Review Article

Molecular Mechanisms behind the Regulation of Rice Tiller Angle: An update

ABSTRACT

In crop plants, architecture is a key agronomic characteristic that has a significant impact on crop productivity. Tiller angle is among the most important factors in crop plant structure, which in response has a significant impact on grain output due to its considerable effect on plant density. It is well recognized that gravity is a basic physical force that affects all life forms. Gravity is sensed by plant organs, which allows them to adjust their growth direction, such as the tiller angle in rice (*Oryza sativa*). Recent developments in research employing the *O. sativa* tiller angle as a research framework are summarized in this review, including knowledge of the domestication of this tiller angle, genetic control of the rice tiller angle, and gravitropism of shoots. Lastly, we believe that recent findings on shoot gravitropism and improved crop tiller/branch angle may be applied to other species, consequently increasing future agricultural productivity.

Keywords: Tiller angle; shoot gravitropism; gravity-sensing tissues; amyloplast sedimentation*; environmental plasticity; transcription factors*

1. INTRODUCTION

Among the most significant crops, rice is among the most essential, providing sustenance for about half of the global population. To fulfill the increased need for rice due to an ever-increasing global population, one successful technique is to improve the architecture of the rice plant. Higher plants, including rice, originate their branches through the axillary meristems of their shoots, and branch orientation is among the most significant plant architecture attributes because it dictates the ideal planting density, affecting production by regulating photosynthetic efficiency [1]. Among rice's most agronomically important traits is the presence of tillers, which are panicle-bearing branches that emerge from the axils of each individual leaf on the basal internodes [2]. In contrast to *Arabidopsis thaliana* rosette and cauline branches, which emerge from the inflorescence stem's leaf axils, tillers grow from the base of the inflorescence [3,4]. Additionally, the tiller angle, which is the angle formed by the side tillers and the vertical line with the greatest inclination, represents the degree to which the rice plant architecture is spreading. *A. thaliana* branch angle is different from the *O. sativa* tiller angle in that it refers to the inclination formed by the inflorescence stems and cauline branches. Excessive spreading and compactness are not favorable to rice grain yield in practice. Plants exhibiting prostrate growth take up excessive space, limiting grain output per unit area, whereas highly compacted rice plants are more prone to disease. Because of this, a good tiller angle is critical for high-density implantation, which is necessary for optimizing grain yield from rice populations.

According to previous research, tiller angle in rice is highly linked to shoot gravitropism [5,6]. In gravitropism, root growth is steered toward the gravitational force while shoot growth is steered away from it [7]. Larger branch/tiller angles are caused by a lack of shoot gravitropism [2,8]. A significant amount of progress has been made in understanding the genetic foundation of shoot gravitropism in *A. thaliana*, but much more work has to be done to understand the regulatory pathway that governs shoot gravitropism and, consequently, tiller angle in rice.

In this study, we emphasize recent breakthroughs in identifying the factors that govern tiller angle in rice, such as analyses of rice tiller angle domestication, asymmetric translocation of auxin engaged in shoot gravitropism, and gravity sensing. We also present some new tactics for enhancing grain productivity in rice by optimizing tiller angle, which may be used for a variety of different species, including fruit trees and ornamental plants

2. DOMESTICATION OF RICE TILLER ANGLE: A MOLECULAR PERSPECTIVE

Crop domestication was essential to the formation of agricultural communities and has contributed significantly to human civilization's progress. Plant architecture changed dramatically as farmed rice evolved from wild rice during domestication. Rice productivity has increased dramatically since the prostrate growth of wild rice transitioned to erect growth in the long course of domestication [9-12].

