence (Wang et al. 2022).

Regulatory role of bHLH transcription factor family

The basic helix-loop-helix (bHLH) TFs play a significant role in regulating leaf senescence. The phytochrome-interacting factors (PIFs) 5, 3, and 4, which are part of bHLH TF family, are shown as possible regulators of ethylene-induced leaf senescence (Cao et al. 2023). These TFs function as negative regulators in light signaling and are key in modulating ethylene production, which accelerates senescence. Notably, *pif4* mutants exhibit reduced ethylene evolution, suggesting that PIFs are integral to the activating ethylene biosynthesis. In contrast, overexpression of *PIF5* and *PIF4* leads to enhanced ethylene production, thereby promoting senescence (Li et al. 2021). PIFs, in conjunction with ENHANCED EM LEVEL (*EEL*), ABSCISIC ACID INSENSITIVE 5 (*ABI5*), and *EIN3*, regulate expression of senescence-associated genes (SAGs), for instance, *SGR1* and *NYC1*, which are involved in chlorophyll degradation (Dkhar & Paul 2023) (Fig. 3). PIFs immediately bind to the promoters of these genes, thereby facilitating ethylene-induced senescence. In *pif4* mutants, which exhibit delayed senescence, ethylene treatment partially reverses the delayed phenotype, further implicating *PIF4* in the ethylene signaling pathway (Liebsch & Keech 2016). Additionally, PIFs regulate *ORESARA1* (*ORE1/ANAC092*), a master TF involved in senescence regulation, underscoring their role in the broader network of senescence-related TFs (Khan et al. 2024). Thus, PIFs are essential for regulating ethylene-induced senescence by modulating ethylene production and the expression of key senescence-associated genes.

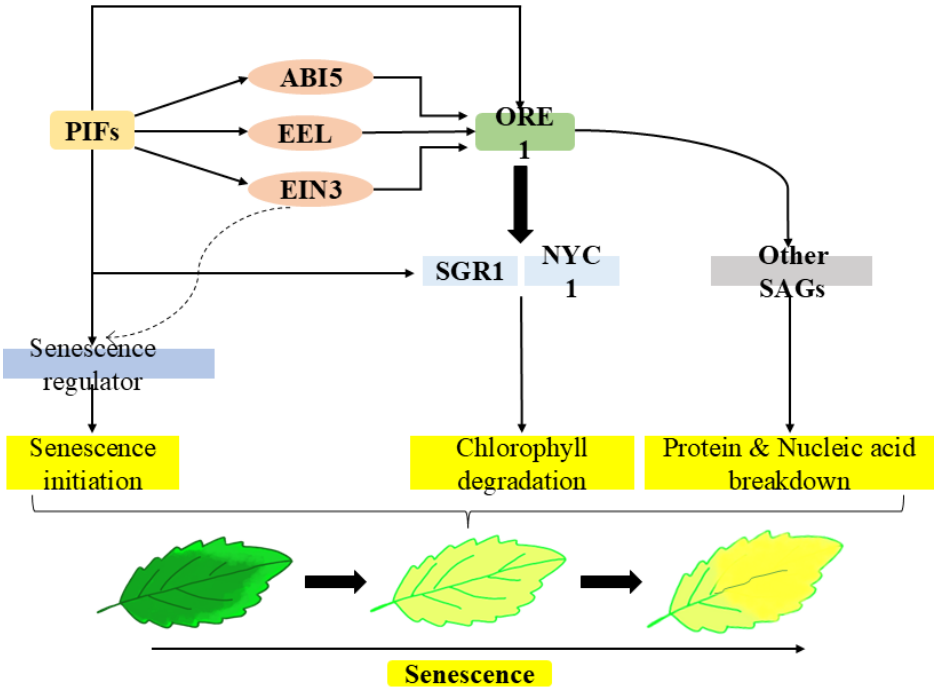

Figure 3. Role of PIFs in ethylene-induced leaf senescence: PIFs regulate ethylene-induced leaf senescence by interacting with *EIN3*, *ABI5*, and *FEL*; these transcription factors collectively stimulate the expression of *ORE1*, a master transcription factor that induces SAGs such as *SGR1* and *NYC1*, leading to chlorophyll degradation and breakdown of proteins and nucleic acids; furthermore, PIFs can directly induce *ORE1* and SAGs; *EIN3* functions as an upstream transcription factor regulating senescence

