Review Article

Maximizing Crop Resilience: Exploring Stay-Green Traits for Sustainable Agriculture and Crop Research

Abstract

The “stay-green” trait, distinguished by detained aging, sustain photosynthetic activity , nutrient use efficiency, offering critical advantages in drought, heat, and nutrient-deficient conditions. This review examines how "stay-green" traits can help crops better withstand the challenges of climate change, ensuring food security for a growing global population while conserving resources in the face of scarcity. This phenomenon is crucial in promoting yield stability, biomass production, and improved grain filling, thereby addressing the global demand for sustainable agriculture. This provides a detailed analysis of stay-green traits in various crop species, emphasizing their genetic basis, physiological mechanisms, and practical applications. It delves into hormonal regulation, reactive oxygen species scavenging, and nutrient remobilization as underlying mechanisms. This paper also underscores advancements in phenotyping technologies and molecular breeding approaches, such as marker-assisted selection and CRISPR-Cas gene editing, for effectively incorporating stay-green traits into crop breeding programs. Real-world examples from cereals such as wheat, maize, and sorghum highlight the significant impact of stay-green traits on crop improvement. The potential of these traits is not limited to agricultural crops; they can also enhance the quality and marketability of horticultural produce. The document discusses emerging biotechnological tools, including nanotechnology and omics-based breeding, as future directions for enhancing stay-green traits and overall crop resilience. By integrating stay-green traits with broader stress tolerance strategies, this review advocates for a sustainable agricultural system that balances productivity and ecological conservation. The insights provided lay the groundwork for future research and innovation in developing resilient crop varieties to ensure climate variability presents concerns to global food security.

Keywords : *Stay-Green Traits , Leaf Senescence , Nutrient Remobilization, Food Security, Climate-Resilient Crops, Carbon Sequestration*

1. Introduction

1.1. Overview of Global Agricultural Challenges

The world’s population is predicted to reach 10,000 million by 2050, with the majority of this rise occurring in emerging areas. Addressing the future food needs sustainably, both environmentally and economically, is one of humanity's greatest challenges. The global agricultural sector is grappling with numerous challenges that complicate efforts to improve crop productivity and resilience (Mohanty *et al.,*2024). To feed a growing global population, agricultural productivity must increase significantly by 2050. However, climate change exacerbates the difficulty (Janni *et al.,*2024). Agriculture faces increasing problems as the population expands and the effects of climate change worsen. At this crucial moment, it is vital to achieve sustainable agriculture to secure food supplies, preserve ecological balance, and foster economic growth. Effective water management is vital, particularly as agriculture demands more water and water shortages intensify. Maintaining healthy soil is crucial for sustainable agricultural practices and is receiving increasing focus. Soil forms a vital part of the ecosystem, intricately linked with water, plants, and animals in a complex and interdependent web. As global temperatures rise and climate patterns shift, traditional planting seasons may be disrupted, presenting challenges for crop growth. Both research groups highlight that changes in climate, including the rise in extreme weather events, pose a significant threat to food security by disrupting the timing and efficiency of agricultural production (Shang *et al.,* 2024; Prajapati *et al.,* 2024).

Food safety is the key goal to sustainable development, as it supports human health, societal stability, and economic prosperity. Climate-related catastrophes like droughts, floods, and storms can worsen food insecurity by destroying crops, animals, and infrastructure, disrupting supply networks. Crop diversification entails growing multiple crops with various features and growth requirements to reduce risk and increase resistance to climatic unpredictability. Planting varied crops can help farmers offset the effects of harsh weather and pests. diseases, resulting in a more consistent and secure food supply. Breeding resilient crop varieties through traditional and biotechnology can improve tolerance to climate-related stresses, leading to improved yields and food safety in the aspect of global heating. Sustainable land management strengthens agricultural systems' resilience to climate change while also promoting soil health, biodiversity, and ecosystem services. Climate-smart crop breeding in India has resulted in resilient crop types that can withstand heat, drought, pests, and diseases. Researchers have utilized participatory plant breeding and genomic selection to develop high-yielding, stress-tolerant crop varieties, such as drought-resistant rice, heat-tolerant wheat, and pest-resistant maize. These improved varieties have significantly enhanced farm productivity and food security for smallholder farmers in vulnerable regions (Toromade *et al*.,2024).

1.2 The Concept of Stay-Green Traits

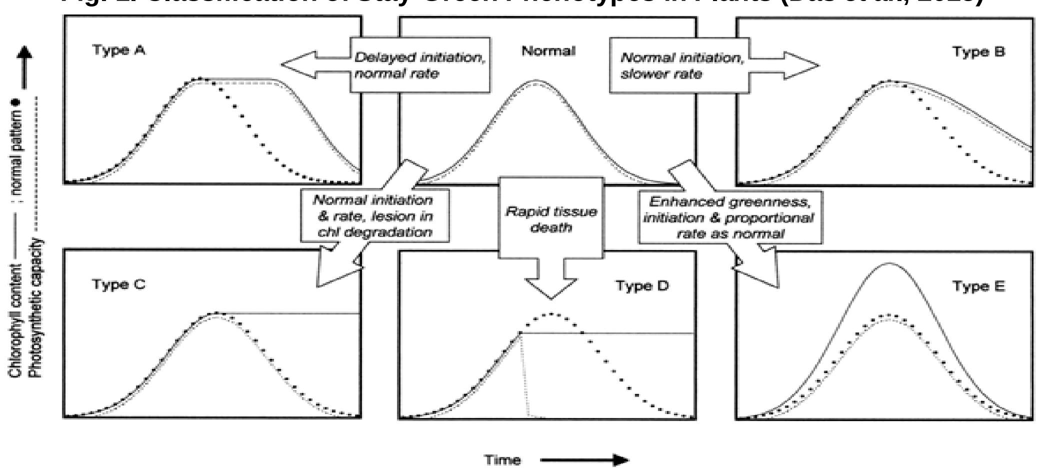
Plant leaves serve as a distinctive and easily accessible genetic system for studying aging, senescence, and death-related processes. Additionally, leaf senescence offers a valuable opportunity to explore the process of orderly degradation, in contrast to the many biological studies that focus on biogenesis and assembly processes (Woo *et al.,*2013). This final stage of development involves the breakdown of cellular components and macromolecules, ensuring the reallocation of nutrients to other growing parts of the plant (Sakuraba *et al.,*2020). In the context of modern agriculture, where maximizing productivity and sustainability is paramount, understanding and manipulating leaf senescence is crucial. Premature senescence can lead to early crop decline, reducing the harvest period and overall yield. Conversely, delayed senescence, or "stay-green" traits, though beneficial in extending photosynthetic activity, can sometimes interfere with nutrient remobilization needed for seed development. Balancing these factors to optimize both yield and quality under various environmental stresses remains a critical and ongoing challenge for crop scientists and geneticists.

The stay green trait, characterized by delayed leaf senescence in plants, has emerged as a promising frontier in agricultural research, offering transformative potential for crop enhancement strategies. This phenomenon, which allows plants to maintain green and photosynthetically active leaves for extended periods compared to conventional genotypes, holds significant implications for enhancing crop resilience and productivity in difficult environmental conditions such as drought, heat stress, and nutritional deprivation. This trait is valuable because it enables vital plant functions such as photosynthesis and nutrient absorption, ultimately resulting in increased grain output and overall plant growth (Verma *et al.,* 2020). Despite its prevalence across various plant species, the molecular mechanisms and genetic underpinnings of stay green remain subjects of intense investigation. In this comprehensive review paper, we delve into the physiological significance of stay green traits, explore the genetic diversity and molecular pathways governing this trait across diverse crop species, and discuss its prospective applications in breeding efforts focused at generating durable and high-yielding agricultural types capable of flourishing in changeable environmental landscapes. By synthesizing current research findings and highlighting recent advancements in the field, This assessment will provide useful perceptions into the promise of stay green as a catalyst for sustainable agriculture. and offer a roadmap for future research directions in crop improvement strategies (Christopher *et al.,* 2008).

1.2.1. Classification of stay green

Stay-green traits in plants manifest through alterations in genetic processes governing senescence initiation and progression, leading to prolonged photosynthetic activity and potentially higher yields. Functional stay green types sustain photosynthesis longer than usual, enhancing productivity. Conversely, non-functional stay green mutants retain chlorophyll due to impaired catabolism but lack photosynthetic competence.

Fig. 1. Classification of Stay-Green Phenotypes in Plants (Das *et al*., 2015)



Classifying stay green into five categories based on senescence timing and duration provides insights into their mechanisms: Type A delays senescence initiation but proceeds normally afterward; Type B initiates senescence timely but progresses slowly; Type C results from chlorophyll degradation defects; Type D maintains green colour until leaf death; Type E maintains chlorophyll content despite reduced enzyme activity. This classification aids in understanding stay green's diverse effects on plant physiology and productivity.

1.3 Objectives of the Review

This review aims to shed light on the importance of this trait in sustainable agriculture and offer insights into future directions for crop improvement strategies. Therefore, expected to give a higher production and productivity of grain as well biomass under biotic and abiotic stress condition. Genetic variation exists in the timing and rate of leaf aging, both between species cum genotypes. Furthermore, mutants also occur whose leave remain green for longer than those of the parental genotype. The presence of this trait leads to an extended period of foliar (leaf) greenness, which is directly linked to delayed senescence, the natural aging and deterioration of leaves. (Xu *et al.,* 2000). Chlorophyll breakdown occurs alongside the aging or ripening of green plant organs. Even so, there exists a genetic variation that slacks up or halts this disintegration process, leading to plants retaining their green color even as they reach the end of their growth cycle. These stay-green mutations predominantly emanate due to alterations in the stay-green protein gene (SGR) (Abdelrahman *et al.,* 2017). The ability of this trait, is considered one of the most thoroughly understood attributes that contribute to drought tolerance in numerous crops.