2.1 Domestication of rice tiller angle

Under natural conditions, wild rice's horizontal growth pattern helps it compete with weeds for space, while cultivated rice's erect growth habit increases yield and planting density. A number of C2H2-type zinc finger transcription factors, such as PROSTRATE GROWTH 7 (PROG7), PROG1, and "RICE PLANT ARCHITECTURE DOMESTICATION" (RPAD), have been discovered to be important for the switch from horizontal to erect development during *O. sativa* domestication [13,14]. Among the varieties of cultivated rice are African cultivated rice and Asian cultivated rice, which have been cultivated from the feral species *Oryza barthii* and *Oryza rufipogon*, respectively [5,6,15]. *The PROG7* gene has controlled the transition of the prostate growth pattern of African wild rice to the erect growth pattern for domesticated African rice, while the *PROG1* gene has experienced an artificial selection of prostate-to-erect growth of Asian feral rice to domesticated rice [9,16,17]. Genes *PROG7* and *PROG1* and their homologs are found in tandem at the *RPAD* gene [18-20]. Prostrate-to-erect growth transitions in African and Asian rice were also influenced by a 113-kb and 110-kb deletion at the *RPAD* gene [8,21,22]. While all of the tested African domesticated rice genotypes have the *prog7* allele and the *rpad*^{113kb} allele, the evaluated Asian domesticated rice genotypes have the *prog1* allele and the *rpad*^{110kb} allele [11,23], indicating that natural selection for the vertical growth pattern occurred simultaneously in both African and Asian domesticated rice.

2.2 Post-domestication selection of rice tiller angle

O. sativa ssp. *indica* and *O. sativa* ssp. *japonica* are two important subspecies of Asian domesticated rice that have undergone post-cultivation selection, exhibiting dramatically different tiller angles [24-27]. As a result of the post-cultivation alterations in *indica* and *japonica* rice, some genes were discovered to be critical factors involved in the various tiller angles in these two rice varieties [13,28,29]. TAC1, a gene that encodes a protein with no known function; contributes significantly to yield potential and is commonly employed in the cultivation of Asian-cultivated *O. sativa* [30,31]. The plant morphology of the *japonica* subspecies is more compact than that of *indica* because of the reduced activity of *TAC1*, which is being widely used in cultivars cultivated in high-altitude temperate zones and high-latitude places where *japonica* variants are commonly produced [4,12,32]. However, the precise mechanisms that drove the evolution of distinct *TAC1* genes in different *indica* and *japonica* rice types are still a mystery to researchers. In forthcoming studies, it will be intriguing to see if the *tac1* gene can be transferred to *indica* varieties in order to increase planting density and, therefore, yield. Several other species, including wheat, *A. thaliana*, peach trees, and *Miscanthus sinensis,* have shown that *TAC1* regulates branching/tiller angle, indicating that *TAC1* may be crucial for improving architecture and yield in many other plant species [16,33].

Although certain genes that are attributed to *O. sativa* cultivation and post-cultivation have been found, the specific molecular networks and regulatory mechanisms through which they interact are still mostly unclear. Exploring these systems in greater depth will help increase wild rice branching angle domestication and improvements using accurate gene editing approaches.

3. SHOOT GRAVITROPISM MEDIATED REGULATION OF RICE TILLER ANGLE

Shoot gravitropism has been implicated in the regulation of *O. sativa* tiller angle in previous research [34,35]. In the current understanding of the gravitropic reaction, gravity sensing, organ curvature, and signal transduction [36-40] are all regarded as consecutive stages. Rice shoot gravitropic response is still completely unknown, despite decades of research on *Arabidopsis* as the primary source of information on the molecular basis of shoot gravitropism.

3.1 Gravity-stimulated tissues in rice aerial portion

When it comes to higher plants, gravity sensing is the initial and most critical step in gravitropism. In accordance with the conventional starch–statolith concept, specialized cells can detect gravity via the deposition of amyloplasts containing starch granules [41,42]. Some shoot sections, notably the pulvinus and coleoptiles of monocots and the inflorescence stems and hypocotyls of dicots, have been found to contain sedimented amyloplasts [15,19,43]. It was discovered that a single endodermal cell layer in *A. thaliana's* inflorescence stems and hypocotyls is responsible for gravity-sensing [21,44]. Rice seedling leaf sheath bases, which have amyloplasts in numerous cell layers, differ from *Arabidopsis* in that they are involved in sensing gravity during the seedling stage [45,46]. In adult Gramineae plants, the pulvinus of the leaf sheath may be important for determining the direction of gravity [2,33,47]. It is yet to be documented that rice has gravity-sensing cells at the maturity phase. We will learn more about the subtle mechanisms that regulate shoot gravitropism and, in turn, the tiller angle of rice in the future from specific studies related to each cell of tissues responsible for gravity-sensing.

