Senescence-associated proteins and nitrogen remobilization in grain filling under drought stress condition

Zohreh Hajibarat and Abbas Saidi*

Abstract

Background: Plants use escape strategies including premature senescence and leaf reduction to cope in response to drought stress, which in turn reduces plant leaves and photosynthesis. This strategy allows the new generation (seeds) to survive under drought but, plants experience more yield loss during stress condition. The amount of damage caused by drought stress is compensated by the expression of genes involved in regulating leaf aging. Leaf senescence alters the expression of thousands of genes and ultimately affecting grain protein content, grain yield, and nitrogen utilization efficiency. Also, under drought stress, nitrogen in the soil will not become as much available and causes the beginning and acceleration of the senescence process of leaves.

The main body of the abstract: This review identified proteins signaling and functional proteins involved in senescence. Further, transcription factors and cell wall degradation enzymes (proteases) related to senescence during drought stress were surveyed. We discuss the regulatory pathways of genes as a result of the degradation of proteins during senescence process. Senescence is strongly influenced by plant hormones and environmental factors including the availability of nitrogen. During maturity or drought stress, reduced nitrogen uptake can cause nitrogen to be remobilized from leaves and stems to seeds, eventually leading to leaf senescence. Under these conditions, genes involved in chloroplast degradation and proteases show increased expression. The functional (proteases) and regulatory proteins such as protein kinases and phosphatases as well as transcription factors (AP2/ERF, NAC, WRKY, MYB, and bZIP) are involved in leaf senescence and drought stress.

Short conclusion: In this review, senescence-associated proteins involved in leaf senescence and regulatory and functional proteins in response to drought stress during grain filling were surveyed. The present study predicts on the role of nitrogen transporters, transcription factors and regulatory genes involved in the late stages of plant growth with the aim of understanding their mechanisms of action during grain filling stage. For a better understanding, the relevant evidence for the balance between grain filling and protein breakdown during grain filling in cereals is presented.

Keywords: Senescence, Chlorophyll degradation, Protease, Drought, Nitrogen remobilization

*Correspondence: abbas.saidi@gmail.com
Department of Plant Sciences and Biotechnology, Faculty of Life Sciences and Biotechnology, Shahid Beheshti University, Tehran, Iran
the reproductive organs and in this process the nutrients are remobilized. Senescence is controlled by complex networks of biochemical, physiological, and molecular mechanisms [1]. In addition, plants cope with drought stress by decreasing current photosynthesis and initiating leaf senescence, inducing a series of complex metabolic changes. Extensive physiological events subject to severe stress lead to chlorophyll degradation and production of reactive oxygen species (ROS), and oxidation of proteins and lipids. ROS produced in chloroplasts and mitochondria during drought may eventually cause leaf senescence and decrease yield [2]. As leaves begin to senesce, chloroplasts are degraded and stromal enzymes are destroyed, eventually reducing photosynthesis [3]. Carbon and nitrogen are important sources that are released during the senescence process or remobilized to other growing parts of plants. Sugars (glucose and fructose) accumulate during stress and in naturally senesced leaves. Although the accumulation of hexoses in older leaves initiates or accelerates the senescence processes, this alone may not cause senescence, but some other factors such as a complex metabolic network (nitrogen) and environmental factors may also be involved [4].

Under drought stress, plants face nitrogen deficiency, eventually leading to senesced leaves. Senescence due to nitrogen deficiency increases nitrogen recycling and remobilization, higher or optimal concentrations of nitrogen cause leaf growth and stay green [5, 6]. Therefore, improving the efficiency of Nitrogen use efficiency (NUE) is important for crops under water shortage conditions. Water deficiency accelerates the senescence process in cereals, leading to an increased loss of leaf nitrogen and leaf chlorophyll and increasing lipid peroxidation, which is important for remobilization of nitrogen to the phloem. If the nitrogen uptake is very low during grain filling, the plant’s nitrogen demand cannot be supplied. This condition decreases cytokinin biosynthesis and leads to degradation of leaf protein. Amino acids secreted by protein degradation are transported to the grain through the phloem. Over 95% of grain proteins are composed of amino acids, remobilized to seeds after degradation of proteins in rosette leaves [7].

Leaf senescence by extensively degrading chloroplast proteins using increased expression or activity of serine, cysteine, aspartic, and metalloproteases in leaves provide the nitrogen needed for seed filling. Senescence is a prerequisite for the mobilization of not only nitrogen but also other important nutrients. Chloroplasts contain a major reservoir of reduced leaf nitrogen. Hence, nitrogen remobilization essentially involves the degradation of chloroplast proteins into different types of amino acids and eventually mobilize to growing seeds [8]. Phytohormones, transcription factors, cellular oxidation state, and source strength cause the reallocation of nutrients, leading to senescence in natural environments or stress. Among the different transcription factors implicated in leaf senescence regulation, NAC and WRKY transcription factors and FTSH and Lon proteases have been surveyed extensively in barley. In this review, we will focus on the regulation of plant senescence in using signaling proteins such as protein kinase and phosphatase, senescence associated proteins, cell wall degradation enzymes and nitrogen remobilization in response to drought stress.

**Main text**

**Leaf senescence in response to drought stress**

A genotype with a stay green (SG) phenotype relies more on current photosynthesis and retains more leaf chlorophyll, enabling them to synthesize carbohydrates and produce assimilates during flowering as well as during seed development. At the onset or delayed senescence, a positive correlation between water use efficiency and final yield in sorghum, wheat, rice, and maize has been observed, allowing the plants to cope under terminal drought stress [9].

The effect of SG phenotype and the share of its photosynthetically active tissue in spikes under terminal drought stress is of great importance in cereals. Recent research has demonstrated the importance of spike photosynthesis and the source of assimilate for effective grain yield under stress [10]. Under stress, senescence causes the remobilization of carbon and nitrogen from vegetative tissues (leaves and stems) to seeds and accelerates the seed filling process. These events alter carbon and nitrogen metabolism and disrupt remobilization mechanisms, leading to sink-source disruption through a complex network of hormones and regulation of genes network [11].

Most of reprograming of the thousands of genes related to senescence were up and down-regulated with the onset of senescence [3]. Many hydrolytic enzymes were targeted to degrade proteins, nucleic acids, and lipids [3]. Nitrogen produced by enzymes that break down proteins and lipids are remobilized through growing leaves to growing seeds and nourishing tissues. This process occurs due to natural conditions at the terminal of the plant growth period or biotic and abiotic stresses [12]. Enzymes involved in protein breakdown are one of the most important proteins related to leaf senescence with an essential role in nutrient recycling, especially nitrogen. Studies of genes expression showed that cysteine proteases are among the most abundant proteases involved during leaf senescence. Reduction of protein degradation in senesced leaf sections of wheat can be achieved by treatment of cysteine protease inhibitors, indicating the involvement of cysteine proteases in senescence [13, 14].
Proteases and signaling proteins play key roles in nitrogen remobilization from senesced leaves to developing seeds under both normal and stress conditions.

Degradation and remobilization of plastid proteins in leaf senescence

Proteases and ubiquitin proteins are involved in degradation of proteins. An excellent example of describing the genetic background of drought resistance is a situation where there is a significant genetic compatibility in a wide range of environments and a high level of drought tolerance [15]. The history of nitrogen mobilization for remobilization from older leaves to growing seeds goes back to more than 30 years. Drought stress Rubisco degradation is enhanced due to nitrogen demand from reservoir sources during leaf aging [16].

