Plant Reprod (2018) 31:3–14
https://doi.org/10.1007/s00497-017-0310-5

REVIEW

Genetic and molecular characterization of photoperiod and thermo-sensitive male sterility in rice

Yourong Fan[1] · **Qifa Zhang**[2]

Received: 30 August 2017 / Accepted: 22 October 2017 / Published online: 2 November 2017

Abstract
Key message **A review on photoperiod and temperature-sensitive genic male sterility in rice.**
Abstract Male sterility in plants, facilitating the development of hybrid crops, has made great contribution to crop productivity worldwide. Environment-sensitive genic male sterility (EGMS), including photoperiod-sensitive genic male sterility (PGMS) and temperature-sensitive genic male sterility (TGMS), has provided a special class of germplasms for the breeding of "two-line" hybrids in several crops. In rice, the finding of the PGMS NK58S mutant in 1973 started the journey of research and breeding of two-line hybrids. Genetic and molecular characterization of these germplasms demonstrated diverse genes and molecular mechanisms of male sterility regulation. Two loci identified from NK58S, *PMS1* and *PMS3*, both encode long noncoding RNAs. A major TGMS locus, *TMS5*, found in the TGMS line Annong S-1, encodes an RNase Z. A reverse PGMS mutant *carbon starved anther* encodes an R2R3 MYB transcription factor. Breeding efforts in the last three decades have resulted in hundreds of EGMS lines and two-line hybrids released to rice production, which have greatly elevated the yield potential and grain quality of rice varieties. The enhanced molecular understanding will offer new strategies for the development of EGMS lines thus further improving two-line hybrid breeding of rice as well as other crops.

Keywords Environment-sensitive genic male sterility · Two-line hybrid · Photoperiod-sensitive genic male sterility · Temperature-sensitive genic male sterility

Introduction

Male sterility, an unfavorable trait for individual plant, has played a critical role for utilization of heterosis by facilitating hybrid breeding and, thus, has contributed greatly to increased productivity of many crops globally. According to the genetic basis, male sterility can be classified as cytoplasmic male sterility (CMS) induced by mutations in cytoplasmic genes, and genic male sterility (GMS) caused by mutations in the nuclear genome. Usually, CMS can be restored by nuclear restorer gene(s), providing the genetic basis for the development of the "three-line" system of hybrid crop varieties consisting of a male sterile line, a maintainer line and a restorer line (Fig. 1a). A number of GMS mutations have been found to be regulated by environmental conditions, such as photoperiod, temperature, or both and, thus, are referred to as PGMS, TGMS, or collectively EGMS. The plants would be male sterile under restrictive environmental conditions and fertile under permissive conditions. These characteristics have provided opportunities to develop "two-line" hybrids of crop varieties, since the male sterile line can be used for hybrid seed production under restrictive conditions and propagate itself under permissive conditions (Fig. 1b). Both two-line and

Communicated by Mengxiang Sun.

A contribution to the special issue 'Plant Reproduction Research in Asia'.

✉ Qifa Zhang
qifazh@mail.hzau.edu.cn

[1] State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources and College of Life Science and Technology, Guangxi University, Nanning 530004, China

[2] National Key Laboratory of Crop Genetic Improvement, National Centre of Plant Gene Research (Wuhan), Huazhong Agricultural University, Wuhan 430070, China

