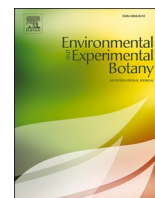


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Comparison of leaf senescence regulation between distantly related plant species uncovers knowledge gaps and opportunities for plant improvement strategies

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ABSTRACT

Leaf senescence is a destructive process that allows the efficient recycling of nutrients from dying leaves to growing parts of the plant. It is the final stage of leaf development that can be induced in response to stress. This makes leaf senescence an adaptive process that is highly beneficial for whole plant survival under unpredictable environmental conditions. Thus, the manipulation of this process has the potential to improve crop plants to become more climate resilient. In this review we compare leaf senescence processes between distantly related species to identify knowledge gaps and opportunities for plant improvement strategies. We describe that main signalling pathways controlled by carbohydrates, reactive oxygen species and hormones are conserved. However, the role of ethylene in age-induced leaf senescence in cereals is obscure. Moreover, downstream senescence regulatory signalling events are largely unknown, and these may be considerably different between members of annual dicots and cereals. Because leaf senescence regulation is so intricately connected to basic metabolic and developmental processes, we propose to increase research efforts to discover natural variation in senescence regulation and pinpoint gene variants that are tried and tested in nature.

1. Introduction: leaf senescence is a beneficial trait in plants

Leaves are a plant's main photosynthetic organs and are critical for plant growth. At their final developmental stage these organs senesce, which involves the organised breakdown of the photosynthetic apparatus. Yet, this destructive process facilitates nutrient recycling from old leaves to newly developing tissues (Guo and Gan, 2005; Jing et al., 2005) and functions as the final opportunity for leaves to contribute to plant growth and development. Efficient nutrient recycling, however, requires a highly ordered progression involving biochemical, physiological, and metabolic alteration, chlorophyll degradation and consequently cessation of photosynthetic activity (Gan and Amasino, 1997; Munné-Bosch and Alegre, 2004). The most notable sign of leaf senescence is the yellowing of leaves (Ougham et al., 2005) and both leaf age and stress are strong inducers of this destructive process (Kanojia and Dijkwel, 2018). Thus, leaf senescence is a highly regulated process that functions to maximise plant survival under changing environments and

contributes to crop productivity (Gan, 2014; Gregersen et al., 2013; Uauy et al., 2006; Kim et al., 2016).

Leaf senescence occurs ubiquitously in both dicotyledonous and monocotyledonous plants, suggesting this beneficial process has evolved well before the two flowering plant groups separated (Thomas et al., 2009). Fossil records of monocots extend to around 130 million years ago, while dicots are thought to have evolved around 110 million years ago (Soltis and Soltis, 1999; Chaw et al., 2004). In this review, we aim to compare major senescence regulatory pathways in some representative model mono- and dicots. Although the study into leaf senescence regulation has been given progressively more attention, there are still numerous unanswered questions. In comparing leaf senescence in distantly related groups of plant species, we explore these fundamental questions: how similar is leaf senescence regulation and do environmental signals incorporate internal age and stress information in similar ways? Leaf senescence in monocots has mostly been researched in model plant and staple crop *Oryza sativa* (rice), while *Arabidopsis thaliana* is still

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a widely used dicotyledonous model plant. Thus, our comparison involves these species mostly, but is supported by research performed in other cereals and annual dicots. In ignoring perennials, we recognise that this limits the scope of the review. Our analysis of modern-day plants does not provide compelling evidence for regulatory processes that preceded the evolutionary split of the two groups. Thus, we aimed to uncover regulatory elements that benefit the fitness of all plants and identify pathways that deserve more research attention. We furthermore hope this review will provoke discussion and more research into the fascinatingly complex area of the regulation of leaf senescence to learn how we can better harness this process for plant improvement.

1.1. The onset of leaf senescence is age and stress-dependent in dicots and cereals

1.1.1. Onset of leaf senescence involves sugars and reactive oxygen species

Despite the pursuit of understanding the concept of leaf senescence, there are still huge gaps in our understanding of how senescence is initiated: what triggers the onset of leaf senescence and is that similar in dicots and cereals, and how is plant age integrated in this unique programme? As senescence is a nutrient recovery programme and sugars play a critical role in the metabolic regulation of plant growth and development, it is not surprising that sugars regulate the onset of leaf senescence (Quirino et al., 2000; Moore et al., 2003; van Doorn, 2008; Wingler, 2018; Asim et al., 2022). The metabolic rate of sugars may affect leaf shelf life and regulate developmental ageing in dicots and cereals. For instance, senescing leaves of tobacco exhibit higher sugar than younger ones and detached barley leaves exposed to light showed symptoms of leaf yellowing and high sugar accumulation (Masclaux et al., 2000; Parrott et al., 2005). Moreover, sugar accumulation and chlorophyll degradation are accelerated in girdled wheat leaves due to the disruption of phloem export (Feller and Fischer, 1994). In sugar signalling pathways, hexoses such as glucose, fructose, and sucrose are important plant molecules involved in perception and transduction of sugar signals in the hexose-mediated signalling pathway (Rolland et al., 2002). In the model plant *Arabidopsis*, sugars promote leaf senescence by regulating the expression of Senescence Associated Genes (SAGs, ie genes that are upregulated during senescence) and overexpression of *Arabidopsis Hxk1* in tomato caused early leaf senescence (Dai et al., 1999; Xiao et al., 2000; Jongebloed et al., 2004). In rice, *Hxk1* is involved in hexose-sensing at an early stage of leaf senescence, based on the finding that the zhefu 142 mutant leaves display elevated expression of *Hxk1* (Zhaowei et al., 2020), suggesting that sugars regulate senescence in both dicots and cereals mainly via *Hxk1*-dependent signalling pathway. Although, sugars may control senescence processes in both plant groups, the specific mechanisms and processes they regulate may differ depending on the plant species and this requires further investigation.