2. Morphological and Physiological Basis of Stay-Green Traits

2.1. Morphological basis

2.1.1 Delayed leaf senescence

Senescence is an active phase of plant development that includes degradation and remobilization activities. Under optimal conditions, the beginning and duration of senescence are predictable and strongly tied to the crop's phenological development. Leaf senescence is a tightly regulated process in which nutrients are transported from the senescent leaf to other sections of the plant, resulting in leaf death. During senescence, the leaf yellows as chlorophyll degrades and photosynthesis decreases (Chibane *et al*., 2021). Senescence of plant tissues or organs is a developmental process in plants that occurs between the vegetative and reproductive stages. Crop yields may be reduced due to premature senescence induction caused by poor environmental circumstances. Several studies have found a positive relationship between leaf area elongation and yield, although many green cultivars have little influence on productivity due to senescence (Naz *et al*., 2023). Drought, salinity, hot or low temperatures, darkness, nutritional inadequacy, and pathogen infection are all common stressors that can cause it. Premature leaf senescence is a degenerative physiological process that lowers photosynthetic efficiency and nutrient buildup, lowering crop production. Abiotic stress induces leaf senescence, which has a considerable impact on agricultural productivity and quality. Delaying leaf senescence can improve drought tolerance and photosynthesis, which is the foundation of high yields. Exploring techniques to delay leaf senescence is thus necessary for sustaining and improving agricultural production under abiotic stress conditions. The differential expression of senescence marker genes, as well as the NAC and WRKY transcription factors, reflects leaf senescence (Yang *et al*., 2023).

2.1.2. Senescence and Stay-green

Senescence is a physiological mechanism in which nutrient stores are mobilised into fruits and seeds. Stay-green is a key trait that helps plants to keep their leaves in an active photosynthetic state even when they are stressed. Senescence influences crop plant assimilation and grain filling at an early stage. Increased green leaf area at maturity, leaf nitrogen status, and transpiration efficiency were all linked to higher grain yield in stay-green genotypes compared to senescent genotypes. The emergence and progression of senescence are phenological indicators of climate change vulnerability, implying that a better understanding of stay-green will aid in the development of potential crop forms. As a result, any defense mechanisms that delay the onset of senescence and hold leaves green are expected to increase crop yield (Hiremath *et al*., 2017). Stay-green is also one of the important parameters to assess the yield under drought condition with good root system (Hilli *et al*., 2021).

2.1.3. Enhanced root system

Roots play an important function in anchoring and resource acquisition. The availability of nutrients can alter the way the root grows in radial or longitudinal directions, impacting the three-dimensional root structure. They generally exhibit plasticity, allowing them to function well by adjusting to their surroundings (Kalra *et al*., 2024). Root architecture is the spatial layout of root systems that determines plant anchoring, water and nutrient absorption, inter- and intra-plant communication, and competition. It is argued that changing the root system design could be a viable alternative way to increasing crop productivity, resulting in a second green revolution. Plants' root systems provide them with morphological, structural, and physiological adaptability in response to environmental changes. As a result, combining root architectural and physiological traits will aid in the development of drought-tolerant genotypes. Breeding for superior root qualities in crops involves not only efficient and improved screening procedures, but also in-depth knowledge of specific functions of roots, such as water extraction and nutrient absorption from the soil (Sofi *et al*., 2021). The most consensus attribute contributing to drought avoidance in highland circumstances is a deep root system, which allows a plant to hunt mineral resources, absorb water from deeper layers, and respond to evaporative demand, assuming water is accessible in places investigated by roots. The development of crops with more effective roots may be dependent on RSA, which includes structural phenes such as root length or elongation, spread, branching, growth angle, and the amount and length of lateral roots, which have been shown to influence root system architecture. An increased quantity of fine roots and root hairs is connected to better water and nutrient intake, as well as increased resilience to stress (Shafi *et al*., 2023).

2.2. Physiological basis

2.2.1 Hormonal regulation

Richmond and Lang were the first to show that cytokinins exhibit antisenescent effects on excised leaves of tobacco and cocklebur plants. (Honig *et al* ., 2018). Cytokinin negatively regulates it and enhances long suffering to some of the abiotic stresses. Pathogens and herbivores frequently employ CK's senescence-delaying feature to create "green islands."(Walters *et al*.2008). The plant hormone ethylene triggers leaf senescence. Salicylic acid (SA), another plant hormone, also plays a crucial role in initiating and progressing leaf senescence, as demonstrated in Arabidopsis research. Moreover, the plant hormone abscisic acid (ABA) facilitates leaf senescence. Rate of leaf senescence is influenced by environmental factors such as light intensity, quality, and the ratio of red to far-red light (Guo *et al.,* 2021).Leaf senescence is a complex, genetically controlled process involving a series of coordinated events, including the breakdown of chlorophyll and other cellular components. This intricate process is finely regulated at multiple levels within the plant including chromatin remodelling, transcription, and post-translational modifications. The existence of auxin-responsive genes that encode ARFs or IAA proteins suggests that it has a part in controlling foliar senescence (Schippers *et al*.2015). Mutants insensitive to ethylene (ETR1-1, EIN2) show delayed aging. Introducing an ARF2 mutation in these plants causes an additional delay in senescence, indicating that ARF2 functions separately from the ethylene pathway (Grbić,bleeker *et al*.,1995).

2.2.2. Reactive Oxygen Species (ROS) Scavenging

ROS are extremely reactive and poisonous chemicals. ROS are usually produced as a byproduct in some of the cell organelles. Superabundance of this species during the external environmental stress response causes oxidative stress.. During stress, their production increases significantly, causing cellular toxicity and damage (Khanna *et al.,* 2013). Many cellular processes are governed by ROS, which operate as essential signaling intermediaries in growth and development and also conformant to varied stress tolerance in plants. (Haider *et al.,* 2021). Stress conditions such as salinity, drought, extreme temperatures, heavy metal exposure, pollution, high light intensity, and pathogen infections can disturb the fragile balance between the production and scavenging of reactive oxygen species (ROS). To counteract this, plants have evolved a robust antioxidant system comprising two key components: (i) enzymatic elements, including SOD, CAT, APX, GPX, GR, MDHAR, and DHAR, and (ii) chemical antioxidants like ABA, reduced GSH, and α. These components collaborate to mitigate ROS levels effectively. (Das *et al.,* 2014). Plants under mild photorespiration release 1O2, O•2−, and H2O2 at the same time, making it difficult to determine their individual roles. Research has revealed that singlet oxygen ($^1O_2$) is the primary source of senescence-related oxidative stress in sage chloroplasts. This conclusion was drawn from the significant degradation of β-carotene and α-tocopherol observed in drought-stressed plants, indicating increased production of singlet oxygen. Hydrogen peroxide (H_2O_2) plays a crucial role in the aging process of plants. It acts as a signaling molecule, accelerating aging in various plant species. Research shows peroxide interacts with other signaling molecules involved in plant development and aging, such as stress hormones and ripening hormones. This complex interplay influences the overall aging process in plants. External application of hydrogen peroxide (H_2O_2) increases the production of mRNAs for enzymes involved in creating oligosaccharides (complex sugars). These sugars help plants survive drought. Furthermore, H_2O_2 can be used by Class III peroxidases in the plant cell wall, which are crucial for defending against plant pathogens (Jajic *et al.,* 2015).

2.2.3. Nutrient Remobilization

2.2.3.1. The Green Essence: Chlorophyll in Plant Life

The green pigment in plants, plays a critical part in photosynthesis—the process by which plants convert sunlight into energy. As leaves age, green pigment degrades, leading to a yellowing of the foliage. However, delaying this degradation, particularly during the reproductive stage, prolongs photosynthetic activity, ultimately boosting yield and biomass production. This continuous photosynthesis is closely related to functional stay-green features, which indicate the transformation from C capture to N mobilization in leaf growth. (Thomas and Oughum, 2014). Thus, preserving chlorophyll content not only maintains leaf greenness but also enhances plant productivity and crop yield. Prolonged leaf longevity in this genotype may improve agricultural yields by revive nutrients from resource allocation under diverse stressors and low nutrient situations.

CN cycles as energy sources begin to reactivate by piling up sugars in the leaves to meet the sink's nitrogen demands. On the other side, a scarcity of nitrogen causes leaf senescence and encourages N recycling and remobilization. Ideal nitrogen concentrations increase leaf greenness and growth, remobilizing N that would otherwise be destroyed by chloroplast protein and making molecules of nitrogen available. These physiological changes impact its metabolism by weakening translocation pathways, leading to an unequal distribution between source and sink. (Munaiz *et al.,* 2020).

