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Communication

# The Formation of Rice Tillers and Factors Influencing It

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**Abstract:** The number of effective rice tillers determines the number of effective panicles and then affects the final yield. Rice tillering ability shows great differences among cultivars and under different environmental conditions, but the underlying mechanisms are not clear. The present paper investigated the formation of rice tillers and examined its genetic regulation, the effects of plant hormones, several environmental factors affecting rice tillering, and nitrogen's regulation of tillers. Finally, the utilization of the tillering ability of weedy and wild rice was investigated. We concluded that many genes are involved in manipulating rice tillering, including *MOC1*, *MOC3*, *FON1*, *LAX1*, *LAX2*, *APC/C*$^{TE}$, *D3*, *D10*, *D14*, *D17*, *D27*, and *D53*, by altering associated hormone contents or coding signal substances. The plant hormones auxin (IAA), gibberellin (GA), and strigolactone (SL) inhibit rice tillering, while cytokinin (CTK) promotes rice tillering. Weak light (light intensity is lower than 200 μmol $m^{-2}$ $s^{-1}$) and low and high temperatures (below 15 °C and above 38 °C) inhibit rice tillering, while optimized water management, such as alternate wetting and moderate drying irrigation, can greatly promote rice tillering. In addition, increasing plant nitrogen concentration can effectively improve rice tillers by adjusting multiple nitrogen metabolism enzymes. Weedy rice and some wild rice showed obvious superiority in tillering ability with respect to cultivated rice, but the underlying mechanisms are not clear and should be further explored. This study can provide theoretical guidance for the breeding and cultivation of high-yield and high-efficiency rice cultivars.

**Keywords:** rice tillering; tiller buds; genetic regulation; plant hormones; environmental factors; weedy rice

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## 1. Introduction

As rice is one of the most important staple food crops on earth, the production of rice is vital for ensuring food security. Although global rice production has continuously increased during the last few decades (Figure 1), it cannot meet humans' demands. In 2022, global cereal crop production was 2.76 billion tons, while its consumption was 2.78 billion tons [1]; the production of food crops has to be improved to meet consumption demands. With the development of society and the economy, new requirements are being proposed for the rice planting industry; that is, high yield and high efficiency should be equally emphasized, and yield and quality should be improved simultaneously. Rice yield is determined by four factors: panicles per area, grains per panicle, grain weight, and seed setting rate [2]. Panicles can be decomposed into two parts: main stem panicles and tiller panicles. Especially in transplanted rice, tiller panicles are a very important part of the total panicles. The number of effective tillers not only determines the number of effective panicles but also has a non-negligible effect on other yield components that play important roles in determining rice yield [3]. With the improvement in the mechanization level of the modern planting rice production industry and the popularization of simplified cultivation modes and high-efficiency planting methods, such as the mechanical transplantation of rice and the direct seeding of rice, new requirements for the production characteristics of rice cultivars have been put forward. The basic goal is to produce more biomass in a short growth period so as to obtain a higher yield, which we refer to as high-efficiency biomass production.

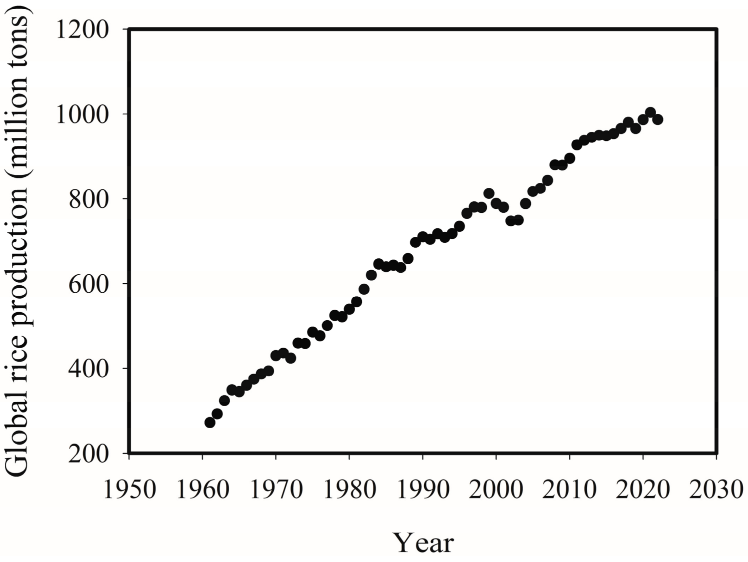

**Figure 1.** Global rice production from 1961 to 2022.

Cultivating high-yield and high-efficiency rice cultivars is important to sustainably develop the rice planting production industry, and the use of a mechanized and simplified rice planting mode is inevitable. High-yield and high-efficiency cultivars must have the characteristics of early development and rapid growth; this is manifested in the rapid growth of tillers in the early growth stage and a high percentage of effective tillers [4]. However, there are still few studies on the physiological mechanisms of early-onset rice tillering and rapid growth, and the cultivar differences in tillering speed and formation mechanisms are not clear.

