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Fine Mapping of a Major QTL for Stay-Green Trait in Maize Using Near-Isogenic Lines

Pingping Yang, Jin Zhou, Minli Xu
Hainan Provincial Key Laboratory of Crop Molecular Breeding, Sanya, 572025, Hainan, China
Corresponding author: minli.xu@hitar.org

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Abstract The greenness retention trait is one of the key agronomic traits determining the stress resistance and high-yield potential of maize (*Zea mays* L.), especially showing significant value under stress conditions such as drought and late maturity. In this study, Near-Isogenic Lines (NILs) were used as research materials to precisely locate a major QTL in corn that was significantly associated with greenness holding traits, reveal its genetic basis and explore candidate gene resources. Through the construction of a high-density molecular marker map and precise phenotypic evaluation, The fine localization region of this QTL on chromosome 9 was identified under multi-environment experiments. Further, through recombinant single-plant analysis, candidate gene expression profiling and functional annotation, multiple key genes that may be involved in regulating chlorophyll degradation, photosynthesis maintenance and antioxidant pathways were preliminarily identified. This study also verified the expression and explored the biological significance of typical candidate genes such as *Stay-Green1* (*SGR1*) and *SAG12*, providing an important basis for the molecular breeding of green-holding traits in maize and potential targets for the improvement of complex traits such as drought resistance and delayed senescence.

Keywords Corn; Green-holding property; QTL fine positioning; Near-isogenic line; Candidate gene

1 Introduction

The high yield of corn does not only depend on the number of kernels, but also on whether the leaves can remain in a "green state" during the filling period. The greenness retention trait refers to the fact that when leaf senescence is delayed, photosynthesis can still continue for a period of time. Especially in abiotic stress environments such as drought and high temperature, once photosynthesis stops too early, the yield often declines accordingly (Wang et al., 2012). Therefore, genotypes that can "preserve greenness" tend to be more stable and more resilient (Belicuas et al., 2014; Zhang et al., 2019).

However, it is no easy task to figure out which group of genes are at work behind this trait. Researchers have identified many regions related to green conservation on corn by using QTL mapping technology. Some major QTLS can even explain a large proportion of the phenotypic differences (Yang et al., 2017). The problem is that the resolution of traditional QTL mapping is often insufficient, and the mapped intervals are too wide, which may contain hundreds of genes - this is not very friendly for gene cloning and subsequent breeding selection (Wang et al., 2018). To solve this "too vague" problem, precise positioning becomes very important. Among them, the near-isogenic line (NIL) is particularly suitable for doing this. Their genetic backgrounds are relatively uniform, with only differences in the target QTL regions. As a result, some background noise can be avoided and the evaluation effect becomes clearer (Eichten et al., 2011). In addition, NIL is also very useful in QTL validation and functional research, which can significantly accelerate the breeding speed of key traits (Zhong et al., 2025).

This study utilized near-isogenic lines (NIL) to precisely locate the major QTL of green retention traits in maize, narrowed the QTL interval to identify candidate genes, and verified the impact of this QTL on green retention traits and yield-related traits, providing genetic resources and molecular markers for breeding projects. This study aims to enhance the efficiency of marker-assisted selection and contribute to the cultivation of high-yield and stress-resistant corn varieties, ultimately ensuring food security in the context of climate change.

2 Physiological Basis and Genetic Characteristics of Stay-Green Trait in Maize

2.1 Definition, classification, and phenotypic evaluation criteria of stay-green trait

It is no accident that some corn varieties can still maintain large green leaves during the grain-filling period. This is actually the green retention trait at work - a genetic ability that enables plants to delay leaf senescence and maintain photosynthetic activity after flowering (Hilli, 2021). But "green" can also be genuine or fake. Some only look green on the surface, but in fact, photosynthesis has already stopped. This is called "appearance" greenness preservation. Another type is the "functional" green preservation that can truly continuously synthesize nutrients and stabilize yields (Thomas and Ougham, 2014). Judging these differences cannot rely solely on the naked eye; data is also necessary. For example, green leaf area score (VSG), number of green leaves (GLNM), SPAD values at flowering and maturity (SPADS, SPADM), and green leaf duration (GLAD), etc. These are all commonly used quantitative standards in breeding work (Zheng et al., 2023; 2024).