Biochemically active proteases (especially acidic pH cysteine endopeptidases) are found in older leaves and are found in vacuolar lithic tissues [16]. Pervious study has showed that plastid proteinolysis stems contain many proteases, including members of the Clp, FtsH, and Lon families, as well as complementar active aminopeptidases [17]. In addition, a series of experiments have shown that isolated chloroplasts incubated in light or dark can initiate Rubisco degradation, resulting in the hydrolysis of its large subunit [18]. Other studies have also shown that the breakdown of this protein and possibly other proteins by oxidative stress may be important to initiate protein catabolism [19, 20]. Transcriptome analysis of old barley leaves showed that serine and cysteine protease genes are abundant, including genes encoding proteins normally found in lytic vacuoles [21]. Proteins and proteases involved in leaf protein degradation are shown in (Table 1). It is probable that chloroplast-based proteases are important for (initiating) the degradation of thylakoid protein. In addition, proteases may provide substrates for complete destruction by autophagy.

Roles of cell wall degradation enzymes in leaf senescence

The cell wall is a complex and selectively permeable layer surrounding the cell. The most relevant function of the cell wall is to provide protection to the cell structure. Thus, the cell wall has evolved to be highly resistant to a wide range of biotic and abiotic stresses. The composition of plant cell walls is mainly composed of polysaccharides arranged in complex structures, while structural proteins are sub-components. The complexity of the cell wall is very important, because it is the first line of defense against biotic and abiotic stresses. In this regard, various plant enzymes involved in cell wall degradation are called cell wall degrading enzymes. Cell wall-degrading enzymes such as β-1,3-glucanase, glycoside hydrolases, β-glucosidase, expansion, and protease play key roles in sucrose metabolism in leaf senescence [29]. These enzymes increase expression in leaf senescence to provide the glucose needed for grain filling through cell wall breakdown. Cell wall degradation enzymes are known as senescence associated proteins.

Glycoside hydrolases (cell wall degradation enzyme) play roles in different biological processes like cell wall metabolism, plant defense, signaling, starch degradation, and remobilization of storage reserves (glucose). Endo 2,4 beta xylanase, Alpha galactosidase, Alpha N arabinofuranosidase A, and Beta D glucosidases were increased in the tolerant genotype. The expression of starch and sucrose metabolism pathway genes like Beta D glucosidase, catalyzing the hydrolysis of the starch, in wheat is altered during drought stress at grain filling stage [30]. Beta D glucosidases are enzymes that hydrolyze cellulose resulting in the formation of glucose. How these enzymes attack starch granule to release glucans is not yet well known, and the pathway of the starch degradation depends on plant species and physiological conditions [31]. It has been reported that cell wall hydrolytic enzymes have many different functions, implicated in stem remobilization during seed filling [31]. We have suggested that the cell wall degradation enzymes play a key role in carbon remobilization during seed filing in the tolerant genotype under drought stress.

Proteases involved in leaf senescence

Leaf senescence is a critical developmental step in plant’s life cycle. During this period, leaf cells affect intricate metabolic modifications and sequential degeneration in the cellular structure. These modifications contain several events namely, significant loss of chlorophyll (Chl), reduction of leaf photosynthetic potential, destruction of chloroplast structures, and the transition of nutrients to other sections of the plant, therefore leading to the death of the senescing leaves [32, 33]. The initiation of leaf senescence can be mainly controlled by different environmental components [34]. Several surveys have suggested that leaf senescence is a stage at which it initiates the programmed cell death (PCD) process [32, 34]. ATP-dependent protease complexes are great and consists of two large subunits of chaperone and proteolytic sections. These energy-dependent proteases along with chaperone system can play as quality control systems and are essential in the state of cell proteins in cell compartments such as cytosol, mitochondria, and chloroplasts [35]. These enzymes are expressed in germinating seeds and function in the remobilization of storage proteins to supply developing seedlings [12]. Most proteases involved in leaf senescence of many plant species are serine and cysteine proteases [12, 13]. Cysteine protease, SAG12, is a senescence-specific gene and is 900 times more pronounced by
glucose. In addition, trehalose 6-phosphate, considered as a signal for the availability of high carbon, is needed for the onset of leaf senescence.

SAG2 and SAG12, both of which encode proteins associated with protein breakdown during senescence, are used as standard markers of leaf senescence. SAG2 transcription is regulated in leaves at all stages of growth, but increases during normal and stress-related senescence in leaves [36]. SAG12 is expressed exclusively in senesced leaves and the encoded protein is contained in the senescence-related vacuoles (SAVs). Senescence-related vacuoles are implicated in the degradation of chloroplast proteins like glutamine synthase and the large subunit of Rubisco [36]. SAG12 is one of the most widely used genes to detect leaf senescence. However, the role of this cysteine protease in nitrogen remobilization and leaf senescence process is not fully understood. The role of SAG12 in nitrogen remobilization has not been well explored, and the few available reports are somewhat controversial. Although, Arabidopsis mutant sag12 did not show any phenotype, overexpression of OsSAG12-1 and OsSAG12-2 in rice moderate senescence progress [37]. In the withering processes, genes involved in senescence such as senescence-associated genes (SAGs), i.e., SAG12 [38, 39], SAG13 [40], were upregulated. Senescence associated proteins are involved in protein degradation, providing essential nitrogen during seed filling.

When plants are exposed to stress conditions, the reaction protein D1 of the PSII is damaged by the ROS species produced near PSII, therefore leading to a reduction in PSII activity. Gene expression of different FtsH has been reported in senescent leaves of Arabidopsis. In Arabidopsis, FtsH2 was expressed most abundantly

### Table 1: Genes and proteins involved in leaf senescence

| Characterization of genes and proteins | Gene/protein name | Description | References |
|--------------------------------------|------------------|-------------|------------|
| **Protein degradation**              | HvSAG12          | Cysteine protease | [22]       |
|                                      | Subtilase        | Subtilases   | [22]       |
|                                      | UBC5             | Ubiquitin.E2 | [22]       |
|                                      | RGLG2            | Ubiquitin.E3.RING | [22]       |
|                                      | UBPS             | Ubiquitin.ubiquitin protease | [22] |
|                                      | HvPAP20          | Cysteine protease | [22]       |
|                                      | HvPAP14          | Cysteine protease | [22]       |
|                                      | ATG8             | Autophagy    | [22]       |
|                                      | RD21             | Cysteine protease | [22]       |
|                                      | RGLG2            | Ubiquitin.E3.RING | [22]       |
| **Regulation of RNA transcription**  | MYB              | MYB-related transcription factor family | [22]       |
|                                      | AtMYB44          | Leaf senescence and abiotic stress responses | [3]        |
|                                      | HvNAC013         | NAC domain transcription factor family | [22]       |
|                                      | HvWRKY12         | WRKY domain transcription factor family | [22]       |
|                                      | IAA16            | Aux/IAA family | [22]       |
|                                      | AFO              | C2C2(Zn) YABBY family | [22] |
|                                      | HvNAC001         | NAC domain transcription factor family | [22]       |
|                                      | HvNAC005         | NAC domain transcription factor family | [22]       |
|                                      | CDF4             | Leaf senescence and floral organ abscission by regulating abscisic acid and reactive oxygen species pathways in Arabidopsis | [23]       |
|                                      | DEAR4            | A member of DREB/CBF family, in leaf senescence and stress response | [24]       |
|                                      | ANAC005 and ANAC019 | An important role in ethylene senescence response | [25]       |
|                                      | RD26             | Leaf senescence and stress response | [26]       |
|                                      | ARF2             | Dark-induced leaf senescence and accumulates for the onset of senescence | [27]       |
|                                      | REVOLUTA (REV)   | Inset of leaf senescence in mature leaves | [28]       |
| **Senescence-related proteins**      | SAG14            | Blue copper-binding protein (membrane) | [29]       |
|                                      | ACS6             | ACC synthase | [29]       |
|                                      | SAG21            | Late embryogenesis-abundant gene | [29]       |
|                                      | SAG113           | Regulates stomatal movement and water loss in senesced leaves | [6]        |
|                                      | SAG12, 21, 29    | Expression only occurs during the senescence of older leaves | [28]       |
while FtsH1 and FtsH5 were downregulated in dark induced leaf senescence. In rice, FtsH2 and DegP play key roles in the regulation of D1 protein turnover and repair PSII cycle through ABA mediated leaf senescence [36]. Mitochondrial Lon and FtsH proteases are implicated in the biogenesis and maintenance of the oxidative phosphorylation system [41]. Mutation of ftsh6 was not able to degrade Lhcb3 and Lhcb1/3 during dark-induced senescence and high-light stress condition, respectively [42]. In oilseed rape, FtsH8 was upregulated under nitrogen deficiency at senescence stage. Whereas, in Arabidopsis and barley, FtsH1, 5, and 6 were upregulated under light deficiency (dark) at senescence stage [42]. The main functions of protease include quality control systems in different organelles, degrade oxidative damaged proteins, and the biogenesis and maintenance of the oxidative phosphorylation [41]. These findings suggest that proteases can be used as important regulatory proteins for senescence in biotechnology systems. Although little information is available about their significance for leaf senescence, proteases have been shown to increase tolerance to abiotic stress conditions. FtsH, Lon, and proteases are implicated in various stresses (light, heat, drought, cold and JA/SA) on protein degradation (Fig. 1).

