

Feature Review

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Molecular Functions and Regulatory Mechanisms of the Temperature-Sensitive Male Sterility Gene *OsTms6* in Rice

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Abstract The temperature-sensitive male sterility gene *OsTms6* plays a crucial role in the reproductive development of rice (*Oryza sativa* L.), particularly under varying thermal conditions. This systematic review synthesizes current research on the molecular functions and regulatory mechanisms of *OsTms6*. The gene has been identified as a key factor in hybrid rice production, with its sterility phenotype being influenced by specific temperature thresholds. Genetic mapping has localized *OsTms6* to chromosome 10, and molecular analyses have revealed its interaction with various regulatory pathways, including those involving noncoding RNAs and microRNAs. The gene's role in pollen fertility is mediated through complex genetic and environmental interactions, which are critical for the development of temperature-sensitive genic male sterile (TGMS) lines. Understanding these mechanisms provides valuable insights for breeding strategies aimed at improving rice yield and resilience to climate change.

Keywords Temperature-sensitive male sterility; *OsTms6*; Rice (*Oryza sativa* L.); Hybrid breeding; Genetic regulation

1 Introduction

In the 1970s, China took the lead in hybrid rice breeding. This attempt was not only a breakthrough in agricultural technology, but also increased rice yield by more than 20%, which brought significant changes to grain production at that time (Li et al., 2007). After that, this method was quickly adopted by Africa, South Asia, America and other regions, indicating that it is quite applicable.

There are two breeding methods for hybrid rice: three-line and two-line. The former mainly relies on cytoplasmic male sterility (CMS), while the latter uses nuclear male sterility (GMS), which is further subdivided into types that are sensitive to light or temperature (Li et al., 2007). Although it sounds a bit complicated, the core issue is actually how to "make rice temporarily infertile" so that hybrid seeds can be produced more conveniently. It is precisely because of this "sterility" method that the time-consuming and labor-intensive work of artificial anther removal has become less necessary. This small biological characteristic is behind the improvement of global hybrid crop productivity (Fan and Zhang, 2017).

Materials such as TGMS (temperature-sensitive male sterility) and PGMS (photoperiod-sensitive male sterility) have contributed to the emergence of a large number of high-yield and high-quality hybrid rice varieties (Li et al., 2007; Fan and Zhang, 2017). Among them, TGMS is particularly noteworthy. It belongs to a type of environmentally sensitive nuclear sterile system (EGMS) and is particularly "picky" about temperature. Simply put, when the temperature changes, its fertility state also changes - this characteristic makes it very practical in two-line hybrid breeding (Reddy et al., 2000; Lee et al., 2005; Liu et al., 2010).

For example, there is a TGMS line called Sokcho MS, which is sterile when the temperature is above 27 °C or below 25 °C, but it can be fertile if the ambient temperature is maintained between 25 °C and 27 °C (Lee et al., 2005). There is also a line called G20S, which is sterile as long as the temperature is below 29.5 °C, which makes it adaptable to more rice-growing areas (Liu et al., 2010). These examples show that TMS is not a "stable sterility" system, but a tool that can be "regulated" by the environment.

As for why it is like this, the mechanism behind it is not simple. It is known that it involves multiple levels of regulation, such as the expression of specific genes, and the role played by non-coding RNA and miRNA (Zhou et al., 2012; Sun et al., 2021).

This review focuses on the gene *OsTms6*, which is closely related to the TGMS trait. We will sort out its role and regulation from multiple perspectives, including genetics, molecular mechanisms, and breeding practices. Understanding the function of *OsTms6* is not only to understand how it makes rice "infertile", but also to use this knowledge to cultivate hybrid rice varieties that are more adaptable to the climate and have higher yields, providing a more reliable foundation for food security.

2 Identification and Cloning of *OsTms6*

2.1 Discovery of *OsTms6*

In hybrid rice breeding research, the exploration of temperature-sensitive male sterility has never stopped. What really attracted widespread attention was a special phenomenon observed in the new TGMS line G20S: as long as the temperature is below 29.5 °C, this material shows the characteristics of complete sterility (Liu et al., 2010). This was quickly noticed by breeders because it meant that it could adapt to more Asian climates. Later, through genetic analysis, researchers confirmed that this sterility was controlled by a recessive gene, temporarily named *tms6(t)* (Liu et al., 2010).