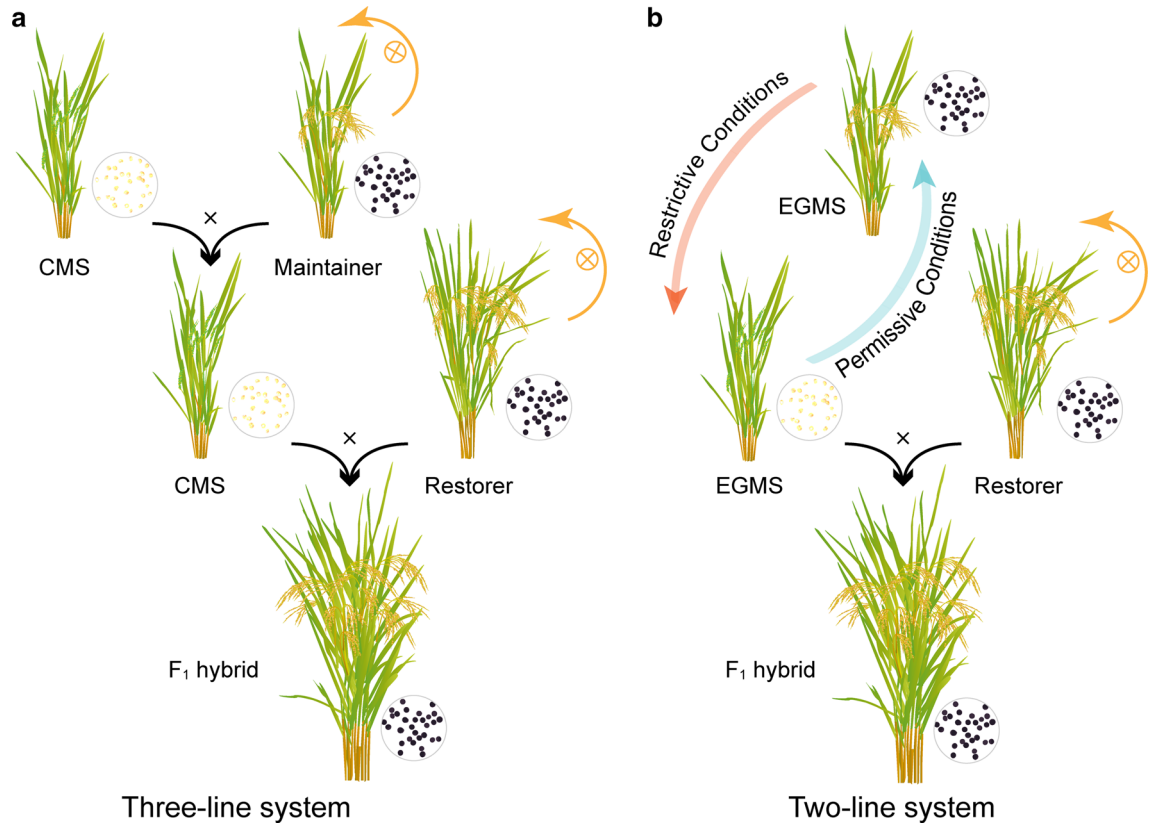

Fig. 1 Three-line and two-line system of utilizing male sterility for hybrid rice production. **a** The scheme of hybrid seed production in three-line system containing a CMS line, a maintainer line and a restorer line. The male sterility of CMS line is maintained by crossing with the maintainer line, and the maintainer line and restorer line are propagated by self-pollination. The F_1 hybrid plants from the cross between CMS line and restorer line have hybrid vigor for trait of interest. **b** The scheme of hybrid seed production in two-line system which only need EGMS line and restorer line. The male sterility of the EGMS line under restrictive conditions (long day for PGMS, or high temperature for TGMS) is recovered under permissive conditions (short day for PGMS, or low temperature for TGMS), without the need for the maintainer line. The pollen fertility of the corresponding line is indicated beside the plants

three-line systems have been extensively used in hybrid breeding of several major crop species for several decades.

In the last decade, tremendous progress has been made in genetic and molecular characterization of genes involved in CMS, PGMS and TGMS, especially in rice. In this review, we will focus on the current understanding of PGMS and TGMS with special emphasis on rice and will also highlight the implications of the findings for plant science research and future crop genetic improvement.

P/TGMS mutants in rice

The photoperiod-sensitive genic male sterile rice Nongken 58S

A spontaneous mutant was found in the field of a *japonica* rice variety Nongken 58 (abbreviated NK58, and the mutant as NK58S) by a breeder Mingsong Shi in 1973 in Hubei Province of central China (Shi 1985). After many years of collaborative work by rice scientists in Hubei Province, it was determined that fertility of NK58S was regulated by day length: it was sterile under natural long-day conditions in the summer of Wuhan and nearby areas and fertile under short-day conditions. This finding started the research and breeding of two-line hybrid rice in China.

Different from the photoperiod-sensitive flowering featuring transition from vegetative growth to reproductive development, the sensitive period of PGMS rice occurred during young panicle development, from the secondary branch differentiation to the pollen mother cell (PMC) formation stage. During this critical period, longer than 14-h day length with no less than 50 lx light intensity could induce sterility of NK58S, while normal fertility under shorter than 13.75-h day length (Yuan et al. 1988; Zhang et al. 1987). Moreover, it was shown that the fertility alternation of PGMS rice is also influenced by temperature (Zhang et al. 1992). There is a compensating effect between the critical day length and the temperature: higher temperature would shorten the critical day length required for fertility alteration, and conversely, lower temperature would lengthen the critical day length. When

the temperature is beyond the physiological upper and lower limits for pollen development, abnormality would occur in pollen development resulting in male sterility regardless of the day length.

It has been observed that the abortive pollen development in NK58S under long-day conditions begins from the early PMC stage and continued in the entire process of pollen development, which was also associated with the abnormal development of tapetum (Shi et al. 2009). This process of degeneration proceeded slowly resulting in the deficiency of nutrient supply for the developing microspores. And programmed cell death (PCD) is also involved in this premature tapetum degeneration, occurring earlier in NK58S than in NK58 (Ding et al. 2012a).

Thermo-sensitive genic male sterile mutants in rice

Several temperature-sensitive male sterile (TGMS) mutants were found by Chinese breeders (Table 1). The first TGMS rice mutant was found in 1986 from a CMS restorer line 5460. Planting in growth chambers revealed that the fertility of 5460S was normal at low temperature, but showing various degrees to complete sterility at high temperature, regardless of the photoperiod (Sun et al. 1989). The TGMS line Annong S-1 (AnS-1) was found in 1987 as a spontaneous mutant from the F_3 populations of the cross Chao 40/H285//6209-3. The induction for TGMS occurred in the PMC formation and meiosis stages (Chen et al. 1994), such that very few of the microspore mother cells could undergo normal meiosis under high temperature resulting in wrinkled abortive pollen grains (Zhou et al. 2014). The TGMS gene (*tms5*, see below) from AnS-1 has been the most widely used TGMS germplasm in two-line hybrid rice breeding and production.

In addition, several other TGMS mutants (Table 1) were also obtained and utilized in rice breeding programs, including Hengnong S-1 (Qi et al. 2014), Zhu 1S (Yang et al. 2000), and Xian S (Peng et al. 2010). The characteristics including thermo-response, anther and pollen development of these TGMS have been studied to various extents.

Reverse P/TGMS mutants in rice

In contrast to the photoperiod response of PGMS rice that shows male sterility under long-day conditions and normal fertility under short days, mutants were also found to show male sterility under short-day conditions and normal fertility under long-day conditions, which were termed reverse PGMS (rPGMS). For example, the rPTGM line Yi D1S was male sterile when the day length was less than 13 h, but fertile when the day length was more than 13.5 h (Li et al. 2006). Another rPGMS mutant showing a carbon starved anther (CSA) phenotype displayed complete male sterility in the paddy field with a photoperiod of 12.5–13.0 h (Zhang et al. 2012), while the anthers and pollen grains were mostly normal if the initiation of panicle development occurred when photoperiod is 13.5–14.0 h.