**Nitrogen remobilization after degradation of proteins in senesced leaves**

The use of nitrogen by plants involves several stages including absorption, mobilization, recovery, and remobilization. Plants are exposed to adverse environmental factors during their growth stages and cannot escape many conditions of abiotic and biotic stress. To cope with these environmental stresses and survive in changing environments, plants remobilize nitrogen and carbon from the phloem of senesced leaves to growing tissues and storage organs such as seeds. Plants can save and use the limited nutrients and energy, to grow and produce seeds [43]. Nitrogen remobilization from protein (plastid) degradation and amino acid metabolism in leaf cell senescence to the protein endosperm stages of cereals involves several short and long distance transitions. Membrane transporters are essential for the transport of amino acids or oligopeptides from vacuoles and chloroplasts. Recently, researchers observed that sucrose-mediated transporters from mesophilic cells to apoplasts in Arabidopsis play an important role in carbon metabolism [44]. Nitrogen remobilization increases plant competitiveness, especially in nitrogen-restricted conditions for agriculture. Nitrogen remobilization efficiency is high because it can reduce the need

---

**Fig. 1** Stress-induced damage to PSII and removal of the damaged D1 by proteases. These stresses induce ROS production leading to oxidation reactive damages. Plants have evolved adaptive systems like responsive genes, protecting plants against oxidative stress damages. Also, FtsH and Lon repair D1 can assist in quality control of damaged proteins.
for nitrogen fertilizers. In crops, nitrogen remobilization after anthesis and during seed maturation is highly related to grain yield and quality [45]. In small grains such as wheat and rice, up to 90% of the grain nitrogen content is remobilized from parts of the vegetative plant, while the proportion of nitrogen remobilization in maize is approximately 35–55% [46]. With the onset and progression of senescence or due to drought stress, several genes associated with senescence are upregulated. Under these conditions, in addition to a small current photosynthesis, plants break down proteins in the leaves and recycle and remobilize the protein to storage materials. Therefore, plants use complex molecular mechanisms with functional proteins such as proteases and regulatory proteins such as phosphatase, protein kinase, and transcription factors to supply energy when the plant needs to produce seeds and offspring of the next generation. The NAC and WRKY transcription factor families play important roles in senescence-related gene regulatory networks in Arabidopsis, rice, and wheat [47–49]. The regulatory network of leaf aging in wheat and barley was investigated, where the transcription factors including NAC and MYB, WRKY, and AP2/EREBP played the most important role [49].

**Senescence signaling and transcription factors in material remobilization under drought stress**

During leaf senescence, the preferred forms of nitrogen remobilization are mostly in the form of amino acids and peptides with carbon remobilization. Researches on proteolysis and nitrogen remobilization during leaf senescence showed that the main remobilization stages include proteolysis of proteins such as rubisco to amino acids by proteases and their transport to the source organ. During the senescence process, proteins and genes associated with nitrogen transport and proteases were upregulated [50]. Nitrogen molecules can be transported from source by their transporters [51]. In wheat, a set of genes were upregulated in the early stages of leaf senescence (NF-YA) while the genes in the late growth stages included CAMTA, GRAS, and NAC. With senescence, bHLH transcription factors, TCP, and MADS_box, were downregulated mainly in the early stages of senescence. While GATA and MADS_box are involved in the later stages of senescence. Regulatory networks include various transcription factors that are themselves regulated by different phyto-hormones. A recent review of 48 barley NAC genes showed that many (but not all) of NAC genes increased expression in senesced barley flag leaf [51]. Among WRKYs, studies have shown that AtWRKY53 is a positive regulator of the senescence process [32, 40]. Limited information is available on the regulation of senescence by transcription factors for wheat and barley. The researchers found that when comparing transcription levels in a number of plant organs, HvWRKY23 expression was positively correlated with AtWRKY53 [52]. Thus, HvWRKY23 is involved in the regulation of leaf senescence. In particular, the mutant line was associated with a stay green phenotype and lower expression of WRKY53 and SAG12 during developmental stages [32].

Proteins involved in the regulation of aging through signal transduction (phosphorylation/dephosphorylation processes, ubiquitin, and hormone signaling) are present in wheat and barley [53, 42]. Genes encoding protein kinases play a role in regulating flowering time. The functional characteristics of these genes are controlled by regulatory networks and are involved in regulation of senescence in cereals and may also use signaling pathways to control flowering time (Table 2). They provide free amino acids for nutrient recovery, where the nutrients are transported to the growing green tissues, either by feeding the metabolism of energy from the tricarboxylic acid cycle, or by providing cell metabolism as well as grain filling for seed production [54]. Study has shown that amino acids accumulate in dark due to senescence and nitrogen deficiency [55]. Several key gene families associated with drought stress were differentially expressed in this study, including TFs and reactive oxygen species scavengers [56]. Based on transcriptome analysis, most of 30 NAC genes increased expression during leaf senescence in Arabidopsis, revealing a strong relationship between hormones and environmental stress. ANAC072, ANAC019, and ANAC055 genes stimulate leaf senescence [57, 58]. A recent survey showed that GhrWRKY27 gene was upregulated in early stages of senescence and its expression varied in various cotton genotypes [59]. ANAC072 expresses the transcription of CV (chloroplast vesiculation), inducing a protein essential for protein degradation and the sugar transport gene SWEET15 [60, 37]. Three WRKYs, namely WRKY18, WRKY25, and WRKY53, were upregulated in the onset and progression of senesced leaves [61].

A report at a transcriptomic level revealed that a higher number of DEGs were observed in the sensitive genotype (IS20351) than in the tolerant genotype (IS22330) [75]. This indicated that the susceptible genotype expresses more genes to complete its growth and life cycle whereas, the tolerant cultivar, instead of enhancing gene expression, stores its energy to complete its grain filling [75]. We can propose several key genes related to drought stress such as TFs, MAPK kinases, sucrose metabolism, starch degradation, and chaperones to be used in breeding and genetic engineering. The transgenic plants developed by overexpressing the transcription factors are given (Table 2).
Phosphorylation of protein kinases and phosphatases play an important role in cellular signaling. Some genes are up-regulated in signal transduction pathway such as protein kinases and calcium signaling pathway in leaf senescence. In bean (*Phaseolus vulgaris*), senescence-associated receptor kinase genes are up-regulated during leaf senescence [76]. Transcriptome analysis of leaf senescence in *Arabidopsis* showed that genes associated to the MAPK phosphorylation were up-regulated during leaf senescence [57]. For example, the membrane-bound receptor protein kinase RPK1 plays a key role in the regulation of leaf senescence in response to ABA. A MAPK kinase kinase9 (MPK9) and MAPK kinase kinase6 (MPK6) play significant roles in controlling leaf senescence [77]. In soybean, GmSARK gene and its *Arabidopsis* homolog, AtSARK, control leaf senescence in response to auxin and ethylene [78]. Mutants of mkk9 or mpk6 can delay senescence, and overexpression of MKK9 gene causes premature senescence [77]. Other protein kinase, the membrane-bound receptor protein kinase RPK1 expressed by abscisic acid (ABA), can affect leaf senescence [79]. Sucrose-nonfermentation1-related protein kinase1 (SnRK1) is a negative regulator in the regulation of leaf senescence [80].

