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REVIEW

Stay-green trait and its potential for durum wheat breeding under water and heat stress conditions: A review

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ABSTRACT

Durum wheat (*Triticum turgidum* ssp. *durum*) is the second-most cultivated species of wheat worldwide, being mostly used for the production of semolina for pasta products. Drought and high temperatures can seriously affect the crop by accelerating senescence and decreasing yield and grain quality, thereby posing risks to food security on a global scale. Certain wheat genotypes exhibit a stay-green trait that enables plants to delay senescence and maintain photosynthetic activity longer. Thus, stay-green plants have an extended grain filling stage, which results in higher yields. Key genes associated with the stay-green trait, such as *SGR1* and *SGR2*, help delay chlorophyll degradation, extending photosynthesis. Additionally, microRNAs (miRNAs) like miR164 and miR319 play a key role in regulating senescence and stress responses in plants. Technologies such as RNA sequencing (RNA-Seq) have been valuable tools for identifying differentially expressed genes associated with photosynthesis and stress resilience, providing valuable information for the development of more resilient durum and bread wheat varieties in wheat breeding programs. The present review provides insights into the advances and importance of the molecular and metabolic characterization of the stay-green trait in durum wheat and aims to get a better understanding of the effect of mRNAs and miRNAs on this trait under water and heat stress conditions.

Key words: Drought, heat, QTL, stay-green, stress resilient wheat.

INTRODUCTION

Durum wheat (*Triticum turgidum* ssp. durum) is an important source of food, feed, and industrial raw materials (Tidiane Sall et al., 2019). Globally, it is grown on around 222 million hectares, with a production of 789 million tons in the 2022-2023 growing season (FAO, 2023). Its protein content and high-quality gluten make it the preferred choice for producing premium pasta and other products such as couscous, freekeh, and bread (Mastrangelo and Cattivelli, 2021; Saini et al., 2023).

Drought and heat stress are the main limiting factors for wheat production worldwide (Beres et al., 2020). In fact, the individual and combined effects of these abiotic factors negatively affect growth, grain yield, and bread-making quality. Unlike intermittent drought, which can occur at any time during the growing season, terminal drought occurs when plants suffer a lack of water during later stages of the phenological cycle, particularly during grain filling or maturation, when water demand is crucial for mobilizing carbohydrates and other nutrients to storage organs (Araus et al., 2008). This leads to an accelerated senescence, thus critically shortening the grain filling stage (Djanaguiraman et al., 2023). When both drought and heat stress occur simultaneously, plant height, number of tillers, ear length, number of kernels, and grain weight are reduced, decreasing biomass production and yield (Sattar et al., 2020).

Due to climate change, wheat yield is projected to decline between 3.5% and 12.9% between 2037 and 2065 (You et al., 2009), while winter wheat yields are likely to decrease by 20%-30% by 2050 (Beres et al., 2020). As feeding the growing population will require increasing food production by at least 2.4% per year by 2050

(Ray et al., 2013), the projected reduction in wheat production and the increasing demand for this cereal may pose serious risks to global food security.

Some plants possess the ability to prolong the period during which their leaves remain green and photosynthetically active, a characteristic known as stay-green (Kusaba et al., 2013; Thomas and Ougham, 2014; Munaiz et al., 2020). This trait is present in wheat (Ren et al., 2022), rice (Singh et al., 2023), tomato (Cui et al., 2024), and soybean (Fang et al., 2014), among other species. In durum wheat, some genotypes can delay senescence under drought and heat stress conditions, prolonging the presence of chlorophyll and photosynthetic activity during grain filling despite adverse abiotic conditions. Thus, the stay-green trait can help increase crop production, particularly under water-limited conditions (Kumar et al., 2022; Ali et al., 2023).

Studies on this trait have revealed that slow-senescing genotypes achieved significantly higher yields compared to those of fast-senescence. Furthermore, vegetation index, chlorophyll index, maximum photochemical efficiency, time to heading, anthesis and maturity, grain weight per spike, 100-grain weight, and biomass content were observed to be positively correlated with grain yield (Soni and Munjal, 2023). Under temperatures above 35 °C, stay-green genotypes exhibit increased stability of thylakoid membranes and improved photosystem II efficiency, resulting in a 30% increase in C assimilation during heat stress (Wang et al., 2021a).

In bread wheat, genes associated with stay-green (*SGR1* and *SGR2*) have been identified. These genes increase their expression during periods of high temperatures and cause a delay in leaf senescence, resulting in higher grain yields (Christopher et al., 2016). On the other hand, it has been determined that microRNAs (miRNAs), which are small non-coding ribonucleic acid (RNA) molecules, play a crucial role in modulating the stay-green trait (Schommer et al., 2008) and in post-transcriptional regulation (Salamon et al., 2021) since they can repress transcription factors and regulate senescence-associated genes. In this sense, some miRNAs have been identified as leaf senescence regulators by controlling transcription factors (Wu et al., 2016).

Transcriptomic analysis through RNA sequencing (RNA-Seq) has been essential for understanding the stay-green trait in durum wheat (Zheng et al., 2023). These technologies enable a comprehensive view of gene expression, providing detailed information on transcriptional changes that occur in response to water and heat stress (Kido et al., 2016). In fact, transcriptomics has allowed the identification of differentially expressed genes associated with photosynthesis, carbohydrate metabolism, and stress response, which is essential for the development of wheat varieties with high productivity under adverse conditions (Bhoite et al., 2021).

This review provides insights into the advances and importance of the molecular and metabolic characterization of the stay-green trait in durum wheat and aims to better understand the effect of mRNAs and miRNAs on this trait under water and heat stress conditions.

PLANT SENESCENCE AND STAY-GREEN PHENOTYPE

Chlorophyll content (Guo et al., 2008), flag leaf senescence (Barakat et al., 2013), and cell membrane stability have been recognized as key indicators of drought tolerance (Elshafei et al., 2013). Chlorophyll loss is the main visible symptom of leaf senescence (Thomas and Ougham, 2014), while abiotic stress conditions such as high temperatures accelerate senescence and decrease the supply of assimilates to the grain, affecting yield. In this context, delayed leaf senescence will increase photosynthesis duration and, ultimately, biomass and yield (Richards, 2000; Aberkane et al., 2021). Stay-green plants can retain the green tissue of their leaves from flowering to physiological maturity instead of senescing, which will positively impact grain filling. Therefore, late leaf senescence can enhance crop performance by allowing sustained photosynthesis during the late grain filling stage, resulting in a positive impact on crop yield (Guo et al., 2021).