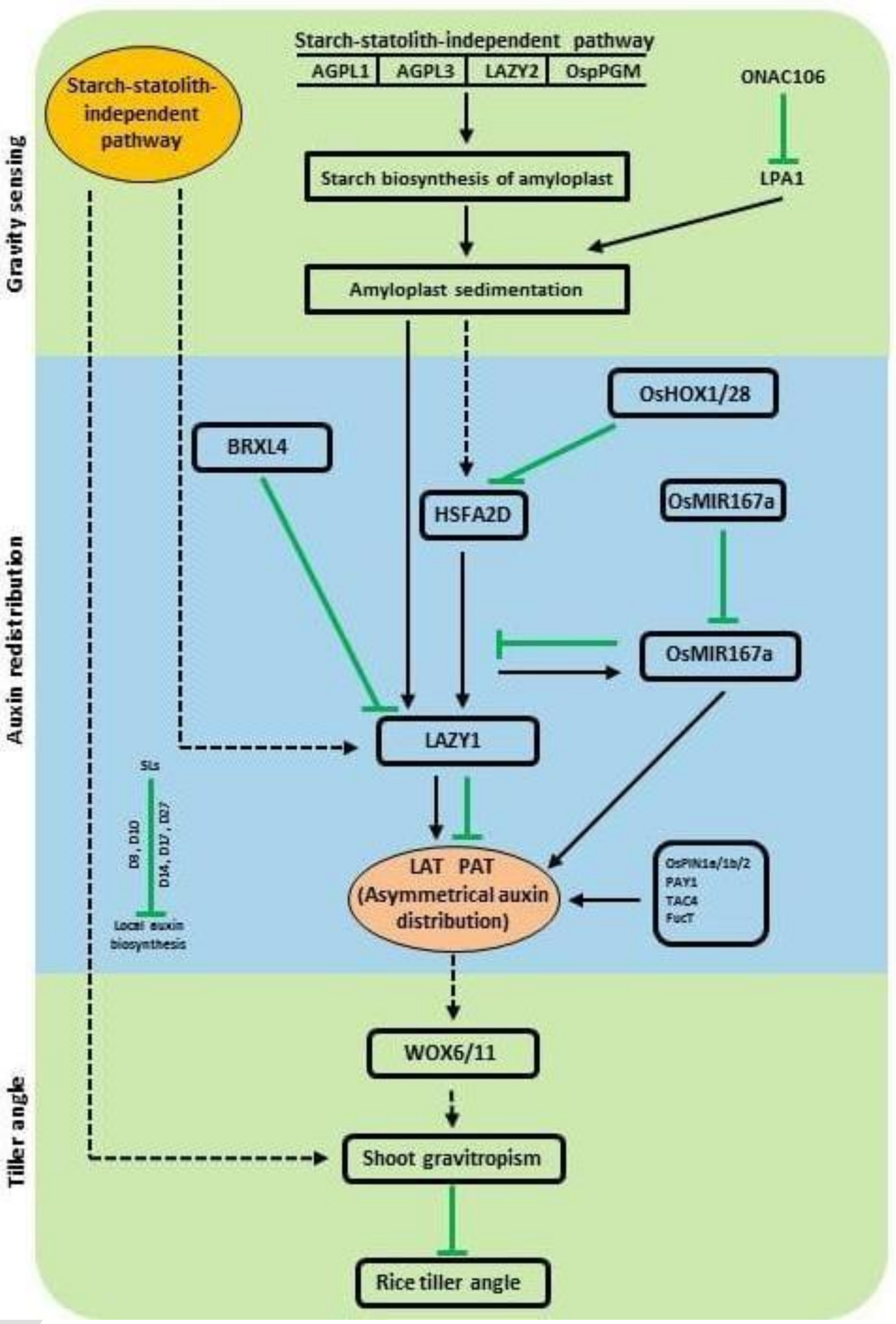

Fig. 1. A proposed model for regulatory mechanisms of shoot gravitropism and tiller angle in rice

