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Research Progress on the Genes Controlling Grain Number in Rice

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Abstract As one of the important factors of rice yield, grains number per panicle has gained wide attention from breeders. The formation of grains number per panicle is a complex biological process, which controlled by many factors, such as spike type, spikelet differentiation rate, and spike differentiation process, etc. With the development of plant functional genomics-related techniques, some progress has been made in the cloning of rice panicle number gene and the study of its mechanism. Recently, the cloning and mechanism study of genes controlling rice grain number has made great progress. In this review, we summarize systematically the recent research progress on the genes controlling grain number from Spike meristem development and spike type etc. We also discuss the problems of current works and future research directions, to provide theoretical basis for rice high-yield breeding.

Keywords Rice; Yield; Grains number per panicle; Gene function; Molecular mechanism

With the continuous growth of population, the problem of food shortage has become increasingly prominent. It is estimated that the world population will reach 9 billion in 2050, and the grain output needs to double on the existing basis to meet the food demand of human beings (Lin et al., 2019). At the same time, food security is facing more severe challenges due to the worsening climate, the reduction of cultivated land, the shortage of water resources and so on (Liu et al., 2016). Rice is an important food crop, and about 60% of the world's population takes rice as its staple food. Therefore, increasing rice production is the key to deal with the problem of food shortage. In order to increase the yield of per unit area of rice, experts and scholars at home and abroad have successively proposed various ideas to increase the yield by using the number of grains per panicle: Yuan Longping proposed a new Super-high-yield plant type with high canopy, low panicle, medium-large panicle and high lodging resistance"; Kai da Zhou designed a "heavy panicle type" rice model; and "large panicle, less tillering" super rice bred by International Rice Institute (Xiao et al., 2013). In recent years, breeding heavy panicle hybrid rice varieties is one of the technical routes for super high yield breeding of rice. Because the number of panicles is easily affected by external conditions, cultivation techniques and other factors, the number of grains per panicle by genetic control has become one of the main directions of high-yield breeding of rice (Gouda et al., 2020b). The formation of grain number per panicle is controlled by many factors, such as the differentiation rate of spikelet meristem, the duration of spikelet differentiation and panicle type, which is a very complex biological process. At present, some progress has been made in gene cloning and mechanism research of grains number per panicle in rice (Qiu et al., 2018).

1 The Number of Grains Per Panicle of Rice and Its Influencing Factors

The conical inflorescence of rice consists of spike, branch and grains, the grains are born on the branches, and the branches are born on the spike. The number of grains per panicle is the total number of grains per panicle, also known as the number of flowers per panicle. Because it grows directly on the branches, so the number of grains per panicle of rice is affected by panicle length, panicle type, number of branches, etc. According to genetic studies, the number of grains per panicle and related traits in rice are both quantitative traits. Through

systematic analysis of panicle traits of rice in BC1 population, F2 segregating population, near isogenic line and other populations, panicle length and primary branch had higher heritability, and panicle traits showed continuous phenotypic variation in segregating offspring, which was greatly influenced by external environment and genetic background. Yu ping Zhang et al. (2010) found that the number of grains per panicle was positively correlated with the panicle length through rice hybridization experiments with different panicle types. Generally, varieties with large panicle length and panicle type had more grains per panicle. Xian ping Zeng (2012) analyzed the relationship between panicle length and number of grains per panicle of hybrid rice varieties approved in Sichuan Province during the past ten years, and found that with the advancement of rice growth period, panicle length showed an increasing trend, and the increasing trend of grain number per panicle was consistent with it. Another factor affecting the number of grains per panicle is the number of branches. A large number of studies have shown that the number of primary and secondary branches are significantly positively correlated with the number of grains per panicle, and the effect of secondary branches is particularly significant. Yong et al. (2009) analyzed the yield-related agronomic traits of rice in the middle and lower reaches of the Yangtze River, and found that cultivars with higher grain yield per panicle usually showed longer panicle length, larger number of primary and secondary branches. Many of the QTLs controlling secondary shoot and grain number per panicle were located at the same locus, thus indicating the close relationship between grain number per panicle and grain number per panicle during rice production.