In addition to existing intraspecific differences, rice tillering ability also shows great differences between cultivated and wild rice. Revealing the mechanisms of the differences in tillering ability between cultivated and wild rice can provide information for the selection of early-onset tillering cultivars. In addition, other kinds of rice can also be used as genetic resources for selecting cultivars that demonstrate early-onset tillering. It has been recorded in Chinese history books that the different weed types 'Nidao', 'Lvdao', and 'Ludao' all refer to non-autotrophic rice. This non-autotrophic rice was once considered by Chinese scholars as a 'companion weed' to rice or 'weedy rice' [5]. Scholars from other countries have also noted the existence of weedy rice. Because weedy rice's seed coat is mostly red or brown, it was originally called 'red rice'. As early as 1846, red rice had become a serious weed in paddy fields in America. Weedy rice is a rice type with the characteristics of both wild and cultivated rice, and it is produced through natural selection and human intervention in common wild and cultivated rice [6]. The seeds of weedy rice are light, have strong dormancy, and easily fall victim to premature dehiscence. The tillering and flowering stages are earlier than those of cultivated varieties, the number of tillers is greater, the tillers are slender, and the fibrous roots are more developed [7,8]. Weedy rice is an important genetic resource with great potential and can be used for rice breeding and research [9]. However, although rice tillering ability has been found to have great cultivar differences, especially between weedy rice and cultivated rice, the underlying mechanisms are not clear. Revealing the underlying mechanisms of the cultivar differences in rice tillering ability and the environmental regulation thereof can provide theoretical guidance for the breeding and cultivation of high-yield and high-efficiency rice.

Under suitable environmental conditions, rice's tillering ability is mainly determined by its genotypes. Generally, hybrid rice cultivars have a stronger tillering ability than that of conventional cultivars; *indica* rice has a stronger tillering ability than that of *japonica* rice [10]. In addition, planting patterns also impact rice tillering; for instance, the early-onset tillering ability of direct-seeding rice is stronger than that of transplanting rice; the number of effective tillers per plant of direct-seeding rice is usually greater than that of transplanting rice [11]. In addition to these factors, environmental factors, including solar radiation, temperature, field water, and especially plant nitrogen concentration, all greatly impact rice tillering ability.

## 2. The Formation of Rice Tillers and Their Contribution to Yield

A rice tiller is a branch of the rice stem that mainly emerges from tillering nodes with short basal internodes [12]. The process of rice tiller formation is divided into two stages: the formation of tiller buds and the elongation of tillers [13–15]. First, axillary meristems (AMs) develop into tiller buds in the axils of each leaf position on the tillering node at the base of the rice plant, which is initially inhibited in dormancy. Then, the tiller buds are activated and continue to differentiate and develop; they differentiate and become elongated in the leaf sheath, and finally, they extract themselves from the leaf sheath to become tillers [16–18]. The structure of tillers is the same as that of the main stem. When there are no more than three leaves on the tillers, the nutrition required for tiller growth is provided by the main rice stem, but when there are more than three leaves on the tillers, they enter the autotrophic stage [19]. The main stem leaves and the tillers simultaneously elongate; that is, when the N$^{th}$ leaf of rice is pulled out, tillers are pulled out at the (N-3)$^{th}$ leaf axil position [20]. Without considering the tillering of coleoptiles, the initial stage of normal tillering in rice is the fourth leaf extraction stage of the main stem. The emergence of primary, secondary, and tertiary tillers differs by three leaf positions; that is, primary tillers begin to appear at the four-leaf stage of the main stem, secondary tillers begin to appear at the seven-leaf stage of the main stem, and tertiary tillers begin to appear at the ten-leaf stage of the main stem [21]. The number of effective tillers of rice directly determines the number of panicles, and the number of panicles is a decisive factor of rice yield, so it is particularly important to ensure the emergence and growth of tillers. The emergence of rice tillers is controlled by environmental factors, hormones, and genetic factors [22].

## 3. Genetic Mechanisms of Rice Tillering

In the field, rice planting density is about 30 plants/m$^2$, each plant usually forms 5–20 tillers, and the number of effective tillers per square meter is usually greater than 200 [23]. Tillering ability shows great cultivar differences. Generally, the tillering ability of *indica* rice is stronger than that of *japonica* rice, and the tillering ability of conventional rice is stronger than that of hybrid rice. The early-onset tillering characteristics of rice cultivars are quite different, but the mechanism is not clear. At present, there are some studies on the genetic regulation of rice tillering, but no research can fully explain its mechanisms. The tiller growth and development of rice are regulated by genes, and their regulatory path is complex. Studies showed that genes regulate rice tillering by regulating other genes' transcription, changing hormone content, encoding signal substances, etc. [24,25].