The onset of senescence triggers the dismantling of chloroplasts, resulting in a decline in photosynthesis (Thomas and Ougham, 2014). In this sense, a distinctive attribute of leaf senescence is chlorophyll degradation. This process is facilitated by six chloroplast-localized enzymes (CCEs): Pheophytin pheophorbide hydrolase (PPH), non-yellow dye 1 (NYC1), NYC1-like (NOL), chlorophyll *a* reductase (HCAR), pheophorbide *a* oxygenase (PAO), and red chlorophyll catabolite reductase (RCCR) (Hörtensteiner and Kräutler, 2011; Kusaba et al., 2013). The stay-green trait is controlled by the stay-green gene (SGR), which encodes proteins that act as key regulators of chlorophyll degradation (Ren et al., 2024).

Several studies have reported that leaves that stay green continue generating energy, promoting growth and development, especially during critical stages like grain filling in cereal crops, which can lead to increased yields (Kusaba et al., 2013; Chibane et al., 2021). Additionally, plants exhibiting this trait demonstrate improved tolerance to environmental stresses, such as drought and high temperatures (Thomas and Ougham, 2014; Kaur and Sarlach, 2020), as they can maintain photosynthetic activity when other plants begin to senesce.

Stay-green mutations are classified as either functional or non-functional (cosmetic) (Archana et al., 2023). Plants possess a functional stay-green phenotype if they are able to photosynthesize for a longer period, i.e., grain filling period is prolonged and yield increases (Ren et al., 2022).

STAY-GREEN AND ABIOTIC STRESS

Drought and heat stress are important abiotic factors that limit plant productivity (Bhunia et al., 2020). In wheat, these conditions can cause yield losses of up to 86% and 69%, respectively (Yang et al., 2021). Globally, most wheat-growing regions experience drought and heat stress during the critical stages of anthesis and grain filling. Their combined effects during both phases can lead to even greater reductions in crop yield (Allahverdiyev and Huseynova, 2015).

Previous research has revealed that the stay-green trait can help mitigate drought-induced premature senescence (Xu et al., 2000; Ghatak et al., 2021). Furthermore, there is evidence that this trait not only improves tolerance to abiotic stress but also contributes to greater nutrient use efficiency and improves grain quality (Gregersen et al., 2013). Therefore, stay-green is a key criterion in breeding programs to develop wheat varieties more resilient to adverse climatic conditions (Thomas and Smart, 1993; Christopher et al., 2016). In addition, the combined use of the stay-green trait with appropriate agronomic practices can enhance its beneficial effect by delaying senescence and improving photosynthetic efficiency under stress conditions (Nawaz et al., 2013). These practices have proven to be effective in improving crop resilience to adverse conditions (Nawaz et al., 2013).

In wheat, specific genes associated with the stay-green trait, such as those regulating chlorophyll degradation and leaf senescence, have been identified (Sánchez-Bragado et al., 2016). Genetic manipulation of these genes has improved drought and heat tolerance, thereby increasing crop yield and yield stability (Zhang et al., 2024). On the other hand, genes associated with stay-green could be used for molecular marker-assisted breeding. This is an effective tool for integrating different traits into new wheat varieties, potentially accelerating the breeding process and allowing for a more precise selection of desired genotypes (Edema and Amoding, 2015), thus contributing to the development of more resistant and productive crops. Several genes (or QTL) associated with stay-green have been reported in rice, soybean, and other crops (Jiang et al., 2004; Nakano et al., 2014; Wang et al., 2018a).

MOLECULAR CHARACTERIZATION OF THE STAY-GREEN PHENOTYPE

Gene expression and regulation

Gene expression is a fundamental cell process that enables the utilization of the information encoded in DNA to produce functional molecules, primarily proteins. The process begins in the cell nucleus with transcription, where the DNA sequence of a gene is transcribed into a messenger RNA (mRNA) molecule. This mRNA is then processed and transported to the cytoplasm, where translation occurs. During translation, the information in the mRNA serves as a template for assembling a chain of amino acids, ultimately resulting in the formation of a protein (Lodish et al., 2016).

Regulation of gene expression is essential for cellular function and takes place at: 1) The transcriptional level, transcription factors and epigenetic modifications dictate which genes are activated or silenced, while post-transcriptional mechanisms, such as alternative splicing and mRNA stability regulation, further influence expression; and 2) the translational level, regulation can occur through the control of translation initiation and protein stability, ensuring that proteins are produced as needed for cell functioning (Lodish et al., 2016). Additionally, gene expression is crucial to determining cellular phenotype and enabling organisms to adapt to environmental changes. This dynamic process varies based on cell type, developmental stage, and environmental conditions. Advances in techniques such as quantitative PCR, microarrays, and RNA sequencing have revolutionized the study of gene expression, allowing researchers to analyze the activity of thousands of genes simultaneously and gain deeper insights into the complex biological processes occurring within cells (Alberts et al., 2015).

Stress tolerance encompasses phenotypic plasticity, physiological adaptations, genetic regulation, epigenetic modifications, and the induced production of protective metabolites. Furthermore, recent studies have increasingly addressed the phenomenon of "stress memory" in plants, offering new avenues for enhancing stress resilience in different crop species (Racette et al., 2020; Liu et al., 2021). In response to abiotic stress signals and developmental cues, epigenetic modifications, including DNA methylation, histone modification, chromatin remodeling, and the activity of small noncoding RNAs can rapidly trigger dynamic changes that influence gene expression at the post-transcriptional level. These effects can be short-term, long-lasting, or even transgenerational (Lämke and Bäurle, 2017).

Identification of QTLs associated with stay-green in wheat

Quantitative trait loci (QTL) are specific regions of the genome associated with variations in a quantitative trait. They do not represent a single gene but a chromosomal location where one or several genes affecting the expression of a given trait are located (Lynch and Walsh, 1998). In recent years, QTLs have become a valuable tool for dissecting the genetic basis of crop performance under stress as they allow the association of genomic information with phenotypic measurements (Shi et al., 2017). Identifying QTLs for the stay-green trait is a key step in understanding the genetics and physiology of this complex phenotype (Christopher et al., 2021).

Currently, multiple QTLs related to the stay-green trait have been identified on several chromosomes. For example, significant QTLs located on wheat chromosomes 2B, 3B, 4A, 6A, 6B, and 7A are associated with chlorophyll retention, green leaf area duration, and yield stability under heat and drought stress conditions (Simmonds et al., 2014; Zhang et al., 2021a; Luo et al., 2021). Similarly, QTLs affecting the rate of chlorophyll loss and other physiological indicators, such as chlorophyll content and normalized difference vegetation index (NDVI), which are used to assess plant health and vigor, have been mapped in wheat populations (Schmidt et al., 2020). For example, QTL located on wheat chromosome 6B have been associated with reduced chlorophyll loss and improved heat and drought tolerance (Schmidt et al., 2020), while QTLs on chromosomes 6A and 7A relate to the duration of active photosynthesis and stability of thylakoid membranes under high temperature conditions (Liu et al., 2014; Simmonds et al., 2014). Currently, statistical tools such as BioMercator and Meta-QTL have simplified the meta-analysis of QTLs identified in several studies, employing specific algorithms for the accurate estimation and recalculation of the genomic position of a given set of QTLs (Wang et al., 2014).