Other protein phosphatases, senescence-suppressed protein phosphatase (SSPP), have negative regulatory roles in leaf senescence signaling [82]. A recent study showed that AtPR5K2 plays a key role in the relationship between ABA-dependent signaling and leaf senescence [83]. Some of the protein kinase and phosphatase proteins decreased or increased in response to leaf senescence. These proteins are important in senescence inhibition and are effective in yield increase.

**Table 2** The transgenic plants developed by overexpressing the transcription factors

| Gene name          | Transgenic plant | Effect                                                                 | References |
|--------------------|------------------|------------------------------------------------------------------------|------------|
| GhWRKY91           | *Arabidopsis*    | Drought stress                                                        | [59]       |
| OsWRKY23           | *Arabidopsis*    | Leaf senescence                                                        | [59]       |
| GhWRKY42           | *Arabidopsis*    | Leaf senescence                                                        | [59]       |
| GhWRKY27           | *Arabidopsis*    | Leaf senescence                                                        | [59]       |
| TaWRKY10           | Tobacco          | Mediating osmotic balance, the production of reactive oxygen species (ROS) | [33]       |
| TaWRKY42-B         | *Arabidopsis*    | Facilitates initiation of leaf senescence by promoting jasmonic acid biosynthesis | [62]       |
| AtWRKY42           | *Arabidopsis*    | Leaf senescence through modulating SA and ROS synthesis                | [63]       |
| AtWRKY25           | *Arabidopsis*    | No accelerate senescence and tolerance to oxidative stress and the intracellular H₂O₂ level | [61]       |
| ZmVQ52             | *Arabidopsis*    | Premature leaf senescence                                              | [64]       |
| CwWRKY71           | *Arabidopsis*    | Promotes flowering and leaf senescence                                 | [65]       |
| GhWRKY17           | *Arabidopsis*    | Accelerated leaf senescence                                             | [59]       |
| NinAC080           | *Arabidopsis*    | Early senescence in leaves                                              | [56]       |
| TaNAC2             | *Arabidopsis*    | Enhanced tolerances to drought, salt, and freezing stresses, senescence | [66]       |
| OsNAC2             | Tobacco          | Early senescence leaves                                                 | [30]       |
| AtNAC075           | *Arabidopsis*    | Delays senescence in *Arabidopsis*                                     | [67]       |
| MINAC5             | *Arabidopsis*    | Drought and cold tolerance and leaf senescence                          | [68]       |
| AtMYBL (At1g49010), | *Arabidopsis*    | as a putative novel transcriptional factor in leaf senescence, and responses to stress caused by exposure to ABA and salt | [69]       |
| PheNAC3            | *Arabidopsis*    | Precocious senescence and abiotic stress tolerance                      | [70]       |
| ScMYBAS1           | Rice             | Biomass accumulation and drought tolerance                              | [71]       |
| MYB4               | *Arabidopsis*    | Leaf senescence                                                         | [72]       |
| ANAC083 (VNI2), ANAC042 | *Arabidopsis* | Tolerance to abiotic stresses, including heat and salt, and delays natural senescence negative regulator of senescence | [73]       |
| GmNAC081           | *Arabidopsis*    | Enhanced senescence, a phenotype associated with accelerated leaf yellowing, reduced photosynthesis rate | [74]       |
Nitrogen homeostasis and senescence associated transcription factors

Under drought conditions, due to the lack of water, the availability of nitrogen in the soil is decreased and as a result, plants are exposed to stress, thus activating a number of molecular mechanisms in the plant. Due to drought stress, the onset of leaf and plant senescence is accelerated. Senescence makes it possible to induce transcription factors and nitrogen remobilization from protein breakdown. This process is a highly complex, regulated, and dynamic process, with some possible side effects. Nutritional starvation, photosynthetic activity, carbon accumulation, carbon to nitrogen ratio, photoperiod, and various other symptoms can lead to the induction of aging of the organ and/or the whole plant. Previous studies have shown that leaf aging is a highly coordinated process, mediating redistribution of metabolites and reproductive maturity and ultimately leading to cell degradation [34, 84].

Environmental stresses such as drought and low nitrogen also cause premature leaf aging by altering gene expression and physiological activities. In addition, certain phyto-hormones, such as abscisic acid (ABA), ethylene (ET), jasmonic acid (JA), and salicylic acid (SA), have been shown to increase leaf senescence, while auxin may increase leaf aging (Fig. 2). ABA initiates and promotes leaf senescence, and as such ABA levels increase with increasing expression of ABA responsive genes during leaf aging [85, 86]. Under low nitrogen conditions, ABA, ET, and JA responsive genes cause inhibition of lateral root and plant growth, eventually leading to leaf senescence. Under high nitrogen conditions, auxin-responsive genes are activated which inhibit transcription factor ARF, leading to induction of root growth and root elongation, resulting in plant growth and development (Fig. 2). In older Arabidopsis leaves, more than 100 transcription factor (TF) genes from different families, including NAC and WRKY, have been upregulated, indicating that transcriptional regulation is an essential step in senescence process [85].

During the senescence process, genes associated with nitrogen transport and proteases show increased

![Fig. 2](image-url)
expression [50]. Inorganic nitrogen molecules can be transported from the leaves in the form of nitrate, ammonium, and urea by their respective transporters [51]. The NRT1.1, NRT1.7, and NRT2.5 transporters are involved in the remobilization of nitrate from source leaves to reservoir organs. The NRT1.6, NRT1.5, and AMT1.5 transporters are involved in nitrate and ammonium transport [86]. In wheat leaf aging process, a set of genes are increased in the early stages of leaf aging (NF-YA) while the genes in the late stages include CAMTA, GRAS, MADS_II, and NAC. With aging, bHLH-transcription factors, TCP, and MADS_box, are increased mainly during the aging stages. WRKY genes are a large TF group in the senescence transcript of Arabidopsis [87]. To date, functional analyses have shown that several WFKY TFs from Arabidopsis positively or negatively regulate leaf aging [88]. For example, WRKY57 acts as a transcription factor for JA and auxin-mediated signaling in JA-induced leaf aging [87]. WRKY45 acts as a positive regulator of aging-induced leaf aging through a gibberellin-mediated signaling pathway (GA) [88]. WRKY25 negatively regulates leaf aging and acts as a positive regulator of WRKY53 expression whereas, WRKY30 negatively regulates leaf senescence [61].