Through the isolation of rice tiller formation mutants, many key tiller formation regulators have been cloned, including *MONOCULM 1* (*MOC1*), *MONOCULM 3* (*MOC3*), *FLORAL ORGAN NUMBER1* (*FON1*), *LAX PANICLE 1* (*LAX1*), *LAX PANICLE 2* (*LAX2*), tiller enhancer, an activator of the anaphase promoting-complex/cyclosome (*APC/C$^{TE}$*), and several tillering dwarf genes including *DWARF 3* (*D3*), *DWARF 10* (*D10*), *DWARF 14* (*D14*), *DWARF 17* (*D17*), *DWARF 27* (*D27*), and *DWARF 53* (*D53*) (Table 1) [22,26–32]. *MOC1* is the first key gene reported to regulate rice tillering. *moc1* mutant (without *MOC1* gene) plants have only a main culm without any tillers, owing to a defect in the formation of tiller buds. *MOC1* encodes a putative GRAS family nuclear protein that is expressed mainly in the axillary buds and functions to initiate axillary buds and to promote their outgrowth [26]. The breeding of cereals with altered gibberellin (GA) signaling propelled the 'Green Revolution' by generating semidwarf plants with increased tiller number. The mechanism by which GAs promote shoot height has been studied extensively, but it is not known what causes the inverse relationship between plant height and tiller number. A recent study illustrated that *MOC1* is protected from degradation by binding to the *DELLA* protein *SLENDER RICE 1* (*SLR1*). GAs trigger the degradation of *SLR1*, leading to stem elongation and also to the degradation of *MOC1* and hence a decrease in tiller number [33]. *MOC3* is a transcription factor with transcriptional activation activity; it binds to the promoter region of *FON1*, a downstream gene of *MOC3*, and activates its expression [27]. *FON1* is expressed in tiller buds, which specifically regulates the elongation of tiller buds without affecting the initiation of tiller buds and eventually causes the *fon1* mutant to show a significant reduction in the number of tillers. A further study found that *MOC3* and *MOC1* are not only key factors for the initiation of tiller buds, but they can also regulate the elongation of tiller buds, and *MOC1* can interact with the *MOC3* protein and further enhance the expression of *FON1* as a co-activator of *MOC3* [28]. *LAX1* is involved in a general mechanism that regulates the formation of all axillary buds throughout rice's vegetative and reproductive phases; *LAX2* is a novel factor that acts together with *LAX1* in rice to regulate the process of axillary meristem formation [29,30]. Lin et al. [31] showed that the rice tiller enhancer (*te*) mutant displays a drastically increased tiller number, *TE* acts as an activator of the anaphase-promoting complex/cyclosome (*APC/C*), and $APC/C^{TE}$ controls tillering by mediating the degradation of *MOC1*.

**Table 1.** Genes regulating rice tillering.

| Genes | Full Name | Functions | Results | Literature |
|---|---|---|---|---|
| *MOC1* | *MONOCULM 1* | Encodes a putative GRAS family nuclear protein | Initiates axillary buds and promotes their outgrowth | Li et al. [26] |
| *MOC3* | *MONOCULM 3* | Is a transcriptional activator of *FON1* | Promotes the outgrowth of axillary buds | Lu et al. [27] |
| *FON1* | *FLORAL ORGAN NUMBER1* | Encodes a transmembrane receptor kinase and is activated by *MOC3* | Promotes the outgrowth of axillary buds | Shao et al. [28] |
| *LAX1* | *LAX PANICLE1* | Encodes basic helix–loop–helix (bHLH) transcription factors | Regulates the formation of axillary meristems (AMs) | Oikawa and Kyozuka [29] |
| *LAX2* | *LAX PANICLE2* | Encodes a nuclear protein with a plant-specific conserved domain | Acts together with *LAX1* to regulate the formation of AMs | Tabuchi et al. [30] |
| $APC/C^{TE}$ | Tiller enhancer, an activator of the anaphase-promoting complex/cyclosome (*APC*) | Encodes a rice homolog of Cdh1 and acts as an activator of *APC/C* | Mediates the degradation of *MOC1* and represses AMs initiation and formation | Lin et al. [31] |
| *D3* | *DWARF 3* | Affects the signal transduction of SL | Promotes rice tillering | Ishikawa et al. [22] |
| *D10* | *DWARF 10* | Affects the synthetic pathway of SL | Promotes rice tillering | Ishikawa et al. 2005 [22] |
| *D14* | *DWARF 14* | Affects the signal transduction of SL | Promotes rice tillering | Ishikawa et al. 2005 [22] |
| *D17* | *DWARF 17* | Affects the synthetic pathway of SL | Promotes rice tillering | Ishikawa et al. [22] |
| *D27* | *DWARF 27* | Affects the synthetic pathway of SL | Promotes rice tillering | Ishikawa et al. [22] |
| *D53* | *DWARF 53* | Affects the signal transduction of SL | Promotes rice tillering | Kinoshita and Takahashi [32] |

The above genes impact rice tillering by modifying the expression of other involved genes, while some genes regulate tillering by affecting the synthesis or signal transduction of strigolactone (SL). For example, many tillering dwarf genes including *D3*, *D10*, *D14*, *D17*, *D27*, and *D53* were found to regulate rice tillering. Ishikawa et al. [22] reported that the five tillering dwarf mutants *d3*, *d10*, *d14*, *d17*, and *d27* all showed reduced plant stature and increased tiller numbers, indicating that the *D3*, *D10*, *D14*, *D17*, and *D27* genes all play important roles in regulating rice tillering.