2.2.3.2. Relation of N_2 With stay green traits

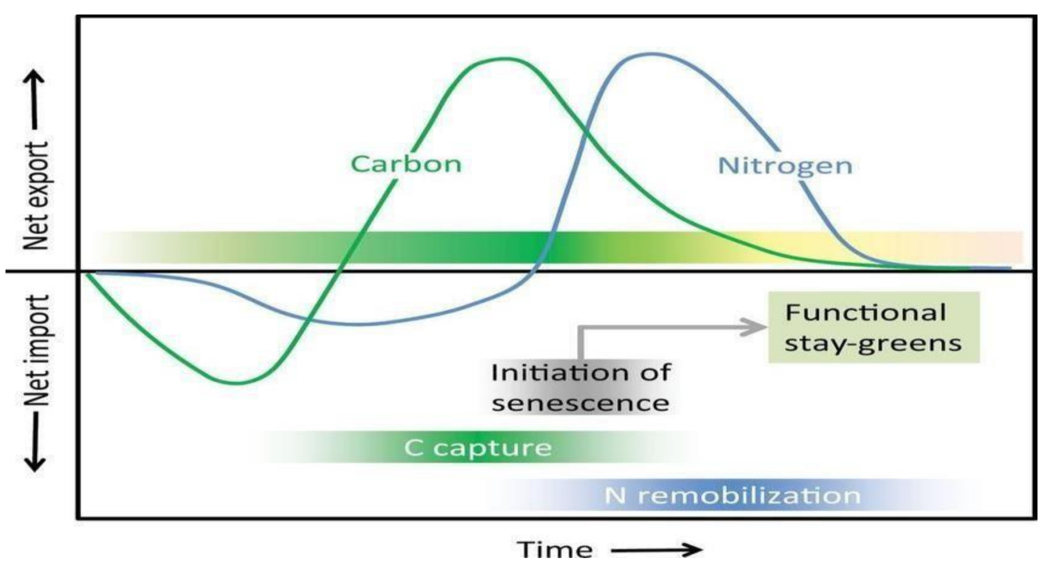


Fig. 2. Carbon sequestration and nitrogen recycling in stay-green plants. (Thomas, H., & Ougham, H. 2014)

Leaves undergo a dynamic transition, shifting from nutrient-demanding consumers to net contributors of photosynthates to the entire plant. This transition signals the functional start of senescence, with the leaf's C-capture phase followed by net organic N remobilization. This mechanism is essential for plant health and productivity.. While laboratory studies provide insights, scaling issues must be considered when extrapolating findings to field conditions. Stay-green genotypes exhibit delayed C-N transition points or slow subsequent yellowing and N remobilization, highlighting their importance in sustaining leaf function and overall plant performance (Lim *et al.,* 2007). Plants remobilize nitrogen and carbon from dying leaves into new tissues and storage organs, allowing them to adapt to changing conditions. Efficient nitrogen remobilization minimizes the need for nitrogen fertilizer and significantly impacts grain yield and quality during seed development. Small grains, like wheat and rice, efficiently recycle up to ninety precent of their nitrogen from vegetative parts, whereas maize recycles only 35-55%.

2.3. Photosynthetic Efficiency and Water-Use

2.3.1. Prolonged Photosynthetic Activity

The environmental importance of the extended grain filling time associated with the SG trait is diverse and crucial for agricultural productivity and resilience. By staying green longer, these plants extend the time for grain filling, leading to improved yield, quality, and ecosystem function (Mahalaskshmi *et al.,* 2002). Firstly, the extended grain filling period allows for prolonged photosynthetic activity, enabling the continued assimilation of carbon dioxide and production of assimilates essential for grain development. This sustained carbon supply enhances the accumulation of dry matter and facilitates optimal grain filling, contributing to increased yield potential. Moreover, the prolonged grain filling duration offers greater flexibility in resource allocation, allowing plants to allocate resources towards grain development over an extended period (Silva *et al*., 2004). This resource partitioning ensures efficient nutrient remobilization from source tissues to developing grains, thereby enhancing nutrient use efficiency and grain quality. Furthermore, the prolonged grain filling period conferred by the stay-green trait enhances the resilience of crops to environmental stresses, particularly drought and heat stress. By maintaining functional green leaves for an extended period, stay-green plants exhibit improved water and nutrient uptake capabilities, reducing the negative impact of water deficiency on grain filling and yield. Additionally, the extended grain filling phase promotes canopy maintenance and ground cover, which reduces soil moisture loss through evaporation, suppresses weed growth, and enhances soil moisture conservation. This contributes to improved soil health, water use efficiency, and ecosystem stability. Overall, the prolonged grain filling period associated with the stay-green trait not only enhances crop yield and resilience to environmental stresses but also has broader ecological implications for sustainable agricultural practices and ecosystem functioning.

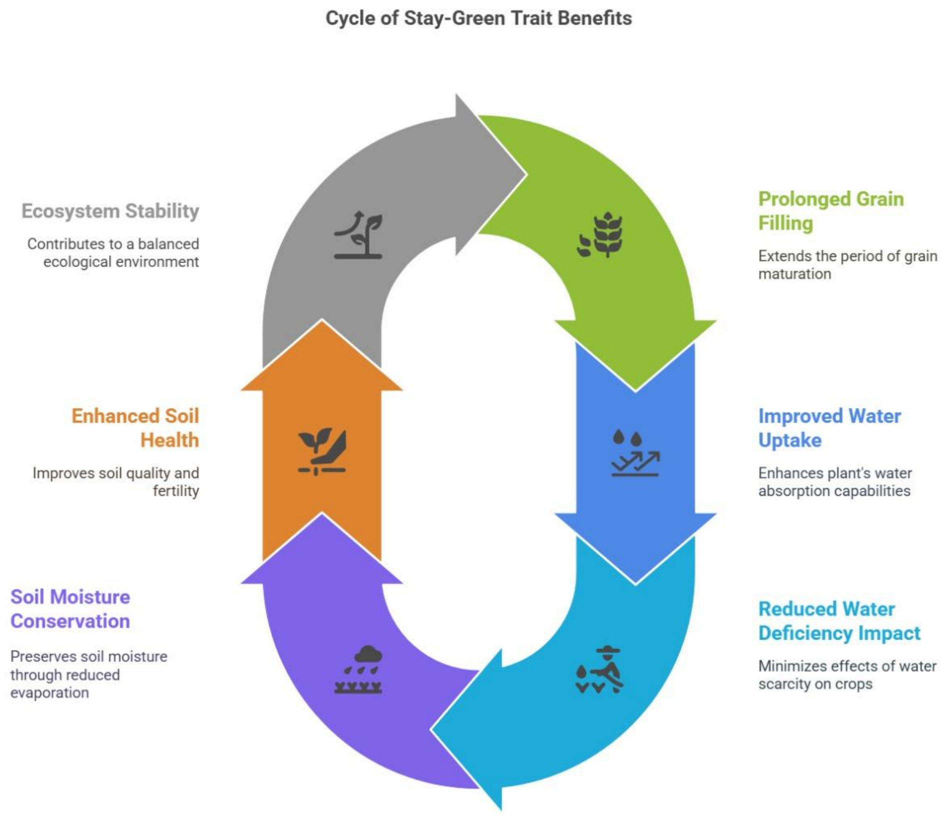


Fig.3. Cycle of stay green benefits

2.3.2. Water-Use Efficiency

Initially, water use efficiency (WUE) was defined as the ratio of crop output (biomass or grain) to water input. This concept evolved to represent crop yield per unit of water lost to the atmosphere (evapotranspiration). Breeding for drought-tolerant crops with improved WUE has been a major focus to combat water scarcity and ensure food security (Mbava *et al.,* 2020). While further WUE improvements are expected, enhancing the efficiency of light reactions in photosynthesis has a profound impact on yield under stress. This efficiency significantly influences a plant's ability to Optimize water and nutrient uptake, Effectively transition from vegetative to reproductive growth and Balance resource allocation between photosynthetic tissues (sources) and growing parts (sinks) throughout its lifecycle (Snowdon *et al.,* 2021). Drought, a critical worry in today's climate, is one of the most severe abiotic stresses affecting regions all over the world. Moisture stress arises when plants cannot adequately meet their water needs through evapotranspiration. Drought significantly impacts plant growth and metabolism, posing a major threat to global agricultural production. It primarily caused by irregular rainfall or insufficient irrigation, significantly impacts crop yields. Factors like soil salinity, poor soil quality, and extreme temperatures can exacerbate drought stress. Throughout the growing season, inadequate water availability, including both rainfall and the soil's ability to retain moisture, limits the crop's potential to reach its maximum yield (Begna *et al.,* 2021). Modifying irrigation and fertilization practices can increase yield by up to 30% under comparable conditions. Understanding the mechanisms that allow crops to grow under limited to severe stress, and applying these insights to build crop resilience methods, could assist improved yield and WUE. Sophisticated technologies allow for the intelligent management of water in agricultural fields. This is achieved by accurately tracking how much water crops need and how they react to water shortages. These technologies can also help plants recover from minor water stress, prevent excessive growth, and regulate the balance between water loss and carbon uptake through signals that travel from the roots to the leaves. (kang *et al*., 2021).

3. Genetic Determinants of Stay-Green Traits

3.1. Identification of Stay-Green Genes

The inheritance pattern of the stay-green trait in plants exhibits a complex interplay of genetic factors across various species. In wheat, (Silva *et al.,* 2001) identified four recessive genes governing stay-green, which segregate independently and interact additively. Similarly, in rice, the recessive variant gene sgr(t) on chr 9 regulates the stay-green phenotype (Cha *et al.,* 2002) and (Jiang *et al.,* 2007). In Arabidopsis, the stay-green trait is controlled by the subordinate gene fiw located on chr 4 (Nakamura *et al.,* 2000). These findings underscore the multi-factorial nature of stay-green inheritance, with different genetic loci contributing to its expression in distinct plant species. To effectively breed crops that can withstand drought and other stresses, it's essential to understand the genetic factors that contribute to the 'stay-green' trait. This knowledge is crucial for developing resilient crop varieties (Munaiz *et al*., 2020).