EPIGENETIC REGULATION OF PLANT LEAF SENESCENCE

In plants, epigenetic mechanisms involve complex modifications, in which the DNA sequence itself does not change, but gene expression is altered. In some cases, cell division may inherit these modifications (Gibney & Nolan 2010). Epigenetic mechanisms, crucial for regulating the transition in plants to the subsequent developmental phases, also significantly influence senescence (Humbeck 2013). These mechanisms dynamically change the chromatin structure at specific loci, making DNA either accessible (euchromatin) or inaccessible (heterochromatin) to TFs, thereby activating or inhibiting senescence-associated genes, respectively (Yolcu et al. 2018). Notably, most research on plant leaf senescence has focused on *Arabidopsis* leaves, which have a very short lifespan, and their senescence may not necessarily reflect that of the whole-plant. Different mechanisms, such as DNA methylation, histone modifications, and ATP-dependent chromatin remodeling, exert the epigenetic regulation of leaf senescence.

DNA methylation and plant leaf senescence

DNA methylation is one of the key epigenetic modifications, in which a methyl group is typically added to cytosine bases by DNA methyltransferases, forming 5-methylcytosine. There are three main contexts of DNA methylation in plants: CG, CHG, and CHH, where H indicates A, T, or C (Rutowicz et al. 2015). *DNA-METHYLTRANSFERASE1* (*MET1*), *CHROMOMETHYLASE3* (*CMT3*), and *DOMAINS-REARRANGED METHYLTRANSFERASE*s (*DRMs*) regulate CG, CHG, and CHH DNA methylation, respectively (Vanyushin & Ashapkin 2011). However, demethylating enzymes, such as DEMETER-LIKE proteins (*DLM2/DML3*) that have the domain DNA glycosylase, DEMETER (*DME*), and *REPRESSOR OF SILENCING1* (*ROS1*) can remove the methyl groups in DNA (Choi et al. 2002; Gehring et al. 2009). DNA methylation can modulate gene expression by altering the methylation state of a gene's coding regions or promoters, thereby affecting their ability to bind in relation TFs (Inamdar et al. 1991). Additionally, DNA methylation may occur at repetitive sequences, including transposable elements

(TEs), thereby stabilizing heterochromatic structure by silencing these repeats (Chan et al. 2005).

The role of DNA methylation in senescence has been reported in multiple aspects, including genes encoding methylase and demethylase enzymes, such as *ROS1*, *MET1*,*CMT3*, *DML2/DLM3*, and *DME*, although the specific mechanisms remains unclear (Ostrowska-Mazurek et al. 2020). In maize, it has been suggested that DNA methylation may contribute to whole-plant senescence, as alterations in DNA methylation were observed during key developmental transitions leading to the silencing of *MuDR* (Mutator-Don Robertson) TEs (Li et al. 2010). In *Arabidopsis*, studies on *MET1* transgenic plants have shown that reduced *MET1* activity either in *met1* mutants or through constitutive expression of the *MET1* antisense gene leads to genomic DNA hypomethylation and developmental anomalies. Kim et al. (2008) further showed that in *DME:MET1 a/s* transgenic plants, suppression of *MET1* expression led to delayed senescence and various developmental abnormalities. Moreover, TEs are released during leaf senescence, as demonstrated by studies in *Arabidopsis* and barley (Ay et al. 2008; Guo & Gan 2012). He et al. (2018) found that among different ecotypes of *Arabidopsis,* the methylation status of a retrotransposon termed *NMR19* (naturally occurring DNA methylation variation region 19) differs. Another class, termed by them *NMR19-4*, appears to be a naturally occurring epiallele involved in the regulation of leaf senescence. They observed that DNA methylation of NMR19-4 suppressed the transcription of the gene *PHEOPHYTIN HEOPHORBIDE HYDROLASE* (*PPH*) that encodes an enzyme responsible for chlorophyll degradation during leaf senescence. In another investigation by Trejo-Arellano et al. (2020) on global methylation levels in dark-induced senescent leaves of *Arabidopsis* downregulation of chromatin-silencing genes during senescence interrupted TE silencing and reactivated young TEs. They also observed that despite decondensation of heterochromatin at chromocenters, the global DNA methylation pattern remained essentially unchanged, with alterations confined to localized CHH methylation. They concluded that while senescence involves global chromatin reorganization, the associated alterations in DNA methylation are mostly localized. Vatov et al. (2022) observed accelerated leaf senescence in two DNA methylation mutants: the triple *dmr1/2 cmt3* and *ros1* knockout. They demonstrated that during senescence, wild-type plants showed a moderate reduction in DNA methylation, primarily in the CG context. In contrast, the most senescent leaves de novo CHH methylation.