As a dual affinity transporter, NRT1.1 can switch between high and low affinity in response to external nitrate concentrations through phosphorylation and dephosphorylation. When nitrate is low, NRT1.1 is phosphorylated, and converted to a high-affinity transporter, triggering a low-level nitrate response. When the nitrate concentration is high, NRT1.1 is dephosphorylated, and converted to a low-affinity transporter, causing a high-level nitrate reaction. Protein kinases interact with NRT1.1 and regulate nitrate signaling. As a positive regulator, protein kinase is specifically involved in low affinity responses, whereas negatively regulatory protein kinase is specifically involved by phosphorylating NRT1.1 in response to low nitrate high affinity responses [89]. Under low nitrate conditions, NRT1.1 can modulate auxin levels and meristem activity to suppress lateral root growth [90]. It also shows the phenotype of root formation in the presence of nitrate, possibly through dephosphorylation of the protein kinase to modulate NRT1.1, which indicates interference with the stress hormone ABA. A study has shown that NRT1.1 may be a sensor for root development [91], but its exact function in nitrate signaling is not yet fully understood. A close relationship between stress response and leaf senescence has been shown by the performance of several NAC- and WRKY family members [55]. For example, transcription factors such as NAC9 and NAC83 mediate osmotic stress signaling during leaf senescence [54].

To regulate gene expression, signals must be transmitted to the nucleus. Several transcription factors involved in the nitrate response have been identified. Among these, NAC transcription factors, TGA1, interact directly with nitrate-related target genes. Recent studies have identified the activation of transcription factors (TFs), including NAC (NAC019) and WRKY53 as key regulators of leaf aging and protein degradation [84]. Genes involved in hormonal signaling, i.e., abscisic acid (ABA) and ethylene, change during leaf senescence [92].

These factors are involved in the regulation of the degradation of chlorophyll, and NAC019 has been identified as a senescence activator in Arabidopsis [26 and 95]. Recently, a NAC factor in Brassica napus, NAC87, has been identified to regulate both ROS-regulating genes and leaf senescence [93].

Transcription factors involved in drought stress

Some of the main families of TFs involved in drought stress include AP2 / ERF, ARF, bZIP/HD-ZIP, C2H2, MYB/MYC, Zinc Finger, and NAC. WRKY TFs have key regulatory activity in growth processes and are also involved in the response to biotic and abiotic stresses [72]. Based on the number and similarity of AP2/ERF domains, the AP2/ERF family is classified into four main subfamilies: AP2 (Apetala 2), RAV (corresponding to ABI3/VP1), DREB (dehydration-responsive binding protein), and ERF. According to previous studies, the largest subfamily of TFs belong to AP2 / ERF. The ERF and DREB subfamilies have been shown to play an important role in responding to cold and dehydration stresses [24, 94].

DREB1 including CBF1, CBF2, and CBF3 play a major role in the response to cold/drought stress and in the aging process [77]. DREB1/CFB TFs specifically interact with DRE/CRT and express several non-living genes. They regulate stress responsiveness [95]. DEAR4 is a member of the DREB family and positively regulates leaf aging and response to multiple stresses in Arabidopsis thaliana. DEAR4 was identified as a regulator of cell death in the root region using the induced hyper-expression strategy. Plants, as sessile organisms, have developed complex mechanisms that are activated and integrated by expressing thousands of genes to cope with a variety of environmental stresses [96]. DREB2 proteins are involved in the response to dryness and heat [97].

Expression of OsDREB2A in rice was expressed under conditions of water scarcity and application of ABA, which can improve drought tolerance [97]. The OsDREB2B transcript was significantly increased under stress conditions and was able to increase drought tolerance [86]. As a result, OsDREB2 plays an important role in drought tolerance in plants. Arabidopsis finger zinc
protein (AZF2), a C2H2 zinc finger TF, positively regulates leaf senescence. Recent studies have shown that ERFs are key regulators in abiotic stress tolerance in several species. Increased ERF expression after drought, salinity, cold, and heat treatments have been reported. For example, ERF1 is involved in the signaling pathways of ethylene and jasmonic acid. OsERF101 promotes leaf senescence through jasmonic acid signaling including OsNAP and OsMYC2 [54]. AtERF1 is considered a key component of the ethylene/JA-mediated defense response in Arabidopsis [98]. Activation of AtERF1 under various stress conditions, such as drought, salt, and heat, requires both ethylene and JA [98]. The SIERF5, a member of the AP2/ERF transcription factor family, acts as a transcriptional regulator and is a member of the ethylene responsive factor (ERF) family. The SIERF5 TF showed high expression in response to abiotic stresses, such as high salinity, drought, and cold temperatures [99]. OsERF71 positively regulates ABA signaling to alter root architecture and confer drought tolerance in rice [100].

The expression of SlARF2A, SlARF2B, SlARF4, SlARF7A, SlARF8A, and SlARF9A were significantly increased in tomato roots under drought stress [101]. TaARF22 was upregulated in response to ABA treatment and showed a 60-fold change under drought stress [23]. ARF2 expression is induced in older leaves and regulates leaf aging and flower drooping [27]. A previous study reported that OsWRKY5 increases leaf aging by regulating ABA biosynthesis [95].

MYC2 was up-regulated in JA-induced leaf senescence by directly activating the expression of Senescence-Associated Gene 29 (SAG29). Abscisic Acid-Insensitive5 (ABI5), a leucine-based zipper (bZIP) of the TF type, was upregulated in ABA signaling and participated in enduring abiotic stress and leaf aging [102, 103]. In addition to MdABI5, MdBT2 was screened as a potential MdZAT10 interaction protein. MdBT2 plays a key role in regulating JA-mediated leaf senescence [104]. AtATF1, a positive senescence-regulated NAC TF, was upregulated by ABA, reactive oxygen species (ROS) treatment, and drought stress [92]. ATF1 possibly induces ABA biosynthesis by interacting with the NCEDs (9-cis-epoxycarotenoid dioxygenases) promoter, which is a key regulatory in ABA biosynthesis [105].

The base leucine zipper family (bZIP) consists of a conserved bZIP domain [33]. In addition, bZIP TFs are involved in plant growth and in responding to abiotic stresses such as drought [106]. Members of the bZIP TF family have been isolated and identified in different eukaryotes. A study showed that OsbZIP23, one of the orthologous close to Arabidopsis, has been reported as a major regulator of ABA-dependent pathway [107].

The histone-binding protein-1b (HBP1b), belonging to the bZIP family of TFs, encoded by SOBIC.009g23000 is induced in sorghum drought-resistant cultivars [106]. These TFs, expressed differentially in response to drought, are mostly responsible for drought stress differences among genotypes.

NAC016 is a positive regulator of aging and can enhance NAP and CCGs directly by binding to the promoter [108]. In Arabidopsis, drought tolerance increased with overexpression of three genes, namely ANAC019, ANAC055, and ANAC072. Similarly, overexpression of stress-responsive NAC1 (SNAC1) in rice provided tolerance to severe drought stress at the reproductive stage under field conditions without changing the phenotype [108]. In addition, OsNAC6/SNAC2 is caused by cold, drought, salinity, and ABA [107]. SINAC6 i, a localized nuclear protein induced by abscisic acid (ABA) or polyethylene glycol (PEG), plays a positive role in tomato plant response to PEG stress [109–111]. Recent findings indicate the presence of various transcription factors inducing resistance in response to drought stress. In this article, we have surveyed various transcription factors that play important roles in drought stress and leaf senescence. Transcription factors play a central role in the aging process and plant defenses against pathogen attacks. In addition, TFs also participate in various processes such as drought tolerance and flowering.