The transcription factors from WRKY background plays an important lead in plant habituation to soil-moisture stress. Recent studies have identified a novel SbWRKY gene, named SbWRKY30, which is predominantly expressed in the taproot and leaves of jowar under water deficit conditions. This suggests that SbWRKY30 functions as an effective regulator of drought response and holds significant potential for improving drought tolerance in various crops. Additionally, other genes—such as SbWRKY45, 79, 83, and 16—also showed high expression in sorghum during water shortage, further highlighting the essential part of SbWRKYs in promoting drought tolerance (Prasad *et al*., 2021).

Table 1. Key Genes Associated with Stay-Green Phenotypes.

Protein	Genetic factor	Variant Phenotype	Progress
Stay-green	SGR,NYE-1SID	sgr = stay-green	**Binding light harvesting complex II and catabolic enzymes, stabilising its complex**
Chlorophyll b reductase	NYC NOL HCAR	nyc (rice and Arabidopsis) = stay-green	**NADPH dependent two-step conversion of chlorophyll b to a**
Phaeophytinase	PPH CRN1 NCY3	pph = stay-green	**Dephytylation ofphaeophytin**

Phaeophorbide a oxygenase	PAO ACD1 LLS1	acd1 = cell death, cosmetic stay-green	**Ferredoxin (Fd)dependent oxidativeopening macrocycle to form RCC**
RCC reductase	RCCR ACD2	acd2 = cell death, cosmetic stay-gree	**Fd dependent reduction of RCC to pFCC**

Senescence onset triggers chloroplast breakdown and stromal enzyme degradation, leading to reduced photosynthesis (Ahlawat *et al*., 2008). Chlorophyll degradation, catalyzed by six chlorophyll catabolic enzymes (CCEs) within chloroplasts, is an ensign of aging.

3.2. Molecular Breeding and Genetic Engineering

3.2.1 MAS

It revolutionizes plant breeding by integrating genetic knowledge into practical applications. It is a cornerstone of modern crop improvement, enabling the development of high-yielding, stress-resilient, and nutritionally enhanced crop varieties, which is crucial for insuring lacking of food insecurity and adapting to environmental fluctuations . MAS is particularly helpful for attributes that are difficult to analyze through conventional breeding methods, such as those controlled by multiple genes (quantitative traits) or expressed only under specific environmental conditions. Furthermore, integrating nanomaterials with genetic engineering facilitates precise gene modification, boosting stress tolerance and sustaining the stay-green phenotype. Although there is limited research on nanotechnology in agriculture, its potential is significant. Nanoscience, with its unique properties, has the potential to revolutionize agriculture and promote sustainability (Chippa *et al.,* 2019).

Marker-Assisted Selection for Drought Tolerance

By 2025, over 65% of the world wide population is expected to face water scarcity. In agricultural systems, drought occurs when plants cannot access sufficient water for transpiration. Drought is a noteworthy stress factor that hampers plant progresss and reproduction, posing a major challenge for scientists. The main goal of plant breeding is to create crops that can withstand or adapt to drought conditions. In the 21st century, developing high-yielding and stable crop varieties that are also drought-resistant is crucial for ensuring a consistent food supply. One of the most effective approaches to achieve this is through MAS. STAY GREEN-related genes in arabidopsis signifies in modulating foliage final developmental period and chlorophyll disintegration under various stress conditions (Sakuraba *et al.,* 2014).

Globally, climate-resilient crops like sorghum are capable of thriving in regions with limited rainfall. However, climate change has exacerbated conditions by increasing temperatures and reducing the frequency of rainfall, thereby impacting crop yields. MAS leverages genetic markers to identify QTLs combined with drought tolerance traits, such as stay-green characteristics. In sorghum, QTLs such as Stg1,2, 3, 4, 3A, and 3B have been linked to high yield and stay-green traits. These QTLs are introgressed into senescent sorghum varieties through marker-assisted backcrossing (MABC), enhancing their drought resilience and productivity (Kumari *et al.,* 2024).

3.2.2. Quantitative Trait Loci (QTL) Mapping

Table 2. Stay-green QTL have been identified

Crop	No. of QTLs	Identified QTL	Chromosome number	State of Observation	Reference
Wheat	3	QSg.bhu-1A QSg.bhu-3B QSg.bhu-7D	1A 3B 7D	Improving yield	**Kumar *et al.,* 2010**
Rice	4	TCS4,Csf16,CSF19/TCs9, Csf12 Yld6,Y1d9-Csf16,TCs9	4,6,9,12 6,9	Improvement of yield	**FU *et al.,* 2011**
Maize	14	sg1.1.1, sg1.6.1, sg2.1.1, sg2.1.2, sg2.2.1, sg2.3.1, sg2.5.1, sg2.8.1, sg3.1.1 ,sg3.2.1,sg3.5.1,sg3.9.1, sg4.1.1, sg4.2.1 2	1,6,1,1,2,3,5,8 ,1,2,5,9,1,2	Post flowering	**Zheng *et al*., 2009**
Sorghum	4(9)	StgB, Stg1, Stg3 and Stg4	-------------------	Drougt tolerance-improving yield	**Kassahun *et al.,* 2010**
	61	-----------------------------	------------------	Post rainy	**Rama Reddy *et al.,*2014**
Barley	10	-----------------------------	3H,4H,5H,6H and 7H	6- terminal heat-stress , 4- terminal water stress	**Gous *et al*., 2016**

The understanding of stay-green traits in plants is fundamental for unraveling the mechanisms that enable prolonged photosynthetic activity, thus contributing to enhanced crop productivity and stress tolerance (Hortensteiner *et al.,* 2011). In (Table 1), several key genes associated with stay-green phenotypes are outlined, each playing a crucial role in chlorophyll degradation and related processes. For instance, SGR (Stay-Green) controls the binding of light-harvesting chlorophyll a/b-binding proteins (LHCII) and catabolic enzymes., thereby stabilizing the catabolic complex essential for chlorophyll breakdown. Similarly, genes like NYC (Non-yellow coloring) and PPH *(Phaeophytinase*) are involved in the stepwise transformation of *chl b* to *chl a* and the dephytylation of phaeophytin, respectively. These molecular components collectively contribute to the maintenance of chlorophyll levels and leaf greenness during plant senescence.In addition to understanding the genetic basis of stay-green traits, the identification of QTLs affliated with these attributes further elucidates their importance in crop improvement. (Table 2) highlights QTLs related to stay-green characteristics identified in various cereal and other crops (Xu *et al.,* 2000). These QTLs, such as *QSg.bhu-1A* in wheat and TCS4 in rice (Park *et* *al.,* 2003), have been linked to improvements in yield potential, particularly under stress conditions like drought. Identifying genomic regions associated with stay-green traits allows researchers to use MAS to incorporate beneficial alleles into elite germplasm, accelerating the development of improved crop varieties.

3.2.3. CRISPR and Gene Editing Technologies

To improve agriculture for future generations, genetic modification technology needs to accelerate domestication. Due to rising food demand, only 15 out of 30,000 edible plants meet 70% of human calorie requirements, highlighting the need for genetic diversity. For this purpose, CRISPR Cas technology provides fast crop variety enhancement. Bacterial type II Cas nine systems have been widely utilized in agricultural research to address several stress, increase production, resist herbicides and diseases, and improve nutrition (Matinvafa *et al.,* 2023). This technology has revolutionized plant genome editing by enabling precise, efficient, and targeted modifications of specific genes. This technology holds immense potential for editing stay-green genes, which are crucial for improving crop resilience to environmental stresses. By altering these genes, CRISPR can help to the development of stress-resistant, high-yielding crops. Recently, researchers successfully utilized this system to modify the lettuce genome by targeting two genes involved in chlorophyll metabolism. The SGR gene encipher a Magnesium -dechelatase enzyme which catalyzes the degradation of chlorophyll a (Chl a). Meanwhile, *BCM* functions as a scaffold protein, playing a pivotal role in maintaining chlorophyll levels by regulating both its synthesis and degradation. Our lssgr lettuce mutant displayed a stay-green phenotype, which has the potential to minimize postharvest food waste (Ito et al. 2024). As in tomato also, The SlSGR1 gene enrolling in the color change during tomato fruit ripening. Using this genome editing to knock out SlSGR1 expression resulted in fruits with a distinct wild fruits have a murky brown color and substantially higher quantities of green pigment and carotenoids. (Ma *et al.,* 2022). A chimeric Cas9-VirD2 protein was designed to enhance HDR performance in plants.VirD2, a bacterial protein, cuts the Ti plasmid at specific sites (Wang *et al.,* 2021b).This method was used to precisely edit the OsALS gene in rice, conferring herbicide resistance (Zafar *et al.,*2023). Moreover, introducing a donor DNA template and a geminivirus-based system enhanced glyphosate resistance in rapeseed (Wu *et al.,* 2020).

4. Applications in Crop Improvement

4.1. Breeding Stay-Green Varieties

4.1.1. Case Studies

Stay Green (SG) is a crucial trait where plants maintain photosynthesis after flowering, even under stress. Stay-green plants exhibit extended grain-filling periods, leading to higher yields. The SG trait has been identified as a valuable characteristic for commercial breeding of cereals, helping to address current yield stagnation while enhancing yield flexibility and stability. Breeding for functional SG has contributed to improved agricultural productivity, especially when paired with other advantageous traits. (Kamal *et al.,* 2019).