*D3*, *D14*, and *D53* regulate rice tillering mainly by affecting the signal transduction of SL. *D3* can be assembled into an $SCF^{D3}$ complex when combined with *D14* to inhibit rice tillering [34]. *D14*, like *D3*, plays a negative role in regulating the number of tillers in rice [35]. A more recent study reported that a low-nitrogen environment in soil enhances the phosphorylation of *D14*, thereby inhibiting protein degradation and enhancing the signal perception of SL; the phosphorylation of *D14* at the N-terminus is an important mechanism by which low-nitrogen signaling inhibits rice tillering [36]. One study proposed that accurate improvement in the phosphorylation site of *D14* can significantly reduce the dependence of rice tillers on nitrogen fertilizer, 'reducing nitrogen fertilizer but not reducing tillers'. *D10*, *D17*, and *D27* affect rice tillering by affecting the synthetic pathway of SL [37].

## 4. Regulation of Rice Tillering by Hormones

Rice tillering is regulated by a variety of hormones. The main hormones affecting rice tillering are auxin (IAA), cytokinin (CTK), gibberellin (GA), and strigolactone (SL) [38,39].

### *4.1. Auxin*

Auxins are a class of endogenous hormones containing an unsaturated aromatic ring and an acetic acid side chain; auxin's chemical essence is indoleacetic acid (IAA) [40]. As the first endogenous plant hormone to be discovered, auxin is mainly synthesized in plant apical tissues, such as plant shoot tips and young leaves [41]. Auxin was reported to inhibit shoot branching in many studies [42,43]. Tanaka et al. [44] found that IAA could cause apical dominance in the main stem and inhibit the growth and development of lateral branches. IAA is transported from the top of the plant to the tiller buds through polar transport, so the tiller buds are dormant, and the growth and development of tiller buds are inhibited. *OsPIN5b* is a member of the *PIN* family of auxin export vectors. The overexpression of *OsPIN5b* causes auxin to lose polar movement and changes the distribution of auxin, thereby reducing plant height, tiller number, seed setting rate, panicle length, and yield; on the contrary, it promotes an increase in the tiller number, root growth, panicle elongation, and yield [45]. Wen et al. [46] found a low-tillering dwarf mutant of *Osdlt10* that showed semidwarfism, a reduced tiller number, an increased grain width, and a reduced seed setting rate.

### *4.2. Cytokinin*

Cytokinin (CTK) is a kind of plant hormone that can promote cell division, induce bud formation, and promote growth. It plays an important role in axillary bud activation, elongation, and plant growth [47]. Unlike IAA, CTK can directly promote the growth and development of tiller buds. CTK is mainly synthesized in the roots of plants, and it can be synthesized in the stems after apical dominance is lifted. CTK is inhibited by exogenous auxin [38], which can promote the germination of lateral buds and is conducive to the growth of tiller buds [48,49]. CTK is generated in the roots and transported to the aboveground part, where it directly promotes the germination of tiller buds [39]. Liu et al. [50] showed that even under low-nitrogen conditions, the application of cytokinins can promote the germination of rice tiller buds. *QsIPT* (adenosine phosphate isopentenyl transferase) is a key enzyme in the process of cytokinin synthesis. After the removal of the rice stem tip, the *QsIPT* gene is expressed in the rice stem, and the expression of the *OsIPT* gene is inhibited after the application of exogenous auxin in the stem tip [51]. Cytokinin oxidase (CKX) is the only known oxidase that can degrade cytokinin and is a key factor in regulating the level of cytokinin in plants [52]. Auxin regulates the content of cytokinin in plants by affecting the expression of the *CKX* gene and *OsIPT* gene, thus forming a regulatory network with cytokinin in rice to regulate tillering [37,53].

### *4.3. Gibberellin*

Gibberellin (GA) regulates the development of the whole life cycle of plants [54]. It is generally believed that GA inhibits the development of rice tiller buds. Spraying GA at the peak tillering stage of rice reduced the number of ineffective tillers [55]. It was reported that, in Zhejiang, early rice was sprayed with GA when the number of tillers reached 90% of the planned panicles; the spike rate reached 82.9%, which was 6.1% higher than that of the control; and the number of filled grains per panicle increased by 10.2 grains. Late rice was sprayed with GA when the number of tillers reached 80% of the planned panicles; the spike rate reached 61.6%, which was 7.8% higher than that of the control; and the filled grains per spike increased by 12.5 grains [55]. Li et al. [56] suggested that GA signal transduction may be related to the expression of the *MOC1* gene. Lin et al. [31] showed that the number of tillers was significantly increased in mutants with the loss of the rice tiller enhancement factor *TE*, and *TE* was an activator of *APC/C* in the late stage of cell division. *TE* and *MOC1* are coexpressed in leaf axils. $APC/C^{TE}$ degrades *MOC1* through ubiquitination and then downregulates the expression of *homeobox 1*, a meristem-determining gene, thereby inhibiting the initiation and formation of the lateral bud meristem. In 2020, Lin et al. [57] further showed that the $APC/C^{TE}$ *E3* ubiquitin ligase complex antagonistically regulates root growth and tillering by affecting the levels of abscisic acid (ABA) and gibberellin (GA).