Reactive Oxygen Species (ROS) include hydrogen peroxide (H_2O_2) and superoxide ($O_2^{\cdot-}$) and are among the most important cellular signalling molecules; however, excess production of ROS can be detrimental and lead to local programmed cell death (PCD) and whole leaf senescence (Khanna-Chopra, 2012; Kanojia and Dijkwel, 2018). As leaves become less stress tolerant over time (Kanojia et al., 2020), there may not be a clear-cut difference between the role of ROS in response to stress and normal development. ROS act as signalling molecules to activate defence mechanisms and induce the expression of stress-related genes (Hu et al., 2017) and their role in leaf senescence is largely conserved between dicots and cereals. Both groups of plants utilise ROS as signalling molecules that can trigger a variety of downstream events, ultimately leading to the degradation of cellular components and breakdown of chloroplasts (Yang et al., 2002; Quan et al., 2008; Choudhury et al., 2016; Li et al., 2018a, 2018b; reviewed in Laloi et al., 2004). Interesting findings using *Arabidopsis* and maize indicate that ROS can induce gene expression changes and the degree of irreversible protein oxidation dramatically decreases rather than increases with the

progression of senescence in older leaves (Rosenwasser et al., 2013; Willems et al., 2016; Locato et al., 2018; Johansson et al., 2004; Foyer and Noctor, 2009), indicating that ROS are important regulators of age-induced senescence in both cereals and dicots (Fig. 1). NADPH oxidase enzyme RBOHD is a main source of ROS production and plays a key role in stress tolerance and leaf senescence (Sagi et al., 2006; Hao et al., 2008; Lin et al., 2009; Jiang et al., 2002; Foyer, 2018). During stress, NADPH oxidases interplay with ABA to activate ROS biosynthesis and simultaneously stimulate antioxidant activity to help cope with the increased oxidative damage (Jajic et al., 2015). In senescing leaves, ROS build up and antioxidant enzymes fluctuate, and NADPH oxidase activity and ABA levels increased during leaf senescence (Hung et al., 2004; Li et al., 2015). Thus, ROS, at least partly synthesised by NADPH oxidases, in concert with ABA seem to be key components that regulate the progression of leaf senescence across dicots and cereals (Fig. 2). Nevertheless, ROS regulate a wide range of cell death processes and it is difficult to tease out ROS signals that specifically regulate age- and stress-induced senescence. Thus, specific regulators and pathways could be different between these two plant groups and further studies on the regulatory mechanism of NADPH oxidase in ROS and ABA signalling during stress-induced senescence are warranted.

1.1.2. Developmental and stress factors are integrated to initiate senescence in dicots and cereals

Plant leaves are critical as they capture energy required for growth and development. However, the process of photosynthesis consumes water and the maintenance of leaves requires nutrients. At the end of a leaf's useful lifespan as a photosynthetic organ, it undergoes senescence and, in the process, provides valuable nutrients for the remainder of the plant. Thus, the optimal lifespan of a leaf depends on the balance between its beneficial role in photosynthesis and its detrimental effects as a water and nutrient-consuming organ. When environmental conditions cause stress, and therefore limit growth, the nutrients that can be recovered from a senescing leaf may outweigh its benefit as an energy-capturing organ. Thus, the longest leaf lifespan is not necessarily the optimal lifespan and plants carefully integrate developmental and stress signals to induce early leaf senescence in order to maximise whole plant survival (Kanojia and Dijkwel, 2018; Kanojia et al., 2020). Both the senescence processes, as well as the rate of senescence progression are determined by diverse external and internal cues including high temperature, salinity, drought, nutrient deficiency, reproductive development and hormones (Sultana et al., 2021). While early stress-induced senescence may be beneficial for whole plant survival, reduced net

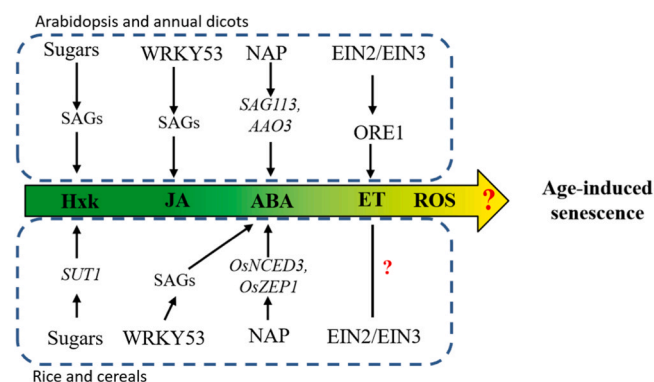


Fig. 1. Age-induced senescence signalling pathways. Illustration showing main pathways regulating age-induced senescence in *Arabidopsis* (top dashed box) and rice (bottom dashed box). Central arrow indicates core senescence signalling components. Question marks mean that signalling occurs through largely unknown pathways. Arrows indicate direction of signalling and line means that direction is unknown. Model is drawn based on research from mainly *Arabidopsis* and rice and we acknowledge that variations may exist in other plant species in the same groups.

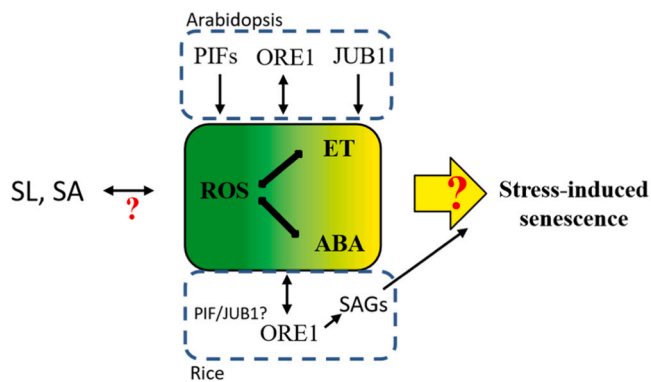


Fig. 2. Stress-induced senescence signalling pathways. Illustration showing main pathways regulating stress-induced senescence in Arabidopsis (top dashed box) and rice (bottom dashed box). Central box indicates core stress signalling components. Question marks mean that signalling occurs through largely unknown pathways. Arrows indicate direction of signalling and double arrow means that direction is two-way. Model is drawn based on research from mainly Arabidopsis and rice, and we acknowledge that variations may exist in other plant species in the same groups.

photosynthesis and precocious cell death can often result in reduced yield in agricultural settings (Gregersen et al., 2008; Gepstein et al., 2013). Phytohormones play various and often complex roles in the integration of developmental and environmental cues to coordinate growth, development and death. As part of the senescence syndrome, a fine-tuned balance between inducers and repressors is maintained to ensure that ordered senescence take place prior to cell death (Schippers et al., 2007). Unsurprisingly, hormones and signalling pathways that regulate developmental senescence also regulate stress-induced senescence. Below, we highlight processes that take place in response to age and stress and compare these elements between the two plant groups.