Similarly spontaneous mutants with reverse TGMS (rTGMS) were also observed. For example, rTGMS lines J207S, G20S, go543S and Diannong S-2 were completely sterile when the temperature was lower than 31, 29.5, 31 and 24 °C, respectively (Jia et al. 2001; Jiang et al. 1997; Liu et al. 2010; Yang and Zhu 1996).

Table 1 Characters of main EGMS lines

EGMS line	Type	Subspecies	Locus	References
NK58S	PGMS	*japonica*	*PMS1*, *PMS2*, *PMS3*	Mei et al. (1999b), Shi (1985) and Zhang et al. (1994)
5460S	TGMS	*indica*	*TMS1*	Sun et al. (1989) and Wang et al. (1995)
Annong S-1	TGMS	*indica*	*TMS5*	Chen et al. (1994) and Zhou et al. (2014)
Hengnong S-1	TGMS	*indica*	*TMS9-1*	Qi et al. (2014)
Zhu 1S	TGMS	*indica*	*TMS9*	Sheng et al. (2013) and Yang et al. (2000)
Mian 9S	PGMS	*indica*	*PMS4*	Huang et al. (2008) and Wang et al. (1999)
Xian S	TGMS	*indica*	*TMSX*	Peng et al. (2010)
Norin PL12	TGMS	*japonica*	*TMS2*	Yamaguchi et al. (1997)
IR32364TGMS	TGMS	*indica*	*TMS3(t)*	Subudhi et al. (1997)
TGMS-VN1	TGMS	*indica*	*TMS4(t)*	Dong et al. (2000)
Sokcho-MS	TGMS	*japonica*	*TMS6*	Lee et al. (2005)
SA2	TGMS		*TGMS*	Reddy et al. (2000)
J207S	rTGMS		*RTMS1*	Jia et al. (2001)
G20S	rTGMS	*japonica*	*TMS6(t)*	Liu et al. (2010)
Yi D1S	rPGMS	*indica*	*RPMS1, RPMS2*	Li et al. (2006) and Peng et al. (2008)

Genetic analysis and mapping of P/TGMS genes

Many studies have been reported in the genetic analysis of male sterility involving NK58S. In general, male sterility of NK58S appeared to be genetically recessive (Shi 1985). Fertility showed single-locus segregation in progenies of crosses between NK58S and its wild-type parent NK58 or a few other *japonica* varieties. Two-locus segregation was observed in crosses between NK58S and many other varieties (Jin and Li 1991).

Using molecular makers, Zhang et al. (1994) identified two loci, *PMS1* and *PMS2*, for PGMS in a cross between Minghui 63 and 32001S, a PGMS line of descendent from NK58S. These two loci were mapped to chromosomes 7 and 3, respectively, and the effect of *PMS1* was much larger than *PMS2*. Using two crosses (NK58S/1514 and NK58S/LH422) involving NK58S as one of the parents, Mei et al. (1999b) identified two loci controlling fertility segregation. One locus corresponded to *PMS1* on chromosome 7, and the other locus was mapped to chromosome 12 designated *PMS3*. They further determined (Mei et al. 1999a; Wang et al. 1997) that *PMS3* was the locus where the original mutation occurred that changed NK58 to NK58S. These two loci showed a classical duplicated genetic effect such that the plant was completely male sterile under long-day conditions only when both *PMS1* and *PMS3* loci were homozygous for the NK58S alleles (Li et al. 2001).

Two loci, *PMS1(t)* and *P/TMS12-1*, were also identified from the TGMS line Peiai 64S derived from NK58S. Further genetic analysis using F_2 populations from the crosses of Peiai 64S/93-11 and Peiai 64S/Peiai 64 mapped *PMS1(t)* and *P/TMS12-1* on chromosomes 7 and 12, respectively (Zhou et al. 2011, 2012). These locations corresponded to *PMS1* and *PMS3,* respectively, from the analysis based on NK58S (Liu et al. 2001; Lu et al. 2005).

Huang et al. (2008) mapped another PGMS gene *PMS4* to a 3.0 cM region on chromosome 4 using an F_2 population derived from the cross Yangdao 6/Mian 9S. The *indica* PGMS line Mian 9S was obtained from the progeny of a cross Feiyin 2A-461/Gu154//CS-6 (Wang et al. 1999), and genetic analysis suggested that the PGMS of Mian 9S was controlled by a single recessive nuclear gene *pms4*.

Due to the relatively rich sources of TGMS lines, more TGMS loci have been identified, including *TMS1*, *TMS-2*, *TMS3(t)*, *TMS4(t)*, *TMS5*, *TMS6*, *TMS9*, *TMS9-1*, *TMSX*, *TGMS* and *PTGMS2-1*. At each of these loci, a single recessive gene was responsible for the male sterility of the respective TGMS line as shown in the respective populations by genetic analysis. Interestingly, one of them, now cloned as *TMS5* from chromosome 2 controlling the TGMS in AnS-1 and Zhu 1S (Zhou et al. 2014), had been identified and mapped many times by different research groups. For example, Xu et al. (2011) identified a single recessive gene *ptgms2-1* by genetic analysis of the F_2 and BC_1F_2 population from the cross between Guangzhan 63S and 1587, in which Guangzhan 63S was obtained from a mutation in the cross between N442S (derived from NK58S) and Guangzhan 63. This gene was mapped to a 50.4 kb region with a nuclear ribonuclease Z gene (LOC_Os02g12290), which coincided with the mapping region of *TMS5* based on AnS-1 (Yang et al. 2007). Genetic analysis of six F_2 populations from crosses between Xian S and other varieties showed that the TGMS in Xian S was controlled by a single recessive gene *tmsX*, and fine mapping also resolved *tmsX* to the region of *TMS5* (Peng et al. 2010). Genetic analysis of the Zhu 1S/R173 F_2 population also resolved the previously designated *TMS9* locus of Zhu 1S to the vicinity of *TMS5* (Sheng et al. 2013) suggesting that *tms5*, *tms9*, *tmsX* and *ptgms2-1* are mutants of the same gene (Fig. 2).