2 Research Progress on the Genes Controlling Grain Number in Rice

2.1 Regulation genes of spikelet differentiation rate and spikelet differentiation duration in rice to control the number of per panicle in rice

During rice development, the symbol of the onset of reproductive growth is the transition from shoot apical meristem (SAM) to inflorescence meristem (IM). IM produces a certain number of lateral meristem (AM), First IM produces a certain number of lateral meristem (AM), Then AM differentiates into primary branch meristem (BM), Finally IM degeneration inactivates the base of the terminal primary branch (Tabuchi et al., 2011). Primary branches can develop into varying numbers of spikelets and secondary branches, and even some secondary branches can develop into three branches, Spikelet meristem (SM) forms after branching meristem.

When the transition from IM to SM is delayed, it will lead to repeated rotation of branches and produce more branching panicles; Conversely, early conversion of IM to SM resulted in a reduction in the number of shoot primordia, which in turn produced fewer spikelets and flowers. Therefore, the number of grains per panicle in rice is affected by the differentiation efficiency of shoot primordium and floret primordium and the duration of differentiation.

The *Gnla* gene encodes cytokinin oxidase. Down-regulation of its expression will result in a large accumulation of cytokinins in the inflorescence meristem, which in turn increases the number of reproductive organs and the number of spikes and grains. *DST* affects panicle-branch and the number grains per panicle in rice by directly regulating *Gnla* expression (Gouda et al., 2020a). The *LOG* gene transforms the inactive cytokinin-nucleotide complex into a free form with biological functions by encoding a cytokinin-activating enzyme with specific phosphoribohydrolase activity. In rice with *LOG* gene loss of function, the development of shoot apical meristem terminated early and the number of grains per panicle decreased significantly. (Kurakawa et al., 2007). In addition, overexpression and interference of the cytokinin-responsive GATA transcription factor *cgal* reduced the number of spike branch and the number of grains per panicle in rice (Hudson et al., 2013). *GNP1* (*GA20ox1*, *qEPD2*), which encodes GA20 oxidase, reduces the accumulation of gibberellin in Rice Panicle inflorescence meristem through a KNOX-mediated transcriptional feedback loop, thereby increasing cytokinin activity and consequently grain number per panicle in rice. *SNBs* are members of the *IDS1* family that are unique to Gramineae and encode two AP2 domains, *SNB* and *OsIDS1* cause the reduction of the grains number per panicle in rice due to premature transformation of inflorescence and branching meristem into the next meristem (Lee and An., 2012). *TAW1* gene can prolong the extension time of shoots by increasing the activity of inflorescence meristem and delaying the differentiation of spikelets, thus

increasing the proportion of secondary branches and leading to an increase in the number of grains per panicle (Yoshida et al., 2013). The certainty of spikelet meristem development is influenced by the newly identified gene *FON4*, which further affects spikelet development by regulating SAM size in rice. The number of florets and grains per panicle increased further in rice with *FON4* mutation (Ren et al., 2019).

LAX1, an important regulator of axillary meristem formation, is transiently expressed in axillary meristem and interacts with LAX2-encoded proteins, which together regulate the formation of lateral meristem in rice (Tabuchi et al., 2011). *APO1* increased the number of grains per panicle of rice by promoting the early formation of spikelet meristem, prolonging the formation time of paddy slices and carpels, and finally positively regulating the number of primary branches. *APO1* regulates the development and formation of panicle, shoot and spike through direct interaction with *APO2* gene. It has also been reported that *APO2* regulates the differentiation of axillary meristem by regulating the expression of *LAX1* (Deshpande et al., 2015).

FZP is a major negative regulator of *APO2*, which determines the timing of transformation from panicle branching to spikelet formation, and controls the number of grains per panicle in rice by regulating the expression of *OsMADS* box genes (Bai et al., 2016).

OsMADS3 and *MADS58* together determine stamen and carpel identity. The other two genes, together with *MADS13*, play an important role in the determination of floral meristem. Both *mads3* and *mads58* were completely lost by the characteristics of reproductive organs represented by mutant rice, and accumulated a large number of plasmalemmas in the third and fourth round of flower organs, resulting in abnormal ear development in rice, which in turn affected the number of grains per panicle (Zhang et al., 2015b). *OsMADS1* and *OsMADS3* interact to promote flower development and maintain floral meristem activity, thereby participating in the formation of floral organ characteristics. In their mutants, stamens and carpels developed into structures similar to the outer and inner barley, and the number of grains per panicle decreased significantly.