3.2 Comparative association between rice tiller angle and starch biosynthesis in gravity sensing cells

The deposition of starch molecules in amyloplasts is crucial in controlling rice branching angle and gravity reaction, as evidenced by analyses of starch overaccumulation and starchless mutants [48,49]. Rice's tiller angle can be widened if starch concentrations in gravity-sensing fibers are reduced. Examples include ADP-glucose pyrophosphorylase (AGP), an enzyme that limits the rate of starch biosynthesis and catalyzes the initial irreversible step [50]. Rice shoot gravitropic response and branching angle are controlled by the genes *OsAGPL3* and *OsAGPL1*, which encode major subunits of the enzyme AGP [51-53]. An increase in the tiller angle was detected in the *agpl1 agpl3* double mutant, which had lower starch accumulation in the stem and leaf sheath compared to that of *agpl1* and *agpl3* single mutants [20,54]. Starch overaccumulation can also lead to a higher tiller angle in *O. sativa*. Examples of this are higher starch levels and hence increased tiller angle by overexpressing *CRCT*, *CO2-Responsive CONSTANS, and CONSTANS-like* genes [19,55].

Nevertheless, this research did not examine the starch concentrations in the cells responsible for gravity-sensing in transgenic CRCT plants. As a result, it is challenging to draw the conclusion that increasing starch concentrations can also result in decreased shoot gravitropism as well as a greater tiller angle. *STARCH EXCESS 1*, in contrast to *CRCT*, encodes an alpha-glucan dikinase that controls starch breakdown by phosphorylating starch-binding proteins [24,56]. The deficiency of *STARCH EXCESS 1* in *Arabidopsis* resulted in an increased starch accumulation with larger starch granules both in inflorescence and hypocotyl, resulting in an increased gravity-sensing [33,57]. These findings suggest that starch's role in gravity manipulation is more nuanced than previously thought and that more research is required.

3.3 Amyloplast sedimentation rate and regulation of rice tiller angle

Both the starch content and sedimentation rate of amyloplasts influence tiller angle and shoot gravitropism in rice. The *SGR5* gene in *Arabidopsis* affects inflorescence stem gravitropism by regulating amyloplast sedimentation rate and amyloplast starch content inside the endodermis [27-29,58]. The *LPA1* gene in *O. sativa* modulates shoot gravitropism and tiller angle by changing the amyloplast sedimentation rate upon gravistimulation [37,59]. Nonetheless, it is not apparent if *LPA1*, like its *Arabidopsis* homolog *SGR5*, can similarly control starch deposition in cells responsible for gravity sensing. Moreover, it was discovered that *PIN1a* and *ONAC106* regulate tiller angle in rice via *LPA1* as downstream and upstream factors, respectively [60]. After further research, it was discovered that *LPA1* may positively regulate the expression of *PIN1a* by binding to its promoter [42,61]. By activating *PIN1a* expression, overexpression of the gene *LPA1* in rice decreases the angle of the tiller and allows for better planting density [28,62].

3.4 Role of starch-statolith-independent pathway in regulating rice tiller angle and rice shoot gravitropism

The presence of a gravity signal in maize coleoptiles even after the surgical excision of the vascular bundle membrane, the supposed gravity-sensing structure that includes the amyloplasts, suggests that the starch–statolith system may not be the only process by which gravity sensing occurs [45,63]. While some experiments have shown that starch particles are important in tiller angle determination and gravitropism, others have shown that the gravitational sensitivity is not explained properly by the concentration of starch particles in amyloplasts. Examples include the starch-deficient *A. thaliana* mutants *pgm* and *esv1* with partially impaired shoot gravitropism [40,64]. Aside from the fact that the *la2* mutant seedlings showed only a partial loss in shoot gravitropism, starch particles were entirely absent among the amyloplasts of gravity-sensitive cells within la2 seedlings [39,65]. According to the findings of these investigations, starch is significant for gravity sensing but is not necessary, indicating there might be a pathway independent from the starch–statolith mechanism.

According to the traditional starch–statolith concept, gravity sensors use statoliths to detect gravitational signals [48,66]. Even in starch-deficient variants, which have no starch in the statolith, there is still a gravitropic response [67]. Empty plastids might still induce residual gravitropism as a result of their bulk, according to previous research. However, starch buildup within the plastids cannot fully explain the gravitropic response. Plastids may consequently be considered statoliths. Amyloplasts are required for a correct gravitropic response, and starch buildup in plastids may speed this process up [68]. A subsequent study, however, showed that the *esv1* mutant's unfilled endodermal plastids could not settle in the path of gravity, disproving the idea above [48,69]. A novel starch-statolith independent mechanism may partially govern the gravitropism of shoots and rice branching angle, according to these results.