**Conclusions**

Herein, a favorable understanding of the mechanism and molecular signaling of remobilization from stem to grain under drought stress conditions has been discussed. We described the important roles of TFs, as a modern tool, to improve plant tolerance to multiple abiotic stresses. Identification of several stress-responsive TF genes and senescence-associated genes regulated by global stress responses or through signaling pathways of various hormones, including ethylene, JA, and SA, were evaluated. Taking all these observations into account, this study discusses the argument that AP2/ERF, NAC, and WRKY transcription factors certainly underlie hormonal signaling pathways that lead to leaf senescence in response to drought stress and play an important role in seed filling. Based on the available information, it can be said that during the terminal stages of growth and grain filling under plant stress conditions, tolerant genotypes can use the stored stem remobilization to supply the carbon and nitrogen needed by degradation of proteins in the leaves for grain filling. A balance should be designed and maintained between protein degradation and high yield towards the plant model along with protein degradation and stay green phenotype until the end of growth under drought stress. Furthermore, by increasing the expression of senescence-associated proteins such as transcription factors, protein kinase, phosphatases,
and proteases, it is possible to improve the performance potential in response to stress. The relationship between senescence- associated proteins and nitrogen remobilization involves a complex network, where a balance between leaf senescence and nitrogen remobilization can provide a high quality and quantity of seed yield. One of the breeders’ objectives is to select cultivars with high nitrogen and carbon remobilization capacity, as well as genotypes with high photosynthetic potential. Researchers also need to understand the genetic basis of yield potential, physiological efficiency (biomass rate and aggregation of grain yield), and drought tolerance mechanisms to utilize effective strategies for genetic improvements of drought tolerant cultivars. Senescence is important at seed filling stage and is enhanced under drought stress. We reviewed transcription factors involved in drought stress and senescence. Significant progress has been made on the role of TFs in tolerating abiotic stress factors such as drought, and a significant number of TF genes have been identified and confirmed. Genetic manipulation of these stress-responsive TF genes is a powerful approach to improve plant tolerance. The present study discussed the significant contribution of transcription factors, transporters, and degrading proteins during senescence and their roles in drought stress response and grain filling. Senescence-associated proteins can be utilized in plant improvement programs.

**Abbreviations**

ROS: Reactive oxygen species; SG: Stay green; PCD: Programmed cell death; SAGs: Senescence-associated genes.

**Acknowledgements**

The authors are thankful to the Department of Plant Sciences and Biotechnology, Faculty of Life Sciences and Biotechnology, Shahid Beheshti University, Tehran, Iran, for receiving necessary help for this project work.

**Authors’ contributions**

AS carried out literature search, designing and editing of the manuscript. ZH wrote and drew all the figures of the manuscript. AS contributed to the final manuscript. All authors have read and approved the manuscript.

**Funding**

There is no funding available for current research.

**Availability of data and materials**

Not applicable.

**Declarations**

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no competing interests.