1.1.3. Abscisic acid plays highly conserved roles in the regulation of age- and stress induced senescence in dicots and cereals

Abscisic acid (ABA) is a sesquiterpenoid hormone that regulates a variety of plant growth and developmental processes, including the ageing of leaves, the growth of shoots and roots, the germination of seeds, and plants' responses to biotic and abiotic stress (Hirayama and Shinozaki, 2010; Lee and Luan, 2012). ABA is synthesised in the leaves and can be transported to other parts of the plant to act as a signal for various developmental processes, including senescence (Breeze et al., 2011; Chen et al., 2020). Evidence indicates that ABA inducible transcription factors (TFs) can promote chlorophyll degradation and enhance leaf senescence (Yang et al., 2014; Liang et al., 2014). In Arabidopsis, AtNAP, an ABA inducible TF, accelerates senescence by inducing *SAG113* (phosphatase-encoding gene) and the ABA biosynthesis gene *AAO3* (Zhang and Gan, 2012; Zhang et al., 2012; Yang et al., 2014), whereas in rice ABA responsive NAC TFs, including *OsNAC2* and *OsNAC054*, activate the expression of ABA biosynthesis genes and increase SAG expression, eventually accelerating leaf senescence (Liang et al., 2014; Mao et al., 2017; Sakuraba et al., 2020).

In addition, stress can increase ABA concentration in leaves to promote leaf senescence by activating various senescence-associated genes (Weaver et al., 1998; Kim et al., 2009; Woo et al., 2021). In both Arabidopsis and rice, dark conditions lead to ABA-induced leaf senescence by activating the expression of TFs including *ORE1*, *AtNAP* and *OsNAP* (ortholog of *AtNAP*) (He et al., 2005; Guo and Gan 2005; Sakuraba et al., 2014; Zhao et al., 2016). Furthermore, ABA-signalling pathways in both plant species include three vital core components, PYRABACTIN RESISTANCE 1 ((PYR1)/PYR1-LIKE (PYL) REGULATORY COMPONENTS OF ABA RECEPTOR (RCAR)), clade A type 2 C PROTEIN PHOSPHATASES (PP2Cs), and subclass III SnRK2s. In transgenic Arabidopsis, overexpression of *PYL9* boosts drought tolerance and leaf

senescence via repressing PP2Cs and triggering SnRK2s (Zhao et al., 2016). Studies have indicated that ABA induces senescence by increasing the biosynthesis of ethylene (ET) (Zhang et al., 2009). This is in contrast to the role of ABA in triggering senescence via core ABA signalling in an ET-independent manner (Zhao et al., 2016) and this should be further studied in cereals.

The senescence-associated subtilisin protease (SBT1.4/AtSASP) in Arabidopsis modulates ABA-induced leaf senescence (Martinez et al., 2015; Wang et al., 2018) and loss-of function of *sasp-1* displayed ABA sensitivity, with enhanced senescence and ROS synthesis. Likewise, rice SASP interacts with *OST1* (*OPEN STOMATA 1*) to regulate ABA and degrade *OST1* suggesting that *AtSASP* and its probable orthologue *OsSASP* might have partially conserved functions during senescence (Martinez et al., 2015). These studies suggest the existence of a significant mechanism linking leaf senescence and ABA signalling and that the role of ABA in leaf senescence may be evolutionarily conserved across dicots and cereals (Fig. 1), and thus that targeting ABA biosynthesis or signalling during the onset of senescence could be beneficial in fine-tuning leaf senescence for optimal nutrient remobilisation in both plant groups. Despite the conserved role of ABA in stress-induced leaf senescence in dicots and cereals, it is difficult to discern to what extent ABA affects senescence differently during stress and developmentally regulated senescence and further study is required (Fig. 2).