However, G20S is not the only example. In fact, as early as in South Korea, a spontaneous mutant japonica rice material called Sokcho MS was also found to have similar traits (Lee et al., 2005). The TGMS gene it carries is also named *tms6* and is located on the long arm of chromosome 5. The two systems are independent but point to the same gene, which undoubtedly strengthens people's understanding of the importance of *OsTms6* in TGMS research.

2.2 Cloning technology used

It is not easy to locate a gene, but the researchers tried many methods and finally successfully cloned *OsTms6*. In the G20S study, they first used SSR markers to perform batch segregation analysis and screened out some markers that may be related to *tms6(t)*. Further co-segregation analysis identified two closely linked markers, RM3152 and RM4455, which allowed the researchers to accurately locate the gene on chromosome 10 (Liu et al., 2010).

The situation is slightly different in Sokcho MS. The research there combined SSR, STS and EST markers, and the positioning work was more detailed, and finally narrowed the target area to between RM3351 and E60663 on chromosome 5 (Lee et al., 2005; Yang et al., 2006). Although the research ideas are different, the results provide precise "coordinates" for the subsequent cloning of *OsTms6*.

2.3 Verification of *OsTms6* as a TMS gene

Location alone is not enough, and verifying its function is the key. On the G20S material, the researchers conducted a complementary experiment. They selected a 2.4-kb DNA fragment containing the wild-type *tms6(t)* allele and introduced it into the sterile plants. As a result, pollen fertility was restored, which basically confirmed the role of *tms6(t)* in TGMS (Liu et al., 2010; Pan et al., 2014).

The verification method of Sokcho MS is not so direct, but it is also very convincing. The genetic analysis there also showed that sterility is controlled by a recessive gene, and the positioning results showed that this *tms6* is not any previously known TGMS gene, but a new one (Lee et al., 2005). This makes people further realize that *OsTms6* is not a phenomenon unique to a single material, but a gene with universal significance.

In general, although these works come from different research groups and use different research materials, they ultimately converge on the same gene point - *OsTms6*. Its discovery, cloning and verification not only give us a clearer understanding of rice temperature-sensitive sterility, but also provide more possibilities for breeding work.

3 Molecular Functions of *OsTms6*

3.1 Gene structure and protein function

The gene *OsTms6* is closely related to temperature-sensitive male sterility (TGMS) in rice. It actually encodes a protein called GMC oxidoreductase, which is related to molecules such as glucose, methanol, and choline. However, what really makes it a research focus is a small mutation: Gly becomes Ser (Zhang et al., 2022). This point mutation directly leads to the TGMS trait. Under high temperature conditions, the pollen wall develops abnormally (Figure 1). Interestingly, this gene itself is also regulated by another key factor, *OsMS188*, which is a transcription factor in the tapetum and is also linked to the development of the pollen wall (Zhang et al., 2022). Understanding the structure of *OsTms6* and what it does is the key to figuring out why rice exhibits sterility or restores fertility at different temperatures.

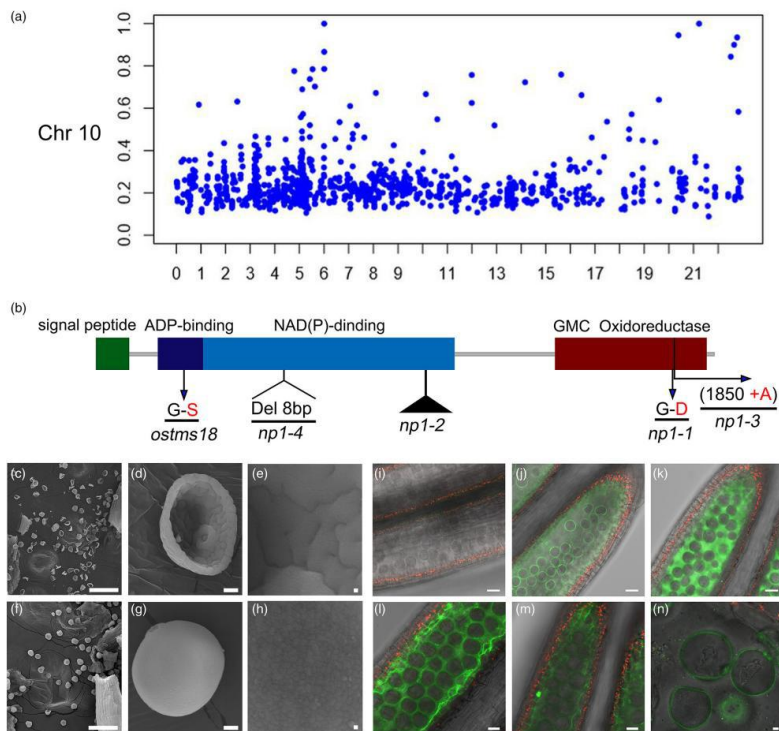


Figure 1 *OsTMS18* encodes an anther-expressed GMC oxidoreductase (Adopted from Zhang et al., 2022)