### *4.4. Strigolactone*

Strigolactone (SL) is a newly discovered phytohormone that is synthesized in the roots and transported upward to the stems. It can inhibit the growth of plant branches by inhibiting the growth of axillary buds [58]. In SL mutants, the number of tillers and the height of rice are usually negatively correlated, and these mutants are mainly dwarf mutants of rice. The functions of related genes in SL synthesis or the signal transduction pathway have been classified. *D10*, *D17*, and *D27* are located in the SL synthesis pathway; *D14*, *D3*, and *D53* are located in the SL signal transduction pathway; and *OsTB1/FC1* is downstream of the SL pathway [59]. The *D27* protein is involved in the *MAX/RMS/D* (more axillary branching) pathway, thereby regulating the biosynthesis of SL. SL plays a negative regulatory role in rice tillering [60]. The *D53* gene is an inhibitor of the SL signal transduction pathway. SL induces *D53* degradation through the *D14-SCF D3* proteasome pathway, relieves the transcriptional inhibition of downstream genes, and activates SL signal transduction, thereby accurately regulating the elongation of axillary buds [61,62]. *OsTB1/FC1* is a gene that acts downstream of SL and plays a negative regulatory role in rice tillering [63]. In addition, SL may affect the polar transport and synthesis of IAA to regulate the level of IAA and, thus, rice tillering [64].

### *4.5. Interacting Effects of Hormones on Rice Tillering*

In summary, IAA, GA, and SL all inhibit rice tillering, while CTK promotes rice tillering. Besides impacting plant tillering individually, these hormones can also affect rice tillering by affecting each other. The interaction of endogenous hormones and the effect of their balance on tillering have become a research hotspot. Generally, a low ratio of IAA to CTK promotes the germination and growth of tillers, and a high ratio of IAA to CTK inhibits the germination and growth of tillers [65]. Liu et al. [66] also found that a low ratio of IAA to CTK promoted the formation of dwarf-scale and multi-tillering traits in rice. As IAA and CTK show opposite effects on rice tillering, the effects of the ratio of IAA to CTK on rice tillering should be the result of the concentrations of the two hormones themselves. In addition to the fact that the ratio of IAA to CTK influences rice tillering, hormones also play roles by regulating other hormones. Phillips [67] reported that the effects of

GAs on plant tillering were achieved by inducing the synthesis of IAA or controlling the decomposition of IAA to have an indirect effect on apical dominance. For SL and CTK, two hormones both regulated by IAA, Ferguson and Beveridge [68] reported that IAA negatively regulates the growth of axillary buds by maintaining a high SL concentration and a low CTK concentration. Recent studies also found that SL and CTK play roles in the regulation of nitrogen and phosphorus in rice tillering. One study showed that under low-nitrogen and -phosphorus nutrition conditions, SL at least partially used the CTK signaling pathway's Type-A family genes to inhibit rice tillering. These studies provided new insights into the interacting effects of hormones on rice tillering and provided guidance for regulating rice tillering by appropriately spraying exogenous hormones.

## 5. Effects of Environmental Conditions on Rice Tillering

Rice tillering, as a typical quantitative trait, is greatly affected by environmental factors. Light, temperature, water, fertilizer, and other environmental factors can directly or indirectly stimulate the synthesis and transmission of related enzymes and hormones in plants, thus promoting or inhibiting the occurrence of tillering [69,70].

### *5.1. Light*

Light is a resource for all creatures, as it is the energy source for green plants through photosynthesis. When there is sufficient light, the photosynthetic rate of rice increases, and enough organic matter is produced to provide a nutritional basis for its vegetative growth and promote the early and rapid development of tillers. On the contrary, when there is insufficient light, the photosynthetic rate is low, and the organic matter in the plant is lacking, resulting in weak seedlings, which are not conducive to the formation of tillers. For example, Martins et al. [71] reported that the photosynthetic rate of Coffee leaves decreased from 12.0 μmol $m^{-2}$ $s^{-1}$ to 7.9 μmol $m^{-2}$ $s^{-1}$ as the growth condition shifted from full sunlight to 10% sunlight. Schmierer et al. [72] found that under a nitrogen supply of 2.8 mmol $L^{-1}$, the No. of rice tillers per plant decreased from 24.0 to 10.3 when the light shifted from full light to 75% illumination and continued to decrease to 6.7 under 20% illumination. Wang et al. [73] showed that when rice was in a weak light environment, in which light intensity is lower than 200 μmol $m^{-2}$ $s^{-1}$, although the chlorophyll content in the leaves increased, the mesophyll conductance of the leaves decreased, resulting in a decrease in carboxylation efficiency, thereby inhibiting rice photosynthesis and affecting the normal occurrence of tillering. By constructing a three-dimensional canopy photosynthesis model of rice, it was found that the light and nitrogen concentration absorbed by each leaf above the canopy determined the morphology of the canopy structure [74]; rice tillers are an important part of the canopy. Adequate light can optimize the canopy structure, thereby promoting the occurrence of tillering and further improving the canopy structure. Therefore, light is a major factor affecting the occurrence of rice tillering.