1.1.4. Ethylene may be a more prominent regulator of senescence in dicots than in cereals

Ethylene is an important and extensively studied senescence-inducing hormone in dicots, and mutants disrupted in ET perception or signalling show delayed senescence, indicating that this hormone is important in regulating the timing of age-induced senescence (Jing et al., 2005; Jibrán et al., 2013). Exogenous application of ethylene accelerates age-induced leaf senescence, while inhibitors of ET biosynthesis or perception prolong leaf senescence (Iqbal et al., 2017). Earlier research on Arabidopsis shows that ET cannot induce leaf senescence until a defined developmental stage is attained (Grbic, and Bleecker, 1995; Jing et al., 2005), suggesting that leaves must acquire the competence to senescence as part of their developmental programme (Schippers et al., 2007). Oh et al. (1997) identified *ETHYLENE INSENSITIVE2* (*EIN2*) as a key regulator of leaf senescence in dicots. *EIN2* is a central component of the ethylene signalling pathway, and it mediates the transcriptional response to ET. Loss of function mutations in the *EIN2* gene delayed age-induced leaf senescence (Oh et al., 1997; Kim et al., 2009), while overexpression of *EIN2* accelerated it (Wen et al., 2012). *EIN3* is also a positive modulator of leaf senescence (Li et al., 2013), which can bind to the *miR164* promoter to inhibit its expression, and then promote *ORE1* expression (Li et al., 2013; Kim et al., 2014). Qiu et al. (2015) showed that *EIN3* modulates the expression of genes involved in chlorophyll degradation and in turn, enhanced leaf senescence in Arabidopsis (Qiu et al., 2015), and in maize, *ZmEIN3* transactivated *ZmNAC126* and modulated chlorophyll degradation of ET-induced senescence (Yang et al., 2020). The transcriptional network downstream of *EIN3* was investigated and revealed that rice homologs exist of about 159 Arabidopsis *EIN3* BOUND-SAGs that have at least one *EIN3* core binding site present in the upstream promoter region (Goodstein et al., 2012), suggesting that parts of the ET signalling pathway controlling leaf senescence regulation may be conserved across dicots and cereals. The mechanism of ET in rice and other cereals is less understood, although recent advances show that rice has distinct and similar ET signalling features as compared to those of Arabidopsis (Zhao et al., 2020a, 2020b). Moreover, evidence suggests that ET interacts with other hormone (JA, SA, and strigolactone) signalling pathways to synchronise leaf senescence in dicots and cereals (Li et al., 2013; Ueda and Kusaba, 2015; Zhou et al., 2019; Wang et al., 2021). While ET treatment induces senescence in detached leaves (Kao and Yang, 1983; Zhang et al., 2012), we did not find publications reporting that it stimulates age-induced senescence in cereals.

These studies suggest that ET may act as a converging point for multiple hormonal and developmental signals that regulate senescence in dicots and cereals. However, differences in ET signalling exist between these major plant groups and there are only few reports on the role of ET in age-induced senescence in cereals, so more research into this area is warranted.

Under diverse stress stimuli, ET biosynthesis can accompany ROS production to induce leaf senescence (Akteer and Islam, 2017; Park et al., 2022). Drought stress-induced ET biosynthesis, in both Arabidopsis and wheat, triggered chlorophyll degradation and leaf senescence (Ceusters and Van de Poel, 2018). For instance, increased expression of *ACC synthase (ACS)*, which affects the first step of ET synthesis, was shown to promote age- and drought-stimulated leaf senescence in both plant groups (Young et al., 2004; Sun et al., 2017), suggesting that ACS plays a conserved role in ET senescence across dicots and cereals. In Arabidopsis, heat stress increases hydrogen peroxide (H₂O₂) abundance and interacts with ET in a self-amplifying feedback loop to enhance ET biosynthesis and accelerate leaf senescence (reviewed by Fatma et al. (2022)). Other studies showed that salinity, high temperature, heavy metals, and ozone (O₃) can trigger stress-induced leaf senescence in an ET-dependent manner (Munné-Bosch and Alegre, 2004; Allu et al., 2014; Khan et al., 2016). In both dicots (cotton and soybean) and rice, disrupting ET signalling with ET biosynthesis inhibitor 1-Methylcyclopropene (1-MCP) has been shown to delay leaf senescence under stress conditions (Djanaguiraman et al., 2011; Yuan et al., 2015; Hussain et al., 2019). The mechanisms underlying ET-modulated, stress-induced leaf senescence involves a wide range of players, including ROS. Thus, this pathway is complex and future study may help shed more light on the role of ET in regulating leaf senescence under stress in different plant species.

1.1.5. Strigolactone and jasmonic acid are poorly researched stress-induced senescence modulators

The plant hormone strigolactone (SL) has recently been shown to play diverse roles in plant growth and development, including shoot branching and leaf senescence (Ha et al., 2014; Ueda and Kusaba, 2015). Mutations in Arabidopsis SL biosynthesis genes, *MORE AXILLARY GROWTH1 (MAX1)*, *MAX3*, and *MAX4*, and the signalling genes *ARABIDOPSIS DWARF 14 (AtD14)* and *MAX2* delayed senescence in response to ET treatment under high light intensity. SL, in concert with ET, accelerates leaf senescence during dark stress, by means of a two-step mechanism involving the initial activation of ET synthesis, followed by SL synthesis (Woo et al., 2001; Ueda and Kusaba, 2015). SL has been shown to regulate stress-induced senescence in rice as well: In SL-deficient mutants, exogenous administration of synthetic SL, GR24, rescued the delayed senescence of detached leaf segments, while early senescence of wild type leaves was observed under phosphate deficit or dark treatments (Yamada et al., 2014). Generally, these studies suggest that SL modulates stress-induced leaf senescence in both dicots and cereals. However, how SL, in concert with other hormones and signalling pathways, regulates stress-induced leaf senescence, remains largely unresolved.

Jasmonic acid (JA) is a lipid derived hormone with major roles in stress responses and plays a key role in promoting leaf senescence (Beltrano et al., 1998; Huang et al., 2017) (reviewed by Wang et al., 2020). In Arabidopsis, exogenously applied MeJA can trigger the expression of senescence-associated genes, degradation of chlorophyll and attenuation of photosynthesis (He et al., 2002). In addition, the JA-induced downregulation of a catalase H₂O₂ scavenger is MYC2-dependent and this enhances ROS abundance and induces leaf senescence (Zhang et al., 2020). The action of JA is complex where it positively regulates leaf senescence, with likely crosstalk with auxin and salicylic acid (Miao and Zentgraf, 2007; Jiang et al., 2014). In rice, JA has also been shown to modulate leaf senescence, involving the TFs *OsMYC2* and *OsTZF1* (Jan et al., 2013). Thus, there is evidence indicating that JA induces leaf senescence across dicots and cereals. Like

other hormones including SL, JA exerts its action in complex ways by acting on multiple signalling pathways. More research is needed to understand how SL and JA integrate environmental signals to positively regulate leaf senescence.