Identification and characterization of genes associated with stay-green in wheat

Several molecular techniques are used to identify the genes responsible for stay-green in crops. Gene expression analyses, including microarrays and RNA sequencing (RNA-Seq), allow the detection of genes that are differentially expressed under diverse conditions. These methods help identify candidate genes based on their relative expression in both controlled and stressful environments (Gao et al., 2020). The RNA-Seq (Figure 1) offers two significant advantages: i) It provides high-resolution and sensitive quantification as well as comparison of gene expression across different conditions; and ii) it can identify transcripts with varying expression levels, splice variants, and novel transcripts (Wang et al., 2009). Furthermore, although gene expression microarrays have some limitations, they remain valuable for simultaneously quantifying thousands of known genes, thus facilitating comparative gene expression studies (Shi et al., 2006).

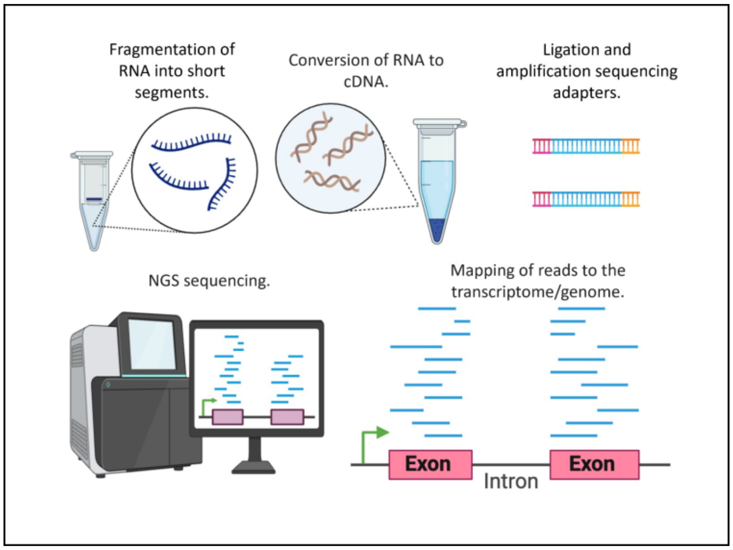

Figure 1. RNA sequencing process using next-generation sequencing (NGS). First, RNA is fragmented into small segments, which are converted into complementary DNA (cDNA) using reverse transcriptase. Then, sequencing adapters are added to the cDNA for amplification. This adapted material is sequenced using specialized equipment that determines the nucleotide sequence. Finally, the obtained readings are mapped against a reference transcriptome or genome, allowing for the identification of exons and introns and quantification of gene expression (modified from Unamba et al., 2015).

Next-generation sequencing (NGS) facilitates massive and parallel sequencing, offering deep coverage and high resolution of the genome, which has enabled the precise identification of genetic variants (Satam et al., 2023). This technique has been crucial to mapping loci associated with important agronomic traits, such as the stay-green phenotype (Goodwin et al., 2016). In turn, the use of PCR and qPCR is essential for the validation and quantification of candidate genes. Real-time PCR (qPCR) enables highly accurate measurement of gene expression, facilitating the validation of genes identified through sequencing (Bustin et al., 2009). Additionally, genotyping by sequencing (GBS) combines high-throughput sequencing with the targeted selection of specific genomic fragments, thus constituting a powerful tool in genome-wide association studies (GWAS) (Metzker, 2010; Elshire et al., 2011). In addition, GWAS identifies loci associated with traits, while transcriptomics functionally validates candidate genes by assessing their differential expression under stress conditions. This integrated approach enhances the understanding of the regulatory networks and biological processes underlying stress resistance (Zhang et al., 2019).

MiRNAs, GENE REGULATION, AND STAY-GREEN

Although miRNAs (Figure 2) are typically about 22 nucleotides in length, they play a crucial role in regulating post-transcriptional gene expression in both plants and animals (Ambros et al., 2003). These small regulatory RNAs influence a diverse array of biological processes, including development, stress response, and senescence (Ruiz-Ferrer and Voinnet, 2009; Sarwat et al., 2013; Pagliarani and Gambino, 2019).

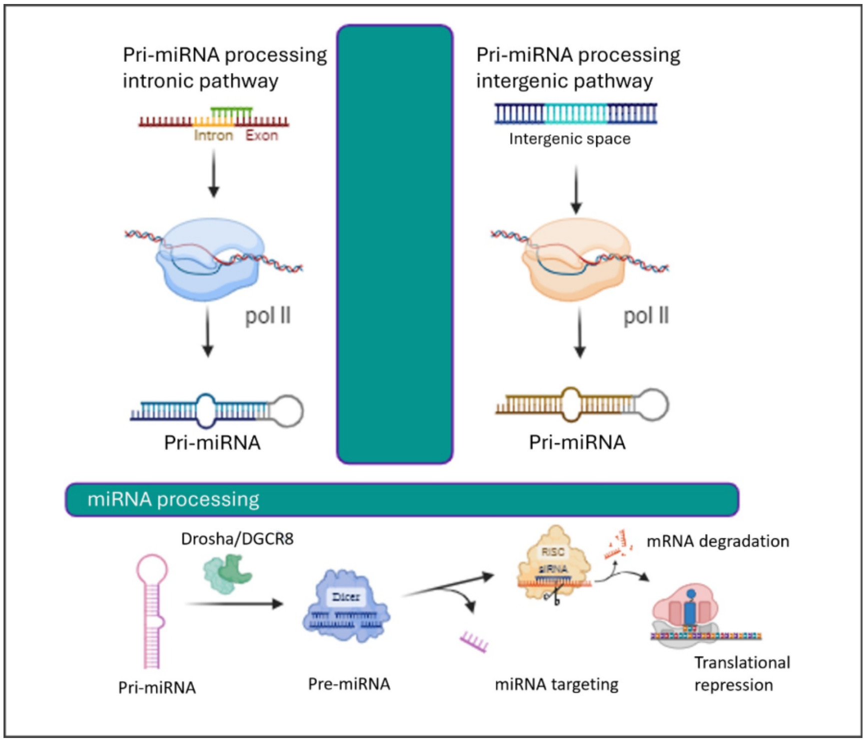

Figure 2. miRNA maturation process, from pri-miRNA to functional miRNA (modified from Suleiman et al., 2024).