2.2 Physiological indicators associated with stay-green

Whether a variety can "retain its green color" is far from enough to just look at its appearance; it is necessary to delve into its physiological manifestations. High SPAD values often indicate that the chlorophyll is well maintained (Kamal et al., 2019), and if the photosynthesis period is prolonged and dry matter can be continuously produced in the later stage of grout filling, it is basically reliable (Yang et al., 2017; Chibane et al., 2021). However, there are other factors supporting this, such as higher leaf moisture, more active antioxidant enzymes (SOD, POD, CAT), and a good hormone ratio, like higher zeaxanthin and lower abscisic acid (Liu et al., 2018). These indicators, when combined, often determine whether a corn plant can withstand adverse conditions and produce stably.

2.3 Genetic control model of stay-green and overview of reported QTLs

In the final analysis, the issue of protecting greenery is still led by genes, but it is not as simple as just one or two genes that control it. This trait is a typical quantitative trait, with both major genes and multiple minor effect genes involved in regulation. Sometimes it also has a slight dominant effect, and the overall heritability is not low (Belicuas et al., 2014). Traits like VSG, GLNM and SPADM can even contribute up to 95% of the major genes in some materials. At present, researchers have identified QTLS related to green conservation on almost all chromosomes of corn. The key regions are concentrated on chromosomes 1, 4, 5 and 6, while chromosome 9 is frequently exposed (Wang et al., 2012). Among them, the gene *nac7* encoding the transcription factor of the NAC domain has been confirmed to play a negative regulatory role in senescence. When its expression level is low, the senescence rate of leaves slows down and the yield can be increased (Sekhon et al., 2019; Zhang et al., 2019). With the integration of technologies such as QTL mapping, GWAS and transcriptomics, the genetic structure of green retention traits in corn has become increasingly clear, providing a solid foundation for future molecular marker selection and functional gene discovery.

3 Construction of Near-Isogenic Lines and Phenotypic Evaluation

3.1 NIL development methods and parental selection strategy

The establishment process of NIL is not complicated, but it is rather cumbersome to operate. The key lies in whether the loop and selection are combined tightly enough. The general practice is as follows: Repeatedly cross the donor parent with the target QTL (such as green-preserving) and the reincycle parent, and then fix the target fragment step by step through self-crossing combined with molecular markers, while the background genome is as close as possible to the reincycle parent (Zhong et al., 2025). For the parents of reincarnation, materials with good agronomic traits but lacking green retention are often selected, such as common superior varieties like B73. Donor parents, on the other hand, place more emphasis on their performance in the target traits. As for screening markers, molecular markers such as AFLP, SSR, and SNP that are closely linked to green-preserving QTL are sufficient and are most suitable for improving breeding efficiency (Eichten et al., 2011; Ying et al., 2025).

3.2 Phenotypic data collection and statistical analysis under multiple environments

The performance of NIL is not consistent in all environments. Whether NIL can "preserve greenery" or not still depends on the performance of multiple environmental tests. The phenotypic data of this type of material usually come from multiple growth cycles and locations, with the aim of capturing the differences in genotype and environmental interactions. In addition to the SPAD value and the number of green leaves, the visual scores during the development period should also be recorded, and even the yield traits should be taken into account. Evaluating this type of data cannot rely solely on intuition. Repeated field trials are standard. Statistically, mixed linear models or BLUP are generally run to estimate QTL effects and the heritability of traits (Li et al., 2020). The ultimate goal is to identify those NIL that remain stable and green in a variable environment.

3.3 Field evaluation standards and stay-green scoring system construction

How does the field evaluate it? In fact, it's not that mysterious. Generally, a visual scoring system from 1 to 9 is used first, and then combined with the readings of the SPAD instrument and the records of the number of green leaves, to suppress the visual subjectivity. The scoring must of course be uniform, especially when it comes to the consistency of standards across years and locations; otherwise, the comparability will be lost (Zheng et al., 2024; Zhong et al., 2025). When this scoring method is combined with molecular markers, it can not only precisely locate QTLS but also improve the selection efficiency of NIL. It is particularly suitable for projects that pursue rapid breeding and precise positioning.