2. Transcriptional regulation of leaf senescence in dicots and cereals

2.1. The integration of hormonal and ROS signals is complex, involves NAC and WRKY transcription factors and may be different between major plant groups

Plant hormones and ROS modulate development and environmental responses not through linear pathways, but via intricate and complex signalling pathways (Balbi et al., 2007). TFs function as important regulatory nodes in these, and also in age- and stress-induced senescence regulatory pathways (Wu et al., 2012a; Penfold and Buchanan-Wollaston, 2014; Huang et al., 2015; Kim et al., 2018). Signalling pathways can integrate both hormone and ROS signals to induce leaf senescence (Liang et al., 2014; Li et al., 2018a, 2018b), however, to what extent this happens in similar ways in dicots and cereals is unclear. TFs, mainly NAC and WRKY, have been identified as important regulators of senescence across diverse species. In dicots and cereals, NAP TFs seem to be conserved in their function as NAC protein members are involved in multiple signalling pathways regulating leaf senescence (Li et al., 2018a, 2018b). In Arabidopsis, inducible overexpression of *AtNAP* led to premature senescence by directly targeting *SENESCENCE-ASSOCIATED GENE 113 (SAG113)* to control stomatal movement and water loss and both *SAG113* and *AtNAP* were induced by ABA during senescence. In rice, the expression of *OsNAP* is age and ABA-dependent and its overexpression enhanced senescence (Guo and Gan, 2006; Liang et al., 2014). Moreover, *OsNAP* positively modulated senescence by targeting genes involved in the breakdown of chlorophyll and nutrient remobilisation (Liang et al., 2014). Mao et al. (2017) further confirmed that this gene regulates leaf senescence by inducing expression of ABA biosynthetic genes *OsNCED3* and *OsZEP1* and suppressing ABA catabolic gene *OsABA8ox1*. Zhang et al. (2020) recently showed that *TaSNAC11-4B*, a homolog of *AtNAP* was up-regulated in response to ABA and drought during the progression of leaf senescence. Interestingly, *TaSNAC11-4B* ectopic expression in Arabidopsis increased ROS levels and accelerated senescence induced by drought, ABA, and age (Zhang et al., 2020), suggesting that NAP TFs in both groups regulate age- and stress-induced leaf senescence mainly via ABA signalling pathway. Sakuraba et al. (2014) identified PhyB as a principal photoreceptor involved in red-light mediated leaf senescence in Arabidopsis, with PHYTOCHROME INTERACTING FACTOR (PIF) 4 and PIF5 identified as positive regulators of dark-induced leaf senescence (Sakuraba et al., 2014; Zhang et al., 2015). Both PIFs stimulate *ORE1* transcription and regulate ABA and ET signalling by activating the expression of *EIN3* and ABA signalling TFs *ABIS* and *ENHANCED EM LEVEL (EEL)*, as well as elevating the transcription of genes encoding chlorophyll catabolic enzymes (Grbic et al., 1995; Ray et al., 1983; Bensmihen et al., 2002; Kim et al., 2009; Mangan and Alon, 2003; Song et al., 2014; Qiu et al., 2015). Although, the mechanism of PhyB-mediated-red-light signalling in modulating leaf senescence was discovered using Arabidopsis (Piao et al., 2015), a few available studies on the cereals rice (OsPIL1; Sakuraba et al., 2017) and maize (zmPIF4; Shi et al., 2018) suggest that PIFs may play similar roles in these plants too (see review by Sakuraba, 2021).

In Arabidopsis, *ORE1* and NITROGEN LIMITATION ADAPTATION (NLA) have been shown to regulate leaf senescence processes under nitrogen stress (Kant et al., 2011; Kim et al., 2009). *ORE1* acts downstream of NLA and *PHO2 (UBC24)* and NLA interact with *ORE1* in the nucleus to control its stability via polyubiquitination employing *PHO2 (UBC24)* as the E3 conjugate. The ubiquitin-specific proteases (*UBP12* and *UBP13*) antagonise NLA E3 ligase activity to retain *ORE1*

homeostasis. Notably, overexpression of UBP12/UBP13 promoted leaf senescence but this was reversed in *ore1* mutants. UBP12/UBP13 overexpression, on the other hand, exacerbated the senescent phenotype of plants overexpressing ORE1 (Derkacheva et al., 2016; Jeong et al., 2017; Park et al., 2019). UBP12/UBP13 deubiquitinate ORE1 to stabilise and promote its activity as a positive regulator of senescence under nitrogen starvation indicating that ORE1 post-translational regulation determines leaf senescence under nitrogen starvation (Park et al., 2018). However, ORE1 and its possible crosstalk with ABA in regulating senescence under nitrogen starvation remain elusive in cereals. Recently, Lim et al. (2020) showed that in rice ETHYLENE RESPONSE FACTOR 101 (ERF101) is a senescence promoter during dark-induced leaf senescence and binds to the OsNAP and OsMYC2 promoters. In *oserf101* mutants, genes involved in chlorophyll degradation, such as *NAM*, *CUC2* (*OsNAP*), *ATAF1/2*, *STAY-GREEN* (*SGR*), *NON-YELLOW COLORING 1* (*NYC1*), and *NYC3*, were downregulated during dark-induced senescence and JA treatment of the mutant resulted in retained chlorophyll abundance, suggesting that OsERF101 is involved in promoting JA-induced leaf senescence.

The Arabidopsis NAC TF JUNGBRUNNEN1 (JUB1) is a recently discovered central regulator of stress- and age-induced senescence. Its expression is H₂O₂ induced, and its overexpression significantly delays senescence and enhances tolerance to abiotic stresses (Wu et al., 2012). JUB1 directly binds to DREB2A to confer abiotic stress responses (Wu et al., 2012; Shahnejat-Bushehri et al., 2017). The small secreted peptide CLAVATA3/ESR-RELATED 14 (CLE14) can activate JUB1 transcription. It is shown that CLE14 interacts with JUB1 to decrease H₂O₂ abundance, delay leaf senescence, and activate ROS scavenging genes, suggesting that CLE14 may act as a brake signal to modulate age- and stress-induced senescence (Zhang et al., 2022). Although, JUB1 in cereals has not been characterised, a NAC gene (*Sb01g006410*) is reported to be a likely ortholog of JUB1. Interestingly, the expression of *Sb01g006410* increased during natural, dark- and drought-induced leaf senescence (Wu et al., 2012; Wu et al., 2016). Further study will help clarify the role of *Sb01g006410* in regulating leaf senescence.