Histone modifications and plant leaf senescence

Histones are the protein components of chromatin and undergo various posttranslational modifications, including methylation, acetylation, phosphorylation, and H2B monoubiquitination. Based on the location and type of these modifications, the gene expression is either promoted or inhibited. For example, histone acetylation generally correlates with transcriptional activation, whereas histone H3K27 and H3K9 methylation are associated with suppressed gene expression (Asensi-Fabado et al. 2017). These modifications regulate gene expression and DNA accessibility by influencing the interaction of histones with the nuclear proteins and DNA (Deal & Henikoff 2011).

Studies explored the genome-wide distribution of histone modifications associated with developmental leaf senescence in *Arabidopsis* using an integrated RNA-seq and chromatin immunoprecipitation sequencing (ChIP-seq) approaches (Ay et al. 2009). Two active histone marks, such as acetylation of lysine 9 on histone H3 protein (*H3K9ac*) and trimethylation of lysine 4 on histone H3 protein (*H3K4me3*) were found to be closely associated with the regulation of leaf senescence. *H3K4me3* was observed to be more dominant than *H3K9ac*, with a subset of senescence-associated genes exhibiting expression patterns that closely correlate with *H3K4me3* levels (Brusslan et al. 2015). The initial evidence supporting a direct connection between histone modifications and the regulation of leaf senescence was provided by a study examining the upstream transcriptional control of multiple senescence regulators. The histone methyltransferase SUPPRESSION(VAR)3-9 homolog2 (*SUVH2*), which mediates H3 lysine methylation, has been shown to play a role in delayed leaf senescence (Ay et al. 2009). The H3K4 demethylase JmjC-domain-containing protein 16 (*JMJ16*) serves as a positive regulator of leaf senescence as its loss-of-function

mutants show delayed senescence and a reduced level of H3K4me3 at the promoter of the senescence-associated gene *WRKY53* (Liu et al. 2019). Both the HISTONE DEACETYLASE-9 (*HDA9*) (Chen et al. 2016) and the *H3K27me3* demethylase RELATIVE OF EARLY FLOWERING6 (*REF6*) (Wang et al. 2019) act as positive regulators of leaf senescence. *HDA9* interacts with POWERDRESS and *WRKY53* to form a regulatory complex, which is guided by *WRKY53* to W-box-containing promoters of negative senescence regulators, such as *WRKY57*, AUTOPHAGY-9 (*ATG9*), and NUCLEAR PROTEIN X1 (*NPX1*), thereby repressing their expression, whereas *REF6* promotes senescence by directly activating key SAGs, such as *ORE1*, *NAP*, and ETHYLENE INSENSITIVE-2 (*EIN2*). HISTONE DEACETYLASE (*HDA15*) associates with WHIRLY1, a single-stranded DNA-binding protein, thereby affecting the *H3K9ac* enrichment at the *WRKY53* promoter. This interaction suppresses *WRKY53* transcription and consequently delays the initiation of leaf senescence (Huang et al. 2018). Furthermore, the histone acetyltransferase *HAC1* has been reported to promote leaf senescence (Hinckley et al. 2019). In contrast, several histone deacetylase (HDACs), including *AtSRT1*, *HD2C*, *HDA9*, and *HDA15*, act as negative regulators of stress-induced senescence in *Arabidopsis* (Hu et al. 2019; Ueda & Seki 2020).

