

Leaf Senescence in Rice

Subjects: Plant Sciences

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Leaf senescence, which is the last developmental phase of plant growth, is controlled by multiple genetic and environmental factors. Leaf yellowing is a visual indicator of senescence due to the loss of the green pigment chlorophyll. During senescence, the methodical disassembly of macromolecules occurs, facilitating nutrient recycling and translocation from the sink to the source organs, which is critical for plant fitness and productivity. Leaf senescence is a complex and tightly regulated process, with coordinated actions of multiple pathways, responding to a sophisticated integration of leaf age and various environmental signals. Many studies have been carried out to understand the leaf senescence-associated molecular mechanisms including the chlorophyll breakdown, phytohormonal and transcriptional regulation, interaction with environmental signals, and associated metabolic changes. The metabolic reprogramming and nutrient recycling occurring during leaf senescence highlight the fundamental role of this developmental stage for the nutrient economy at the whole plant level. The strong impact of the senescence-associated nutrient remobilization on cereal productivity and grain quality is of interest in many breeding programs.

Keywords: rice ; leaf senescence ; productivity ; chlorophyll breakdown ; stay-green ; transcription factors ; phytohormones ; nitrogen remobilization

1. Introduction

Leaf senescence is easily observed because Chl degradation leads to leaf yellowing ^[1]. Stay-green is the heritable delayed senescence phenotype observed in comparison with a reference genotype, and *stay-green* mutants refer to genotypes that retain green leaves during senescence ^{[2][3]}. Maintaining leaf Chl levels and active photosynthetic capacity extends the time for assimilation processes and grain development, thereby increasing crop yield ^{[4][5]}. The genetic and physiological ways to obtain seemingly similar stay-green phenotypes are diverse, and five types of stay-green plants have been reported ^[2]. Their differences are based on the Chl behavior during senescence and their photosynthetic activities ^{[2][6]}.

2. Development

The Type A stay-green plants initiate senescence late but lose Chl at a normal rate. In Type B stay-green plants, senescence is started on schedule, but thereafter, the decline of the photosynthetic activity is comparatively slower than in WT. In Type C stay-green plants, Chl may be retained more or less indefinitely because of defects in pigment breakdown, but functional senescence occurs on a normal time-scale beneath the cosmetic surface of retained pigmentation. Therefore, Type C stay-greens are named cosmetic stay-green. The Type D stay-greens are described as pseudo-stay-greens because their leaves die before or in the middle of the senescence process as if freezing, and subsequently, the plant still appears green after death. The Type E stay-green plants accumulate higher levels of Chl in photosynthetic tissues, resulting in a delay of senescence and the conservation of green tissue. However, the photosynthetic capacity of Type E stay-greens follows the normal ontogenetic pattern. Both Type A and B stay-green plants are termed functional stay-greens as the duration of the photosynthetic capacity is extended. These stay-green types are sought by breeders as they can result in higher yield. Several studies have reported a synergistic effect by combining functional stay-green and other useful traits such as tolerance to drought and heat stress ^[7]. On the contrary, the Type C, D, and E plants are categorized as non-functional stay-green that retain greenness due to the impairment of Chl catabolism but lack the maintenance of leaf functionality during senescence ^{[2][8]}. Most CCE mutants in rice display a stay-green phenotype during senescence but lack an extended photosynthetic capacity and grain yield advantage; therefore, these mutants are regarded as non-functional stay-green plants.

Due to the high importance of maintaining photosynthesis longer and/or in promoting nutrient recycling and mobilization throughout the plant, the stay-green traits were investigated in many plant species, including rice, maize, Arabidopsis,

soybean, barley, tomato, pepper, and wheat, and they were used as markers in plant breeding programs [9][10][11][12][13][14][15].

Several studies report that the Chl content in rice is regulated by a quantitative trait locus (QTL) [10][16][17][18]. Analyses of Chl content and the degree of greenness in the flag and second leaves identified 46 QTLs that were associated with delayed senescence [16]. Cha et al. mapped the *stay-green* (*sgr*) locus, which is responsible for maintaining greenness during leaf senescence, but not photosynthetic activity, to the long arm of chromosome 9 [10]. Further studies identified *SGR* as a senescence-associated gene encoding a novel chloroplast protein and Mg²⁺-dechetalase mediating Chl breakdown, which confirmed that *sgr* was a cosmetic stay-green locus [19][20].