Received: 19 April 2022  Accepted: 14 June 2022  Published online: 11 July 2022

**References**

1. Munné-Bosch S (2008) Do perennials really senesce? Trends Plant Sci 13:216–220
2. Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19
3. Sakuraba Y, Park SY, Kim YS, Wang SH, Yoo SC, Hörtenstein S, Paek NC (2014) Arabidopsis STAY-GREEN2 is a negative regulator of chlorophyll degradation during leaf senescence. Mol Plant 7:1288–1302
4. Pourtau N, Marès M, Purdy S, Quentin N, Ruel A, Wingler A (2004) Interactions of abscisic acid and sugar signalling in the regulation of leaf senescence. Planta 219:765–772
5. Diaz C, Purdy S, Christ A, Morot-Gaudry JF, Wingler A, Masclaux-Daubresse C (2005) Characterization of markers to determine the extent and variability of leaf senescence in Arabidopsis. A metabolic profiling approach Plant Physiol 138(2):898–908
6. Saidi A, Hajibarat Z, Ghaffari MR (2021a) The role of effective factors in cell senescence and material remobilization in cereals. JGEB 10(1):81–90.
7. Fait A, Nesi AN, Angelovicr V, Lehmann M, Pham PA, Song L, Haslam RP, Napier JA, Gallii G, Ferrie N (2011) Targeted enhanced of glutamate-to γ-aminobutyrate conversion in Arabidopsis seeds affects carbon-nitrogen balance and storage reserves in a development-dependent manner. Plant Physiol 157(3):1026–1042
8. Distelfeld A, Avni R, Fischer AM (2014) Senescence, nutrient remobilization, and yield in wheat and barley. J Exp Bot 65:3783–3798. https://doi.org/10.1093/jxb/eru477
9. Condon AG, Richards RA, Rebertzke GJ, Farquhar GD (2004) Breeding for high water-use efficiency. J Exp Bot 55:2447–2460. https://doi.org/10.1093/jxb/erh277
10. Kohl S, Hollmann J, Erban A, Kopka J, Riewe D, Weschke W, Weber H (2015) Metabolic and transcriptional transitions in barley leaves reveal a role as transitory resource buffers during endosperm filling. J Exp Bot 66:1397–1411. https://doi.org/10.1093/jxb/eru492
11. Thomas H, Ougham H (2014) The stay-green trait. J Exp Bot 65:3889–3900. https://doi.org/10.1093/jxb/eru337
12. Diaz-Mendoza M, Velasco-Arruy B, Santamaria ME, González-Melendi P, Martinez M, Díaz J (2016) Plant senescence and proteolysis: two processes with one destiny. Genet Mol Biol 39:329–338
13. Bhalerao R, Kesikalo J, Sterky F, Erlendsen R, Bjorkbacka H, Birve SJ, Karlsson J, Gardestrom P, Gustafson P, Lundeborg J, Jansson S (2003) Gene expression in autumn leaves. Plant Biol 131:430–442
14. Rawlings ND, Barrett AJ, Finn R (2016) Twenty years of the MEROPS database of proteolytic enzymes, their substrates and inhibitors. Nucl Acid Res 44:D343–D350
15. Fan Y, Shabala S, Ma Y, Xu R, Zhou M (2015) Using QTL mapping to investigate the relationships between abiotic stress tolerance (drought and salinity) and agronomic and physiological traits. BMC Genom 16:43. https://doi.org/10.1186/s12864-015-1243-8
16. Feller U, Anders I, Mae T (2007) The FtsH protease heterocomplex in Arabidopsis: dispensability of type-B protease activity for proper chloroplast development. Plant Cell 22(11):3710–3725
17. Schuhmann H, Adamska I (2012) Deg proteases and their role in protein quality control and processing in different subcellular compartments of the plant cell. Physiol Plant 145(1):224–234
18. Zhang D, Kato Y, Zhang L, Fujimoto M, Tsutsumi N, Sakamoto M (2010) The FtsH protease heterocomplex in Arabidopsis: dispensability of type-B protease activity for proper chloroplast development. Plant Cell 22(11):3710–3725
19. Desimone M, Wagner E, Johannngmeier U (1998) Degradation of active-oxygen-modified ribulose-1,5-biphosphate carboxylase/oxygenase by chloroplastic proteases requires ATP-hydrolisis. Planta 205:459–466
20. Ishida H, Nishimori Y, Sugisawa M, Makino A, Mae T (1997) The large subunit of ribulose-1,5-biphosphate carboxylase/oxygenase is fragmented into 37-kDa and 16-kDa polypeptides by active oxygen in the lysates of chloroplasts from primary leaves of wheat. Plant Cell Physiol 38:471–479
21. Jukant AK, Fischer AM (2008) A high-grain protein content locus on barley (Hordeum vulgare) chromosome 6 is associated with increased flag leaf proteolysis and nitrogen remobilization. Physiol Plant 132:426–439
22. Hollmann J, Gregeren PL, Krupinska K (2014) Identification of pre-
dominant genes involved in regulation and execution of senescence-
associated nitrogen remobilization in flag leaves of field-grown barley. J
Exp Bot 1(65)(14):3563–73.
23. Xu L, Wang D, Liu Y, Fang Z, Su S, Guo C, Zhao C, Tang Y (2020) Compre-
hensive atlas of wheat (Triticum aestivum L.) AUXIN RESPONSE FACTOR
expression during male reproductive development and abiotic stress.
Front Plant Sci 11:586144
24. Zhang Z, Li W, Gao X, Xu M, Guo Y (2020) DEAR4, a member of DREB/
CBF family, positively regulates leaf senescence and response to multi-
ple stressors in Arabidopsis thaliana. Front Plant Sci 31(11):367
25. Iqbal N, Khan NA, Ferrante A, Trivellini A, Francini A, Khan MI (2017) Eth-
ylene role in plant growth, development and senescence: interaction
with other phytohormones. Front Plant Sci 8:475
26. Hickman R, Hill C, Penfold CA, Breeze E, Bowden L, Moore JD, Zhang P ,
Jackson A, Cooke E, Bewicke-Coley F, Mead A (2018) A local regulatory
network around three NAC transcription factors in stress responses and
senescence in Arabidopsis leaves. Plant J 75(1):26–39
27. Ellis CM, Nagpal P, Young JC, Hagen G, Guilfoyle TJ, Reed JW (2005)
AUXIN RESPONSE FACTOR1 and AUXIN RESPONSE FACTOR2 regulate
senescence and floral organ abscission in Arabidopsis thaliana. Devel-
opment 132(20):4563–4574
28. Bresson J, Doll J, Vasseur F, Stahl M, von Roepenack-Lahaye E, Kilian J,
Stadelhofer B, Kremer JM, Kilb D, Wenzel S, Zentgraf U (2022) The
genetic interaction of REVOLUTA and WRKY53 links plant development,
senescence, and immune responses. PLoS ONE 17(3):e0254741
29. Zhaowei Li, Qian ZH, Fangmin CH (2020) Sugar starvation enhances leaf
senescence and genes involved in sugar signaling pathways regulate early
leaf senescence in mutant rice. Rice Sci 27(3):201–214
30. Mao C, Lu S, Li B, Zhang B, Shen J, He J, Luo L, Xi Q, Chen X, Ming F
(2017) A rice NAC transcription factor promotes leaf senescence via
ABA biosynthesis. Plant Physiol 174(3):1747–1763
31. Smith AM, Zeeman SC, Smith SM (2005) Starch degradation. Annu Rev
Plant Biol 56(5):73–98
32. Fischer AM (2012) The complex regulation of senescence. Crit Rev
Plant Sci 31:124–147
33. Wang F, Liu J, Chen M, Zhou L, Li Z, Zhao Q, Cheng F (2016) Involvement
of asbiscic acid in PSI photodamage and D1 protein turnover for
light-induced premature senescence of rice flag leaves. PLoS ONE
11(8):e0161203
34. Lim PO, Nam HG (2007) Ageing and senescence of the leaf organ. J
Plant Bio 503(291):301–306
35. Leidhold C, Voss W (2007) Chaperones and proteases—guard-
ians of protein integrity in eukaryotic organelles. Ann NY Acad Sci
1113(1):72–86
36. Otegui MS, Noh YS, Martinez DE, Vila Petroff MG, Staelen HL, Amasino
RM, Guiaumet JJ (2005) Senescence-associated vacuoles with intense
proteolytic activity develop in leaves of Arabidopsis and soybean. Plant
J 41:831–844
37. James M, Poret M, Mascia-Daubresse C, Marmagne A, Coquet
L, Jouenne T, Chan P, Trouverie J, Etienne P (2018) SAG12, a major
cytosine protease involved in nitrogen allocation during senescence
for seed production in Arabidopsis thaliana. Plant and Cell Physiol
59(10):2052–2063
38. Noh YS, Amasino RM (1999) Regulation of a developmental senes-
cence is conserved between Arabidopsis and Brassica napus. Plant Mol
Biol 41:195–206
39. Pistelli L, Perata P, Alpi A (1992) Effect of leaf senescence on glyoxylate
cycle enzyme activities. Aust J Plant Physiol 19:723–729
40. Lohman KN, Gan S, John MC, Amasino RM (1994) Molecular analy-
sis of natural leaf senescence in Arabidopsis thaliana. Physiol Plant
92(2):322–328
41. Janska H, Piechota J, Kwasniak M (2010) ATP-dependent proteases in
early leaf senescence in mutant rice. Rice Sci 27(3):201–214
42. Leidhold C, Voos W (2007) Chaperones and proteases—guard-
ians of protein integrity in eukaryotic organelles. Ann N Y Acad Sci
1113(1):72–86
43. Avila-Ospina L, Morson M, Yoshimoto K, Masclaux-Daubresse C (2014)
Autophagy, plant senescence, and nutrient recycling. J Exp Bot
1(65)(14):3799–811.
44. Chen FL, Jiang B, Zhang K, Zheng H, Xiao Y, Ouyang YZ, Yu NM (2011)
Relationships between initial chemical composition of forest leaf litter
and their decomposition rates in degraded red soil hilly region of South
China. Chin J Appl Ecol 22(3):575–580
45. Kichey T, Hiri B, Heumes Z, Dubois F, Le Georges J (2007) In winter wheat
(Triticum aestivum L.), post-anthesis nitrogen uptake and remobilisa-
tion to the grain correlates with agronomic traits and nitrogen physi-
ological markers. Field Crops Res 102(1):22–32
46. Hiri B, Andrieu B, Valadier MH, Renard S, Quillere I, Chelle M, Pommel
B, Fournier D, Drouet JL (2005) Physiology of maize leaf II: identification
of physiological markers representative of the nitrogen status of maize
(Zea mays) leaves during grain filling. Physiol Plant 124(2):178–188
47. Saidi A, Hajibarat Z (2021) Phytohormones: Plant switchers in develop-
mental and growth stages in potato. Journal of Genetic Engineering
and Biotechnology 19(1):1–17
48. Schippers JH (2015) Transcriptional networks in leaf senescence. Curr
Opin Plant Biol 12(7):77–83
49. Roberts IN, Caputo C, O’Dowd MV, Funk C (2012) Senescence-associated
proteases in plants. Physiol Plant 145(1):130–139
50. Masclaux-Daubresse C, Daniel-Vedele F, Dechorgnat J, Chardon F, Gau-
fichon L, Suzuki A (2010) Nitrogen uptake, assimilation and remobiliza-
tion in plants: challenges for sustainable and productive agriculture.
Ann Bot 105(7):1141–1157
51. Mangelsen E, Kilian J, Berendzen KW, Kolukisaoglu ÜH, Harter K, Jansson
C, Wanke D (2008) Phylogenetic and comparative gene expression
analysis of barley ( Hordeum vulgare) WRKY transcription factor family
reveals putatively retained functions between monocots and dicots.
BM Genom 9(1):1–7
52. Krugman T, Chaque v , Peleg Z, Balzerque S, Just J, Korol AB, Nevo E,
Saanga Y, Chalihoub B, Fahima T (2010) Multilevel regulation and signal-
ling processes associated with adaptation to terminal drought in wild
emmer wheat. Funct Integr Genomics 10(2):167–186
53. Lim C, Kang K, Shim Y, Sakuraba Y, An G, Paek NC (2020) Rice ETHYLENE
RESPONSE FACTOR 101 promotes leaf senescence through Jasmonic
acid-mediated regulation of OsNAP and OsWMC2. Front Plant Sci
11:1096
54. Katoh H, Nishihama R, Weijers D, Kohchi T (2018) Evolution of nuclear
auxin signalling: Lessons from genetic studies with basal land plants. J
Exp Bot 69:291–301
55. Li W, Li X, Chao J, Zhang Z, Wang W, Guo Y (2018) NAC family transcription
factors in tobacco flowers and their potential role in regulating leaf
senescence. Front Plant Sci 21(9):1900
56. Guo Y, Gan S (2006) AtNAP, a NAC family transcription factor, has an
important role in leaf senescence. Plant J 46:601–612. https://doi.org/
10.1111/j.1365-313X.2006.02723.x
57. Hu R, Qi G, Yingzhen Kong, Deijing Kong, Qian Gao, and Gongke Zhou
(2010) “Comprehensive Analysis of NAC Domain Transcription Factor
Gene Family in Populus Trichocarpa.” BMC Plant Biol 10(1):145
58. Guo L, Ma Q, Zhang C, Wang C, Wei H, Wang H, Yu S (2019) The cotton
GhWRKY91 transcription factor mediates leaf senescence and
responses to drought stress in transgenic Arabidopsis thaliana. Front
Plant Sci 29(10):1352
59. Kamranfar I, Xue GP, Tohge T, Sedaghatmehr M, Fernie AR, Balazadeh
S, Mueller-Roeber B (2018) Transcription factor RD26 is a key regulator
of metabolic reprogramming during dark-induced senescence. New
Phytol 218:1543–1557. https://doi.org/10.1111/nph.15127
60. Doll J, Muth M, Riester L, Nebel S, Bresson J, Lee HC, Zentgraf U (2020)
Arabidopsis thaliana WRKY25 transcription factor mediates oxidative
stress tolerance and regulates senescence in a redox-dependent man-
ner. Front Plant Sci 23(10):1734
61. Zhao MM, Zhang XW, Liu YW, Li K, Tan Q, Zhou S, Wang G, Zhou C (2020)
A WRKY transcription factor, TaWRKY42-B, facilitates initiation of
leaf senescence by promoting jasmonic acid biosynthesis. BMC Plant
Biol 20(1):1–22
63. Niu F, Cui X, Zhao P, Sun M, Yang B, Deyholos MK, Li Y, Zhao X, Jiang YQ (2020) WRKY42 transcription factor positively regulates leaf senescence through modulating SA and ROS synthesis in Arabidopsis thaliana. Plant J 104(1):171–184