Image caption: (a) SNP index for mapping the *OsTMS18* by the BSA-seq approach. (b) Identification of the mutated point of *OsTMS18* in a WT plant and *ostms18* (Adopted from Zhang et al., 2022)

3.2 Expression pattern of *OsTms6*

The location of *OsTms6* expression is also very particular, mainly concentrated in the anther wall cells, especially in the period before and after meiosis. To put it bluntly, it is "full-time" to do the reproductive work. When the temperature rises, its expression will be enhanced, like "emergency" to help stabilize the vitality of pollen (Lin et al., 2023). But this process is not fixed, it is also affected by the environment, such as temperature fluctuations (Shi et al., 2022). So the expression of this gene is like a temperature sensor. Once the external environment changes, its expression level will also adjust accordingly, which will affect the survival status of pollen.

3.3 Functional studies in model plants

Regarding the function of *OsTms6*, scientists have not only studied it in rice, but also found its "relatives" in Arabidopsis. It turns out that the genes in this family seem to be a bit "afraid of heat". For example, in Arabidopsis, once the temperature rises, the mutants of homologous genes will also show a decrease in fertility (Zhang et al., 2022). This is even more obvious in rice. The mutation directly leads to TGMS, and the pollen wall cannot be formed. The pollen will be useless if it is hot. Similar phenomena occur in different plants, indicating that the function of this gene is very conservative, and it may have been involved in regulating male fertility since a long time ago. This feature is of great significance for hybrid breeding.

3.4 Phenotypic effects of *OsTms6* mutation

What will happen if *OsTms6* is knocked out? The answer is quite intuitive-pollen development will go wrong. For example, in the *ostms18* mutant, the pollen wall cannot be formed at all, especially under high temperature conditions, and the sterility is very stable (Zhang et al., 2022). Not only that, this mutation will also cause the tapetum cells to "overgrow", as if they are suddenly out of control; at the same time, the starch in the anthers also decreases (Shi et al., 2022). When these changes are combined, the final result is that pollen cannot develop normally. In short, *OsTms6* plays an indispensable role in maintaining normal pollen development, especially in maintaining fertility in hot environments.

4 Regulatory Mechanism of *OsTms6*

4.1 Transcriptional regulation

4.1.1 Promoter-related information

If you want to understand how a gene "starts working", the promoter region is the key, and *OsTms6* is no exception. This region is just in front of the gene and is a special DNA sequence with many "binding sites" that transcription factors can recognize. When different signals come, transcription factors may attach to it to start or inhibit the expression of *OsTms6*. Studying this part is actually to find out how it is regulated in different environments (Wu et al., 2019).

4.1.2 Related transcription factors

But having a promoter alone is not enough, who will recognize it? At this time, transcription factors come in handy. They bind to the promoter region and determine whether *OsTms6* is expressed or not. When studying the photothermosensitive male sterile line (PTGMS) of rice, some people noticed that some miRNAs, such as miR156, miR5488 and miR399, did not directly regulate *OsTms6*, but targeted certain transcription factors, thereby indirectly affecting the expression of genes related to male sterility (Sun et al., 2018; 2021). The regulatory relationship between these miRNAs and *OsTms6* is very obvious, especially when encountering temperature fluctuations.

4.2 Post-transcriptional regulation

4.2.1 mRNA stability

After *OsTms6* is transcribed, whether its mRNA can be stable is also a very important thing. The regulation at this stage is more affected by miRNA. For example, some miRNAs (such as miR-2118 and miR-2275) will affect the generation of phasiRNA, and these phasiRNAs can regulate the stability of mRNA in rice reproductive organs (Ding et al., 2021; Shi et al., 2022). As a result, the stability of *OsTms6* mRNA is affected, and the protein production changes accordingly.