ATP-dependent chromatin remodeling and plant leaf senescence

Remodeling of ATP-dependent chromatin regulates DNA accessibility for RNA polymerase II and other TFs, and thereby regulates gene transcription inside the chromatin structure (Kusch & Workman 2007; Chodavarapu et al. 2010). Such dynamic alterations in DNA accessibility affects processes such as flowering time, senescence, and responses to environmental changes and stress in plants (Berr et al. 2011; Miryeganeh 2021). Studies have demonstrated that alterations in chromatin structure by chromatin-remodeling enzymes play a significant role in the regulation of leaf senescence (Ostrowska-Mazurek et al. 2020). Ay et al. (2009) reported remodeling of euchromatic and heterochromatic regions within the nuclei of senescing cells, along with their distinct association with dense chromocenters. During leaf senescence, the transcriptionally inactive heterochromatic regions become distinguishable from the surrounding euchromatic regions, which exhibit comparatively higher transcriptional activity. However, it remains unclear whether chromatin condensation in centromeric and pericentromeric regions during the initiation of senescence is a secondary effect of nuclear disintegration or a regulated event that initiates senescence (Ay et al. 2014). The overexpression of *ORESARA7* (*ORE7*), an AT-hook chromatin remodeler has been shown to delay leaf senescence significantly (Lim et al. 2007). *ORE7* suppresses decondensation of chromatin, thereby preventing the accessibility of senescence-associated TFs. Additional chromatin-remodeler proteins involved in senescence-associated gene expression include members of the SUCROSE NONFERMENTING-2 (SNF2) family, notably *CHR10* (ALTERED SEED GERMINATION3, *ASG3*) and *CHR19* (*ETL1*), which are upregulated during the process of senescence (Breeze et al. 2011).

POSTTRANSLATIONAL REGULATION OF PLANT LEAF SENESCENCE

Posttranslational regulation plays a vital role in cellular signaling. In senescing leaves, although various protein modifications, such as glycosylation and phosphorylation have been strongly associated with the regulation of signaling cascades (Ahmad & Guo 2019), protein degradation has emerged as the most extensively studied form of posttranslational regulation. This process is essential not only for signal transduction but also for senescence. Among the major degradation pathways, the ubiquitin-proteasome system (UPS) and autophagy play central roles, which collectively facilitate the removal of damaged or aggregated proteins and organelles, ensuring efficient nutrient recycling and maintaining the homeostasis of key senescence regulators. The UPS mediates the covalent attachment of ubiquitin molecules, marking them for recognition and subsequent degradation by the 26S proteasome (Vierstra 2009). While UPS primarily targets individual proteins, autophagy degrades protein complexes, aggregates, and even entire organelles (Schreiber & Peter 2014). Notably, these two degradation pathways play contrasting

roles in regulating senescence. Autophagy generally delays or prevents senescence, whereas the proteasome acts as a positive regulator promoting its initiation (Wang & Schippers 2019). Interestingly, recent finding suggest that during leaf senescence, the UPS and the autophagy pathway can function synergistically in the regulation of chloroplast protein degradation (Kikuchi et al. 2020).

Initiation of leaf senescence is accompanied by upregulation of *ATG* genes (Masclaux-Daubresse et al. 2014). In *Arabidopsis*, disruption of various *ATG*s, including *ATG2*, *ATG4a/4b*, *ATG5*, *ATG7*, *ATG8*, *ATG9*, *ATG10*, and *ATG18a*, impairs autophagy and promotes premature leaf senescence, particularly under nutrient-limited conditions such as low nitrate availability (Minina et al. 2018; Wang & Schippers 2019). Although autophagy was historically regarded as a nonselective, bulk protein-degradation pathway, accumulating evidences indicate that it can also mediate the selective degradation of specific cellular components. Although autophagy was once viewed as a nonselective degradation pathway, recent studies show that it can selectively target specific cellular components, such as chloroplasts (Izumi et al. 2017), mitochondria (Li et al. 2014), proteasome (Marshall et al. 2015), endoplasmic reticulum (Yang et al. 2016), peroxisomes (Shibata et al. 2013), and ribosomes (Hillwig et al. 2011). For example, *ATG8*-INTERACTING PROTEIN-1 (*ATI1*) facilitates the selective degradation of mitochondria-associated proteins and vesicles and mediates autophagy-dependent vesicular trafficking of chloroplast proteins to the vacuole during leaf senescence (Li et al. 2014; Michaeli et al. 2014). Although autophagy is generally considered to delay senescence, *ATG8*, via its interaction with ABNORMAL SHOOT3 (*ABS3*), a multidrug and toxic compound extrusion (MATE) transporter can induce senescence and protein degradation at the late endosome (Jia et al. 2019), which shows the dual role played by autophagy both as executioners and procrastinators during senescence, maximizing the recycling of residual nutrients. In contrast to the global upregulation of the *ATG* gene, only specific proteasome subunit genes show elevated expression during leaf senescence (Guo & Gan 2012). Nevertheless, the proteasome exhibits high activity in senescing leaves of *Arabidopsis*, barley, and oilseed rape (Poret et al. 2016; Velasco-Arroyo et al. 2016), and knockout of proteasome subunit genes in *Arabidopsis* often delays senescence (Lin et al. 2011).