### *5.2. Temperature*

Temperature is one of the most important environmental factors affecting the occurrence of rice tillering. When rice is in a low-temperature environment, it is prone to dwarfism, a thin appearance, and less tillering. Liu et al. [69] showed that between 20.52 and 21.55 °C, when the average temperature in the rice tillering stage was 1 °C lower, the tiller number in the low-temperature treatment was significantly lower than that in the normal-temperature treatment, and the final spike number was significantly reduced. Ding et al. [75] suggested that the most suitable temperature for rice tillering was between 30 °C and 32 °C and that tillers would stop growing when the temperature was lower than 15 °C or higher than 38 °C. High temperatures lead to a decrease in the chlorophyll content in leaves, thus inhibiting the photosynthesis of rice and affecting the normal occurrence of rice tillering [76]. Therefore, temperature has a critical influence on the occurrence of rice tillering.

### 5.3. Water

The humidity and irrigation depth of paddy fields have a non-negligible effect on the formation and growth of rice tillers. Zhang et al. [77] suggested that drought could significantly inhibit the growth of tillers, as the tiller stems were too thin, the leaves could not develop normally, and the tillers even died in severe cases. Land drought leads to too many ineffective tillers, and the spike rate is greatly reduced [78]. For example, Xu et al. [79] reported that under normal field water conditions, the number of effective rice tillers per hill was about 22, while under a field capacity of 60–65%, the number of effective rice tillers per hill decreased to about 15; videlicet, drought can effectively decrease the number of rice tillers. Jiang et al. [80] found that the three young stages and the leaf primordium stage are environmentally sensitive periods for rice tiller buds. When the $n^{th}$ leaf is extracted, deep irrigation and other measures are taken, and the buds of the n-1 node are effectively controlled and become dormant buds. When shallow water management is adopted, tillers break their dormancy and can elongate and grow. Lv et al. [81] clarified that alternating dry–wet irrigation can promote the early development of rice tillers, increase the number of effective panicles and the seed setting rate, and, thus, increase the yield compared with those in traditional flooding and wet irrigation. Reasonable water management can also reduce overgrowth and increase efficiency. For instance, Yang et al. [82] reported that a moderate wetting and drying condition (soil water potential was kept at $-5$ to $-10$ kPa during effective tillering stage and $-15$ to $-20$ kPa during jointing stage, $-8$ to $-12$ kPa during panicle differentiating and heading stages, $-10$ to $-15$ kPa during early and mid-grain filling stages, and $-15$ to $-20$ kPa during late grain filling stage) clearly reduced the number of ineffective tillers and increased the spike rate. Therefore, the alternating wetting and drying irrigation method has gradually become more widely used.

## 6. Effect of Nitrogen on Rice Tillering

Nitrogen is one of the essential nutrient elements in the growth and development of rice. Nitrogen is not only an important part of amino acids, chloroplasts, ATP, and other substances but also a key regulator of protein synthesis, amino acid metabolism, and carbon metabolism [83]. Nitrogen can regulate the growth and development of tillers. When the nitrogen content is too low, the growth of tillers is slow or may even stop, the tillers are weak, and the number of tillers is small. In the vegetative growth period of rice, sufficient nitrogen can promote the elongation of tillers [84], while the lack of nitrogen greatly reduces the number of effective tillers [85]. When the nitrogen concentration was in the range of 10–90 mg $L^{-1}$, the relationship between the number of rice tillers and nitrogen concentration had a quadratic curve. Jiang et al. [85] clarified the relationship between stem–sheath nitrogen content and the tillering of rice seedlings. When the stem–sheath nitrogen content was 2.7–3.3%, rice tillering could occur normally. When the stem–sheath N content was lower than 1.3%, the tiller buds remained in the post-differentiation stage—the three early stages and the leaf primordium stage. When the nitrogen content was between 1.3% and 2.7%, the differentiation process of tiller buds was slow, and the occurrence and elongation times of the tillers were delayed; when the nitrogen supply was improved, the tiller buds of rice plants stayed in the late differentiation stage of three young and one leaf primordium stage because the response to nitrogen deficiency could be reactivated, so they continued to grow and develop into new tillers.

Forde et al. [86] pointed out that nitrogen mainly regulates the growth and development of plants through two approaches. The first approach is the effect on the physiological metabolism and development of plants by regulating the nutrients required for plant growth and development. The second approach is the regulation of the physiological metabolism of plants through a series of signals. Nitrogen can increase the activity of nitrate reductase and glutamine synthetase in leaves, thus promoting the synthesis of soluble protein and the accumulation of nonstructural carbohydrates and promoting the elongation and growth of rice tillers. Liu et al. [50] suggested that although nitrogen and cytokinin also play an important role in the germination of rice tiller buds, they are essentially different.

Cytokinin can promote the germination of branch buds, but after germination, tiller buds need many nutrients to continue to grow into tillers, and nitrogen can provide the nutrients needed for plant growth and development.

In addition to impacting rice tillering by adjusting plant growth as a nutrient element, nitrogen also impacts rice tillering by affecting rice carbon and nitrogen metabolism, which are closely related to the emergence, growth, and decline of tillers [66]. Carbon and nitrogen metabolism in plants affect and determine the distribution and utilization of photosynthetic products, protein synthesis, the absorption of minerals, and other life activities.