4. GENETIC PATHWAY ELUCIDATING THE REGULATION OF RICE TILLER ANGLE

Rice tiller angle and shoot gravitropism are regulated by a number of genes, including those involved in gravity perception, auxin translocation, and transport upon gravistimulation. The dissection of the signaling pathways that regulate rice branching angle has made substantial progress during the last few years.

4.1 Role of *LAZY1* in determining rice tiller angle through asymmetric auxin redistribution

Amyloplast sedimentation, as previously indicated, may cause the signal transmission to alter auxin movement and drive uneven translocation of auxin within gravity-responsive tissues [55,70]. Auxin's asymmetrical distribution is critical for controlling rice shoot gravitropic response and, as a result, tiller angle [61,71]. Growing maize with a horizontal growth habit was labeled as "lazy" by plant biologists as early as the 1930s [72]. It wasn't until 2007 that the equivalent gene, *LA1*, was cloned for the rice mutant *lazy1* with impaired shoot gravitropism, which led to the characteristic horizontal growth habit [53,73]. Further research has shown that *LA1* affects shoot gravitropism and tiller angle by regulating the uneven translocation of auxin following gravistimulation [17,74]. Rice shoot gravitropic response and branching angle is controlled by *LA1*, which is expressed within vascular bundles at the ventral sections of developing rice stems and leaves. In the *IGT* family of genes, it was discovered that *TAC1* and *LA1* belong to two distinct lineages; the most significant morphological distinction between these two *IGT* lineages is the presence of the conserved CTD V, which is absent from TAC1 [60,75]. Due to the EAR-like pattern in CTD V, it might be fascinating to examine its functional importance in the *LA1* gene.

BRXL4 has been shown to regulate gravitropism and rice branching angle by influencing the *LA1's* nuclear localization, which is required for its functioning, according to a recent study [76]. If *BRXL4* increases protein breakdown of *LA1* within the nucleus or facilitates the transfer of *LA1* from the nucleus to the plasma membrane, it is currently unclear what tends to happen when *LA1* comes into contact with *BRXL4*. A number of additional plant species were also found to have homologs of LA1 that are involved in shoot gravitropic response [22,77]. It has been shown that *LA1*, *AtLA1*, and *ZmLA1* have distinct functions in maize inflorescence development, showing that *LA1*, *AtLA1*, and *ZmLA1* may have distinct activities, most likely due to their limited protein-encoding resemblance or diverse expression patterns [13,45,56]. If *LA1*, a major regulator associated with the adjustment of tiller angle in rice, has undergone artificial selection, it will be worthwhile to investigate if there are superior genotypes of *LA1* in domesticated rice that may be exploited to attain the optimum plant architecture in the long term.

4.2 Role of WOX6 and WOX11 transcription factors in determining rice tiller angle through asymmetric auxin redistribution

Tiller angle in rice is controlled by genetic regulatory networks that can be identified using high-resolution and high-throughput technologies such as vibrant transcriptome sequencing. As part of a rice branching angle control study, a vibrant transcriptome examination was carried out [78,79]. In addition, the upstream protein *HSFA2D* promotes the uneven translocation of auxin, therefore promoting the asymmetrical expression of the duplicated downstream transcription proteins *WOX6* and *WOX11* [80]. Tiller angle in rice is controlled by these two genes, which play a role in the organ folding response to gravistimulation.

Additional important components acting within the HSFA2D-LA1-WOX6/WOX11 network have been discovered recently, as indicated in Figure 1 [56]. OsHOX28 and OsHOX1, two class II HD-Zip proteins, actively control rice branching angle by binding directly to the *HSFA2D's* promoter, which inhibits lateral auxin transportation, therefore suppressing the transcription of *WOX6*/*WOX11* in the shoot base during gravistimulation [72,81]. Rice shoot gravitropic response and branching angle are influenced by the uneven translocation of auxin, which is mediated by *OsmiR167a*, which suppresses its targeted auxin response factors OsARF25, OsARF17, and OsARF12 [66,82]. Nevertheless, an understanding of the role of auxin response factors, which are crucial to the signaling process, in the regulation of auxin distribution is not simple.