2.2 Influencing the grains number per panicle in rice by regulating the genes regulating panicle type

Panicle formation includes a series of processes such as axillary meristem development, inflorescence morphology establishment and grain formation. Rice panicle size and panicle morphological structure not only affect the shading canopy area and photosynthetic efficiency, but also affect the spatial distribution of branches and grains, thus determining the number of grains per panicle. The *DEP1* gene controls the phenotype of erect panicles in rice. The dominant *DEP1* allele is a gain-of-function mutation resulting from the truncation of the protein. The role of *DEP1* is to improve meristem activity, resulting in a decrease in inflorescence internode length and an increase in grain number per panicle. *OsSPL18* and *IPA1* positively regulate the expression level of *DEP1* by directly binding to the *DEP1* promoter, thus affecting the branching of Rice Panicles and then affecting the grain weight and panicle size of rice (Yuan et al., 2019). *IPA1* positively regulates panicle branching differentiation during rice reproductive growth to produce larger Panicles in rice, which in turn increases the number of grains per panicle (Wang et al., 2017). Genes such as *DEP2*, *DEP3*, *EP3* and *PAP2* can all cause rice to exhibit the phenotype of shorter panicle stem node and increased shoot density, and this change in erect panicle type ultimately leads to changes in the number of grains per panicle in rice. (Qiao et al., 2011; Yu et al., 2015). Changes in the length of rice spike-stalk and branches can also change the structure of rice panicle, thereby regulating the number of shoots and grains per panicle in rice. *OsLGI*, which encodes the SBP protein, affects the formation and development of spikes by affecting parenchyma cells in the gap between the spike axis and branches, thereby regulating spike-type tightness and affecting the number of grains per spike (Ishii et al., 2013). *Spd1-D* encodes a triangular pentapeptide repeat protein that may shorten the length of floret pedicels and secondary pedicels by blocking *GID1L2*, *RFL* and *WOX3*, thereby altering panicle structure and ultimately leading to changes in the number of grains per panicle (Jiang et al., 2014).

miRNAs are a class of non-coding short RNAs with nucleotide length of about 21 bp that are involved in post-transcriptional regulation of target gene expression by cleavage of target mRNA or translation inhibition. An increasing number of studies have revealed the regulation of miRNAs in plant growth and development. *SPL* gene negatively controls tillering but positively regulates inflorescence meristem and spikelet transition. Insufficient or overproduction of *SPL* can reduce the branching of rice panicles. In order to obtain the optimal panicle size, *SPL* levels can be fine-tuned by *miR156* and *miR529* (Wang et al., 2015).

Overexpression of *OsmiR535* reduces primary and secondary branching of panicles and shortens panicle length, which in turn reduces the number of grains per panicle. *OsPIL15* activates *OsmiR530* expression by directly binding to G-box elements in the promoter. *OsmiR530* directly targets *OsPL3*, which encodes a protein containing the PLUS3 domain, to negatively regulate grain yield. Panicle branching was significantly reduced in *OsmiR530* overexpressing plants, which in turn reduced the number of panicles and grain yield (Sun et al., 2020).

2.3 Genes regulating grain number per panicle in rice while regulating other important agronomic traits

Some agronomic trait-related genes showed obvious one-cause pleiotropy, which regulated other important agronomic traits besides the number of grains per panicle. For example, *MOC1* and *MOC3*, *LAX1*, *LAX2*, etc., their mutants can reduce both the number of panicle branches and the number of tillers (Tabuchi et al., 2011; Shao et al., 2019). *OsDES4*, a highly homologous BRU1 in *Arabidopsis thaliana*, encodes a triangular pentapeptide repeat structural protein that participates in rice DNA repair mainly in axillary bud and young spike meristem. The expression of *LAX1*, *LAX2* and *MOC1* was significantly down-regulated in the *des4* mutant, and showed the phenotypes of dwarf, reduced tillering, reduced spikelet number and reduced the grains number per panicle (Ni et al., 2019). *PAY1* significantly increased the number of secondary branches while significantly decreased the number of tillers (Zhao et al., 2015). The enhanced expression of *Ghd7* under long-day conditions not only delayed heading and increased plant height, but also increased the number of grains per panicle. *OsMFT1*, a downstream gene of *Ghd7*, delays heading stage of rice by inhibiting *Ehd1* expression and positively regulates panicle structure. The overexpressed plants showed delayed heading stage, dense shoot spikelets and increased number of grains per panicle (Song et al., 2018).