A total of six QTLs (*csfl2/tcs2*, *tcs4*, *tcs5*, *csfl6*, *csfl9/tcs9*, and *csfl12*) were identified in recombinant inbred line populations derived from intra- and inter-subspecific crosses of rice varieties [21]. The functional stay-green *japonica* rice 'SNU-SG1' is mapped on chromosome 9. The presence of SNU-SG1 improved grain yield by maintaining photosynthetic activity in the flag and second leaves during grain filling, and by increasing sink strength due to high seed-setting rate [17]. Fine mapping performed by Lim et al. identified eleven main-effect loci in the *japonica* rice SNU-SG1 that were responsible for functional SG phenotypes [22]. Fifteen strong candidate genes were identified that explained these main-effect QTLs using the whole-genome sequence [22]. All these genes represent interesting candidates for further plant breeding. The *qCC2* major QTL for Chl content was identified using a population derived from an interspecific cross between *O. sativa* and *O. grandiglumi* [18]. The *GW2* gene that encodes an E3 ubiquitin ligase is located in the *qCC2* region and is responsible for leaf senescence through the transcriptional regulation of phytohormone signaling pathways [18]. Whether the *qCC2* QTL is explained by *GW2* allelic variations in *O. sativa* and *O. grandiglumi* remains to be determined. Ten stable QTL regions for six delayed senescence traits have been identified [23]. Expression analysis of five candidate genes displayed the differential transcript levels, suggesting their strong association with the senescence pattern in the flag and second leaves and possible contribution in enhancing grain yield through genomics-assisted breeding.

A genome-wide association study (GWAS) of a diverse worldwide collection of rice accessions identified forty-six significant association loci in natural variation of Chl content (CC) [24]. Among them, the *Grain number, plant height, and heading date7* (*Ghd7*) was a major locus for natural variations of Chl content that was involved in the repression of Chl and chloroplast biosynthetic genes [24]. As indicated by its name, this locus is a functional stay-green locus that controls also grain number, plant height, and heading date. Another candidate revealed by GWAS is *Narrow leaf1* (*NAL1*) [24]. A high degree of polymorphism in the 5' UTR and four non-synonymous single nucleotide polymorphisms (SNPs) in the coding region of *NAL1* was shown to confer natural variations of Chl content [24]. Whether pleiotropic effects of *NAL1* in regulating flag leaf width and spikelet number per panicle might be helpful for rice breeding remains to be determined. In another GWAS study, 25 known genes for CC and stay-green (SG) traits were identified in natural rice variations [25]. Non-synonymous SNPs were detected in six of the genes and three SNPs in the promoter region of *OsSG1* [25]. Another GWAS revealed fourteen regions associated with CC and strong SG phenotypes [25]. From them, twenty-five candidate genes identified around the GWAS signals are genes with known important roles in CC and SG phenotypes. This suggests that these genes could be involved in the genetic variation of CC or SG. Non-synonymous SNPs within six of these genes, and three SNPs in the promoter of *OsSG1*, were unveiled. The impact of each of these genes on plant performance remains to be explored.

Two representative rice subspecies, *japonica* and *indica*, display distinct morphological and physiological features as well as clear variation in genomic sequences [26]. Furthermore, *indica* displays early leaf senescence, whereas *japonica* displays late leaf senescence [27]. Then, QTL mapping was conducted to determine the genetic factors responsible for the differential senescence patterns between *indica* and *japonica* [20]. Results showed that allelic polymorphisms in the *OsSGR* promoter in *indica* result in higher and earlier induction of *OsSGR*, thereby triggering earlier senescence. The introgression of *japonica* *OsSGR* alleles into elite *indica* cultivars produced near isogenic lines (NILs) with delayed leaf senescence and extended photosynthetic competence, leading to improved grain filling rate and yield. Then, the *japonica* *OsSGR* alleles represent technical solutions for a beneficial breeding strategy in rice.

In addition to QTL and GWAS approaches, experiments leading to the characterization of mutants were carried out. The screen of ethyl methansulphonate (EMS)-induced rice mutants led to the identification of three stay-green mutants that also displayed drought tolerance [28]. Amongst them, *SGM-3* was characterized as a novel functional stay-green mutant with extended photosynthetic capacity during senescence, increased harvest index, and higher grain yield under irrigated as well as drought conditions which can be further used for the development of high-yielding lines [28]. The exact function of *SGM-3* remains to be determined.