64. Yu T, Li X, Bae Y, Mei X, Guo Z, Liu C, Cai Y (2019) Overexpression of the maize transcription factor ZmVQ25 accelerates leaf senescence in Arabidopsis. PLoS ONE 30(14):e0221949.

65. Huang R, Liu D, Huang M, Ma J, Li Z, Li M, Sui S (2019) CIPKR7/1, a WRKY transcription factor gene of Wintersweet (Chimonanthus praecox), promotes flowering and leaf senescence in Arabidopsis. Int J Mol Sci 21(21):5325.

66. Mao X, Zhang H, Qian C, Li A, Zha G, Jing R (2012) TaNAC2, a NAC-type wheat transcription factor conferring enhanced multiple abiotic stress tolerance in Arabidopsis. J Exp Bot 63(8):2933–2946

67. Kan C, Zhang Y, Wang HL, Shen Y, Xia X, Guo H, Li Z (2021) Transcription factor NAC075 delays leaf senescence by deterring reactive oxygen species accumulation in Arabidopsis. Front Plant Sci 24;12:164.

68. Yang X, Wang X, Ji L, Yi Z, Fu C, Ran J, Hu R, Zhou G (2015) Overexpression of a Miscanthus lutarioriparius NAC gene MANCOS confers enhanced drought and cold tolerance in Arabidopsis. Plant Cell Rep 34(6):943–958

69. Zhang X, Ju HW, Chung MS, Huang P, Ahn SJ, Kim CS (2011) The R-type MYB-like transcription factor, ATMYBL, is involved in promoting leaf senescence and modulates an abiotic stress response in Arabidopsis. Plant Physiol 52(11):138–148

70. Xie L, Cai M, Li X, Zheng H, Xie Y, Cheng Z, Bai Y, Li J, Mu S, Gao J (2020) Senescence-Suppressed Protein Phosphatase directly interacts with the cytoplasmic domain of Senescence-Associated Receptor-Like Kinase and negatively regulates leaf senescence in Arabidopsis. Plant Physiol 169:1275–1291

71. Kihara T, Mokdad R, Gepstein S (2000) Cloning and characterization of a soybean dual-specificity kinase, GmSARK, and its Arabidopsis homolog, AtMYBH, participates in regulation of leaf senescence and modulates an abiotic stress response. Plant Mol Bio 88(3):269–286

72. Lee S, Masclaux-Daubresse C (2021) High-resolution temporal profiling of transcripts during Arabidopsis leaf senescence reveals a distinct chronology of processes and regulation. Plant Cell 23(3):873–894

73. Iba Y, Tanaka K, Yamaguchi-Shinozaki K (2007) Regulation and functional analysis of ZmDREB2A in response to drought and heat stresses in Zea mays L. Plant J 50:54–69. https://doi.org/10.1111/j.1365-313X.2007.03034.x

74. Lee IC, Hong SW, Whang SS, Lim PO, Nam HG, Koo JC (2011) Age-and dark-induced leaf senescence in Arabidopsis. Plant Physiol 52(2):651–662

75. Bouzayen M, Zouine M (2018) Auxin response factors (ARFs) are potential mediators of auxin action in tomato response to biotic and abiotic stress (Solanum lycopersicum). PLoS ONE 13(2):e0193517

76. Xu X, Wan W, Jiang G, Li Y, Huang H, Cai J, Chang Y, Duan CG, Mangrauha SK, Peng X, Zhu JK (2019) Nucleocytoplasmic trafficking of the...
Arabidopsis WD40 repeat protein XIW1 regulates ABA5 stability and abscisic acid responses. Mol Plant 12(12):1598–1611

103. Tamowski L, Rodriguez MC, Brzywczy J, Piecho-Kabacik M, Krókova Z, Martinec J, Wawrzyńska A, Sirko A (2020) A selective autophagy cargo receptor NBR1 modulates abscisic acid signalling in Arabidopsis thaliana. Sci Rep 10(1):1–5

104. Yang K, An JP, Li CY, Shen XN, Liu YJ, Wang DR, Ji XL, Hao YJ, You CX (2021) The apple C2H2-type zinc finger transcription factor MdZAT10 positively regulates JA-induced leaf senescence by interacting with MdBT2. Horticulure research 1:8

105. Jensen MK, Lindemose S, De Massi F, Reimer JJ, Nielsen M, Perera V, Workman CT, Turk F, Grant MR, Mundy J, Petersen M (2013) ATAF1 transcription factor directly regulates abscisic acid biosynthetic gene NCED3 in Arabidopsis thaliana. FEBS Open Bio 3:321–327

106. Abdel-Ghany SE, Ullah F, Ben-Hur A, Reddy AS (2020) Transcriptome analysis of drought-resistant and drought-sensitive sorghum (Sorghum bicolor) genotypes in response to PEG-induced drought stress. Int J Mol Sci 21(3):772

107. Todaka D, Shinozaki K, Yamaguchi-Shinozaki K (2015) Recent advances in the dissection of drought-stress regulatory networks and strategies for development of drought-tolerant transgenic rice plants. Front Plant Sci 18(6):84

108. Jian W, Zheng Y, Yu T, Cao H, Chen Y, Gui Q, Xu C, Li Z (2021) SNAC6, a NAC transcription factor, is involved in drought stress response and reproductive process in tomato. J Plant Physiol 264:153483

109. Liu G, Li X, Jin S, Liu X, Zhu L, Nie Y, Zhang X (2014) Overexpression of rice NAC gene SNAC1 improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton. PLoS One 28(9(1):e86895.

110. Zientara-Rytter K, Lukomska J, Moniuszko G, Gwozdecki R, Surowiecki P, Lewandowska M, Liszewska F, Wawrzyńska A, Sirko A (2011) Identification and functional analysis of Joka2, a tobacco member of the family of selective autophagy cargo receptors. Autophagy 7(10):1145–58

111. Saidi A, Hajibarat Z (2020) Application of Next Generation Sequencing, GWAS, RNA seq, WGRS, for genetic improvement of potato (Solanum tuberosum L.) under drought stress. Biocatal Agric Biotechnol 28:101801.

Publisher’s Note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.