Rice

(Reynolds *et al* ., 2010) investigated drought tolerance in rice by examining three "stay-green" (SG) mutants derived from the wild-type rice, Nagina 22 (N22). The stay-green characteristic of the mutants was confirmed through dark-induced senescence experiments. Researchers evaluated the mutants' performance under both normal and drought conditions by measuring agronomic traits, the activity of enzymes related to oxidative stress, and the expression levels of 15 genes associated with chlorophyll breakdown and senescence. Whole-genome sequencing provided the genetic information for these candidate genes. Two mutants, SGM-1 and SGM-2, showed a complete absence of senescence, while SGM-3 exhibited delayed senescence. Gene expression in the mutants remained relatively stable over time, unlike the wild type. However, SGM-3 showed a significant increase in ATG6a gene expression over time. While all rice varieties performed better under drought, only SGM-3 produced a higher grain yield. Under drought conditions, all 15 genes were over expressed, with N22 and SGR-30 showing the highest levels of up-regulation.

Sorghum

According to (Crasta *et al.,* 1995), sorghum is the 5th significant cereal crop, after remaining prime cereal crops . Most US sorghum is grown without irrigation, making water availability the main yield limiter. Drought stress impacts sorghum differently depending on the growth stage. Post-flowering drought often causes leaves to prematurely age, especially during grain development. Genetic studies show that the stay-green trait, which delays leaf aging, is primarily controlled by a single dominant gene. (Mwamahonje *et al.,* 2021) certain sorghum varieties exhibit the stay-green trait, where green, productive leaves are maintained under drought stress during grain filling, making the crop essential for ensuring food and nutritional security. Conventional methods rely on phenotyping the SG trait, being complex due to its polygenic nature, environmental interactions. MAS, involves QTL mapping and introgression of stay-green traits into senescent varieties through MABS, guided by field phenotypic data.

Wheat

(Christopher *et al.,* 2018) had been Stay-green wheat maintains green leaves longer after flowering, boosting biomass and yield. Developing stay-green wheat varieties can increase yields under drought stress while maintaining productivity in other conditions. This trait might arise from early changes in plant structure (canopy and roots). The objective of this study was to identify genetic regions (QTLs) associated with SG traits in a doubled haploid wheat population, including leaf greenness, senescence onset and duration, and senescence rate, across eight subtropical environments. The relationship between these stay-green traits and yield varied depending on drought conditions.

Maize

(Trachsel *et al.,* 2016) focuses on identifying genetic regions that influence phenotypic variation of the trait associated with vitality and SG traits that contribute to drought tolerance in tropical maize. By analyzing two connected advanced backcross populations, the researchers aimed to uncover genetic factors that enhance early growth and delay senescence under drought conditions. The identification of these QTLs provides valuable insights for breeding programs targeting improved water defecit endurance in tropical one. The findings highlight the potential of marker-assisted selection in developing maize varieties with enhanced early vigor and stay-green traits, contributing to increased resilience against drought stress. It advances our knowledge on heritable basis of drought tolerance in maize and offers practical applications for crop improvement in water-limited environments.

Cucumber

(Dong *et al*., 2023) studied the genetic basis of low-temperature (LT) tolerance in cucumbers. Using genome-wide association, a specific genetic variation (SNP) within the *STAYGREEN* (*CsSGR*) gene, located at the *gLTT5.1* locus, was identified as being linked to LT tolerance. CRISPR-Cas9 gene editing was used to create *CsSGR* knockout mutants, which displayed improved LT tolerance, specifically by maintaining higher chlorophyll levels and accumulating less harmful reactive oxygen species (ROS) under cold stress. The *CsSGR* gene was found to be activated by the *CsCBF1* transcription factor. Further investigation revealed that the LT-sensitive version of *CsSGR* (*CsSGRHapA*), unlike the LT-tolerant version (*CsSGRHapG*), interacts with *CsNYC1* to promote chlorophyll breakdown.

Tomato

(Yang *et al*., 2023) Research has identified that mutations in the STAY-GREEN 1 (SGR1) gene inhibit chlorophyll degradation during tomato fruit ripening. This inhibition leads to the retention of chlorophyll, and when combined with the accumulation of lycopene, results in a brown or "green flesh" phenotype. A study titled "Recoloring Tomato Fruit by CRISPR/Cas9-Mediated Multiplex Gene Editing" demonstrated that targeted mutations in the SGR1 gene, along with other genes involved in pigment biosynthesis, can effectively alter fruit coloration.

4.1.2. Challenges and Opportunities

The intricate interactions between traits and environmental variability make precise trait predictions difficult. Smaller breeding programs with constrained resources often face challenges in accessing advanced technologies. Overcoming these obstacles requires coordinated efforts and collaboration among scientists, breeders, policymakers, and other stakeholders (Chaudhary *et al.,*2024).The challenge in introgressing these QTLs lies in the low level of genetic polymorphism between the both parents. The understanding of the stay-green trait and the genetic regulation of mechanisms underlying its expression in sorghum remains incomplete. For example, recent findings showed that alleles from the B35 (BTx642) donor parent at the stay-green QTL Stg1 enhanced water extraction in the moderately senescent caudatum variety S35 but did not have the same effect in the highly senescent durra variety R16. This highlights the need to identify optimal germplasm donors for each component which may vary depending on genetic forms as well as specific external conditions where improved drought tolerance is sought. The lack of alternative SSRs and limited polymorphism posed a significant challenge. Many of the stay-green QTLs targeted for introgression were associated with broad confidence intervals between flanking markers, combined with a lack of flanking SSR polymorphisms between the donor and recurrent parents. (Vadez *et al.,* 2013).

Early maturation in wheat is advantageous for avoiding abiotic stresses such as drought and heat, thereby enhancing resilience in unpredictable climates. However, accelerating the growth cycle can lead to reduced biomass accumulation, potentially compromising grain yield and quality. This trade-off necessitates a careful balance between achieving early maturity and maintaining optimal yield and quality. Discussion emphasizes the importance of understanding the genetic and physiological mechanisms underlying early maturation to develop wheat varieties that can effectively balance these competing factors. By identifying and manipulating specific genetic determinants, breeders can aim to produce early-maturing wheat cultivars that do not sacrifice yield or quality, thereby meeting the demands of both farmers and consumers. While early maturation offers significant benefits in adapting to changing environmental conditions, it presents challenges that require a nuanced approach to wheat breeding, ensuring that the advantages of early maturity do not come at the expense of other critical agronomic traits (Singh *et al.,*2024).

Breeding crops with the SG attributes , presents notable challenges due to trade-offs with other agronomic traits. For instance, while stay-green can enhance drought tolerance by maintaining photosynthetic activity during stress, it may also reduce nitrogen remobilization efficiency, potentially impacting grain filling and yield. Furthermore, the leaf longivety trait has been linked to reduced tillering and altered stomatal behavior in sorghum, which could affect overall plant architecture and water use efficiency. Future research opportunities include dissecting the various mechanisms underlying this trait to mitigate these trade-offs. Advancements in molecular breeding and genomic selection could facilitate the development of stay-green varieties that maintain yield and quality. Moreover, exploring the interaction between stay-green traits and environmental factors may provide insights for optimizing crop performance under varying conditions (Lu *et al.,* 2024).

4.1.3. Significance of stay green

4.1.3.1. Stay-green attribute vital for crop resilience and productivity

The stay-green trait in plants is indispensable in diverse agricultural and ecological settings, particularly in environments where plants encounter stressors or constraints that can impede their growth and productivity (Rosenow *et al.,* 1983) and (Wahid *et al.,* 2007). Specifically, it is important in drought and heat stress conditions to maintain leaf greenness over an extended period, especially throughout the grain loading stage, thereby enhancing grain yield (Spano *et al.,* 2003).

4.3.1.2. Significance of stay-green traits in agricultural and horticultural crops

Their performance extends across both agronomical and horticultural crops, offering multifaceted advantages crucial for sustainable agriculture. In agronomical crops, delayed senescence, particularly in stay-green plants, emerges as a cornerstone for enhancing yield and biomass production. This trait facilitates elevated nitrogen uptake during grain filling, a pivotal stage for crop productivity, compared to senescent genotypes (Gregersen *et al.,* 2008). Moreover, stay-green genotypes exhibit enhanced nutrient uptake and utilization by postponing leaf senescence, thus optimizing resource allocation, especially in nutrient-deficient soils. As climate change increases the frequency and intensity of weather events, agronomic crops' resilience becomes critical, with stay-green features playing a crucial role in enabling improved adaptation to changing climatic conditions. (Borrell *et al.,* 2014). Additionally, the sustained activity of leaves in stay-green crops mitigates the need for excessive fertilizer and irrigation, promoting more sustainable agricultural practices (Thomas and Howarth, 2000). Furthermore, the trait contributes to lodging resistance and bolsters resilience against biotic and abiotic stresses, ensuring crop stability and productivity in challenging environments.

In horticultural crops, the importance of stay-green traits transcends mere productivity and extends to enhancing market value and produce quality. The preservation of greenness prolongs the harvest period and improves the marketability of fruits, vegetables, and ornamental plants. Various approaches, including manipulation of hormone levels or responses in transgenic plants, have been employed to mitigate postharvest yellowing, thereby extending post-harvest shelf life and facilitating long-term transportation. By maintaining visual appeal and quality, stay-green traits boost market value and reduce post-harvest losses, ensuring economic viability and endurability throughout the agricultural supply chain.