Carbon metabolism provides carbon skeleton and energy for nitrogen metabolism, while nitrogen metabolism also provides the necessary enzymes for carbon metabolism; at the same time, carbon and nitrogen metabolism also need the same reducing power and ATP [87–89]. Photosynthesis is a very important part of carbon metabolism. The main photosynthates are sugars. Rice tillering needs energy; all energy is sourced from sugar metabolism. Many studies showed that nitrogen greatly affects the accumulation of photosynthate; generally, increasing N input improves the accumulation of photosynthates, ultimately improving tillers [89]. Therefore, increasing N input remarkably improves rice tillering ability [90].

In addition to affecting rice tillering by modifying carbon metabolism, nitrogen also affects rice tillering by adjusting nitrogen metabolism. There are many enzymes involved in carbon and nitrogen metabolism, including glutamine synthetase, glutamate dehydrogenase, sucrose phosphate synthase, phosphoenolpyruvate carboxylase, peroxidase, superoxide dismutase, nitrate reductase, and so on. Most of these enzymes are more or less associated with nitrogen. Nitrogen's regulation of carbon and nitrogen metabolism is complex. Benzhuang et al. [91] reported that nitrogen fertilizer levels were positively correlated with the activities of glutamine synthetase, phosphoenolpyruvate carboxylase, and sucrose phosphate synthase. However, conclusions on the effects of nitrogen fertilizer on the key enzymes in carbon and nitrogen metabolism are not consistent. In some studies, it was suggested that nitrogen fertilizer may inhibit the activity of sucrose phosphate synthase. For example, Luo et al. [92] showed that by increasing the amount of nitrogen applied, the activity of sucrose phosphate synthase in leaves was decreased; at lower nitrogen levels, the level of activity of sucrose phosphate synthase was higher, and the sugar content in leaves showed the same response.

As a photosynthate, plant nonstructural carbohydrate (NSC, including soluble sugar and starch) concentration is an important index of carbon metabolism in plants [79]. Yang et al. [93] considered that a higher soluble sugar content in tillers was beneficial to their growth and development, thus increasing the spike rate in wheat. At the same time, it was pointed out that the total nitrogen content and soluble sugar content of wheat at each growth stage affected the development of tillers. Zhang et al. [94] showed that the emergence, growth, and death of wheat tillers were closely related to the metabolism of sugar and nitrogen in tiller nodes. Frank et al. [95] pointed out that the soluble sugar content in plant stems significantly affected the number of tillers and the survival rate. In summary, nitrogen fertilizer can not only directly affect the growth and development of tillers but also regulate their growth and development by affecting carbon and nitrogen metabolism.

## 7. The Prospect of Utilizing the Tillering Ability of Weedy and Wild Rice

Weedy rice (*Oryza sativa f.spontanea*) is a major invasive weed in paddy fields. It is a plant of the genus *Oryza* and resembles cultivated rice in its appearance [96]. Weedy rice is widely distributed all over the world, with strong growth and reproductive abilities. It generally germinates and tillers earlier than cultivated rice, and it has strong competitiveness for resources [97]. With the deepening of genetic research on weedy rice, it has been found that the main origin of weedy rice is the de-domestication of cultivated rice (including modern cultivated rice and local species), followed by the introgression of genes from local wild rice (such as in Southeast Asian weedy rice) and inter-subspecific hybridization (such as in Brazilian weedy rice) [98–100]. In the process of evolution, weedy rice can continuously obtain new dominant genes, retain dominant traits that are conducive to its own growth and development, and have rich genetic diversity through long-term natural selection [100]; thus, it can provide excellent genes for the genetic improvement of cultivated rice. There is an abundant number of studies on the genetic basis of early-onset tillering and fast tillering in weedy rice, but the physiological basis is still unclear [101,102]. In the last two years, we explored the underlying physiological mechanisms of the stronger tillering ability of weedy rice in comparison with that of cultivated rice, and we found that the tillering rate and biomass tillering efficiency of weedy rice were significantly higher than those of cultivated genotypes; there was an obvious super-extension phenomenon; that is, leaf and tiller extension followed a law of $N = n - 2$. The stronger tillering ability of weedy rice than that of cultivated rice is attributed to its stronger nitrogen absorption and utilization abilities, photosynthetic production capacity, and root activity. Additionally, we found that weedy rice expressed more of the tillering-associated gene *OsMADS57*. The early tillering characteristics of weedy rice are significantly better than those of cultivated varieties, which makes it an important germplasm resource for cultivating high-yield and high-efficiency rice cultivars [103]. Genes regulating tillering ability should be further excavated and used.

In addition to weedy rice, some wild rice genotypes have shown outstanding tillering ability compared with that of cultivated rice. Kang [101] reported that the number of effective tillers of *Oryza rufipogon* Griff. reached 80 per plant, which was far higher than the number in cultivated rice, which was only about 15 tillers per plant. If the strong tillering ability of wild rice can be transferred into cultivated rice cultivars, the number of panicles and yield will be greatly improved. The mechanisms of the stronger tillering ability in weedy and wild rice should be further investigated and used.