Rapid regulation of stress-responsive gene expression by miRNA is particularly advantageous in abiotic stress response. These small regulators are recognized to play a key role in plant survival under environmental stress. Small non-coding RNAs (sncRNAs) are diverse in both their origins and functions. Non-coding RNAs comprise a diverse group of transcripts, including housekeeping ncRNAs: Ribosomal RNAs, transfer RNAs, small nuclear RNAs, small nucleolar RNAs, and many regulatory ncRNAs (Cech and Steitz, 2014). The sncRNAs in plants are diverse and include miRNAs, piwiRNAs (piRNAs), small nuclear RNAs (snRNAs), small nucleolar RNAs (snoRNAs), and long ncRNAs. All these sncRNAs have some common features, including their biogenesis (Mallory and Vaucheret, 2006; Pattanayak et al., 2013). The application of sequencing techniques, such as NGS and bioinformatics analysis, has enhanced the identification of specific miRNAs involved in trait regulation in plants (Unamba et al., 2015).

The miRNAs are not always related to the response to abiotic stresses, such as drought or water deficit, and their function is not limited exclusively to these processes. In fact, miRNAs are also involved in a wide range of physiological regulatory mechanisms, including defense against pathogens, regulation of plant development, response to oxidative stress, and adaptation to adverse environmental conditions (Pagano et al., 2021; Luo et al., 2024).

In wheat, several miRNAs with different expression levels have been identified in stay-green plants (Wei et al., 2009; Wu et al., 2016). For example, the miR164 and miR319 play an important role in regulating genes linked to senescence and stress responses, contributing to the regulation of leaf senescence and the maintenance of photosynthetic functionality (Li et al., 2013; Ma et al., 2022). Specifically, miR164 negatively regulates the expression of NAC genes (*NAM*, *ATAF1/2*, *CUC2*), a family of transcription factors involved in the regulation of senescence and stress responses in plants, which may delay senescence and help maintain photosynthetic functionality in plants that remain green (Kim et al., 2009). Similarly, miR319 regulates TCP genes (TEOSINTE BRANCHED1, CYCLOIDEA, and PROLIFERATING CELL FACTOR), a family of transcription factors that control cell division and expansion, which are essential processes for maintaining leaf vigor under stress conditions (Schommer et al., 2008). By downregulating TCP genes, miR319 modulates growth and stress response. Furthermore, miR398 enhances the expression of genes encoding the enzyme superoxide dismutase

(SOD), a key enzyme in the protection against oxidative damage induced by environmental stress. Furthermore, the upregulation of miR398 may help plants stay green by managing oxidative damage more effectively (Jagadeeswaran et al., 2009).

STAY-GREEN TRAIT AND DURUM WHEAT BREEDING

Plant breeders recognize that leaf senescence can improve wheat yield by remobilizing nutrients from the leaves. Furthermore, a recent study conducted by Soni and Munjal (2023) has confirmed that the stay-green trait can serve as a strategy to further increase wheat yield and tolerance to abiotic stresses. The stay-green phenotype in durum wheat is characterized by prolonged chlorophyll retention and continued photosynthetic activity during grain maturation, reflecting a complex regulation of multiple gene expressions. Genes associated with leaf senescence encode enzymes responsible for chlorophyll degradation, such as chlorophyllases, and typically exhibit reduced or delayed expression. In contrast, genes involved in the biosynthesis and signaling of cytokinin hormones that help delay senescence may demonstrate increased expression or prolonged activity (Zhang et al., 2021b).

The expression of genes associated with N metabolism is also essential for the stay-green trait. In senescence-delaying durum wheat varieties, genes that encode key enzymes involved in N assimilation and remobilization, such as glutamine synthase, may exhibit altered expression patterns that promote N retention in leaves (Akhtar et al., 2019). Additionally, genes involved in responding to oxidative stress and protecting against cellular damage are often overexpressed in stay-green plants, including those encoding antioxidant enzymes like superoxide dismutase and catalase (Wang et al., 2021b). The regulation of gene expression in durum wheat that stays green is orchestrated by specific transcription factors, which in turn are tightly regulated and control the activation or repression of gene sets related to senescence and the maintenance of photosynthetic activity (Borrell et al., 2014).

Transcriptomic analysis has facilitated the identification of differentially expressed genes in stay-green plants under stress, revealing an overexpression of genes associated with photosynthesis, nutrient transport, and stress defense (Distelfeld et al., 2014). Additionally, gene co-expression network analysis has identified clusters of genes that collaborate to sustain photosynthetic functionality and delay senescence, thereby contributing to a better understanding of the key regulatory pathways involved in this trait (Wang et al., 2018b). Validation of candidate genes identified through genome-wide association studies (GWAS) is commonly conducted using transcriptomic analysis. The differential expression of these genes under stress conditions confirms their role in mediating the stay-green trait, providing additional evidence for their functional significance (Zhang et al., 2019).

In durum wheat, RNA-Seq was used to compare gene expression in leaves of genotypes exhibiting the stay-green trait with those lacking it, which were grown under water stress conditions, identifying stress response genes that were significantly overexpressed in stay-green plants (Distelfeld et al., 2014). In addition, candidate genes associated with the stay-green trait were identified and validated by integrating GWAS and transcriptomic data. Additionally, RNA-Seq facilitated the analysis of the expression of these genes under heat stress, thereby confirming their role in regulating senescence and photosynthesis (Zhang et al., 2019).

CONCLUSIONS

The productivity of wheat is vulnerable to environmental changes. Therefore, for breeding purposes, it is essential to identify and integrate traits that provide this crop with greater resilience to such conditions.

Functional stay-green crops extend photosynthesis during the grain filling stage, leading to enhanced productivity and yield stability under water and heat stress. The capacity to delay senescence and maintain photosynthetic activity is essential for optimizing crop production in Mediterranean regions, where climate change poses significant challenges to yield. Molecular characterization of the stay-green trait is critical to improving durum wheat performance under such conditions. The use of molecular technologies, including transcriptomic analysis through RNA-Seq, has enabled the precise identification of genes and miRNAs—such as miR164 and miR319—that play a direct role in regulating senescence and responding to environmental stress.

These molecular tools have facilitated a better understanding of the stay-green regulation and the integration of this trait in crop breeding programs, which could contribute to accelerating the development of more stress-tolerant varieties. Furthermore, studies on miRNA provide new insights into post-transcriptional regulation, underscoring the importance of these small non-coding RNAs in modulating key processes for plant adaptation. Their ability to regulate the expression of genes that control chlorophyll degradation and stress response presents an innovative approach to enhance not only drought and heat tolerance but also nutrient use efficiency and crop yield.

In the future, the integration of molecular tools such as marker-assisted selection with a comprehensive approach that considers both the genome and the transcriptome will enable progress toward sustainable and efficient agriculture. This knowledge will not only improve durum wheat productivity under adverse conditions but will also contribute to global food security through the development of crops that are better adapted to the challenges of climate change.