4 Preliminary QTL Mapping and Validation

4.1 Construction of QTL linkage maps and definition of target regions

At the beginning, to identify the green-holding trait of corn, most studies start with constructing a linkage map. Not all graphs are complex, but there are also versions drawn with over 100 SSR markers, covering 10 linkage groups relatively comprehensively, with a total length even exceeding 1 400 cM (Trachsel et al., 2016). In this case, multiple QTLS at different developmental stages can be identified. The distribution locations are basically throughout the entire genome. Of course, some of the major QTLS themselves can explain about 13.5% of the phenotypic variations (Wang et al., 2012; Yang et al., 2017), which can be regarded as relatively "strong signal" segments. As for the target areas that are planned to be further precisely positioned later, they are usually placed between the markers close to both sides of the target QTL, which is more convenient for operation.

4.2 QTL effect validation in different genetic backgrounds

Sometimes, a QTL that stands out in one material may not be "effective" when its genetic background is changed. Therefore, verification work cannot be carried out only on one group. Researchers often infuse principal QTLS into different strains, such as heterogeneous inbred lines, to see if they can still control the aging process or yield performance in other materials. QTLS related to NAC domain transcription factors like nac7 have been verified in multiple genetic contexts. After down-regulation, the leaves age more slowly and the yield increases instead (Zhang et al., 2019). Similar validations have also emerged in other materials and populations. Some QTLS have repeated results in different studies, indicating that their performance is not accidental (Belicuas et al., 2014).

4.3 Correlation analysis between preliminary QTL and stay-green phenotypes

If QTL is truly useful for traits, it must be able to "bring out" some phenotypes, such as chlorophyll content, green leaf area, and yield. Many analyses have indeed shown that materials with green-preserving alleles have a significant advantage in these phenotypic indicators (Zheng et al., 2009; Wang et al., 2012). Interestingly, there is overlap between the regional and production-related QTLS of green conservation QTLS. This "collision" actually validates the value of these QTLS in turn (Bhadmus et al., 2022). Therefore, in breeding, this type of QTL is very suitable for use as a marker-assisted selection, which helps to simultaneously enhance stress resistance and yield stability.

5 Fine Mapping and Candidate Gene Identification

5.1 Development of high-density molecular markers and recombinant line screening

To precisely lock the greenish retention trait of corn to a small chromosomal interval, relying solely on traditional mapping techniques is far from sufficient. Nowadays, a more common approach is to use high-density molecular markers such as SNPS and SSRS in combination with a hybrid separation strategy of next-generation sequencing (NGS) and BSA-seq to quickly lock onto the target region. As in a recent study, F_2 populations of chlorogenic and non-chlorogenic parents were used for BSA-seq, and a large candidate region containing 778 genes was screened on chromosome 9 (Figure 1) (Zheng et al., 2023). Of course, when the area is large, it is not easy to operate. Therefore, researchers introduced weighted correlation network analysis (WGCNA) and RNA-seq data integration to further refine the candidate library. These combined methods are more precise and efficient in locating QTLS compared to a single technical approach.