Ubiquitination and deubiquitination, which regulate ubiquitin dynamics within cells, are among the most prevalent posttranslational modifications (PTMs) and participate in a wide range of biological processes in plants. Components of the ubiquitination cascade, including specific enzymes and their targets, act as key regulators of leaf senescence (Shu & Yang 2017). For instance, the F-box protein *ORE9* acts as a positive regulator of senescence (Woo et al. 2001), whereas the U-box E3 ubiquitin ligases *PUB12* and *PUB13* act as negative regulators of stress-induced leaf senescence (Zhou et al. 2015). Another U-box ligase, *PUB44*, which is also referred to as SENESCENCE-ASSOCIATED E3 UBIQUITIN LIGASE1 (*SAUL1*) and NOT ORE-SARA1 (*NORE1*) integrates humidity and temperature-dependent defense signals with the regulation of leaf senescence (Vogelmann et al. 2012). *ARABIDOPSIS TOXICOS EN LEVADURA31* (*ATL31*), a RING-type ubiquitin ligase, exhibits a significant role in senescence under high CO_2/low N status. Depending on the C/N status of plants, *ATL31* is directly activated by *WRKY53*, thereby linking primary metabolism to senescence regulation (Aoyama et al. 2014). Moreover, HECT-type E3 ubiquitin ligase family members (*UPL1–UPL7*) are also associated with the process of leaf senescence (Lan & Miao 2019). Notably, knockout of UPL5 results in accumulation of *WRKY53* and premature leaf senescence (Miao & Zentgraf 2010).

In contrast to the well-studied roles of E3 ligases, the specific functions of deubiquitinating enzymes (DUBs) in regulating leaf senescence have emerged recently. Ubiquitin-specific proteases (*UBP*s) constitute the largest group of DUBs with diverse roles in plants (Zhou et al. 2017). *UBP12* and *UBP13* exhibit deubiquitinating activity, and mutations in these genes, either the *ubp12*-mild or the *ubp12ubp13* double mutants, lead to alterations in senescence phenotypes, circadian rhythms, and flowering time (Cui et al. 2013). Furthermore,

UBP12 and *UBP13* (Table 4) promote leaf senescence by deubiquitinating and stabilizing the *ORE1* protein (Park et al. 2019). Thus, proper ubiquitin dynamics within cells is crucial for maintaining protein function during plant development.

Overall, autophagy and the proteasome exert distinct yet interconnected effects on plant aging and the initiation of senescence. Evidence suggests that these two degradation pathways interact in regulating senescence processes. For instance, since proteasomes themselves can be degraded through autophagy (Havé et al. 2018), the excessive accumulation of proteasomes observed in autophagy-deficient mutants may contribute to their premature senescence phenotype. This accumulation could also serve as a compensatory response to the reduced proteolytic activity resulting from impaired autophagy.