Shoot gravitropic response and tiller angle in rice are both controlled by WOX6 and WOX11 transcription factors, which work downstream of auxin (Figure 1). In the gravitational signal transduction system, LA1 may operate as a critical node between amyloplast aggregation and downstream auxin transfer. Identifying new downstream and upstream components of *LA1* may help us better understand the rice branching angle regulation network.

5. ENVIRONMENTAL PLASTICITY OF RICE TILLER ANGLE

Plants have a unique ability to modify their structures to the ever-changing environment because of their amazing developmental flexibility. While several endogenous elements influence the rice branching angle, it is important to note that environmental factors also play an important role in influencing this parameter [76,83]. Plants growth and maintenance are heavily influenced by the availability of light. Light has the ability to cause higher plants to change the direction of their growth. Rice plants grown in a growth chamber or out in the field with shorter photoperiods tend to have a more upright structure [42,55,84]. Furthermore, light quality may change the tiller angle in rice by influencing the phytochrome-interacting factorlike15 levels, which is dependent on phytochrome B, a major photoreceptor, to recognize the low red and far-red proportion of shade light [34,37]. *TAC1* controls branch angle in *Arabidopsis* and is light-dependent, being inhibited by prolonged far-red light [85,86]. There are two major phases in the growth of a rice tiller: the initial spread phase and the later compact phase [87]. During the initial spread phase, the juvenile plant occupies more area for further tiller growth, and during the later compact phase, the matured plant reduces the degree of leaf shade and improves its photosynthetic rate in a congested growing environment [64,88]. As with its *Arabidopsis* ortholog, *TAC1's* dynamic expression will need to be tested in future research to see whether it affects the angle of the tiller in response to photosynthetic cues. Light-responsive components in the promoter region of *ZmLA1* in maize were discovered by bioinformatics research; shorter photoperiods have been shown to suppress *ZmLA1* production [59,89]. According to this research, photoperiods may influence maize shoot gravitropic response by altering the *ZmLA1* expression rate.

According to prior research, temperature and gravitational signals are linked throughout the tropical development of plant components [27,90]. As a result, plants' tiller angle and gravitropism are influenced by temperature. Frost-resistant wheat may be improved by increasing its tiller angle during the seedling stage due to temperature-related changes [91]. Because of the gravitropism in the inflorescence stems in *Arabidopsis*, both temperature extremes may both reduce the plant's gravitropic response and alter the branch angle [92]. Inflorescence stem gravitropism may be regulated by cold temperatures, possibly by reducing stem elongation after gravitational signal reception [82,93]. High temperatures, as opposed to low temperatures, reduce the shoot gravitropic response by reducing the detection of gravity signals. A molecular mechanism for this gravity–temperature connection may be explained by accelerating *SGR5* alternative splicing, which results in high rates of *SGR5b* inhibiting the function of *SGR5a* via the formation of nonfunctional *SGR5a/SGR5b* heterodimers [88,94]. Although comparable phenomena occur in *Arabidopsis*, the flexibility of tiller angle and the shoot gravitropic response in rice in reaction to temperature have received significantly less attention to date. Insight into the mechanisms that underpin the environmental flexibility of tiller angle can be beneficial in the development of higher-yielding varieties that are more tolerant of certain environmental conditions.

Table 1. List of genes involved in the regulation of rice tiller angle

Gene names	**Specie**	**Accession numbers**	**Functional annotation**	**References**
TAC1	Wheat, maize and *Arabidopsis*	LOC_Os09g35980	IGT family protein	[3,23,83]
TAC4		LOC_Os02g25230	Unkown	[37]
AGPL1/3		LOC_Os05g50380 LOC_Os03g52460	Subunit of ADP-glucose pyrophosphorylase	[55]
LAZY1	*Arabidopsis*, tea plant, maize	LOC_Os11g29840	IGT family protein	[22,92]
BRXL4		LOC_Os08g36020	Brevis Radix-Like 4	[67]
OsHOX1/28		LOC_Os10g41230/ LOC_Os06g04850	HD-ZIP II transcription factor	[25]
WOX6/11		LOC_Os03g20910/ LOC_Os07g48560	WUSCHEL-related homeobox	[33]
PAY1		LOC_Os08g31470	Trypsin family protein	[11]
OsMIR167a		MI0000676	MicroRNA	[41]