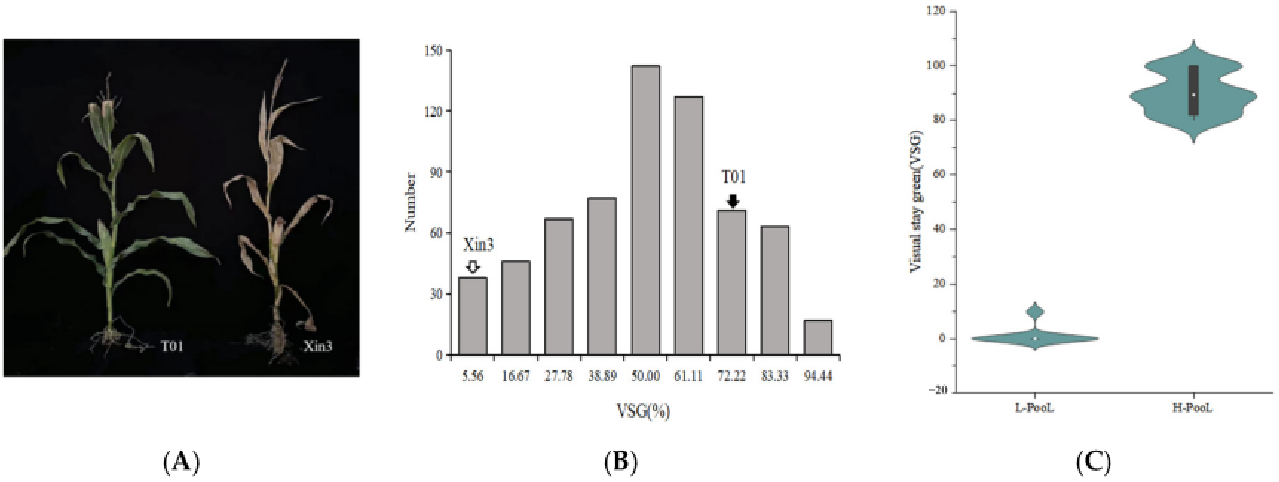


Figure 1 (A) The phenotype of visual stay-green trait in T01 and Xin3. (B) Frequency distribution of visual stay-green in the F_2 population of maize. (C) The performance of visual stay-green in two extreme mixed pools of visual stay-green (Adopted from Zheng et al., 2023)

5.2 Recombination event analysis and interval narrowing of target regions

The narrowing of candidate regions often depends not on luck but on whether one can seize those key recombination individual plants. In the analysis of recombination events, researchers rely on these "useful mutations" to gradually minimize the interval. Take the region of chromosome 9 for example. By integrating the BSA-seq and RNA-seq data, only three candidate genes of key concern remained in the end: *Zm00001eb378880*, *Zm00001eb383680* and *Zm00001eb384100* (Zheng et al., 2023). Moreover, this method does not rely solely on sequencing data. It also needs to be combined with phenotypic data to truly link functional sites with phenotypes, just as Fang et al. (2012) did, in order to achieve the goal of precise localization.

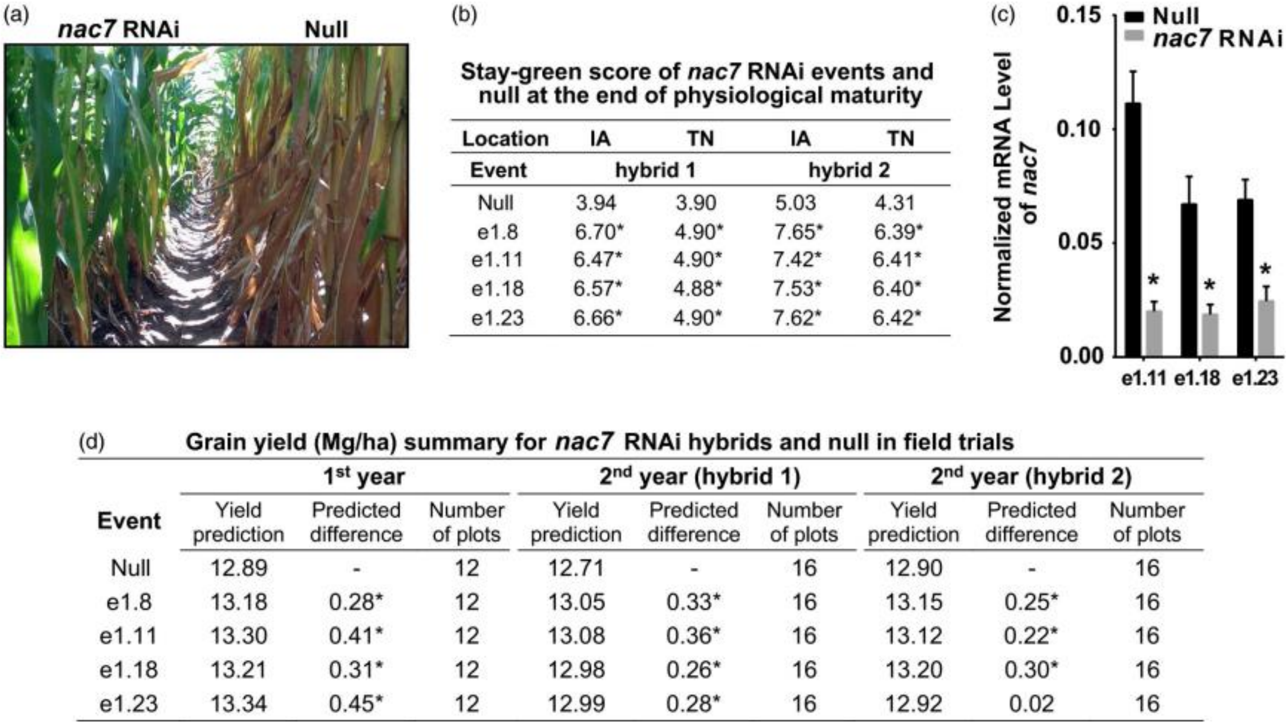
5.3 Functional annotation, expression analysis, and prediction of candidate genes