4.2. Phenotyping Technologies for Stay-Green Traits

4.2.1. High-Throughput Phenotyping

Plant breeding is a lengthy and expensive process, constrained by several factors. These include the breeder's confidence in the selected phenotype and its relationship to the underlying genotype, as well as the capacity to anticipate phenotypic performance across different conditions. By focusing on variables that capture dynamic fluctuations in leaf greenness and canopy architecture, we may be able to link stay-green features to changes in leaf area and N remobilization during grain loading. To assist with this, the CSIRO High Resolution Plant Phenomics Centre created a portable Phenomobile that incorporates a Greenseeker® for precise NDVI measurement and LiDAR to analyze the vertical distribution of green leaf biomass and leaf area throughout the canopy. With Global Positioning System –linked spatial coding, the device can rapidly and non-destructively assess canopy architecture traits across one hectare of breeding lines (approximately 1,000 plots) in under an hour. For instance, the evolution of NDVI during grain filling was evaluated for sixty four wheat genotypes with contrasting canopy architectures (Rebetzke *et al.,* 2016).

Advancements in high-throughput phenotyping (HTP) methods, particularly remote sensing and imaging technologies, have significantly enhanced the assessment of stay-green traits in crop breeding programs. These technologies allow for quick, precise, and non-harmful assessment of plant traits in large groups, facilitating the selection of desirable traits such as delayed senescence. Remote sensing tools, including multispectral and image spectroscopy, provide deep insights on plant health and physiology by measuring reflectance at various wavelengths. This allows for the monitoring of chlorophyll content and photosynthetic activity, which are indicative of stay-green traits. Imaging technologies, such as RGB cameras and thermal imaging, provide insights into canopy structure, leaf area, and temperature profiles, further informing assessments of plant vigor and stress responses.The integration of these HTP methods into breeding programs accelerates the identification and development of crop varieties with enhanced stay-green characteristics, contributing to improved yield stability and resilience under stress conditions. For example, in sorghum, HTP of dynamic canopy characteristics associated with SG has been successfully carried out utilizing these modern methods. (Liedtke *et al.,* 2020).

4.2.2. Field-Based Phenotyping

Observers have concentrated from base level enhancements in production potential to encourage this type of phenotyping. Below-ground it is a significant bottleneck, and novel methods for measuring root-related traits are necessary (Roitsch *et al.,* 2019).These platforms are widely acknowledged as the sole appliance capable of providing the necessary throughput in plant, as well as an An errorless depiction of characteristic expression in the real world.Plants in controlled circumstances often have substantially less soil volume than plants in the field, which has an impact on nutrition and water regimes, as well as disrupting normal growth and development patterns. Enclosed controlled surroundings make it difficult to describe reactions that might occur in the field. These include both ground and air-based techniques. Ground-based phenotyping platforms include adapted vehicles and detection equipment, also known as 'phenomobiles'. Outdoors, accessible photos provide information on canopy cover and hue.. Using a color threshold, an image processing method can predict canopy cover. In the outdoors, a stereo camera system or images from several sites enable extensive reconstruction and investigation of the canopy structure, providing crucial variables (Li *et al.,* 2014).

Field-based phenotyping is essential for understanding the expression of SG traits in crops under real-world conditions. Evaluating this trait in natural field environments allows researchers and breeders to observe how it interacts with variable factors such as soil type, climate, and management practices. By conducting phenotyping directly in the field, it is possible to assess the performance and adaptability of stay-green traits across diverse environmental conditions. Advances in robotic sensing platforms have aided HTP's success. The development of unmanned aircraft systems (UASs), often referred to as drones, has significantly advanced High-Precision Phenotyping (HPP). Red, Green, Blue, multispectral, hyperspectral, and infrared cameras are among the image sensors mounted on UAS. Advances in IoT sensors, such Field Server, have benefited HTP, underlining the necessity to understand G×E (genotype-environment interaction) (Ninomiya *et al.,* 2022). Machine learning advancements have allowed for fast phenotyping of crop stresses such as drought, pests, and diseases. These projects range in scale from the leaf to the field level. The success of disease evaluation employing ground mobile platforms, such as sugar beet cercospora leaf spot and wheat STB, has led to the widespread usage of such aircraft systems for field-level disease assessment using RGB and multispectral images with CNN. (Guo *et al.,* 2021).

5. Conclusion

5.1. Summary of Key Findings

Stay-green characteristics play an important role in improving crop resilience and yield under stress circumstances like drought, heat, and nutrient constraints. These traits, characterized by the delayed senescence of leaves, contribute to prolonged photosynthetic activity, improved resource use efficiency, and sustained biomass production during critical growth phases. Crops can maximize water and nutrient intake by keeping green foliage, while decreasing the deleterious consequences of stress-induced premature leaf loss. Stay-green traits also enhance grain filling and overall yield stability, making them invaluable in breeding programs aimed at improving food security. Furthermore, stay-green crops exhibit better root development, which enables deeper soil exploration for moisture and nutrients, crucial for survival in arid or degraded soils. Their ability to endure abiotic stresses without considerable loss in output is crucial in the context of climate change and increasing environmental unpredictability. These tarits also indirectly contribute to carbon sequestration, soil health,and ecosystem sustainability by extending vegetation cover. Modern molecular breeding and genetic engineering technologies have enabled the identification and inclusion of stay green features into numerous crop species, hence expediting the production of resistant cultivars.. The integration of these traits into crop improvement strategies aligns with global efforts to ensure sustainable agricultural systems. Stay-green traits thus represent a cornerstone in the developing crops resilient to harsh conditions, safeguarding food production for future generations

5.2. Implications for Sustainable Agriculture

The adoption of stay-green crops is a promising strategy to achieve sustainable agricultural systems that balance productivity with environmental conservation. By enhancing resource use efficiency, improving stress resilience, and mitigating environmental degradation, stay-green crops contribute to sustainable food production systems that can withstand the challenges of climate change. Their widespread adoption could significantly contribute to global food security while preserving ecological balance .Enhanced yield stability as improved grain filling and biomass production, ensuring stable yields even under stress conditions, consistent productivity, critical for meeting the growing global food demand despite erratic weather patterns. Stay-green (SG) traits are closely linked to improved tolerance to abiotic stresses such as drought, heat, and salinity. These crops utilize available water and nutrients more efficiently, making them resilient in water-scarce environments. Sustained chlorophyll content during heat stress ensures continued photosynthetic efficiency, mitigating yield losses caused by climate-induced stress. Resource Use Efficiency: Reduced transpiration losses and prolonged canopy greenness improve water use efficiency, Stay-green crops make better use of applied fertilizers by extending the photosynthetic phase, reducing nutrient runoff and environmental pollution. Mitigation of Climate Change Impacts such as Sequestering carbon, Prolonged green foliage increases the duration of carbon capture through photosynthesis and Efficient use of inputs like water and fertilizers decreases emissions associated with intensive farming practices. Contribution to Food Security in the form of resilience of stay-green crops ensures reliable food production in regions affected by climate variability reffering to Adaptability and Improved storage and quality i.e., Extended leaf greenness can lead to higher-quality grains and longer post-harvest shelf life, ensuring food availability. Promoting Sustainable Farming System in which crops support long-term soil health by reducing soil erosion and improving organic matter content.

References

Abdelrahman, M., El-Sayed, M., Jogaiah, S., Burritt, D. J., & Tran, L. S. P. (2017). The "STAY- GREEN" trait and phytohormone signaling networks in plants under heat stress. *Plant Cell Reports*, *36*, 1009-1025.

Ahlawat, S., Chhabra, A. K., Behl, R. K., & Bisht, S. S. (2008). *South Pacific Journal of Natural Sciences*, 26:73-81

Begna, T. (2021). Impact of drought stress on crop production and its management options. *International Journal of Research in Agronomy*, *4*(2). http://dx.doi.org/10.20431/2454-6224.0812001

Borrell, A. K., Hammer, G. L., & Henzell, R. G. (2000). Does maintaining green leaf area in sorghum improve yield under drought? I. Leaf growth and senescence. Crop Science, 40(4), 1037–1048.

Cha, K. W., Lee, Y. J., Koh, H. J., Lee, B. M., Nam, Y. W., & Paek, N. C. (2002). A simple method for extracting high-quality DNA from rice seeds*. Theoretical and Applied Genetics*, 104(3-4), 526– 532.

Chaudhary, D., Pal, N., Arora, A., Prashant, B. D., & Venadan, S. (2024). Plant Functional Traits in Crop Breeding: Advancement and Challenges. In *Plant Functional Traits for Improving Productivity* (pp. 169-202). Singapore: Springer Nature Singapore.

Chhipa, H. (2019). Mycosynthesis of nanoparticles for smart agricultural practice: A green and eco-friendly approach. In: Shukla, A., & Iravani, S. (eds.) Green Synthesis, Characterization and Applications of Nanoparticles (1st edition). Elsevier Inc., pp. 87–109

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*(2), 276.)

Christopher, J. T. (2008). Stay-green traits to improve wheat adaptation in well-watered and water-limited environments. Journal of Experimental Botany, 59(13), 3537-3546.

Christopher, M., Chenu, K., Jennings, R., Fletcher, S., Butler, D., Borrell, A., & Christopher, J. et al. (2018). QTL for stay-green traits in wheat in well-watered and water-limited environments. *Field crops research*, *217*, 32-44. https://doi.org/10.1016/j.fcr.2017.11.003

Crasta, O. R. (1995). *Molecular genetic analysis of stay-green, a post-flowering drought resistance trait in grain sorghum (Sorghum bicolor L. Moench)*. Texas Tech University.