4.2.2 Relationship between miRNA and siRNA

Don't underestimate these small RNA molecules. Although miRNA and siRNA do not encode proteins themselves, they can accurately identify target mRNA and then either degrade it or prevent it from being translated. In the regulation of male fertility related to *OsTms6*, miR156, miR5488 and miR399 have been found to affect key genes in anther development (Sun et al., 2021). More complicatedly, proteins like AGO1d bind to miR2118 and miR2275 to guide the synthesis of phasiRNA (Shi et al., 2022). The whole system is like a network, and *OsTms6* is just one link.

4.3 Environmental regulation

4.3.1 Effect of temperature

When the temperature changes, the performance of *OsTms6* also changes. Some sterile lines, such as Beijing sterile 366 (BS366), are prone to problems at low temperatures: the expression levels of miRNAs and their target genes change, which ultimately leads to abnormal pollen development and male sterility (Liu et al., 2022). Studies have also found that AGO1d also plays a role in this process, which again shows that temperature does not act alone, but affects the expression of *OsTms6* through a series of molecular regulation (Shi et al., 2022).

4.3.2 Involvement of other environmental factors

In addition to temperature, light and water supply also affect *OsTms6*. For example, in PTGMS materials such as PA64S, male sterility is only exhibited under specific temperatures and photoperiods (Sun et al., 2021), indicating that photoperiods also have a place in regulating fertility genes. As for water, there is not much direct evidence to show that it has a significant effect on *OsTms6*, but existing studies show that water stress may work together with other factors such as temperature and light to affect its expression (Campo et al., 2013).

5 Association of *OsTms6* with other Genetic Pathways

5.1 Cross-influence with other sterility genes

Not all studies on *OsTms6* treat it as a "single-soldier" gene. Instead, it often plays a role in a larger genetic network, especially in male sterility. Transcription factors such as OsAL5 regulate *OsTMS5*, linking drought stress signals to thermosensitive male sterility (Wen et al., 2021). Of course, similar regulation also occurs in pollen wall development - OsMS188 transcription factors regulate *OsTMS18*, which directly affects the stability of pollen at different temperatures (Ni et al., 2021; Zhang et al., 2022). In other words, *OsTms6* may not directly control male sterility, but indirectly affect rice fertility and response to the environment by collaborating with other genes.

5.2 Involvement with hormone pathways

When it comes to regulating male sterility, hormone pathways should not be ignored. miRNAs such as miR156, miR5488, and miR399 have been found to affect genes related to fatty acid synthesis or secondary metabolism, which are critical for anther development and pollen activity (Sun et al., 2021). In this context, SPL transcription factors are particularly noteworthy, including OsSPL2, SPL4, SPL16, SPL17, etc., which affect programmed cell death (PCD) and male fertility by regulating the synthesis of flavonoids and controlling the level of ROS in the tapetum (Sun et al., 2022). Although *OsTms6* itself may not be directly involved in these pathways, it is likely to be "linked" to them. The studies of Ding et al. (2012) and Wan et al. (2019) also support this idea of interactive regulation.

5.3 Genetic modifiers affecting the action of *OsTms6*

The regulatory effect of *OsTms6* is not entirely "determined by itself". For example, studies on TGMS lines have found that the control of temperature responsiveness often involves the influence of multiple QTLs or specific loci (Reddy et al., 2000). Genes in PGMS lines, such as *rpms1* and *rpms2*, are also considered to be involved in regulating the function of *OsTms6* (Peng et al., 2008). Although these "modifying factors" may not be the protagonists, they do "pull the strings" behind the scenes to regulate the expression of *OsTms6* under different conditions. Therefore, when studying this gene, it is difficult not to consider its genetic background.

Overall, the relationship between *OsTms6* and other genes, hormones, and even larger genetic regulatory networks is far more complicated than imagined. If you want to really make good use of it to improve rice fertility or stress resistance, it is not enough to study it alone, but you have to put it into the whole picture.

6 Application of *OsTms6* in Rice Breeding

6.1 Formation process of TMS line

In rice hybrid breeding, in order to establish an efficient breeding system, we must first have a suitable sterile material. For example, the temperature-sensitive male sterile line (TGMS line) is a key tool. In lines like G20S, people found a gene called *OsTms6*, which is located on chromosome 10 of rice and is a recessive inheritance (Liu et al., 2010). One of the special features of this gene is that it only causes male sterility when the temperature is below 29.5 °C, which makes it more flexible than the traditional TGMS line and applicable to a wider area (Liu et al., 2010). In the process of locating such genes, researchers also used many molecular markers such as SSR and InDel. With the help of these tools, the development of new TGMS lines has become more precise (Kadirimangalam et al., 2019; Khilaimongkhon et al., 2019).