After narrowing down the intervals, the next step is naturally to "dig out" each candidate gene one by one to see which one is more like the main cause. Researchers usually conduct functional annotations first, that is, by using methods such as gene ontology and homology comparison, to figure out what these genes usually do. Immediately after, the differences of these genes in green-preserving and non-green-preserving materials are examined through expression profile data (such as RNA sequencing). If a certain gene is "abnormally active" or obviously "silent" in the processes of photosynthesis, chlorophyll metabolism, and aging, then it is the key suspect. Like nac7, it has been proven to be a negative regulatory factor of senescence. As long as its expression is inhibited, leaf senescence slows down and yield increases (Zhang et al., 2019; Zhou and Liang, 2024). Strategies like this one that integrates "expression + annotation + functional prediction" have laid a solid foundation for subsequent marker-assisted selection and trait improvement.

6 Case Study: Fine Mapping of Stay-Green QTLs

6.1 Fine mapping of a stay-green QTL on chromosome 9 in maize

Not all QTLS can be successfully located to specific genes, but there are exceptions. Taking a QTL related to greenness retention on chromosome 9 as an example, researchers gradually narrowed down the scope to a NAC domain transcription factor gene in a population with significantly different aging processes, which was later named nac7 as the target gene. In the transgenic corn experiment, after down-regulating the expression of nac7 through RNAi technology, leaf senescence was delayed, the biomass of the plants increased, and the nitrogen accumulation capacity was also strengthened. These changes basically indicate that nac7 is a typical negative regulatory factor. Such results were achieved through high-density marker analysis combined with functional genomics techniques, and the accuracy was obviously much higher than that of traditional QTL mapping (Figure 2) (Zhang et al., 2019).



(b)

Stay-green score of *nac7* RNAi events and null at the end of physiological maturity

Location	IA	TN	IA	TN
Event	hybrid 1		hybrid 2	
Null	3.94	3.90	5.03	4.31
e1.8	6.70*	4.90*	7.65*	6.39*
e1.11	6.47*	4.90*	7.42*	6.41*
e1.18	6.57*	4.88*	7.53*	6.40*
e1.23	6.66*	4.90*	7.62*	6.42*

(d) **Grain yield (Mg/ha) summary for *nac7* RNAi hybrids and null in field trials**

Event	1st year			2nd year (hybrid 1)			2nd year (hybrid 2)		
	Yield prediction	Predicted difference	Number of plots	Yield prediction	Predicted difference	Number of plots	Yield prediction	Predicted difference	Number of plots
Null	12.89	-	12	12.71	-	16	12.90	-	16
e1.8	13.18	0.28*	12	13.05	0.33*	16	13.15	0.25*	16
e1.11	13.30	0.41*	12	13.08	0.36*	16	13.12	0.22*	16
e1.18	13.21	0.31*	12	12.98	0.26*	16	13.20	0.30*	16
e1.23	13.34	0.45*	12	12.99	0.28*	16	12.92	0.02	16

Figure 2 Down-regulation of *nac7* in maize increased gain yield in two-year field trials (Adopted from Zhang et al., 2019)