Different from *tms9*, *tms9-1* was a recessive gene governing the TGMS in Hengnong S-1, which was mapped to a 162 kb interval on chromosome 9, where a PHD finger protein (LOC_Os09g27620) was identified as the candidate (Qi et al. 2014). The *TMS1* locus from the TGMS line 5460S co-segregated with the RFLP marker TGMS1.2 on chromosome 8 with a distance 6.7 cM (Wang et al. 1995). In addition, preliminary mapping information has also been obtained for five other TGMS genes *TMS-2*, *TMS3(t)*, *TMS4(t)*, *TMS6* and *TGMS* (Table 1 and Fig. 2) that are located on chromosomes 7, 6, 2, 5, and 9, respectively (Dong et al. 2000; Lee et al. 2005; Reddy et al. 2000; Subudhi et al. 1997; Yamaguchi et al. 1997).

Several rPTGM/TGMS genes were identified and mapped. Analysis of an F_2 population from a cross between rPTGM line Yi D1S and 8528 identified two rPTGM loci *RPMS1* and *RPMS2*, which were mapped to regions of 998 kb and 68 kb on chromosomes 8 and 9, respectively (Peng et al. 2008). Genetic analysis identified two loci *TMS6(t)* and *RTMS1*, controlling male sterility of rTGMS lines G20S and J207S, respectively, both of which were mapped to chromosome 10 (Jia et al. 2001; Liu et al. 2010) (Fig. 2).

The molecular mechanisms of P/TGMS genes regulating male sterility

Recently, studies of P/TGMS genes in rice have made great progress as several important P/TGMS genes have been cloned, and their molecular mechanisms of regulating P/TGMS have been gradually unveiled.

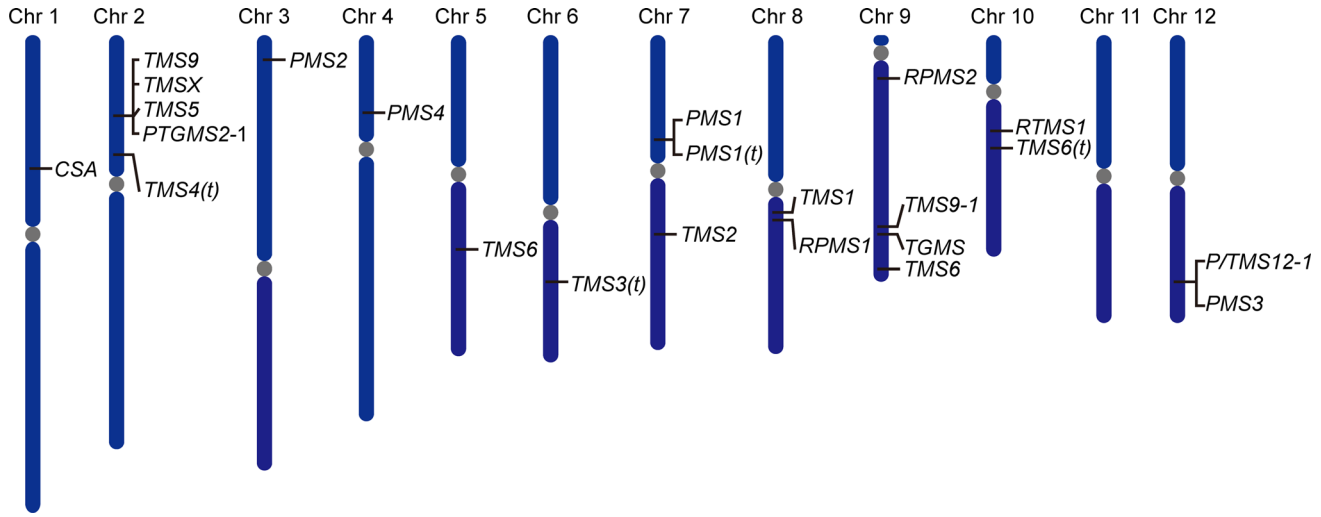

Fig. 2 Distribution of genetic loci for P/TGMS in rice

Long noncoding RNAs regulate PGMS

The gene *PMS3* which has been determined previously was the original mutation that changed NK58 to NK58S (Li et al. 2001; Mei et al. 1999a, b). Fine mapping and comparative sequencing found a single SNP resulting from substituting guanine (G) in NK58 with cytosine (C) in NK58S (Lu et al. 2005). This SNP was located within a long noncoding RNA (lncRNA). Overexpression of the fragment from NK58 in NK58S could recover the fertility under long-day conditions. An lncRNA named as *LDMAR* (long-day-specific male-fertility-associated RNA) was identified as the candidate of the *PMS3* locus (Ding et al. 2012a). *LDMAR* was expressed in almost all of the tissues, but higher in young panicles, and highest in NK58 under long-day conditions compared with NK58S under both long day and short day and also NK58 under short-day conditions. It was hypothesized that sufficient level of the *LDMAR* is required for normal pollen development of plants grown under long-day conditions. The G-to-C SNP may alter the secondary structure of *LDMAR* from a stem to the loop, together with increased methylation in the putative promoter region of *LDMAR*, reducing the gene transcription in the young panicles under long-day conditions, eventually causing PGMS (Fig. 3a) (Zhu and Deng 2012). Moreover, three predicted small RNAs were detected within the LDMAR (Ding et al. 2012a). A follow-up study showed that this DNA methylation was likely directed by a 21-nt small RNA *Psi-LDMAR* generated from the promoter of *LDMAR* (Ding et al. 2012b).