6.2 Application in hybrid breeding

If breeders consider simplifying the process and improving the efficiency of seed production, then *OsTms6* is a very good choice. The "two-line method" breeding using the TGMS line does not require a maintenance line, which is easier to operate (Lee et al., 2005). At the same time, the genetic information and positioning research of *OsTms6* itself also give people a clearer understanding of its mechanism of action, which provides a basis for the development of new TGMS lines (Lee et al., 2005). Moreover, similar genes, such as TMS5, can be precisely edited by CRISPR/Cas9, which also means that similar methods are likely to work on *OsTms6* and can speed up the generation of "non-transgenic" breeding materials (Zhou et al., 2016).

6.3 Field performance and trait stability

However, whether a line can be truly used depends on its performance in the field. TGMS materials with *OsTms6* have shown strong drought resistance in actual environments, which is an advantage for areas with tight water resources (Wen et al., 2021). Some studies have also found that the transcription factor OsAL5, which regulates similar genes (such as *OsTMS5*), can also enhance the drought resistance and temperature sensitivity of plants if it is highly expressed. Although this conclusion is based on other genes, the idea is the same, indicating that *OsTms6* may also be able to enhance its practicality through similar means (Wen et al., 2021). In addition, under suitable environmental conditions, this type of TGMS line can also maintain relatively good fertility, which is also critical for the stable production of hybrid seeds (Kadirimangalam et al., 2019).

6.4 Attempts and prospects of gene editing

Regarding *OsTms6*, the use of CRISPR/Cas9 tools has given everyone a lot of room for imagination. Previously, someone had successfully performed site-directed mutagenesis on TMS5 using this technology, indicating that it is not a fantasy to use it to manipulate *OsTms6* (Figure 2) (Zhou et al., 2016). As long as the target site is designed in the coding region of this gene, its function can be accurately changed, and even new traits can be introduced. The TGMS strains produced in this way are not only fast to develop, but also avoid transgenic problems and meet the requirements of commercial promotion (Zhou et al., 2016). With the continuous deepening of the understanding of the relevant mechanisms of TGMS, the application value of *OsTms6* may be further explored (Jiang et al., 2015; Fan and Zhang, 2017).

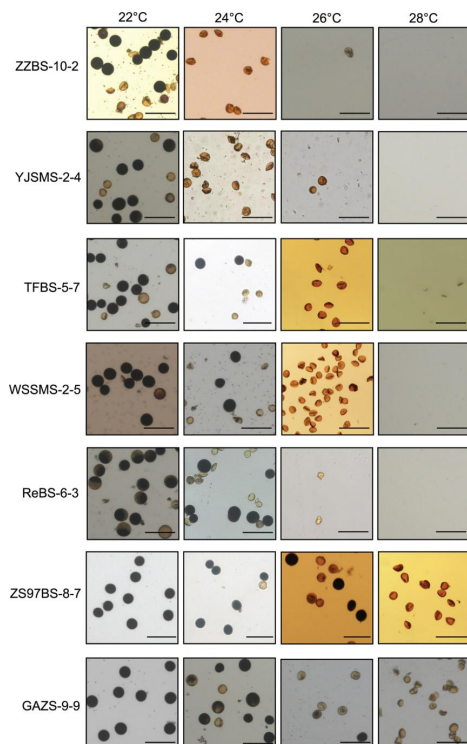


Figure 2 Pollen fertility of TGMS lines induced by the TMS5ab construct at different temperatures (Adopted from Zhou et al., 2016)

7 Challenges and Future Directions

7.1 Current blind spots in understanding

Although researchers have made many steps in studying the temperature-sensitive male sterility gene *OsTms6* in rice, such as clarifying some of its functions and regulatory methods, things are not yet completely clear. In particular, the molecular details of how it causes male sterility step by step under different temperature conditions are still unclear.

Some studies have indeed found related pathways, such as the involvement of certain non-coding RNAs or specific transcription factors (Zhou et al., 2012; Fan and Zhang, 2017), but for the entire network, who moves first, who moves later, and how they affect each other, there is still a lack of a complete picture. In addition, whether *OsTms6* and other stress resistance genes have "cooperation performances", such as the response mechanism to drought or high temperature (Raza et al., 2020; Wen et al., 2021), is still unclear. These "blank areas" are where we need to fill in the next step.