The WRKY family of TFs performs important roles in hormone and ROS signalling pathways to regulate age-induced leaf senescence in both dicots and cereals (Miao and Zentgraf, 2007; Zhao et al., 2020a, 2020b; Yu et al., 2021a, 2021b). For example, in Arabidopsis, the *AtWRKY6* and *AtWRKY53* TFs regulate ET, SA and JA-induced leaf senescence by enhancing the expression of SAGs (Pieterse and van Loon, 1999; Miao et al., 2004), and H₂O₂ regulates *WRKY53* expression during age-induced leaf senescence (Miao et al., 2004). *WRKY71* directly elevated *EIN2* and *ORE1* expression within the ET signalling pathway, and enhanced ET biosynthesis by directly activating *ACS2*, to promote leaf senescence in Arabidopsis (Yu et al., 2021a, 2021b). Jiang et al. (2014) showed that *WRKY57* is involved in JA-Auxin-mediated signalling in JA-enhanced senescence. In cereals, the role of WRKY TFs in regulating leaf senescence is less well-studied, but there is evidence to suggest that they are involved in similar signalling pathways, although differences exist in some areas. In comparing WRKY TFs, *AtWRKY53* regulates senescence mainly via the JA signalling pathway (Miao et al., 2004). *OsWRKY53*, (this is not the *AtWRKY53* ortholog, as the numbers are not related) regulates age-induced leaf senescence via the ABA signalling pathway: *OsWRKY53* binds to the promoters of ABA catabolic genes including *OsABA8ox1* and *OsABA8ox2* to suppress their expression which in turn, increases endogenous ABA levels and induces premature leaf senescence (Xie et al., 2022). In another study, *OsWRKY42* overexpression caused premature leaf senescence by inducing ROS levels and reducing chlorophyll abundance (Han et al., 2014). Meanwhile, a wheat WRKY TF *TaWRKY42-B* overexpression in Arabidopsis triggered leaf senescence by altering JA biosynthesis genes (*AtLOX1*, *AtLOX2*, *AtLOX3* (*TaLOX3*), and *AtVSP2*) expression. Interestingly, *TaWRKY42-B* and *AtWRKY53* both belong to the group III WRKYs and functional conservation to initiate age-induced leaf senescence was demonstrated in Arabidopsis (Zhao et al., 2020a).

Overall, it appears that in dicots and cereals NAC TFs control age- and stress-induced leaf senescence mainly through the ABA signalling pathway. Considering the importance of WRKY TFs in age-induced leaf senescence, more studies are needed to explore yet unidentified WRKYs and their interactions with hormone- and ROS signalling. While both *AtWRKY53* and *OsWRKY53* regulate age-induced senescence, their hormonal pathways seem different (Fig. 1). WRKY and NAC family of TFs appear to be important regulators of leaf senescence in dicots and cereals via hormonal and ROS signalling pathways, while important differences exist in how, especially ET and ABA, regulate leaf senescence. Also, stress-induced senescence seems to share similar signalling pathways via TFs and ORE1 may be a conserved regulator of leaf senescence in various hormone signalling pathways across dicots and cereals (Fig. 2). However, there is still much to learn about how environmental signals, through the action of hormones and ROS, regulate the onset of leaf senescence.

3. Progression and execution of leaf senescence mainly involve autophagy and SAG12 in dicots and cereals

3.1. The autophagy pathway for remobilisation of nutrients is evolutionarily conserved in dicots and cereals

The vegetative growth stage is a critical stage where plant nitrogen and other essential nutrients are distributed to growing parts of the plant (Schulze et al., 1994; Makino et al., 1997). It is estimated that 75–80% of nitrogen in C₃ plants is distributed to chloroplasts, mostly as photosynthetic proteins such as Rubisco (Makino and Osmond, 1991; Makino et al., 2003). Rubisco and most stromal proteins degrade during senescence and under suboptimal environmental stimuli, and this facilitates nitrogen release to growing organs and seeds (Mae et al., 1983). Part of this process involves autophagy and in both plant groups, autophagy greatly enhances the remobilisation of nutrients from source to sink organs (Guiboileau et al., 2012). In Arabidopsis, ATG8 plays a crucial role during autophagosome membrane formation and cargo sequestration and in autophagosomes; ATG8 interacts and sequesters cargos via receptors (reviewed by Sakuraba et al., 2021). The Arabidopsis *ATG8* and *OsATG8* isoforms were recently identified and overexpression of these genes stimulates autophagy flux and promotes nitrogen remobilisation by enhancing enzymes involved in nitrogen metabolism (Chen et al., 2019; Zhen et al., 2021). Moreover, Htwe et al. (2009) revealed that *GmATG8c* and *GmATG8i* expression was enhanced in leaves but declined during seed maturation, suggesting that enhanced nitrogen-use efficiency and synthesis of storage proteins in growing seeds might signal the leaf to trigger autophagy and senescence. Subsequently, they showed that the altered source-sink balance by de-podding, impacted the expression of ATGs (including, *GmATG8c*, *GmATG8i*, *GmATG4* and *GmATG9*) leading to delayed leaf senescence and high nitrogen content in soybean (Htwe et al., 2011). While the specific ATG genes and regulatory mechanisms may vary between dicots and cereals, the fundamental role of autophagy in nutrient remobilization is conserved. Both plant groups depend on autophagy to recycle nutrients during age- and stress-induced senescence. This process guarantees the efficient use of internal nutrient stores and enables plants to adapt and survive in increasingly challenging environments.