Interestingly, almost at the same time, another group reported the isolation of the locus they named *P/TMS12-1* from the TGMS line Peiai 64S (Zhou et al. 2012). The *P/TMS12-1* locus is the same as *PMS3*, since Peiai 64S was bred by introgressing the PGMS trait of NK58S into the *indica* variety Peiai 64 genetic background. However, the *PMS3* (*P/TMS12-1*) locus confers TGMS in this genetic background rather than PGMS. The point mutation between NK58 and NK58S is at position 11 of a 21-nt small RNA, named osa-smR5864w and osa-smR5864m in wild-type and P/TGMS lines, respectively. As the central region of small RNA is very important for the recognition and regulation of their targets (Franco-Zorrilla et al. 2007), the authors hypothesized that osa-smR5864w suppressed the expression of the targets, while the mutation would lead to a loss-of-function of osa-smR5864m in targeting different genes in the *japonica* and *indica* genetic backgrounds, resulting in PGMS and TGMS, respectively (Zhou et al. 2012).

More recently, Fan et al. (2016) reported the cloning of the *PMS1* locus that also encodes an lncRNA. By analyzing the genetic effects in progenies from a cross between NK58S and NIL(MH), a near isogenic line containing an introgressed genomic fragment from Minghui 63 in NK58S background, they showed that the PGMS trait controlled by *PMS1* is semi-dominant rather than completely recessive as previously assumed (Zhang et al. 1994). This allele was thus designated as *Pms1*, which encodes an lncRNA *PMS1T* that has no intron and located in an intergenic region (Fan et al. 2016; Guo and Liu 2017). Transformation of the *PMS1T* into the NIL(MH) resulted in male sterility under long-day conditions. Although there is 65-bp insertion in the *PMS1T* of NK58S relative to Minghui 63, this inserted sequence is not related to PGMS. They identified a SNP S2 as the causal polymorphism. The lncRNA *PMS1T* was targeted by a 22-nt microRNA miR2118, preferentially expressed in the immature inflorescence and triggers 21-nt phased small interfering RNAs (phasiRNA) biogenesis in plants (Johnson et al. 2009). Small RNA sequencing results from the young panicles displayed that