Das, K., & Roychoudhury, A. (2014). Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. *Frontiers in environmental science*, *2*, 53. http://www.frontiersin.org/Environmental_Science/editorialboard

Das, S., Roy, N., Chakraborty, I., Sutradhar, M., & Sarma, D. SIGNIFICANCE OF STAY-GREEN TO FOSTER CROP PRODUCTION UNDER STRESS ENVIRONMENT-A MINI-REVIEW.

Dong, S., Li, C., Tian, H., Wang, W., Yang, X., Beckles, D. M., ... & Zhang, S. (2023). Natural variation in STAYGREEN contributes to low-temperature tolerance in cucumber. *Journal of Integrative Plant Biology*, *65*(12), 2552-2568.

Fu, J. D., Yan, Y. F., Kim, M. Y., Lee, S. H., & Lee, B. W. (2011). Population-specific quantitative trait loci mapping for functional stay-green trait in rice (Oryza sativa L.). *Genome*, *54*(3), 235-243.

Gous, P. W., Hickey, L., Christopher, J. T., Franckowiak, J., & Fox, G. P. (2016). Discovery of QTL for stay-green and heat-stress in barley (Hordeum vulgare) grown under simulated abiotic stress conditions. *Euphytica*, *207*(2), 305-317.

Grbić, V., & Bleecker, A. B. (1995). Ethylene regulates the timing of leaf senescence in Arabidopsis. The Plant Journal, 8(4), 595-602. https://doi.org/10.1046/j.1365-313X.1995.8040595.x

Gregersen, P. L., Culetic, A., Boschian, L., & Krupinska, K. (2008). Plant senescence and crop productivity. Plant Molecular Biology, 67(1-2), 37-48.

Guo, W., Carroll, M. E., Singh, A., Swetnam, T. L., Merchant, N., Sarkar, S., ... & Ganapathysubramanian, B. (2021). UAS-based plant phenotyping for research and breeding applications. *Plant Phenomics*.

Haider, M. S., Jaskani, M. J., & Fang, J. (2021). Overproduction of ROS: underlying molecular mechanism of scavenging and redox signaling. In *Biocontrol Agents and Secondary Metabolites* (pp. 347-382). Woodhead Publishing. https://doi.org/10.1016/B978-0-12-822919-4.00014-4

Hilli, H.J. and Immadi, S.U. 2021. Evaluation of stay-green sunflower lines and their hybrids for yield under drought conditions.

Hiremath, G., & Nadaf, H. L. (2017). Assessment of stay green genotypes of sunflower for root traits under different soil moisture regimes. *Int. J. Curr. Microbiol. App. Sci*, *6*(11), 1156-1166.

Hönig, M., Plíhalová, L., Husičková, A., Nisler, J., & Doležal, K. (2018). Role of cytokinins in senescence, antioxidant defence and photosynthesis. *International journal of molecular sciences*, *19*(12), 4045.

Hörtensteiner, S., & Kräutler, B. (2011). Chlorophyll breakdown in higher plants. Biochimica et Biophysica Acta (BBA) - *Bioenergetics*, 1807(8), 977–988. https://doi.org/10.1016/j.bbabio.2010.12.007

Ito, T., Yamatani, H., Nobusawa, T., & Kusaba, M. (2024). Development of a CRISPR-Cas9-Based Multiplex Genome-Editing Vector and Stay-Green Lettuce. In *Gene Editing in Plants: CRISPR-Cas and Its Applications* (pp. 405-414). Singapore: Springer Nature Singapore.

Jajic, I., Sarna, T., & Strzalka, K. (2015). Senescence, stress, and reactive oxygen species. *Plants*, *4*(3), 393-411. https://doi.org/10.3390/plants4030393

Janni, M., Maestri, E., Gullì, M., Marmiroli, M., & Marmiroli, N. (2024). Plant responses to climate change, how global warming may impact on food security: a critical review. *Frontiers in Plant Science*, *14*, 1297569. https://doi.org/10.3389/fpls.2023.1297569

Jiang, H. W., Li, M. R., Liang, N. B., Yan, H. B., Wei. Y. L., Xu, X., Liu, J. F., Xu, Z., Chen, F., & Wu, G. J. (2007). Molecular cloning and expression analysis of eight PgDREB genes from Panax ginseng responsive to abiotic stresses. *The Plant Journal*, 52(2), 197–209.

Kalra, A., Goel, S., & Elias, A. A. (2024). Understanding role of roots in plant response to drought: Way forward to climate-resilient crops. *The Plant Genome*, *17*(1), e20395.

Kamal, N. M., Gorafi, Y. S. A., Abdelrahman, M., Abdellatef, E., & Tsujimoto, H. (2019). Stay-green trait: a prospective approach for yield potential, and drought and heat stress adaptation in globally important cereals. *International journal of molecular sciences*, *20*(23), 5837. https://doi.org/10.3390/ijms20235837

Kang, J., Hao, X., Zhou, H., & Ding, R. (2021). An integrated strategy for improving water use efficiency by understanding physiological mechanisms of crops responding to water deficit: Present and prospect. *Agricultural Water Management*, *255*, 107008. https://doi.org/10.1016/j.agwat.2021.107008

Kassahun, B., Bidinger, F. R., Hash, C. T., & Kuruvinashetti, M. S. (2010). Stay-green expression in early generation sorghum [Sorghum bicolor (L.) Moench] QTL introgression lines. *Euphytica*, *172*, 351-362.

Khanna-Chopra, R., Nutan, K. K., & Pareek, A. (2013). Regulation of leaf senescence: role of reactive oxygen species. In *Plastid development in leaves during growth and senescence* (pp. 393-416). Dordrecht: Springer Netherlands.DOI 10.1007/978-94-007-5724-0_17.

Kumar, U., Joshi, A. K., Kumari, M., Paliwal, R., Kumar, S., & Röder, M. S. (2010). Identification of QTLs for stay green trait in wheat (Triticum aestivum L.) in the 'Chirya 3'×'Sonalika'population. *Euphytica*, *174*, 437-445.

Kumari, M., Dubey, A. K., Kumar, R., & Kumar, A. (2024). Marker-assisted selection in plant breeding for stress tolerance. In *Improving Stress Resilience in Plants* (pp. 371-387). Academic Press.

Li, L., Zhang, Q., & Huang, D. (2014). A review of imaging techniques for plant phenotyping. *Sensors*, *14*(11), 20078-20111. https://doi.org/10.3390/s141120078

Liedtke, J. D., Hunt, C. H., George-Jaeggli, B., Laws, K., Watson, J., Potgieter, A. B., ... & Jordan, D. R. (2020). High-throughput phenotyping of dynamic canopy traits associated with stay-green in grain sorghum. *Plant Phenomics*. https://doi.org/10.34133/2020/4635153

Liedtke, J. D., Hunt, C. H., George-Jaeggli, B., Laws, K., Watson, J., Potgieter, A. B., ... & Jordan, D. R. (2020). High-throughput phenotyping of dynamic canopy traits associated with stay-green in grain sorghum. *Plant Phenomics*. https://doi.org/10.34133/2020/4635153

Lim, P. O., Kim, H. J., & Nam, H. G. (2007). Leaf senescence. Annual Review of Plant Biology, 58, 115-136.

Lu, J. (2024). *Traits and trade-offs: dissecting nitrogen use efficiency in maize using plant modeling* (Doctoral dissertation, Wageningen University).

Ma, L., Zeng, N., Cheng, K., Li, J., Wang, K., Zhang, C., & Zhu, H. (2022). Changes in fruit pigment accumulation, chloroplast development, and transcriptome analysis in the CRISPR/Cas9-mediated knockout of Stay-green 1 (slsgr1) mutant. *Food Quality and Safety*, *6*, fyab029. https://doi.org/10.1093/fqsafe/fyab029

Mahalakshmi, V., & Bidinger, F. R. (2002). Identification of QTLs for grain yield of pearl millet [*Pennisetum glaucum* (L.) R. Br.] in environments with variable moisture during grain filling. Crop Science, 42(3), 965–974.

Matinvafa, M. A., Makani, S., Parsasharif, N., Zahed, M. A., Movahed, E., & Ghiasvand, S. (2023). CRISPR-Cas technology secures sustainability through its applications: a review in green biotechnology. *3 Biotech*, *13*(11), 383.

Mbava, N., Mutema, M., Zengeni, R., Shimelis, H., & Chaplot, V. J. A. W. M. (2020). Factors affecting crop water use efficiency: A worldwide meta-analysis. *Agricultural Water Management*, *228*, 105878. https://doi.org/10.1016/j.agwat.2019.105878

Mohanty, L. K., Singh, N. K., Raj, P., Prakash, A., Tiwari, A. K., Singh, V., & Sachan, P. (2024). Nurturing crops, enhancing soil health, and sustaining agricultural prosperity worldwide through agronomy. *Journal of Experimental Agriculture International*, *46*(2), 46-67.DOI: 10.9734/JEAI/2024/v46i22308

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*(4), 790. https://doi.org/10.3390/en13040790

Mwamahonje, A., Eleblu, J. S. Y., Ofori, K., Deshpande, S., Feyissa, T., & Tongoona, P. (2021). Drought tolerance and application of marker-assisted selection in sorghum. *Biology*, *10*(12), 1249.

Nakamura, M., Nobuyoshi, M., & Nagatan (2000). Role of cytokinins in the regulation of senescence in detached rice leaves. *Plant Cell Physiology*, 41(1), 94-103.