6. UNDERSTANDING THE MECHANISMS BEHIND THE REGULATION OF RICE TILLER ANGLE: A WAY FORWARD

6.1 Tiller angle optimization and crop productivity

The rice branching angle, which controls the cropping density in a unit area and has a significant impact on grain yield, is critical to the appropriate rice architecture. Rice farmed in high-latitude temperate regions and at high elevations, where *japonica* rice types are often used, has been shown in previous research to benefit greatly from *tac1*, which leads to a dense plant architecture having a smaller tiller angle [95]. Earlier research has shown that certain genes, such as *LA2* and *LA1*, are uniquely involved in the regulation of shoot gravitropic response and rice branching angle, with no substantial damaging impacts on other agronomic characteristics [96]. These genes may be manipulated by utilizing precise gene-editing techniques to create more elite variants that may be exploited to boost grain yields.

Increased cropping density may also assist in minimizing the quantity of synthetic fertilizers used and boost crop fertilizer use efficiency by breeding for the optimum tiller angle. According to a recent finding, cropping density and the quantity of nitrogen fertilizer applied have a substantial impact on rice tillering capability [97]. More nitrogen input is required for greater planting densities than at lower densities to compensate for the reduced population density [98]. Greater wheat planting densities and lower nitrogen fertilizer applications have been proven to develop bigger populations with improved yields and fertilizer use efficiency, according to research [75]. Sustainable agriculture may be achieved by minimizing nitrogen fertilizer inputs by adopting the ideal tiller angle to enhance canopy photosynthesis and improve crop population.

6.2 Rice as a model plant for modifying tiller angle in other crop plants

In studying the molecular processes that regulate tiller angle, considerable success has been achieved using *O. sativa* as a framework. It is possible that the processes controlling tiller angle in various plants may be revealed by the findings of these studies. To regulate tiller angle in various other plants, orthologs of the rice genes *TAC1* and *LA1* are suitable candidates. *TAC1* homologs have been shown to have retained roles in Prunus species, peach trees, *Miscanthus sinesis*, maize, *Arabidopsis,* and wheat [99]. Several species, including *Arabidopsis*, tea plants, and maize, have also now revealed the conserved activities of *LA1* homologs in the control of the tiller angle [100]. As a result, gaining a better knowledge of the molecular processes that govern tiller angle in rice will provide insight into the genes controlling architecture in various other plants.

7. FUTURE PERSPECTIVE AND CONCLUSION

We initially outlined the factors behind variations in rice branching angles throughout domesticated and post-domesticated rice derived from their wild counterparts in this review. The genetically controlled pathway that regulates branching angle and shoot gravitropic response in rice was next explored, with an emphasis on gravity perception and asymmetrical auxin redistribution being a particular focus. Finally, we outlined a number of sensible strategies for enhancing the tiller/branch angle in plants via the application of principles obtained from improving the rice tiller angle. By providing a complete overview of the genomic basis for tiller angle, we want to stimulate further research into previously unknown genetic regulatory networks that regulate tiller angle and shoot gravitropism in rice.

Some critical elements of gravity sensing, downstream auxin response, asymmetric translocation of auxin, and organ flexibility have been discovered to govern shoot gravitropic response and, consequently, tiller angle using rice as an experimental model (Table 1). Examining the processes that govern rice tiller angle determination helps in understanding shoot gravitropism, a major scientific subject. In the past few years, it has been demonstrated that various key elements, including *OsAGPL1*, *OspPGM*, and *LA2*, play their roles in gravity sensation. In addition to providing additional data in favor of the conventional starch–statolith theory, these investigations show that plants use a starch-statolith-independent mechanism to perceive gravity. It is possible to identify new gravity-sensing genes by separating gravity-sensing cells from rice, extracting their transcripts, and constructing sequencing libraries that are linked to the individual gravity-sensing cells, facilitating systematic analyses of the regulatory networks that underpin the sense of gravity in *O. sativa* as well as other crops. Moreover, several significant components, including *LA1*, *HSFA2D*, *WOX6/WOX11*, *HOX1/HOX28*, and *BRXL4*, operate as the fundamental regulatory network controlling tiller angle in rice (Figure 1).

In summary, understanding the genetic mechanisms that control branching angle will not only help us further perceive the molecular process that underpins the tiller angle in rice, but it will also aid breeders in generating new crop types with an optimal tiller/branching angle for certain environmental conditions.

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