Beyond protein degradation, numerous senescence-associated proteins undergo diverse post-translational modifications (PTMs). According to the Plant PTM Viewer database, 207 PTMs have been identified on SAG proteins in *Arabidopsis* (Willems et al. 2019). These include lysine methylation, acetylation, ubiquitination, phosphorylation, reversible cysteine oxidation, and more (Wang & Schippers 2019). Among these modifications, phosphorylation appears to play a particularly significant role during the initiation of senescence, as mitogen-activated protein kinase (MAPK) cascades have been shown to modulate the timing of senescence in *Arabidopsis* (Zhou et al. 2009; Zentgraf et al. 2010; Xiao et al. 2015; Ren et al. 2017). Taken altogether, a deeper understanding of the functional role of PTMs in senescence-associated proteins during plant senescence is highly crucial.

Table 4. Gene/protein names and abbreviations

Number	Gene/protein abbreviation	Full gene/protein name
1	*SAGs*	Senescence-Associated Genes
2	*SAG101*	Senescence-Associated Gene 101
3	*SGR1*	STAY-GREEN 1
4	*NYC1*	NON-YELLOW COLORING 1
5	*NYC3*	NON-YELLOW COLORING 3
6	*PAO*	Pheophorbide a Oxygenase
7	*PPH*	Pheophytin Pheophorbide Hydrolase
8	*LOX1*	Lipoxygenase 1
9	*NAC TFs*	NAM/ATAF/CUC Transcription Factors
10	*ORE1* (*ANAC092*)	ORESARA1
11	*AtNAP* (*ANAC029*)	NAC-like Activated by AP3/PI
12	*ORS1* (*ANAC059*)	ORE1 SISTER 1
13	*ANAC016*	NAC Domain Protein 16
14	*VNI2*	VND-INTERACTING 2
15	*JUB1* (*ANAC042*)	JUNGBRUNNEN1
16	*ATAF1* (*ANAC002*)	Arabidopsis Transcription Activation Factor 1
17	*RD26* (*ANAC072*)	Responsive to Desiccation 26
18	*NTL4*	NAC with Transmembrane Motif-Like 4
19	*SlNAP2*	*Solanum lycopersicum* NAC Protein 2
20	*WRKY6*	WRKY Transcription Factor 6
21	*WRKY53*	WRKY Transcription Factor 53
22	*WRKY54*	WRKY Transcription Factor 54
23	*WRKY70*	WRKY Transcription Factor 70
24	*WRKY22*	WRKY Transcription Factor 22
25	*WRKY30*	WRKY Transcription Factor 30
26	*WRKY33*	WRKY Transcription Factor 33
27	*WRKY75*	WRKY Transcription Factor 75
28	*SlWRKY37*	Tomato WRKY37
29	*AtERF8*	Ethylene Response Factor 8
30	*AtERF4*	Ethylene Response Factor 4