Naz, M., Hussain, S., Zaib, S., Zubair, A., Tariq, M., Dai, Z., & Du, D. (2023). Cereal Performance and Senescence. *Cereal Crops*, 67-78

Ninomiya, S. (2022). High-throughput field crop phenotyping: current status and challenges. *Breeding Science*, *72*(1), 3-18. doi: 10.1270/jsbbs.21069

Park, J. H., & Lee, B. W. (2003). Study on the growth and leaf area index of the cultivars of rice *(Oryza sativa* L.) in plastic house condition. *Journal of Crop Science*, 48, 216–223.

Prajapati, H. A., Yada, K., Hanamasagar, Y., Kumar, M. B., Khan, T., Belagalla, N., ... & Malathi, G. (2024). Impact of climate change on global agriculture: Challenges and adaptation. *International Journal of Environment and Climate Change*, *14*(4), 372-379. https://doi.org/10.9734/ijecc/2024/v14i44123

Prasad, V. R., Govindaraj, M., Djanaguiraman, M., Djalovic, I., Shailani, A., Rawat, N., ... & Prasad, P. V. (2021). Drought and high temperature stress in sorghum: Physiological, genetic, and molecular insights and breeding approaches. *International Journal of Molecular Sciences*, *22*(18), 9826. https://doi.org/10.3390/ijms22189826

Rama Reddy, N. R., Ragimasalawada, M., Sabbavarapu, M. M., Nadoor, S., & Patil, J. V. (2014). Detection and validation of stay-green QTL in post-rainy sorghum involving widely adapted cultivar, M35-1 and a popular stay-green genotype B35. *BMC genomics*, *15*, 1-16.

Rebetzke, G. J., Jimenez-Berni, J. A., Bovill, W. D., Deery, D. M., & James, R. A. (2016). High-throughput phenotyping technologies allow accurate selection of stay-green. *Journal of experimental botany*, *67*(17), 4919-4924. https://doi.org/10.1093/jxb/erw301

Reynolds, M. P., Hays, D., & Chapman, S. (2010). Breeding for adaptation to heat and drought stress. In *Climate change and crop production* (pp. 71-91). Wallingford UK: CABI.

Roitsch, T., Cabrera-Bosquet, L., Fournier, A., Ghamkhar, K., Jiménez-Berni, J., Pinto, F., & Ober, E. S. (2019). New sensors and data-driven approaches—A path to next generation phenomics. *Plant Science*, *282*, 2-10. https://doi.org/10.1016/j.plantsci.2019.01.011

Rosenow, D. T., Quisenberry, J. E., Wendt, C. W., & Clark, L. E. (1983). Drought tolerant sorghum and cotton germplasm. Agricultural Water Management, 7, 207–222.

Sakuraba, Y., Li, J., Park, S., & Paek, N. C. (2020). Regulatory mechanisms of leaf senescence under environmental stresses. *Frontiers in Plant Science*, *11*, 1293.https://doi.org/10.3389/fpls.2020.01293

Sakuraba, Y., Park, S. Y., Kim, Y. S., Wang, S. H., Yoo, S. C., Hörtensteiner, S., & Paek, N. C. (2014). Arabidopsis STAY-GREEN2 is a negative regulator of chlorophyll degradation during leaf senescence. *Molecular plant*, *7*(8), 1288-1302.

Schippers, J. H., Schmidt, R., Wagstaff, C., & Jing, H. C. (2015). Living to die and dying to live: the survival strategy behind leaf senescence. Plant Physiology, 169(2), 914-930. https://doi.org/10.1104%2Fpp.15.00498

Shafi, S., Shafi, I., Zaffar, A., Zargar, S. M., Shikari, A. B., Ranjan, A., & Sofi, P. A. (2023). The resilience of rice under water stress will be driven by better roots: Evidence from root phenotyping, physiological, and yield experiments. *Plant Stress*, 100211.

Shang, M., & Xie, J. (2024). Agricultural sustainable development: Soil, water resources, biodiversity, climate change, and technological innovation. *Advances in Resources Research*, *4*(2), 181-204. DOI: 10.50908/arr.4.2_181

Silva, S. A., Carvalho, FIF, Nedel, J. L., Vasconcellos, NJS, Cruz, P. J., Simioni, D., & Silva, JAG (2004). Differential levels of pigmentation affect morphological and anatomical traits in corn (*Zea mays* L.) seedlings. *Ciência Rural*, 34(3), 679-683.

Silva, S. A., Carvallo, FIF., Caetano, V. R., Oliveira, A. C., Coimbra, JLM., Vasconcellos, NJS., & Lorencetti, C. (2001). A comparison of root system morphology and anatomy of ratooning and non- ratooning sugarcane cultivars. *Journal of New Seeds*, 2(2), 55-68.

Singh, C., Yadav, S., Khare, V., Gupta, V., Kamble, U. R., Gupta, O. P., & Tiwari, R. (2024). Unraveling the Secrets of Early-Maturity and Short-Duration Bread Wheat in Unpredictable Environments. *Plants*, *13*(20), 2855. https://doi.org/10.3390/plants13202855

Snowdon, R. J., Wittkop, B., Chen, T. W., & Stahl, A. (2021). Crop adaptation to climate change as a consequence of long-term breeding. *Theoretical and Applied Genetics*, *134*(6), 1613-1623. https://doi.org/10.1007/s00122-020-03729-3

Sofi, P. A., Rehman, K., Gull, M., Kumari, J., Djanaguiraman, M., & Prasad, P. V. V. (2021). Integrating root architecture and physiological approaches for improving drought tolerance in common bean (Phaseolus vulgaris L.). *Plant Physiology Reports*, *26*, 4-22.

Spano, G., Di Fonzo, N., Perrotta, C., Platani, C., Ronga, G., Lawlor, D. W. & Napier, J. A., & Shewery, P. R. (2003). Physiological characterization of ‘stay green’ mutants in durum wheat. Journal of Experimental Botany, 54(383), 1415-1420.

Thomas, H. & Howarth, C. J. (2000). Senescence in wheat: the use of mutants to probe leaf development and photosynthesis. *Journal of Experimental Botany*, 51:329–337.

Thomas, H. and Ougham, H. (2014). Senescence and crop performance. In: Sadras VO, CalderiniDF, eds. *Crop physiology*. Applications for genetic improvement, agronomy and farming systems, 2nd edn. New York: Academic Press

Toromade, A. S., Soyombo, D. A., Kupa, E., & Ijomah, T. I. (2024). Reviewing the impact of climate change on global food security: Challenges and solutions. *International Journal of Applied Research in Social Sciences*, *6*(7), 1403-1416. DOI: 10.51594/ijarss.v6i7.1300

Trachsel, S., Sun, D., SanVicente, F. M., Zheng, H., Atlin, G. N., Suarez, E. A., & Zhang, X. et al. (2016). Identification of QTL for early vigor and stay-green conferring tolerance to drought in two connected advanced backcross populations in tropical maize (Zea mays L.). *PloS one*, *11*(3), e0149636. https://doi.org/10.1371/journal.pone.0163400

Vadez, V., Deshpande, S., Kholova, J., Ramu, P., & Hash, C. T. (2013). Molecular breeding for stay-green: Progress and challenges in sorghum. *Translational genomics for crop breeding: abiotic stress, yield and quality*, *2*, 125-141.

Verma, V., & Jha, P. (2020). Deciphering the genetic basis of stay-green trait in crops. Plant Physiology and Biochemistry, 151, 54-64.

Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. (2007). Heat tolerance in plants: An overview. Environmental and

Experimental Botany, 61(3), 199-223.

Walters, D. R., McRoberts, N., & Fitt, B. D. (2008). Are green islands red herrings? Significance of green islands in plant interactions with pathogens and pests. Biological Reviews, 83(1), 79-102. https://doi.org/10.1111/j.1469-185X.2007.00033.

Wang Z, Wan L, Xin Q et al (2021b) Optimizing glyphosate tolerance in rapeseed by CRISPR/Cas9-based geminiviral donor DNA replicon system with Csy4-based single-guide RNA processing. J Exp Bot 72:4796–4808. https://doi.org/10.1093/jxb/erab167

Woo, H. R., Kim, H. J., Nam, H. G., & Lim, P. O. (2013). Plant leaf senescence and death–regulation by multiple layers of control and implications for aging in general. *Journal of cell science*, *126*(21), 4823-4833. doi: 10.1242/jcs.109116

Wu J, Chen C, Xian G et al (2020) Engineering herbicide-resistant oilseed rape by CRISPR/Cas9-mediated cytosine base-editing. Plant Biotechnol J 18:1857–1859. https://doi.org/10.1111/pbi.13368

Xu, W., Subudhi, P. K., Crasta, O. R., Rosenow, D. T., Mullet, J. E., & Nguyen, H. T. (2000). Molecular mapping of QTLs conferring stay-green in grain sorghum (*Sorghum bicolor* L. Moench). *Genome*, 43(3), 461–469.

Yang, K., Sun, H., Liu, M., Zhu, L., Zhang, K., Zhang, Y., & Li, C. (2023). Morphological and physiological mechanisms of melatonin on delaying drought-induced leaf senescence in cotton. *International Journal of Molecular Sciences*, *24*(8), 7269.)

Zafar K, Khan MZ, Amin I, et al (2023) Employing template-directed CRISPR-based editing of the OsALS gene to create herbicide tolerance in Basmati rice. AoB Plants 15:. https://doi.org/10. 1093/aobpla/plac059

Zheng, H. J., Wu, A. Z., Zheng, C. C., Wang, Y. F., Cai, R., Shen, X. F., & Dong, S. T.et al. (2009). QTL mapping of maize (Zea mays) stay-green traits and their relationship to yield. *Plant breeding*, *128*(1), 54-62.