Author contributions

Manuscript writing and revision: M.V., J.Ch. Preparation, completion of the main concept, and editing: D.C., M.G. Manuscript revision: I.M. The submitted version of the article was approved by all authors who contributed to it.

References

Aberkane, H., Belkadi, B., Kehel, Z., Filali-Maltouf, A., Tahir, I.S., Meheesi, S., et al. 2021. Evaluation of drought and heat tolerance of durum wheat lines derived from interspecific crosses using physiological parameters and stress indices. Agronomy 11:695. doi:10.3390/agronomy11040695.

Akhtar, S., Ahmad, A., Jha, S.R., Ahmad, J. 2019. Regulation of leaf senescence by macromolecule degradation and hormones. p. 61-97. In Akhtar, S., Hayat, S. (eds.) Senescence signalling and control in plants. Academic Press, London, UK.

Alberts, B., Bray, D., Hopkin, K., Johnson, A.D., Lewis, J., Raff, M., et al. (eds.) 2015. How genes and genomes evolve. p. 289-343 In Essential cell biology. 4th ed. Garland Science, Taylor & Francis Group, New York, USA.

Ali, A., Ullah, Z., Sher, H., Abbas, Z., Rasheed, A. 2023. Water stress effects on stay green and chlorophyll fluorescence with focus on yield characteristics of diverse bread wheats. Planta 257:104. doi:10.1007/s00425-023-04140-0.

Allahverdiyev, T.I., Huseynova, I.M. 2015. Effect of drought stress on some physiological parameters, yield, yield components of durum (*Triticum durum* Desf.) and bread (*Triticum aestivum* L.) wheat genotypes. Ekin Journal of Crop Breeding and Genetics 1:50-62.

Ambros, V., Bartel, B., Bartel, D.P., Burge, C.B., Carrington, J.C., Chen, X., et al. 2003. A uniform system for microRNA annotation. RNA 9:277-279. doi:10.1261/rna.2183803.

Araus, J.L., Slafer, G.A., Royo, C., Serret, M.D. 2008. Breeding for yield potential and stress adaptation in cereals. Critical Reviews in Plant Sciences 27:377-412. doi:10.1080/07352680802467736.

Archana, R., Vinod, K.K., Krishnan, S.G., Vadhana, E.D.C., Bhowmick, P.K., Singh, V.J., et al. 2023. Quantitative trait loci for stay-greenness and agronomic traits provide new insights into chlorophyll homeostasis and nitrogen use in rice. Plant Breeding 142:312-326. doi:10.1111/pbr.13086.

Barakat, M.N., Wahba, L.E., Milad, S.I. 2013. Molecular mapping of QTLs for wheat flag leaf senescence under water-stress. Biologia Plantarum 57:79-84. doi:10.1007/s10535-012-0138-7.

Beres, B.L., Rahmani, E., Clarke, J.M., Grassini, P., Pozniak, C.J., Geddes, C.M., et al. 2020. A systematic review of durum wheat: enhancing production systems by exploring genotype, environment, and management (G×E×M) synergies. Frontiers in Plant Science 11:568657. doi:10.3389/fpls.2020.568657.

Bhoite, R., Si, P., Siddique, K.H.M., Yan, G. 2021. Comparative transcriptome analyses for metribuzin tolerance provide insights into key genes and mechanisms restoring photosynthetic efficiency in bread wheat (*Triticum aestivum* L.) Genomics 113:910-918. doi:10.1016/j.ygeno.2021.02.004.

Bhunia, P., Das, P., Maiti, R. 2020. Meteorological drought study through SPI in three drought-prone districts of West Bengal, India. Earth Systems and Environment 4:43-55. doi:10.1007/s41748-019-00137-6.

Borrell, A.K., Mullet, J.E., George-Jaeggli, B., van Oosterom, E.J., Hammer, G.L., Klein, P.E., et al. 2014. Drought adaptation of stay-green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. Journal of Experimental Botany 65:6251-6263. doi:10.1093/jxb/eru232.

Bustin, S.A., Benes, V., Garson, J.A., Hellemans, J., Huggett, J., Kubista, M., et al. 2009. The MIQE guidelines: Minimum information for publication of quantitative real-time PCR experiments. Clinical Chemistry 55:611-622. doi:10.1373/clinchem.2008.112797.

Cech, T.R., Steitz, J.A. 2014. The noncoding RNA revolution—trashing old rules to forge new ones. Cell 157:77-94. doi:10.1016/j.cell.2014.03.008.

Chibane, N., Caicedo, M., Martinez, S., Marcet, P., Revilla, P., Ordás, B. 2021. Relationship between delayed leaf senescence (stay-green) and agronomic and physiological characters in maize (*Zea mays* L.) Agronomy 11:276. doi:10.3390/agronomy11020276.

Christopher, J.T., Christopher, M.J., Borrell, A.K., Fletcher, S., Chenu, K. 2016. Stay-green traits to improve wheat adaptation in well-watered and water-limited environments. Journal of Experimental Botany 67:5159-5172. doi:10.1093/jxb/erw276.

Christopher, M., Paccapelo, V., Kelly, A., Macdonald, B., Hickey, L., Richard, C., et al. 2021. QTL identified for stay-green in a multi-reference nested association mapping population of wheat exhibit context dependent expression and parent-specific alleles. Field Crops Research 270:108181. doi:10.1016/j.fcr.2021.108181.

Cui, L., Zheng, F., Li, C., Li, G., Ye, J., Zhang, Y., et al. 2024. Defective mutations in *STAY-GREEN*$_1$, *PHYTOENE SYNTHASE*$_1$, and *MYB*$_{12}$ genes lead to formation of green ripe fruit in tomato. Journal of Experimental Botany 75:3322-3336.

Distelfeld, A., Avni, R., Fischer, A.M. 2014. Senescence, nutrient remobilization, and yield in wheat and barley. Journal of Experimental Botany 65:3783-3798. doi:10.1093/jxb/ert477.

Djanaguiraman, M., Gowsiga, S., Govindaraj, M., Habyarimana, E., Senthil, A., Thavaprakaash, N., et al. 2023. Impact of root architecture and transpiration rate on drought tolerance in stay-green sorghum. Crop Science 64:2612-2629. doi:10.1002/csc2.21108.

Edema, R., Amoding, G.L. 2015. Validating simple sequence repeat (SSR) markers for introgression of stay-green quantitative trait loci (QTLs) into elite sorghum lines. African Journal of Biotechnology 14:3101-3111. doi:10.5897/AJB2015.14821.