31	*NtERF3*	Nicotiana ERF3
32	*SlERF36*	*Solanum lycopersicum* ERF36
33	*RAV1*	Related to ABI3/VP1
34	*GmRAV1*	Soybean RAV1
35	*SUB1A*	Submergence Tolerance 1A
36	*CRF6*	Cytokinin Response Factor 6
37	*CBF2*	C-repeat Binding Factor 2
38	*CBF3*	C-repeat Binding Factor 3
39	*COR15*	Cold-Regulated 15
40	*RD29*	Responsive to Desiccation 29
41	*PIF4*	Phytochrome-Interacting Factor 4
42	*PIF5*	Phytochrome-Interacting Factor 5
43	*PIF3*	Phytochrome-Interacting Factor 3
44	*EEL*	ENHANCED EM LEVEL
45	*ABI5*	Abscisic Acid Insensitive 5
46	*MYBL*	MYB-like TF
47	*ARF2*	Auxin Response Factor 2
48	*SR1/CAMTA3*	Signal Responsive 1/Calmodulin Binding TF
49	*ETR1*	Ethylene Resistant 1
50	*CTR1*	Constitutive Triple Response 1
51	*EIN2*	Ethylene Insensitive 2
52	*EIN3*	Ethylene Insensitive 3
53	*EILs*	EIN3-Like Proteins
54	*ABCG40*	ABA Transporter ABCG40
55	*NCED3*	9-cis-Epoxycarotenoid Dioxygenase 3
56	*DREB2A*	Dehydration Responsive Element Binding Protein 2A
57	*RCD1*	Radical-Induced Cell Death 1
58	*MYC2*	MYC Transcription Factor 2
59	*SlMYC2*	*Solanum lycopersicum* MYC2
60	*AUX/IAA*	Auxin/Indole-3-Acetic Acid Proteins
61	*ERFVII TFs*	Ethylene Response Factor VII
62	*PDC*	Pyruvate Decarboxylase
63	*ADH*	Alcohol Dehydrogenase
64	*phyB*	Phytochrome B
65	*phyA*	Phytochrome A
66	*ATG2*	Autophagy Gene 2
67	*ATG4a/4b*	Autophagy Gene 4 Isoforms
68	*ATG5*	Autophagy Gene 5
69	*ATG7*	Autophagy Gene 7
70	*ATG8*	Autophagy Gene 8
71	*ATG9*	Autophagy Gene 9
72	*ATG10*	Autophagy Gene 10
73	*ATG18a*	Autophagy Gene 18a
74	*ATI1*	ATG8-Interacting Protein 1
75	*ABS3*	Abnormal Shoot 3
76	*ORE9*	F-box Protein ORE9
77	*PUB12*	Plant U-box 12
78	*PUB13*	Plant U-box 13
79	*PUB44/SAUL1*	Senescence-Associated E3 Ubiquitin Ligase 1
80	*ATL31*	ARABIDOPSIS TOXICOS EN LEVADURA 31
81	*UPL1-7*	Ubiquitin Protein Ligase Family 1-7
82	*UPL5*	Ubiquitin Protein Ligase 5
83	*UBP12*	Ubiquitin-Specific Protease 12
84	*UBP13*	Ubiquitin-Specific Protease 13
85	*MET1*	Methyltransferase 1
86	*CMT3*	Chromomethylase 3
87	*DRM*	Domains Rearranged Methyltransferase
88	*DME*	Demeter
89	*ROS1*	Repressor of Silencing 1

90	*DML2/3*	Demeter-Like 2/3
91	*SUVH2*	Suppressor of Variegation 3-9 Homolog 2
92	*JMJ16*	JmjC Domain Demethylase 16
93	*HDA9*	Histone Deacetylase 9
94	*REF6*	H3K27 Demethylase REF6
95	*HDA15*	Histone Deacetylase 15
96	*HAC1*	Histone Acetyltransferase 1
97	*SRT1*	Sirtuin 1
98	*HD2C*	Histone Deacetylase HD2C
99	*ORE7*	AT-hook Chromatin Remodeler ORE7
100	*CHR10/ASG3*	Chromatin Remodeler CHR10
101	*CHR19/ETL1*	Chromatin Remodeler CHR19

TFs – transcription factors

CONCLUSION AND FUTURE PERSPECTIVE

Leaf senescence under water stress represents a highly coordinated developmental transition regulated by complex networks integrating transcriptional, epigenetic, and post-translational mechanisms. NAC, WRKY, ERF, and bHLH transcription factors act as central nodes linking hormonal and stress signaling with remodeling of chromatin architecture and protein turnover. Recent evidence indicates that epigenetic modifications, such as DNA methylation and histone remodeling, dynamically shape the senescence transcriptome by fine-tuning the activation of senescence-associated genes. At the same time, ATP-dependent chromatin remodelers further modulate transcriptional accessibility. Post-translational modifications, including ubiquitination, deubiquitination, and phosphorylation, together with the interplay of proteasome and autophagy pathways, ensure precise regulation of protein stability and nutrient recycling. Future research should focus on spatiotemporal mapping of epigenetic landscapes and PTM networks during stress-induced senescence to explore functional cross-talk among regulatory layers. Integrating single-cell multi-omics and genome editing will enable the dissection of transcription factor-chromatin-protein interaction circuits. These advances will accelerate the development of crops with optimized senescence timing, enhanced stress resilience, and improved productivity under adverse environmental conditions.

Author contribution statement
KS – A – Research concept and design, D – Writing the article
NA – D – Writing the article, E – Critical revision of the article
PKM – E – Critical revision of the article
SYJ – A – Research concept and design, D – Writing the article, E – Critical revision of the article, F – Final approval of the article

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