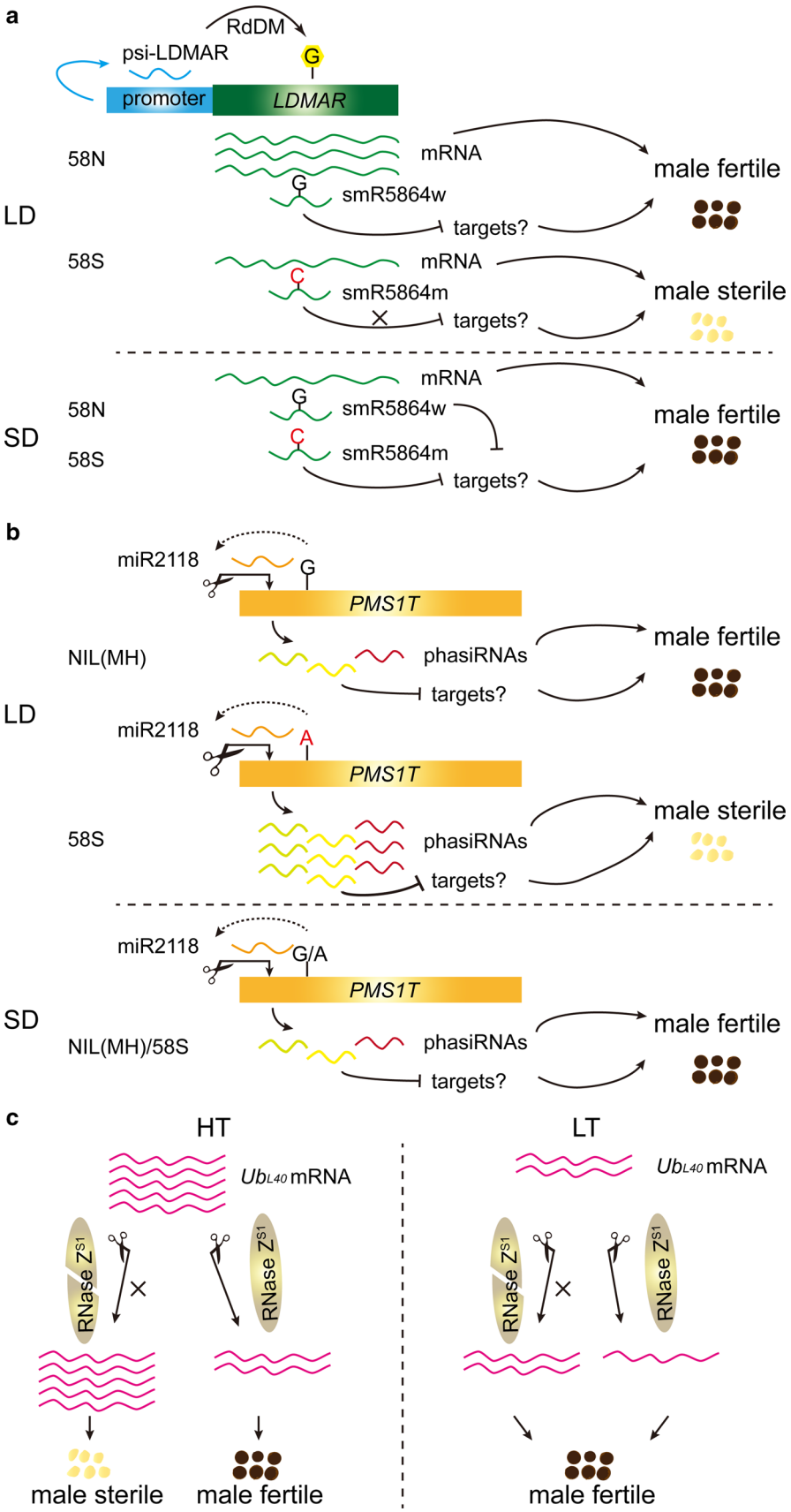

Fig. 3 Models of the current understanding for the three cloned EGMS genes. **a** An lncRNA *LDMAR* controls the PGMS trait at the *PMS3* locus. A small RNA psi-LDMAR generated from the promoter mediated the DNA methylation of LDMAR regulating the level of transcript for pollen development under long-day conditions. Or alternatively, a G-to-C mutation leads to a loss-of-function of small RNA osa-smR5864m in targeting different genes, resulting in PGMS. **b** An lncRNA *PMS1T* targeted by the miR2118 confers the PGMS at the *PMS1* locus. The SNP nearby the cleavage site may influence the cleavage efficiency for higher accumulation of phasiRNAs, causing male sterility in 58S under long-day conditions. **c** The TGMS gene *TMS5* encodes RNase Z^{S1} processing Ub_{L40} mRNA whose expression is temperature-sensitive. The loss-of-function mutation of RNase Z^{S1} results in the over-accumulation of Ub_{L40} mRNA, leading to male sterility at high temperature. LD, long-day conditions; SD, short-day conditions; HT, high temperature; LT, low temperature

18 pairs of 21-nt phasiRNAs were generated from the *PMS1T* transcript, beginning right from the cleavage site of miR2118. Comparative analysis revealed that the quantities of 21-nt *PMS1T*-phasiRNAs were higher in NK58S under long days at PMC stage than NK58S under short day and NIL(MH) under both long- and short-day conditions. They also showed that the causal polymorphism of *PMS1T*, SNP S2, was located in one of phasiRNA, 24 nt downstream of the cleavage site directed by miR2118. This location indicated the likely roles of SNP S2 in regulating PGMS: it may alter the RNA secondary structure to change the cleavage efficiency mediated by miR2118 to result in more phasiRNAs in NK58S at long-day conditions; it may also cause difference in efficiency for targeting the downstream genes for male sterility by these phasiRNAs (Fig. 3b).

PMS1 and *PMS3* both regulate the PGMS in rice, and they have similar gene structure and expression patterns; both encode lncRNAs producing small RNAs; causal mutations are SNPs (Table 2). But there are also some differences between them: dominant-recessive trait, the small RNA type, DNA methylation status and the targets of the small RNAs (Table 2). How these two loci function in the same plant to cause male sterility should be an interesting highlights in future studies.

The findings that both *PMS1* and *PMS3* loci encode lncRNAs have general implications for plant science research (Guo and Liu 2017). LncRNAs are a new class of functional RNAs that are longer than 200 nucleotides without protein translation capacity and play important roles in the regulation of gene transcription, post-transcriptional gene regulation and epigenetic regulation (Fatica and Bozzoni 2014; Mercer et al. 2009; Wilusz et al. 2009). So far, only a few lncRNAs in plant have been functionally characterized, which are mainly involved in process like flowering, fertility, phosphate starvation and immunity (Ding et al. 2012a; Fan et al. 2016; Franco-Zorrilla et al. 2007; Heo and Sung 2011; Seo et al. 2017; Swiezewski et al. 2009; Zhou et al. 2012). Moreover, phasiRNAs are a special class of small RNAs. It was known that phasiRNAs are generated in 21-nt or 24-nt intervals from transcripts of precursor RNAs called *PHAS* genes or loci (Johnson et al. 2009). They are triggered by the cleavage of 22-nt miR2118 or miR2275 to generate 21-nt or 24-nt phasiRNAs, respectively (Johnson et al. 2009; Komiya et al. 2014; Song et al. 2012a, b). In maize, the 21-nt and 24-nt phasiRNAs are specifically abundant in premeiotic and meiotic anthers, respectively (Zhai et al. 2015). Clearly the results of PGMS studies have demonstrated a rare opportunity for understanding functions of noncoding RNAs.

RNase Z regulates TGMS

A single-locus *TMS5* was identified as controlling the TGMS trait in the TGMS line AnS-1 and Zhu 1S, and mapped many times by different research groups because of its wide use in two-line hybrid rice breeding (Jiang et al. 2006; Wang et al. 2003b; Yang et al. 2007). The *TMS5* gene was cloned by Zhou et al. (2014). Comparative sequencing of the *TMS5* region revealed a C-to-A mutation at the gene LOC_02g12290 creating a premature stop codon. This candidate gene was verified by genetic complementation and RNA interference. *TMS5* encodes a conserved ribonuclease Z (RNase Z) and belongs to the short-form group, referring as RNase Z^{S1}. No differences in protein accumulation and mRNA expression were detected between low and high temperatures indicating that RNase Z^{S1} itself is temperature-insensitive. It was then hypothesized that some targets of RNase Z^{S1} should be sensitive to the temperature. RNA-seq analysis identified three mRNAs of $Ub_{L40}1$, $Ub_{L40}2$ and $Ub_{L40}4$, all from the genes of ubiquitin-60S ribosomal protein L40 family (Ub_{L40}),