Elshafei, A.A., Saleh, M., Al-Doss, A.A., Moustafa, K.A., Al-Qurainy, F.H., Barakat, M.N. 2013. Identification of novel SRAP markers linked to leaf chlorophyll content, flag leaf senescence and cell membrane stability traits in wheat under water stress conditions. Australian Journal of Crop Science 7(6):887-893. doi:10.3316/informit.365078361876788.

Elshire, R.J., Glaubitz, J.C., Sun, Q., Poland, J.A., Kawamoto, K., Buckler, E.S., et al. 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLOS ONE 6(5):e19379. doi:10.1371/journal.pone.0019379.

Fang, C., Li, C., Li, W., Wang, Z., Zhou, Z., Shen, Y., et al. 2014. Concerted evolution of *D1* and *D2* to regulate chlorophyll degradation in soybean. The Plant Journal 77(5):700-712. doi:10.1111/tpj.12419.

FAO. 2023. Food outlook: Biannual report on global food markets. FAO, Rome, Italy. Available at http://www.fao.org/3/cb4479en/cb4479en_wheat.pdf (accessed October 2024).

Gao, C., Sun, J., Dong, Y., Wang, C., Xiao, S., Mo, L., et al. 2020. Comparative transcriptome analysis uncovers regulatory roles of long non-coding RNAs involved in resistance to powdery mildew in melon. BMC Genomics 21:125. doi:10.1186/s12864-020-6546-8.

Ghatak, A., Chaturvedi, P., Bachmann, G., Valledor, L., Ramšak, Ž., Bazargani, M.M., et al. 2021. Physiological and proteomic signatures reveal mechanisms of superior drought resilience in pearl millet compared to wheat. Frontiers in Plant Science 11:600278. doi:10.3389/fpls.2020.600278.

Gregersen, P.L., Culetic, A., Boschian, L., Krupinska, K. 2013. Plant senescence and crop productivity. Plant Molecular Biology 82:603-622. doi:10.1007/s11103-013-0013-8.

Goodwin, S., McPherson, J.D., McCombie, W.R. 2016. Coming of age: Ten years of next-generation sequencing technologies. Nature Reviews Genetics 17:333-351. doi:10.1038/nrg.2016.49.

Guo, P., Baum, M., Varshney, R.K., Graner, A., Grando, S., Ceccarelli, S. 2008. QTLs for chlorophyll and chlorophyll fluorescence parameters in barley under post-flowering drought. Euphytica 163:203-214. doi:10.1007/s10681-007-9629-6.

Guo, Y., Ren, G., Zhang, K., Li, Z., Miao, Y., Guo, H. 2021. Leaf senescence: progression, regulation, and application. Molecular Horticulture 1:5. doi:10.1186/s43897-021-00006-9.

Hörtensteiner, S., Kräutler, B. 2011. Chlorophyll breakdown in higher plants. Biochimica et Biophysica Acta-Bioenergetics 1807:977-988. doi:10.1016/j.bbabio.2010.12.007.

Jagadeeswaran, G., Saini, A., Sunkar, R. 2009. Biotic and abiotic stress down-regulate miR398 expression in *Arabidopsis*. Planta 229:1009-1014. doi:10.1007/s00425-009-0889-3.

Jiang, G.H., He, Y.Q., Xu, C.G., Li, X.H., Zhang, Q. 2004. The genetic basis of stay-green in rice analyzed in a population of doubled haploid lines derived from an *indica* by *japonica* cross. Theoretical and Applied Genetics 108:688-698. doi:10.1007/s00122-003-1465-z.

Kaur, A., Sarlach, R.S. 2020. Leaf area, relative water content and stay-green habit of Iranian landraces (*Triticum aestivum* L.) under water stress in field conditions. Advances in Research 21:1-13. doi:10.9734/air/2020/v21i930227.

Kido, É.A., Ferreira-Neto, J.R.C., Pandolfi, V., de Melo Souza, A.C., Benko-Iseppon, A.M. 2016. Drought stress tolerance in plants: Insights from transcriptomic studies. p. 153-185. In Hossain, M., Wani, S., Bhattacharjee, S., Burritt, D., Tran, LS. (eds.) Drought stress tolerance in plants. Vol 2. Springer, Cham, Switzerland. doi:10.1007/978-3-319-32423-4_6.

Kim, J.H., Choi, D., Kende, H. 2009. The AtGRF family of putative transcription factors is involved in leaf and cotyledon growth in *Arabidopsis*. Plant Journal 36(1):94-104. doi:10.1046/j.1365-313x.2003.01862.x.

Kumar, R., Harikrishna, B., Barman, D., Ghimire, O.P., Gurumurthy, S., Singh, P.K., et al. 2022. Stay-green trait serves as yield stability attribute under combined heat and drought stress in wheat (*Triticum aestivum* L.) Plant Growth Regulation 96:67-78. doi:10.1007/s10725-021-00758-w.

Kusaba, M., Tanaka, A., Tanaka, R. 2013. Stay-green plants: What do they tell us about the molecular mechanism of leaf senescence. Photosynthesis Research 117:221-234. doi:10.1007/s11120-013-9862-x.

Lämke, J., Bäurle, I. 2017. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. Genome Biology 18:124. doi:10.1186/s13059-017-1263-6.

Li, Z., Peng, J., Wen, X., Guo, H. 2013. *ETHYLENE-INSENSITIVE3* is a senescence-associated gene that accelerates age-dependent leaf senescence by directly repressing *miR164* transcription in *Arabidopsis*. The Plant Cell 25(9):3311-3328. doi:10.1105/tpc.113.113340.

Liu, H., Able, A.J., Able, J.A. 2021. Small RNAs and their targets are associated with the transgenerational effects of water-deficit stress in durum wheat. Scientific Reports 11:3613. doi:10.1038/s41598-021-83074-7.

Liu, G., Jia, L., Lu, L., Qin, D., Zhang, J., Guan, P., et al. 2014. Mapping QTLs of yield-related traits using RIL population derived from common wheat and Tibetan semi-wild wheat. Theoretical and Applied Genetics 127:2415-2432. doi:10.1007/s00122-014-2387-7.

Lodish, H., Berk, A., Kaiser, C.A., Krieger, M., Bretscher, A., Ploegh, H., et al. 2016. Molecular cell biology. 8th ed. W.H. Freeman and Company, New York, USA.

Luo, C., Bashir, N.H., Li, Z., Liu, C., Shi, Y., Chu, H. 2024. Plant microRNAs regulate the defense response against pathogens. Frontiers in Microbiology 15:1434798.

Luo, Q., Zheng, Q., Hu, P., Liu, L., Yang, G., Li, H., et al. 2021. Mapping QTL for agronomic traits under two levels of salt stress in a new constructed RIL wheat population. Theoretical and Applied Genetics 134:171-189. doi:10.1007/s00122-020-03689-8.

Lynch, M., Walsh, B. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, Massachusetts, USA.