3. conclusion

In summary, we can see that both the quantitative genetics and mutagenesis approaches successfully identified several functional stay-green genes that play a role in plant productivity. Although the function of many of these genes and loci still remains to be elucidated, their positive alleles could be used in marker-assisted plant breeding programs.

References

1. Hörtensteiner, S. Chlorophyll degradation during senescence. *Annu. Rev. Plant Biol.* 2006, 57, 55–77.
2. Thomas, H.; Howarth, C.J. Five ways to stay green. *J. Exp. Bot.* 2000, 51, 329–337.
3. Thomas, H.; Ougham, H. The stay-green trait. *J. Exp. Bot.* 2014, 65, 3889–3900.
4. Borrell, A.K.; Hammer, G.L.; Oosterom, E.V. Stay-green: A consequence of the balance between supply and demand for nitrogen during grain filling. *Ann. Appl. Biol.* 2001, 138, 91–95.
5. Morales, F.; Ancín, M.; Fakhret, D.; González-Torralba, J.; Gámez, A.L.; Seminario, A.; Soba, D.; Ben, M.S.; Garriga, M.; Aranjuelo, I. photosynthetic metabolism under stressful growth conditions as a bases for crop breeding and yield improvement. *Plants* 2020, 9, 88.
6. Kusaba, M.; Tanaka, A.; Tanaka, R. Stay-green plants: What do they tell us about the molecular mechanism of leaf senescence. *Photosynth. Res.* 2013, 117, 221–234.
7. Kamal, N.M.; Alnor Gorafi, Y.S.; Abdelrahman, M.; Abdellatef, E.; Tsujimoto, H. Stay-Green trait: A prospective approach for Yield Potential, and Drought and Heat Stress Adaptation in Globally Important Cereals. *Int. J. Mol. Sci.* 2019, 20, 5837.
8. Tian, F.; Gong, J.; Zhang, J.; Zhang, M.; Wang, G.; Li, A.; Wang, W. Enhanced stability of thylakoid membrane proteins and antioxidant competence contribute to drought stress resistance in the *tasg1* wheat stay-green mutant. *J. Exp. Bot.* 2013, 64, 1509–1520.
9. Barry, C.S.; McQuinn, R.P.; Chung, M.Y.; Besuden, A.; Giovannoni, J.J. Amino Acid Substitutions in Homologs of the STAY-GREEN Protein Are Responsible for the green-flesh and chlorophyll retainer Mutations of Tomato and Pepper. *Plant Physiol.* 2008, 147, 179–187.
10. Cha, K.W.; Lee, Y.J.; Koh, H.J.; Lee, B.M.; Nam, Y.W.; Paek, N.-C. Isolation, characterization, and mapping of the stay green mutant in rice. *Theor. Appl. Genet.* 2002, 104, 526–532.
11. Duvick, D.; Smith, J.; Cooper, M. Long-term selection in a commercial hybrid maize breeding program. *Plant Breed. Rev.* 2004, 24, 109–152.
12. Fang, C.; Li, C.; Li, W.; Wang, Z.; Zhou, Z.; Shen, Y.; Wu, M.; Wu, Y.; Li, G.; Kong, L.A.; et al. Concerted evolution of D1 and D2 to regulate chlorophyll degradation in soybean. *Plant J.* 2014, 77, 700–712.
13. Grbić, V.; Bleecker, A.B. Ethylene regulates the timing of leaf senescence in *Arabidopsis*. *Plant J.* 1995, 8, 595–602.
14. Rampino, P.; Spano, G.; Pataleo, S.; Mita, G.; Napier, J.A.; di Fonzo, N.; Shewry, P.R.; Perrotta, C. Molecular analysis of a durum wheat ‘stay green’ mutant: Expression pattern of photosynthesis-related genes. *J. Cereal Sci.* 2006, 43, 160–168.
15. Gous, P.W.; Warren, F.; Gilbert, R.; Fox, G.P. Drought-proofing barley (*Hordeum vulgare*): The effects of stay green on starch and amylose structure. *Cereal Chem.* 2017, 94, 873–880.
16. Jiang, G.H.; He, Y.Q.; Xu, C.G.; Li, X.H.; Zhang, Q. The genetic basis of stay-green in rice analyzed in a population of doubled haploid lines derived from an indica by japonica cross. *Theor. Appl. Genet.* 2004, 108, 688–698.
17. Yoo, S.-C.; Cho, S.-H.; Zhang, H.; Paik, H.-C.; Lee, C.-H.; Li, J.; Yoo, J.-H.; Koh, H.-J.; Seo, H.S.; Paek, N.-C. Quantitative trait loci associated with functional stay-green SNU-SG1 in rice. *Mol. Cells* 2007, 24, 83–94.
18. Shim, K.-C.; Kim, S.H.; Jeon, Y.-A.; Lee, H.-S.; Adeva, C.; Kang, J.-W.; Kim, H.-J.; Tai, T.H.; Ahn, S.-N. A RING-Type E3 Ubiquitin Ligase, OsGW2, Controls Chlorophyll Content and Dark-Induced Senescence in Rice. *Int. J. Mol. Sci.* 2020, 21, 1704.
19. Park, S.Y.; Yu, J.W.; Park, J.S.; Li, J.; Yoo, S.C.; Lee, N.Y.; Lee, S.K.; Jeong, S.W.; Seo, H.S.; Koh, H.J.; et al. The Senescence-Induced Staygreen Protein Regulates Chlorophyll Degradation. *Plant Cell* 2007, 19, 1649–1664.
20. Shin, D.; Lee, S.; Kim, T.H.; Lee, J.H.; Park, J.; Lee, J.; Lee, J.Y.; Cho, L.H.; Choi, J.Y.; Lee, W.; et al. Natural variations at the Stay-Green gene promoter control lifespan and yield in rice cultivars. *Nat. Commun.* 2020, 11, 2819.