Image caption: (a) *nac7* RNAi plants driven by an Ubi promoter showed stay-green phenotype in a yield trial under normal nitrogen condition. Pictures were taken postanthesis. (b) Stay-green score of two hybrid lines expressing *nac7* RNAi in Iowa and Tennessee with 2 plots per location. Scores ranged from 1 to 9 with '9' being a fully green canopy and '1' being completely senesced with no green. Stay-green score was analysed by linear unbiased prediction model. Significance between transgenic events and null comparator was determined at the $P < 0.1$ level shown with *. (c) *nac7* was down-regulated in three *nac7* RNAi events under field conditions as measured by qPCR ($n = 8$). Transcript level of *nac7* relative to the endogenous reference eIF4g, a maize eukaryotic translation initiation factor, was calculated by the ΔCt method. Significant difference between each transgenic event and its null was determined using the t-test, $^*P < 0.001$. (d) Yield tests in two years demonstrated that down-regulation of *nac7* increased yield in three hybrid lines. Yield was analysed by linear unbiased prediction model and shown as the best linear unbiased predictions (BLUPs). Summary table shows the yield and yield difference between nulls and the transgenic events in megagram/hectare (Mg/ha) at multilocations under normal nitrogen and well-watered conditions. Statistical significance was determined at the $P < 0.05$ level shown with * (Adopted from Zhang et al., 2019)

6.2 Multi-location trials of NILs for stable QTL expression analysis

Molecular verification in the laboratory alone is not enough; the true value can only be seen in the fields. In multi-site and multi-year field trials, the research team selected parents with nac7 RNAi backgrounds to hybridize with some superior inbred lines, and the test species were evaluated in multiple environments. The results were quite consistent: the green leaves were retained for a longer time, and the yield also increased, with an average increase of 0.29 tons per hectare. Converted, this is approximately an increase of 4.6 bushels per acre. The significance of such multi-point experiments lies in that they not only verify the stability of QTL but also directly reflect the breeding potential of this trait (Zhang et al., 2019).

6.3 Functional verification and biological significance of candidate genes such as *Stay-Green1* and *SAG12*

When it comes to the functions of candidate genes, some have already provided initial clues. Like nac7, research shows that it may regulate a whole set of genes involved in photosynthesis, chlorophyll degradation and protein renewal, and these processes are also closely related to the green-retaining trait. As for genes like *Stay-Green1* and *SAG12*, although there is currently a lack of direct evidence in corn, they have been proven to be related to aging regulation and adaptation to environmental stress in other crops. Combining expression profile data and transgenic analysis, it is not difficult to see that these candidate genes provide many useful molecular targets for green-preserving traits, and also provide support for subsequent marker-assisted selection and genetic improvement (Zhang et al., 2019).

7 Conclusion and Perspectives

People have actually been paying attention to the green retention property of corn for a long time. Especially in terms of increasing yield and stress resistance, maintaining the green color of leaves for a longer time is regarded as a practical trait. At present, through meta-analysis, a large number of QTLS related to green conservation, yield and stress resistance have been identified and integrated, among which some regions share multiple traits. Transcription factors in the NAC domain like nac7 are believed to be closely related to the regulation of aging and resource allocation. Although these genes have long existed in the corn genome, it is precisely because of the current methods such as BSA-seq, RNA-seq, and GWAS, along with high-throughput genotyping and better mapping populations, that these key loci have been able to be precisely located and their functions further verified.

Not all QTL mapping work can directly guide breeding, but those markers known to be closely linked to green-retaining traits undoubtedly bring more initiative to breeders. With these tools, breeders can precisely introduce outstanding alleles into target varieties, which not only extends the photosynthetic duration of corn but also makes its resistance more stable. More importantly, under different environmental conditions, strains with these excellent QTLS tend to perform better. This means that even in the face of adverse conditions such as drought and high temperatures, the output can still be maintained at a relatively ideal level.

Of course, relying solely on green retention is not enough. How to combine it with other important traits such as drought resistance and maturity period is the difficulty and key point in actual breeding. Interestingly, many green-preserving QTLS are precisely aligned with traits such as drought tolerance and yield. That is to say, while choosing one trait, another may have been improved incidentally. In this regard, the introduction of marker-assisted backcrossing and genomic selection techniques is very timely. They give breeders the opportunity to integrate stably expressed QTLS and environmentally sensitive QTLS, thereby cultivating hybrid corns that are both green-preserving and drought-tolerant, and can also adapt to the maturity requirements of different regions. This approach of integrating multiple traits might just be the direction for future corn improvement.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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