Ma, X., Zhao, F., Zhou, B. 2022. The characters of non-coding RNAs and their biological roles in plant development and abiotic stress response. International Journal of Molecular Sciences 23(8):4124. doi:10.3390/ijms23084124.

Mallory, A.C., Vaucheret, H. 2006. Functions of microRNAs and related small RNAs in plants. Nature Genetics 38(Suppl 6):S31-S36. doi:10.1038/ng1791.

Mastrangelo, A.M., Cattivelli, L. 2021. What makes bread and durum wheat different? Trends in Plant Science 26:677-684. doi:10.1016/j.tplants.2021.01.004.

Metzker, M.L. 2010. Sequencing technologies—the next generation. Nature Reviews Genetics 11:31-46. doi:10.1038/nrg2626.

Munaiz, E.D., Martínez, S., Kumar, A., Caicedo, M., Ordás, B. 2020. The senescence (stay-green)—an important trait to exploit crop residuals for bioenergy. Energies 13:790. doi:10.3390/en13040790.

Nakano, M., Yamada, T., Masuda, Y., Sato, Y., Kobayashi, H., Ueda, H., et al. 2014. A green-cotyledon/stay-green mutant exemplifies the ancient whole-genome duplications in soybean. Plant and Cell Physiology 55:1763-1771. doi:10.1093/pcp/pcu107.

Nawaz, A., Farooq, M., Cheema, S.A., Yasmeen, A., Wahid, A. 2013. Permanent green character during grain filling ensures resistance to terminal drought in wheat. International Journal of Agricultural Biology 15(6):1272-1276.

Pagano, L., Rossi, R., Paesano, L., Marmiroli, N., Marmiroli, M. 2021. miRNA regulation and stress adaptation in plants. Environmental and Experimental Botany 184:104369. doi:10.1016/j.envexpbot.2021.104369.

Pagliarani, C., Gambino, G. 2019. Small RNA mobility: spread of RNA silencing effectors and its effect on developmental processes and stress adaptation in plants. International Journal of Molecular Sciences 20:4306. doi:10.3390/ijms20174306.

Pattanayak, D., Solanke, A.U., Kumar, P.A. 2013. Plant RNA interference pathways: Diversity in function, similarity in action. Plant Molecular Biology Reporter 31:493-506. doi:10.1007/s11105-012-0520-9.

Racette, K., Zurweller, B., Tillman, B., Rowland, D. 2020. Transgenerational stress memory of water deficit in peanut production. Field Crops Research 248:107712. doi:10.1016/j.fcr.2019.107712.

Ray, D.K., Mueller, N.D., West, P.C., Foley, J.A. 2013. Yield trends are insufficient to double global agricultural production by 2050. PLOS ONE 8(6):e66428. doi:10.1371/journal.pone.0066428.

Ren, T., Fan, T., Chen, S., Chen, Y., Ou, X., Jiang, Q., et al. 2022. Identification and validation of quantitative trait loci for the functional stay green trait in common wheat (*Triticum aestivum* L.) via high-density SNP-based genotyping. Theoretical and Applied Genetics 135:1429-1444. doi:10.1007/s00122-022-04044-9.

Ren, H., Yu, Y., Huang, C., Li, D., Ni, J., Lv, W., et al. 2024. Genome-wide identification and characterization of Tea SGR family members reveal their potential roles in chlorophyll degradation and stress tolerance. Agronomy 14:769. doi:10.3390/agronomy14040769.

Richards, R.A. 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. Journal of Experimental Botany 51(suppl_1):447-458. doi:10.1093/jexbot/51.suppl_1.447.

Ruiz-Ferrer, V., Voinnet, O. 2009. Roles of plant small RNAs in biotic stress responses. Annual Review of Plant Biology 60:485-510. doi:10.1146/annurev.arplant.043008.092111.

Saini, P., Kaur, H., Tyagi, V., Saini, P., Ahmed, N., Dhaliwal, H.S., et al. 2023. Nutritional value and end-use quality of durum wheat. Cereal Research Communications 51(2):283-294. doi:10.1007/s42976-022-00305-x.

Salamon, S., Żok, J., Gromadzka, K., Błaszczyk, L. 2021. Expression patterns of miR398, miR167, and miR159 in the interaction between bread wheat (*Triticum aestivum* L.) and pathogenic *Fusarium culmorum* and beneficial *Trichoderma* fungi. Pathogens 10(11):1461. doi:10.3390/pathogens10111461.

Sánchez-Bragado, R., Molero, G., Reynolds, M.P., Araus, J.L. 2016. Photosynthetic contribution of the ear to grain filling in wheat: a comparison of different methodologies for evaluation. Journal of Experimental Botany 67(9):2787-2798. doi:10.1093/jxb/erw116.

Sarwat, M., Naqvi, A.R., Ahmad, P., Ashraf, M., Akram, N.A. 2013. Phytohormones and microRNAs as sensors and regulators of leaf senescence: Assigning macro roles to small molecules. Biotechnology Advances 31:1153-1171. doi:10.1016/j.biotechadv.2013.02.003.

Satam, H., Joshi, K., Mangrolia, U., Waghoo, S., Zaidi, G., Rawool, S., et al. 2023. Next-generation sequencing technology: Current trends and advancements. Biology 12:997. doi:10.3390/biology12070997.

Sattar, A., Sher, A., Ijaz, M., Ullah, M.S., Ahmad, N., Umar, U.U. 2020. Individual and combined effect of terminal drought and heat stress on allometric growth, grain yield and quality of bread wheat. Pakistan Journal of Botany 52:405-412. doi:10.30848/PJB2020-2(5).

Schmidt, J., Garcia, M., Brien, C., Kalambettu, P., Garnett, T., Fleury, D., et al. 2020. Transcripts of wheat at a target locus on chromosome 6B associated with increased yield, leaf mass and chlorophyll index under combined drought and heat stress. PLOS ONE 15(11):e0241966. doi:10.1371/journal.pone.0241966.

Schommer, C., Palatnik, J.F., Aggarwal, P., Chetelat, A., Cubas, P., Farmer, E.E., et al. 2008. Control of jasmonate biosynthesis and senescence by miR319 targets. PLOS Biology 6(9):e230. doi:10.1371/journal.pbio.0060230.

Shi, S., Azam, F.I., Li, H., Chang, X., Li, B., Jing, R. 2017. Mapping QTL for stay-green and agronomic traits in wheat under diverse water regimes. Euphytica 213:246. doi:10.1007/s10681-017-2002-5.

Shi, L., Reid, L.H., Jones, W.D., Shippy, R., Warrington, J.A., Baker, S.C., et al. 2006. The MicroArray Quality Control (MAQC) project shows inter- and intraplatform reproducibility of gene expression measurements. Nature Biotechnology 24:1151-1161. doi:10.1038/nbt1239.