7.2 Technical requirements

Some technologies have been put to use, such as RNA-seq and small RNA sequencing, which have indeed helped us see some transcriptional maps related to sterility (Shimono et al., 2016; Sun et al., 2021). But the problem is that although these technologies have a large amount of information, they may not be detailed enough.

In order to see more clearly how *OsTms6* is expressed and how it works at the cellular level, more sophisticated technologies such as single-cell RNA sequencing are particularly important. CRISPR-Cas9 is also suitable for verifying gene function. At the same time, integrating proteomics and metabolomics may be able to see how *OsTms6* affects the state of rice under heat stress from a holistic perspective (Raza et al., 2020; Kan and Lin, 2021).

7.3 Next research directions

7.3.1 Mechanism exploration needs to be more in-depth

To understand the role of *OsTms6*, the current surface information alone is not enough. Later, we need to find its target in more depth to see how it affects sterility step by step. In particular, the "reaction logic" of these target genes may change at different temperatures. Methods such as ChIP-seq or yeast two-hybrid have been proven to be quite effective in finding protein-DNA and protein-protein interactions and can be used (Lee et al., 2005; Zhou et al., 2012; Fan and Zhang, 2017).

7.3.2 Breeding strategies to cope with climate change

The climate is becoming more and more extreme, which is not a trivial matter for rice yield. Future breeding work must use this type of temperature-sensitive sterility mechanism. Take *OsTms6* for example. If we can translate our understanding of it into practical breeding methods, such as introducing these traits into high-yield varieties through molecular markers or genomic selection, it will be a solution to deal with temperature fluctuations (Chen et al., 2010; Shimono et al., 2016; Raza et al., 2020).

7.3.3 Multiple methods to improve stability

It is difficult to solve practical problems by relying on one gene or one angle alone. The next focus should be to take genetics, physiology and environmental factors into consideration. For example, while using thermosensitive male sterility, adding drought and heat resistance traits may be able to breed truly stable and high-yield varieties.

At this time, it is not just the job of molecular biologists alone. Breeding experts and agronomists must also participate, and cooperation is the key. In addition, computational modeling is becoming increasingly useful, and it can help predict how different varieties will perform in different climates (Kan and Lin, 2021; Wen et al., 2021; Zhang et al., 2022). If these problems can be gradually solved, the research on *OsTms6* will not only be an academic breakthrough, but will also provide practical technical support for food production under the background of climate change. If necessary, I can continue to use the same method to handle the next section or the overall unified style of the whole article.

8 Conclusion

The researchers discovered the *tms6* gene in a rice mutant line called Sokcho MS. One of the special features of this rice is that it will be completely sterile when the temperature is above 27 °C or below 25 °C, and can only breed normally between 25 °C and 27 °C. Later, this gene was located on the long arm of chromosome 5, specifically between the two molecular markers RM3351 and E60663. In fact, this is not the only case. Genetic analysis of some other thermosensitive male sterile lines also shows that this type of trait is usually controlled by a recessive gene, but the location is different. Some are on other chromosomes, with different markers related to the *tms* gene.

It is worth noting that temperature sensitivity is not simply determined by a certain gene, but the product of genetic and environmental factors intertwined. In the study, some candidate genes have obvious responses to temperature changes in rice panicles. In addition, the transcription factor OsAL5 has also entered the research field of vision-it can regulate *OsTMS5*, thereby linking drought stress and thermosensitive male sterility. This discovery opens up new ideas for breeding TGMS rice varieties with both drought resistance and sterility.

From a breeding perspective, thermosensitive sterility genes like *tms6* are very useful. It can be used as a control switch in a two-line hybrid breeding system to help improve the production efficiency of hybrid seeds. The involvement of molecular markers is also critical - with these markers, breeders can screen out ideal lines more quickly. In addition, as the mechanism of action of regulatory factors such as OsAL5 becomes increasingly clear, we may be able to breed new rice varieties that are both high-yielding and able to cope with adverse environments such as drought in the future. This dual ability of "both being able to produce grain and being able to withstand disasters" is obviously what modern agriculture needs.

Looking ahead, there is still a lot of room for research on TGMS. To understand the ins and outs of these sterility mechanisms, we have to delve into the details of their molecular regulation. Once we have a clearer understanding of these regulatory networks, perhaps we can more confidently breed rice with stronger adaptability and more stable performance. Moreover, intersections like OsAL5 remind us that it is not a fantasy to combine sterility research with stress resistance mechanisms. In the future, using genomic tools and biotechnology to accelerate the breeding of new varieties may become an important step in promoting global rice production capacity and food security.

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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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