3.2. The role of Senescence Associated Gene 12 may differ between major plant groups

Marker genes are extremely useful for identifying pathways and processes that are activated in response to developmental or environmental cues. *Senescence Associated Gene 12* (*SAG12*) of Arabidopsis was first described by Lohman et al. (1994), encodes a papain-like cysteine protease and is perhaps the most used and reliable marker for age-induced senescence (Desclos et al., 2009; Guo et al., 2004; Lohman et al., 1994; Noh and Amasino, 1999; Poret et al., 2016; Safavi-Rizi et al.,

2018). Expression is very low in green tissue but increases dramatically upon induction of senescence (Noh and Amasino, 1999). Nevertheless, its functional role during senescence is still shrouded in some mystery as the knock-out mutant of Arabidopsis did not show any senescence phenotype (Otegui et al., 2005). Recently, James et al. (2018) showed this protease is required for optimal seed yield when grown under nitrogen limiting conditions. Later they showed a function in nitrogen remobilisation for SAG12 in roots (James et al., 2019), which means its role in senescing leaves is still unclear. The SAG12 protein accumulates in senescence-associated vacuoles, which are shown to degrade chloroplast proteins, mainly glutamine synthase and Rubisco (Otegui et al., 2005). Surprisingly, the two rice structural homologues of Arabidopsis SAG12, *OsSAG12-1* and *OsSAG12-2*, are negative regulators of senescence and cell death (Singh et al., 2013; Singh et al., 2016). Still, the expression of SAG12 orthologs in barley (Jukanti et al., 2008; Parrott et al., 2010; Hollmann et al., 2014) and wheat (Gregersen and Holm, 2007; Ruuska et al., 2008) was upregulated in senescing flag leaves during nitrogen remobilisation. Thus, SAG12 may have opposing roles in dicots and cereals and further study is encouraged to clarify the role of SAG12 in nitrogen remobilisation during age-induced leaf senescence.

4. Harnessing natural variation in senescence signalling pathways to improve crop yield

In nature, evolutionary pressures optimise senescence regulation to maximise survival. However, in agriculture, natural processes are actively managed to optimise yield and the ideal senescence regulation for maximum yield may not be the same as the ideal regulation to survive in nature. Thus, modifying senescence signalling pathways may result in improved yield. However, the hormone and ROS signalling pathways described above regulate multiple aspects of plant development and are intrinsically integrated in stress responses. So, how have breeding programmes harnessed natural variation that optimises senescence under field conditions? It is often considered that delaying senescence can increase crop yield because carbohydrates can be captured for longer. Delayed senescence - also known as "stay-green" - phenotypes have been shown to carry a variety of positive effects,

including accelerated root development and carbon accumulation, reducing the time between anthesis and silking, and increased chlorophyll content (Peng et al., 2008; Borell et al., 2001; Gregersen et al., 2013; Thomas and Ougham, 2014). Dozens of stay-green genes have been identified and some of these regulate chlorophyll levels (Kusaba et al., 2007). However, their application in breeding programmes is less established. A proposed haplotype approach, whereby genome sequence information is combined with phenotypic information to predict breeding outcomes, has recently indicated a possibility of harnessing natural allelic variants in diverse accessions for developing superior varieties (Bevan et al., 2017). A summary of haplotype analysis for leaf senescence in some key genes is presented in Table 1.

The well-known pea green cotyledon *i* mutant, used by Gregor Mendel, has a mutation in the *STAY-GREEN* (*SGR*) gene and this results in a defective chlorophyll break-down pathway and a cosmetic stay-green phenotype (Aubry et al., 2008). Nevertheless, Shin et al. (2020) found that polymorphisms in the promoter of the *SGR* homolog in rice, *OsSGR*, were significantly associated with chlorophyll content in rice flag leaf, and four of the *OsSGR* haplotypes displayed delayed senescence and increased yield. Notably, introgression of japonica *OsSGR* alleles in the indica background resulted in increased grain filling rate and higher yield. Moreover, in wheat, the superior haplotypes in *TaSGR* genes increased the chlorophyll content as well as grain yield. Because knock-down of *TaSGR* delayed leaf senescence without yield benefits, the occurrence of allelic variation in the promoter of *TaSGR* likely resulted in increased yield (Islam et al., 2022). *SGR* positively controls Chl degradation via interaction with chlorophyll catabolic enzymes and light harvesting complex II proteins (Sakuraba et al., 2015), and it has been shown that rice *sgr* mutants often exhibit a stay-green phenotype due to chl-protein complex and thylakoid membrane structure stability (Jiang et al., 2007). This indicates that in cereals changes in *SGR* expression may positively affect yield, while its knock-out only causes cosmetic changes. It will be important to understand the mechanism of this and interesting to see if the same occurs in dicots.

In higher plants, multiple enzymes and steps taking place in plastids are required for catabolising leaf Chl (reviewed by Kuai et al., 2017). NON-YELLOW COLORING 1 (NYC1) and NYC1-like (NOL) are key

Table 1
Natural variation associated with leaf senescence.

Species	Genes	No. of haplotypes	Effects of allelic variation	Functional description	Reference
Rice	<i>OsPME1</i> , <i>OsTSD2</i>	9	Elevated JA-Ile and JA-Ala contents	i. Protein phosphatase methyltransferase 1	Fang et al. (2016)
	<i>NOL</i>	6	Significant association with chlorophyll content (CC) and chlorophyll accumulation (ACC)	ii. Putative methyltransferase chloroplast-localised short chain dehydrogenase/reductase	Zhao et al. (2019)
	<i>SSG4</i> , <i>CHR729</i> ,	3	High chlorophyll content	iii. Amyloplast membrane protein SUBSTANDARD STARCH GRAIN4	Islam et al. (2022)
	<i>OsFRDL1</i> , <i>OsSG1</i>	8	Variation in the promoter region influence leaf senescence, life span, and life cycle	iv. Chromodomain-helicase/ATPase-DNA-binding domain (CHD) family	
	<i>OsSGR</i>			v. Citrate transporter family	
Wheat	<i>TaPPH-7A-1</i>	2	High chlorophyll content at grain filling stage	vi. Glutamine synthetase (cytosolic GS1)	
	<i>TaSGR-5A</i>	4	High spikelet number per spike, grain per spike, thousand-grain weight, yield per plant and chlorophyll content with reduced transcription of <i>TaSGR-5A</i>	vii. Oxidoreductase, short chain dehydrogenase/reductase family domain containing protein	Wang et al. (2019)
	<i>TaSGR-5B</i>	3	High chlorophyll content and normalised difference vegetation index	viii. Putative signal recognition particle 54 kDa protein	Islam et al. (2022)
<i>Brassica napus</i>	<i>BnNYE1-A01</i>	3	High chlorophyll level	ix. chlorophyll-degrading Mg ⁺ + -dechelataze Pheophytin pheophorbide hydrolase (Pheophytinase, PPH)	Qian et al. (2016)
Arabidopsis	<i>GVS1</i>	26	Highly associated with leaf senescence response	Mg-dechelataze	Lyu et al., 2018