Simmonds, J., Scott, P., Leverington-Waite, M., Turner, A.S., Brinton, J., Korzun, V., et al. 2014. Identification and independent validation of a stable yield and thousand grain weight QTL on chromosome 6A of hexaploid wheat (*Triticum aestivum* L.) BMC Plant Biology 14:191. doi:10.1186/s12870-014-0191-9.

Singh, A.K., Yadav, N., Singh, A., Singh, A. 2023. Stay-green rice has greater drought resistance: one unique, functional SG Rice increases grain production in dry conditions. Acta Botanica Plantae 2(31):38. doi:10.5281/zenodo.8167229.

Soni, A., Munjal, R. 2023. Characterisation and evaluation of wheat genetic resources for heat stress tolerance using stay-green traits. Crop and Pasture Science 74:581-595. doi:10.1071/CP22303.

Suleiman, A.A., Al-Chalabi, R., Shaban, S.A. 2024. Integrative role of small non-coding RNAs in viral immune response: A systematic review. Molecular Biology Reports 51:107. doi:10.1007/s11033-023-09141-6.

Thomas, H., Ougham, H. 2014. The stay-green trait. Journal of Experimental Botany 65:3889-3900. doi:10.1093/jxb/eru037.

Thomas, H., Smart, C.M. 1993. Crops that stay green1. Annals of Applied Biology 123(1):193-219. doi:10.1111/j.1744-7348.1993.tb04086.x.

Tidiane Sall, A., Chiari, T., Legesse, W., Seid-Ahmed, K., Ortiz, R., Van Ginkel, M., et al. 2019. Durum wheat (*Triticum durum* Desf.): Origin, cultivation, and potential expansion in Sub-Saharan Africa. Agronomy 9(5):263. doi:10.3390/agronomy9050263.

Unamba, C.I., Nag, A., Sharma, R.K. 2015. Next generation sequencing technologies: The doorway to the unexplored genomics of non-model plants. Frontiers in Plant Science 6:1074. doi:10.3389/fpls.2015.01074.

Wang, Z., Gerstein, M., Snyder, M. 2009. RNA-Seq: A revolutionary tool for transcriptomics. Nature Reviews Genetics 10:57-63. doi:10.1038/nrg2484.

Wang, P., Hou, S.Y., Wen, H.W., Wang, Q.Z., Li, G.Q. 2021b. The stay-green mutation contributes to enhanced antioxidative competence and delays leaf senescence in soybean hybrid Z1. International Journal of Agriculture and Biology 25:361-372. doi:10.17957/IJAB/15.1676.

Wang, N., Liu, Z., Zhang, Y., Li, C., Feng, H. 2018a. Identification and fine mapping of a stay-green gene (*Brnye1*) in pakchoi (*Brassica campestris* L. ssp. *chinensis*). Theoretical and Applied Genetics 131:673-684. doi:10.1007/s00122-017-3028-8.

Wang, F., Sun, H., Rong, L., Li, Z., An, T., Hu, W., et al. 2021a Genotypic-dependent alternation in D1 protein turnover and PSII repair cycle in rice *psf* mutant rice (*Oryza sativa* L.) as well as its relation to light-induced leaf senescence. Plant Growth Regulation 95:121-136. doi:10.1007/s10725-021-00730-8.

Wang, S., Wong, D., Forrest, K., Allen, A., Chao, S., Huang, B.E., et al. 2014. Characterization of polyploid wheat genomic diversity using a high-density 90,000 single nucleotide polymorphism array. Plant Biotechnology Journal 12:787-796. doi:10.1111/pbi.12183.

Wang, Y., Zheng, W., Zheng, W., Zhu, J., Liu, Z., Qin, J., et al. 2018b. Physiological and transcriptomic analyses of a yellow-green mutant with high photosynthetic efficiency in wheat (*Triticum aestivum* L.) Functional & Integrative Genomics 18:175-194. doi:10.1007/s10142-017-0583-7.

Wei, L., Zhang, D., Xiang, F., Zhang, Z. 2009. Differentially expressed miRNAs potentially involved in the regulation of defense mechanism to drought stress in maize seedlings. International Journal of Plant Sciences 170(8):979-989. doi:10.1086/605122.

Wu, X., Ding, D., Shi, C., Xue, Y., Zhang, Z., Tang, G., et al. 2016. microRNA-dependent gene regulatory networks in maize leaf senescence. BMC Plant Biology 16:73. doi:10.1186/s12870-016-0755-y.

Xu, W., Rosenow, D.T., Nguyen, H.T. 2000. Stay-green trait in grain sorghum: Relationship between visual rating and leaf chlorophyll concentration. Plant Breeding 119:365-367.

Yang, H., Hu, W., Zhao, J., Huang, X., Zheng, T., Fan, G. 2021. Combined genetic improvement and seed priming with ethephon improved grain yield and drought resistance of wheat exposed to soil water deficit at tillering stage. Plant Growth Regulation 95:29-39. doi:10.1007/s10725-021-00749-x.

You, L., Rosegrant, M.W., Wood, S., Sun, D. 2009. Impact of growing season temperature on wheat productivity in China. Agricultural and Forest Meteorology 149:1009-1014. doi:10.1016/j.agrformet.2008.12.004.

Zhang, Y.M., Jia, Z., Dunwell, J.M. 2019. The applications of new multi-locus GWAS methodologies in the genetic dissection of complex traits. Frontiers in Plant Science 10:100. doi:10.3389/fpls.2019.00100.

Zhang, W., Peng, K., Cui, F., Wang, D., Zhao, J., Zhang, Y., et al. 2021b. Cytokinin oxidase/dehydrogenase OsCKX11 coordinates source and sink relationship in rice by simultaneous regulation of leaf senescence and grain number. Plant Biotechnology Journal 19(2):335-350. doi:10.1111/pbi.13467.

Zhang, Z., Qu, Y., Ma, F., Lv, Q., Zhu, X., Guo, G., et al. 2024. Integrating high-throughput phenotyping and genome-wide association studies to improve drought resistance and yield prediction in wheat. New Phytologist 243(5):1758-1775. doi:10.1111/nph.19942.

Zhang, J., She, M., Yang, R., Jiang, Y., Qin, Y., Zhai, S., et al. 2021a. Yield-related QTL clusters and the potential candidate genes in two wheat DH populations. International Journal of Molecular Sciences 22:11934. doi:10.3390/ijms222111934.

Zheng, R., Deng, M., Lv, D., Tong, B., Liu, Y., Luo, H. 2023. Combined BSA-Seq and RNA-Seq reveal genes associated with the visual stay-green of maize (*Zea mays* L.) International Journal of Molecular Sciences 24:17617. doi:10.3390/ijms242417617.