GSNI encoded protein kinase phosphatase *OsMKP1* negatively regulates the *OsMKK10*-*OsMKK4*-*OsMPK6* cascade, which affects panicle type and number of grains per panicle by regulating differentiation and proliferation of meristem. Material mutated in *GSNI* exhibited a phenotype of reduced branching, reduced number of grains per panicle, enlarged grains, and loose spike pattern (Guo et al., 2018). *Ghd8* (*DTH8*, *OsHAP3H*, *LHD1*, *EF8*, *OsNF-YB11*, *CAR8*) can control heading stage, tiller number, plant height, primary branch number, secondary branch number and grain number per panicle of rice (Feng et al., 2014). *PROG1*, a key gene of rice creeping property, alters rice plant type and also increases the number of primary and secondary branches in erect rice compared with creeping rice, which ultimately leads to changes in the number of primary branches and grains per panicle (Tan et al., 2008). *OsMCA1* recessive mutants showed a significant reduction in dwarf poles, short leaves and secondary branches, which led to a reduction in the number of grains per panicle in rice (Liu et al., 2015). *An-1*, a gene controlling rice awn, causes rice long awn to disappear while increasing panicle grain number. *GAD1*, a gene controlling rice awn, may reduce cytokinin content in vivo by activating the expression of *DST* while regulating awn character, thereby negatively regulating panicle grain number in rice (Jin et al., 2016). *QNGR9* has been identified as synonymous with *DEP1*, carrying the dominant *dep1-1* allele leading to increased grain number and yield per panicle by increasing nitrogen uptake and assimilation in plants (Zhang et al., 2015a). The research also found that *OsDHH1* is an alternative splicing variant of *Os02g0819100* in rice, which can increase both tiller number and grain number per panicle of rice (Zhou et al., 2017). Many genes related to male and female gamete development also affect the number of grains per panicle in rice, such as the rice pollen-specific gene *OsAGO17*, which affects the number of grains per panicle by affecting pollen fertility to reduce the setting rate (Yao et al., 2018).

3 Prospects

Rice grains number per panicle is an important agronomic trait affecting rice yield. Research on genes related to grains number per panicle can provide genetic information for further improving rice yield and provide new ideas for high-yield rice breeding. The formation of grains number per panicle is a complex biological process controlled by many factors. It is difficult to fully elucidate the molecular mechanism of grains number per panicle by cloning the related genes. Identification of these genes and elucidation of their molecular mechanisms are of great significance for rice production management and genetic improvement.

With the rapid development of sequencing technology and functional genomics research technology, a large number of genes related to grains number per panicle have been cloned. However, the molecular mechanism analysis process of grains number per panicle is still relatively slow, and there are few genes that can be used to improve grains number per panicle. The main reasons are as follows: rice grains number per panicle is a quantitative trait, which is easily to be affected by the environment and is difficult to be cloned and identified; the genes controlling grains number per panicle is difficult to study, which are linked to other important agronomic traits; at present, there are few genes which have important breeding value for improving grains number per panicle, most of the cloned genes have been applied in long-term domestication or breeding practice .

With the development of sequencing technology and multi-omics, G enome-wide association study (GWAS) which is used to analyze complex traits of crops has become the development direction of future gene identification. This technology can construct a high-density genetic map through phenotypic traits of natural population and tiny single nucleotide polymorphisms (SNPs) in the genome to finely locate genes (QTL). This provides strong technical support for exploring potential functional genes of grains number per panicle, and accelerates the process of high-yield breeding by genetic regulation of grains per panicle. In the future, studies on grains number per panicle in rice should be strengthened in the following four aspects: analyzing the domestication process of grains number per panicle and identifying the genes related to grains number per panicle through G enome-wide association study; increasing the identification of the dominant haplotypes of the genes related to grains number per panicle; constructing mapping population cross (such as MAGIC-Cross) with rich genetic resources, carrying out QTL and identifying functional genes for further improving the regulation network of grains number per panicle; identifying the genetic potential of different gene combinations to provide guidance for molecular design and breeding of rice. Recently, the certainty of the newly identified gene FON4 spikelet meristem has an important role, and it can influence spikelet development by regulating SAM size in rice. The number of florets in small panicles of rice with mutated FON4 increased, leading to more grains.

Authors' contributions

Li Li is the conceiver and responsible person of this review and guides the writing of the review throughout. Hao Dong is the main author of this review, who is responsible for consulting references and writing papers; Yixing Li, Shufeng Song, Tiankang Wang, Mudan Qiu, Licheng Zhang, Lei Li and Yanxia Li participated in the review and revision of some references; All authors have read and agreed to the final text.

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