enzymes involved in Chl b degradation and reports have indicated that NYC1 loss-of-function limited Chl degradation in ageing leaves and resulted in cosmetic stay-green in Arabidopsis (Horie et al., 2009), rye grass (Xu et al., 2019), and rice (Sato et al., 2009). In contrast, the *atnol* mutant in Arabidopsis showed no stay-green phenotype, while its counterpart *osnol* mutant in rice exhibited a cosmetic stay-green phenotype, suggesting a possible existence of genetic diversity in how NOL functions in Arabidopsis and rice (Kusaba et al., 2007; Sato et al., 2009). Moreover, darkness, ABA and JA treatment elevated the expression of NYC1 (Kusaba et al., 2007) and knock-down of *LpNOL* in perennial ryegrass caused a functional stay-green phenotype, at least partly due to altered ABA biosynthesis and signalling (Yu et al., 2021a, 2021b). The natural variants found in *NOL*, *NYC1*, *SSG4*, *CHR729*, *OsFRDL1*, and *YGL138* (*t*) increased chlorophyll content and displayed stay-green phenotypes and it was revealed that non-synonymous SNPs within these genes represent possible functional sites. Phylogenetic analysis and signature identification indicated that genes regulating chlorophyll content and stay-green phenotype were positively selected for during crop domestication in rice (Zhao et al., 2019). More recently, Wang et al. (2023) found that senescence-associated genes were under intense selection during domestication of sorghum, based on haplotype analysis. Among the SAGs, *Sobic.004G299500*, *Sobic.004G299600*, and *Sobic.004G299700* homologues of Arabidopsis *ATYSL3* and *OsYSL15* are involved in leaf senescence progression. These genes encode iron (III)-deoxymugineic acid transporters and have been reported to modulate leaf senescence processes (Inoue et al., 2009; Kumar et al., 2017). In Arabidopsis, a SNP variant in *Genetic Variant for leaf Senescence1* (*GVS1*) showed significant correlation with senescence phenotypes. Two key haplotypes displayed distinct leaf senescence phenotypes and loss-of-function of *gvs1* alleles resulted in delayed senescence and increased sensitivity to oxidative stress, indicating that *GVS1* controls responses to developmental and environmental cues (Lyu et al., 2019). Unsurprisingly, breeding for delayed senescence has obtained lines that contain increased chlorophyll content. Perhaps surprisingly, natural variants in genes chiefly involved in chlorophyll degradation can cause functional stay-green phenotypes. Some of the genes selected for control chlorophyll content and degradation, while the function of others is unclear. A relationship with oxidative stress and ABA signalling suggests that some natural variants work to integrate age and environmental signals. Since these natural variants have stood the test of time in nature, they could potentially be critical in breeding efforts to obtain optimal yield in response to challenging environmental conditions. It will be essential to understand how these variants function on a molecular level in order to develop climate-change resilient crops. Considering the importance of genome variation for leaf senescence regulation, further studies should explore natural allelic variation present in senescence genes to improve yield.

5. Concluding remarks

The recent past has seen enormous advances in the understanding of leaf senescence. The regulation of onset and progression of leaf senescence is shown to be affected by internal and external cues in both dicots and cereals and to a large extent; similar cellular processes seem to be evolved. This is especially true for major signalling pathways involving phytohormones and ROS and key TFs: ABA signalling is an important modulator of age and stress-induced leaf senescence, the TF ORE1 regulates leaf senescence through ABA signalling (Mao et al., 2017; Sakuraba et al., 2020; La et al., 2022) and EIN2 and EIN3 are main regulators of leaf senescence in ET signalling pathways. However, the exact mechanisms by which EIN2 and EIN3 regulate leaf senescence in cereals still remain elusive. While ABA interacts with ET to induce leaf senescence in dicots, ABA in cereals is shown to promote senescence via ABA core signalling in an ET-independent manner. ROS are general inducers of leaf senescence in both plant groups and NADPH oxidase enzymes are a main source of ROS biosynthesis. However, it is unclear

whether similar ROS regulatory mechanisms exist in ROS and ABA signalling during stress-induced senescence. Thus, while main regulatory pathways are conserved, it is largely unclear how downstream regulatory pathways drive senescence in dicots and cereals, or even within these groups (Figs. 1 and 2).

Given that the manipulation of senescence regulation can contribute considerably to sustainable food production, we suggest that major advances in insight, and consequently potential for production gain, can be found in studying natural variation in the regulation of stress-induced senescence. We consider that natural variants have evolved to allow optimal survival under varied environmental conditions. Because the major hormone and ROS signalling pathways can affect a wide range of developmental programmes, we further think that research of these natural variants may identify more downstream signalling pathways. Given the similarities in senescence regulation across all plants, discoveries made in one species may be widely applicable to others. Then, gene editing technology may efficiently allow the development of stay-green crops with superior stress tolerance and yield properties. Here, integrating phenome data with other “omics” resources should give a holistic view of the connection existing between genetic and external factors to influencing the onset, progression, and termination of senescence.

CRedit authorship contribution statement

All authors contributed to the Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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