Table 2 Parallels of between *PMS1* and *PMS3*

Characteristic	*PMS3*	*PMS1*
Genetic relationship	Recessive	Semi-dominant
Transcript	*LDMAR*	*PMS1T*
Gene structure	No intron; lncRNA	
Gene location	Overlaps with other transcripts	Intergenic region
Expression level	Low	
Expression pattern	Preferentially expressed in young panicles; lower in NK58S under LD; without rhythm	
Causal mutation	SNP	
MiRNA recognize	Unknown	miR2118
Small RNA type	Psi-LDMAR in promoter; osa-smR5864m	phasiRNAs
DNA methylation level	Higher in NK58S	No differences
Mechanism	RdDM	phasiRNAs
Small RNA targets	Unknown	Unknown

accumulate at higher level in *tms5* plants at high temperature than low temperature. *RNase* Z^{S1} could process these three mRNAs, which are expressed in PMCs both in vitro and in vivo. Overexpression of $Ub_{L40}1$ or $Ub_{L40}4$ alone could also lead to male sterility at high temperature while knockdown of either one could restore the male fertility. As the TGMS gene, RNase Z^{S1} itself is temperature-insensitive, but the loss-of-function mutation in the TGMS lines blocks the processing Ub_{L40} genes by RNase Z^{S1}, resulting in over-accumulation of Ub_{L40} mRNAs leading to male sterility at high temperature (Fig. 3c). The result should be directly useful for application in developing male sterile lines in hybrid rice breeding, in addition to enhanced understanding of male fertility development in plants (Fan and Zhang 2014).

An R2R3 MYB transcription factor regulates reverse PGMS

Zhang et al. (2010) isolated the gene for rPGMS showing a carbon starved anther (CSA) phenotype. The *CSA* (LOC_Os01g16810) encodes an R2R3 MYB transcription factor and is mainly expressed in vascular tissues and the tapetum. It directly regulates the *OsMST8*, a monosaccharide transporter (Zhang et al. 2010). The mutation of *CSA* greatly reduced the expression of *OsMST8*, causing defect in sugar partitioning from the flag leaf to the lemma/palea and anther via stem, resulting in male sterility. Interestingly, the *csa* mutant caused male sterility only under short-day conditions, while under long-day conditions, the plant would still show normal sterility (Zhang et al. 2012). This recovery of fertility of the *csa* mutant under long-day conditions is probably due to the functional replacement of the *CSA-OsMST8* pathway by two CSA homologs or other proteins in male reproductive development. Alternatively, a BR-signaling factor *OsBZR1* could bind to the promoter of *CSA* and directly promote its expression. Knockdown of *OsBZR1* causes reduced male fertility and seed size and weight, independent of the day length (Zhu et al. 2015). Introduction of the *csa* fragment into other *japonica* or *indica* background could express the rPGMS trait very well, which could be used as male sterile line to produce two-line hybrid (Zhang et al. 2012).

Development and utilization of two-line hybrids in rice breeding and production

The availability of the EGMS germplasms facilitated the development of two-line hybrids, which has demonstrated a number of advantages compared to three-line hybrids. First, the EGMS rice can be used to propagate itself under permissive conditions, and to produce hybrid seeds under restrictive conditions, thus would reduce the costs in labor, time and resources in production. Second, the EGMS rice has a broad spectrum of restoration; all normal rice varieties can restore the fertility of the F_1 hybrid. Therefore, deliberately bred restorer lines are not required, thus providing much more freedom for making crosses thus raising the opportunities to obtain superior hybrid combinations.

Large efforts have been invested in the development of two-line hybrid rice especially in China in the last three decades, which has made tremendous progress. The first two-line hybrid rice combination was planted in large area in 1995 in China. Since then, hundreds of two-line hybrids have been released by various institutions and the proportion of two-line hybrid rice in all hybrid rice and the total planting area have been increasing sturdily and reached 5 million ha in 2013 (Hu et al. 2016).

Possible interactions between PGMS and TGMS in the breeding process

Presently, 99 PGMS/TGMS lines have been developed and passed the examination and approval for use in commercial hybrid rice breeding (http://www.ricedata.cn/variety). Zhang et al. (2015) surveyed the distribution of the cloned PGMS and TGMS genes in 90 of the released PGMS and TGMS lines, most of which were developed based on NK58S, AnS-1 and Zhu 1S. Genotyping with two functional molecular markers of PGMS gene *PMS3* and TGMS gene *TMS5* show that out of the 47 EGMS lines bred using the PGMS line NK58S as the male sterility parent, 12 carried the PGMS gene *pms3*, 29 had the TGMS gene *tms5*, two possessed both genes, while the remaining four lines contained neither of them. Conversely, all the 18 lines derived from AnS-1 or Zhu 1S carried the *tms5* gene, without *pms3*. All P/TGMS descendants from crosses between Peiai 64S (a NK58S derivative) and AnS-1 carried the *tms5* gene. In the two lines derived from a cross between Peiai 64S and Zhu 1S, one carried both *pms3* and *tms5*, the other had *tms5*. In addition, of the 16 EGMS lines obtained without deriving germplasm from NK58S, AnS-1 or Zhu 1S, six had *pms3*, nine carried *tms5*, while the remaining one had neither *pms3* nor *tms5*.

Furthermore, the data also showed that large shift from PGMS-based to TGMS-based two-line hybrids occurred in rice production in China during 1993–2012, and by 2012 the *tms5*-containing hybrids occupied $> 95\%$ planting area in the two-line hybrid rice production (Zhang et al. 2015).