21. Fu, J.D.; Yan, Y.F.; Kim, M.Y.; Lee, S.H.; Lee, B.W. Population-specific quantitative trait loci mapping for functional stay-green trait in rice (*Oryza sativa* L.). *Genome* 2011, 5, 235.
22. Lim, J.H.; Yang, H.J.; Jung, K.H.; Yoo, S.C.; Paek, N.-C. Quantitative Trait Locus Mapping and Candidate Gene Analysis for Plant Architecture Traits Using Whole Genome Re-Sequencing in Rice. *Mol. Cells* 2014, 37, 149–160.
23. Singh, U.M.; Sinha, P.; Dixit, S.; Abbai, R.; Venkateshwarlu, C.; Chitikineni, A.; Singh, V.K.; Varshney, R.K.; Kumar, A. Unraveling candidate genomic regions responsible for delayed leaf senescence in rice. *PLoS ONE* 2020, 15, e0240591.
24. Wang, Q.; Xie, W.; Xing, H.; Yan, J.; Meng, X.; Li, X.; Fu, X.; Xu, J.; Lian, X.; Yu, S.; et al. Genetic Architecture of Natural Variation in Rice Chlorophyll Content Revealed by a Genome-Wide Association Study. *Mol. Plant* 2015, 8, 946–957.
25. Zhao, Y.; Qiang, C.; Wang, X.; Chen, Y.; Deng, J.; Jiang, C.; Sun, X.; Chen, H.; Li, J.; Piao, W.; et al. New alleles for chlorophyll content and stay-green traits revealed by a genome wide association study in rice (*Oryza sativa*). *Sci. Rep.* 2019, 9, 2541.
26. Hu, C.; Shi, J.; Quan, S.; Cui, B.; Kleessen, S.; Nikoloski, Z.; Tohge, T.; Alexander, D.; Guo, L.; Lin, H.; et al. Metabolic variation between japonica and indica rice cultivars as revealed by non-targeted metabolomics. *Sci. Rep.* 2014, 4, 5067.
27. Abdelkhalik, A.F.; Shishido, R.; Nomura, K.; Ikehashi, H. QTL-based analysis of leaf senescence in an indica/japonica hybrid in rice (*Oryza sativa* L.). *Theor. Appl. Genet.* 2005, 110, 1226–1235.
28. Ramkumar, M.K.; Senthil Kumar, S.; Gaikwad, K.; Pandey, R.; Chinnusamy, V.; Singh, N.K.; Singh, A.K.; Mohapatra, T.; Sevanthi, A.M. A Novel Stay-Green Mutant of Rice with Delayed Leaf Senescence and Better Harvest Index Confers Drought Tolerance. *Plants* 2019, 8, 375.

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