## 8. Conclusions

The number of effective tillers in rice determines the number of effective panicles and ultimately impacts yield. Rice tillering ability shows great cultivar differences, especially between cultivated and weedy or wild genotypes, but the underlying mechanisms behind this are not clear. The genetic regulation of rice tillering, the effects of plant hormones, and the effects of environmental factors on rice tillering were summarized in the present study (Figure 2), which showed that many genes are involved in determining rice tillering ability by altering associated hormone contents or coding signal substances. The plant hormones auxin (IAA), gibberellin (GA), and strigolactone (SL) inhibit rice tillering, while cytokinin (CTK) promotes it. Weak light and low and high temperatures inhibit rice tillering, while optimized water management, such as alternate wetting and moderate drying (AWMD) irrigation, can greatly promote rice tillering. Increasing plant nitrogen concentration can effectively improve rice tillers by adjusting multiple nitrogen metabolism enzymes. The interacting effects of genes, hormones, and environmental factors on rice tillers should be further explored to reveal the underlying mechanisms of the difference in rice tillering ability and provide strategies for early-onset rice varieties breeding. The superiority of the tillering ability in weedy and wild rice should be further exploited for the breeding of high-yield and high-efficiency rice cultivars.

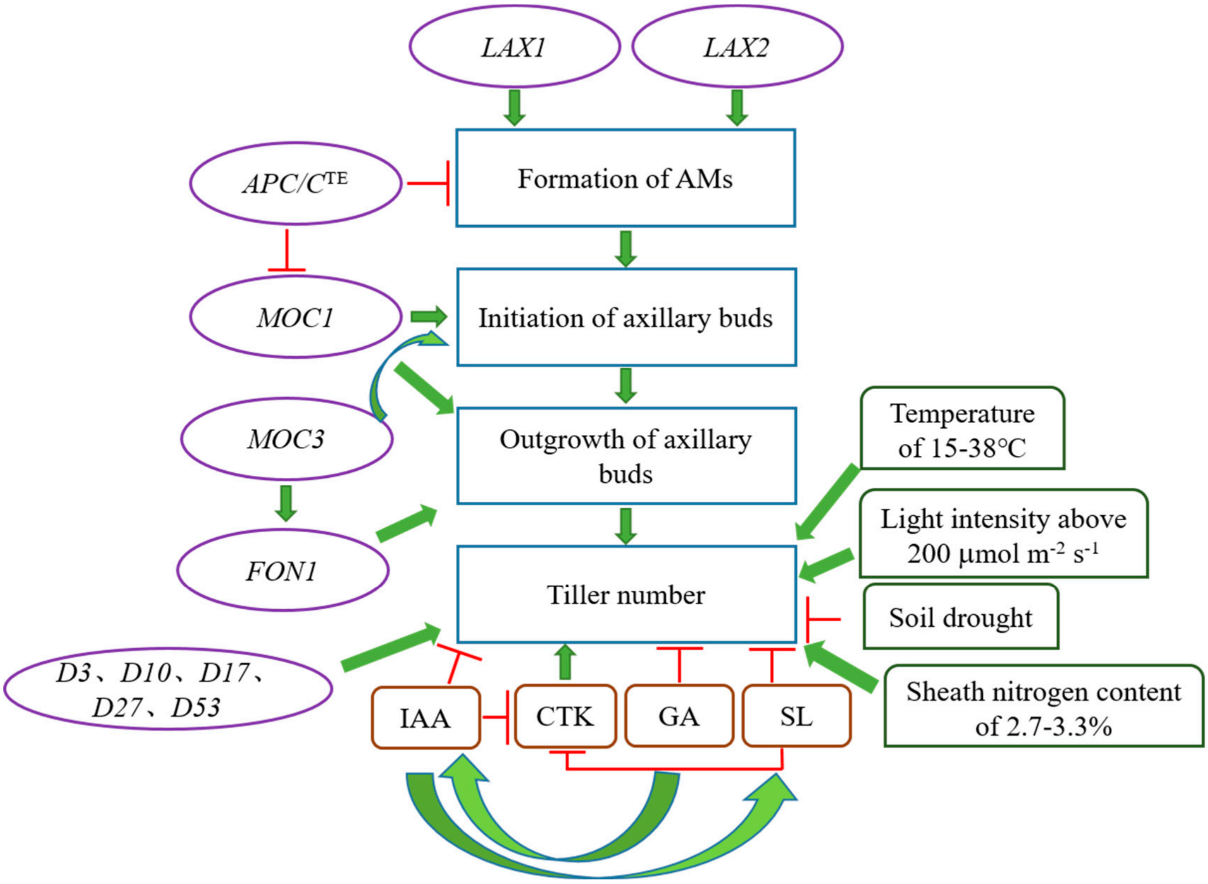

**Figure 2.** Effects of various factors on number of rice tillers. AMs, axillary meristems; *MOC1*, *MONOCULM 1*; *MOC3*, *MONOCULM 3*; *FON1*, *FLORAL ORGAN NUMBER1*; *LAX1*, *LAX PANICLE1*; *LAX2*, *LAX PANICLE2*; *APC/C$^{TE}$*, *Tiller enhancer, an activator of the anaphase-promoting complex/cyclosome (APC)*; *D3*, *DWARF 3*; *D10*, *DWARF 10*; *D17*, *DWARF 17*; *D27*, *DWARF 27*; *D53*, *DWARF 53*; IAA, auxin; CTK, cytokinin; GA, gibberellin; SL, strigolactone. The Green arrow means promotion; the red bars mean inhibition.

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