Although it seems puzzling on why and how the transition from PGMS to TGMS took place in the process of male sterility breeding, the data certainly suggest very interesting problems for future investigation. It also suggested that combined utilization of the identified EGMS

genes may benefit the development of new EGMS lines with more stable sterility and fertility conversion in different environments.

The EGMS in other crops

Efforts have also been made to identify EGMS mutants for development of two-line hybrids in other crops. In upland cotton (*Gossypium hirsutum* L.), the pursuit for acquiring EGMS lines started in 1990s in China. The first EGMS mutant 48043 with a useful morphological marker of yellow first true-leaf was found in the field of Jing 86162, Hubei Province (Shao and Liu 2000). Other EGMS lines, such as 396A (Niu et al. 2016), Temian S-1 (Yu et al. 2003), Xiang-QB (Zeng et al. 2013) and TMS-2 (Zhou et al. 2007) were subsequently found to be sterile under the long-day and high-temperature conditions in higher latitudes, but fertile under the short-day and low-temperature conditions in lower latitudes. A new PGMS line CCRI 9106 was recently obtained from CCRI 040029 by so-called "space mutation" (Ma et al. 2013). CCRI 9106 was fertile with an 11–12.5 h photoperiod when the temperature was higher than 21.5 °C in the winter nursery in Sanya (Hainan Province), China, providing a short-day condition, and was sterile with a 13–14.5 h photoperiod in Anyang (Henan Province) in the summer providing a long-day condition. Genetic analysis indicated that the PGMS trait of CCRI 9106 was controlled by a single recessive gene *ys*-1, which was located on the chromosome D12 (Zhang et al. 2017).

In *Brassica napus*, the first EGMS line Xiangyou 91S was found in 1991, with its fertility sensitive to the temperature by showing male sterility at high temperature and normal fertility at low temperature (Xi et al. 1994). Two-line hybrids have been developed based on Xiangyou 91S and used in production in China. Other TGMS lines such as SP2S, 104S and H90S were also reported, and some preliminary genetic analyses were conducted (Li et al. 1997; Wang et al. 2003a; Wu et al. 2009; Yu et al. 2015).

In wheat, environment-sensitive male sterility was first reported in the D^2-type wheat which showed photoperiod-sensitive cytoplasmic male sterility. Since then, many EGMS lines were reported and two-line hybrid wheat have undergone demonstration and application phase in China. Among them, BS series were PGMS, C49S, BNS and 337S series were TGMS, while ES series were sensitive to both photoperiod and temperature (Zhao 2010). Contrary to the EGMS trait in rice, the EGMS wheat was sterile under short-day and/or low-temperature conditions but fertile under long-day and/or high-temperature conditions. Different types of EGMS wheat showed different characteristics of fertility transformation, including the critical day length, critical temperature and even the sensitive stages in the development of plant. Genetic analysis indicated that the male sterility of different EGMS lines in wheat was governed by one, two or multiple recessive major genes (Dong et al. 2012). It was difficult to fine map the genes in wheat because of the polyploidy, only a single locus named as *WTMS1* conferring the TGMS in BNY-S has been mapped on chromosome 2B (Xing et al. 2003).

Future perspectives of EGMS research and breeding application

With rapid development of the rice functional genomic research, genes for EGMS have been identified in recent years, revealing that the molecular natures of the EGMS genes are very different from each other. We anticipate that more genes for EGMS will be cloned both in rice and other crops in the near future. Gene cloning will provide more opportunities for elucidating the regulatory mechanisms, with regard to both environmental sensitivity and male sterility.

Although many of the EGMS germplasms have been successfully utilized in two-line hybrid breeding and many hybrids have been planted in large scale, there are still two major problems encountered in the breeding of two-line hybrids based on the EGMS lines. The first is the instability of the male sterility under restrictive conditions (usually long day/high temperature) in the fields caused mostly by temperature fluctuation resulting in fertile pollen and selfed seeds. Such selfed seeds would reduce the purity of the seeds and produce male sterile plants thus causing yield loss. The second is insufficient reversibility to fertile pollen under permissive conditions (short-day/low-temperature), which limit the amount of seeds produced for propagating the male sterile lines. Understanding the molecular nature of the genes may help solve the problems.

Conceptually, it was expected that PGMS should provide more stable sterility and fertility conversion in terms of withstanding against the environmental fluctuation than TGMS and, thus, should be much more reliable for hybrid rice breeding. This is because the photoperiod is stable for any given geographical region, while temperature fluctuates unpredictably. The results that PGMS lines shifted to TGMS in the breeding process together with the changes of the genes seemed quite surprising and puzzling. Nonetheless, such results have opened an area for future investigation. With the accumulation of data from expression profiles, genes with essential functions in pollen development with clear photoperiod-dependence might be identified. Modifying such genes by gene editing may produce "ideal PGMS" lines.

Moreover, there has been a rapid movement in China toward "green varieties", a notion that has been elucidated by Zhang (2007) as "Green Super Rice", to develop new cultivars with resistances to multiple diseases and insects and abiotic stresses, high nutrient-use efficiency thus requiring less pesticides, fertilizers and irrigation, and at the same time higher yielding and producing better grain quality. In the practice of hybrid rice breeding, the male sterile lines of the hybrids may be designed to harbor genes for the "green traits", while the restorer lines should be continuously improved for combining ability for yield potential. The accelerated progress in rice functional genomic research will help realize such goals, facilitating development of resource saving and environment-friendly agriculture systems.

Author contribution statement FY and ZQ wrote the manuscript. All authors read and approved the manuscript.

Acknowledgements This work was supported by grants from the National Natural Science Foundation (No. 91540101) and the National Key Research and Development Program (2016YFD0100903) of China.

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