Food and Energy Security

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Molecular Control of Tiller Angle and Its Role in Rice Domestication

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Received: 30 December 2025 | **Revised:** 18 April 2026 | **Accepted:** 23 April 2026

Keywords: cultivated rice | domestication | gene regulatory network | plant architecture | tiller angle | wild rice

ABSTRACT

Plant architecture is a key determinant of rice (*Oryza sativa*) productivity, with tiller angle playing a central role in optimizing plant density, light interception, and yield. During domestication, rice underwent a critical transition from the prostrate growth habit of wild relatives such as *Oryza rufipogon* to the erect architecture of cultivated varieties, driven by selection for reduced tiller angle. While numerous studies have identified genes associated with tiller angle regulation, a comprehensive synthesis integrating domestication genetics, physiological mechanisms, and emerging biotechnological approaches remains limited. This review provides a critical and integrative perspective on the molecular control of tiller angle, distinguishing between genes that directly regulate gravitropism and shoot orientation (e.g., *PROG1*, *TAC1*, *LAZY1*) and those that indirectly influence plant architecture through hormonal or developmental pathways (e.g., *D3*, *D14*, *D53*, *sd1*). We highlight key domestication genes, including *PROG1*, *PROG7*, *TIG1*, and the RPAD locus, and clarify the current status of BTA8 as a candidate locus associated with basal tiller angle whose molecular function and regulatory interactions remain unresolved. Importantly, we move beyond descriptive summaries to propose a conceptual framework linking gene regulatory networks, auxin-mediated gravitropism, and evolutionary selection during domestication. We further evaluate how recent advances in multiomics, single-cell technologies, and CRISPR/Cas-based genome editing can address current bottlenecks in dissecting complex traits such as tiller angle. By integrating genetic, physiological, and technological perspectives, this review identifies key knowledge gaps and outlines future research directions, including network-level analysis and precision breeding strategies. These insights provide a foundation for exploiting wild rice genetic diversity to develop climate-resilient, high-yielding cultivars with optimized plant architecture.

1 | Introduction

Rice (*Oryza sativa L.*) is not only a major global staple food crop but also serves as an important model species for plant biology and agricultural research (Bandumula 2018; Xu and Sun 2021). Among the various traits shaping rice plant architecture, tiller angle has emerged as a crucial trait determinant of plant density, light interception, disease susceptibility and ultimately grain yield (Bai et al. 2018; Zhang et al. 2018). During the domestication of rice, modification of tiller angle played a pivotal role in transitioning from prostrate growth in wild species to the erect architecture characteristic of modern cultivars (Wang, Gao, et al. 2022; Wang, Tu, et al. 2023). Tiller angle is defined as the angle between the main culm and the side tillers with the greatest inclination, influencing the spatial distribution of tillers and overall plant compactness (Yang and Hwa 2008).

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Axillary meristems at the basal nodes initiate side tillers, whose growth orientation defines the plant architecture. While larger tiller angles are beneficial during early establishment phases, facilitating soil coverage and water retention, compact architectures with smaller tiller angles are critical for high-density planting and mechanized farming (Marone et al. 2020; Wang, Gao, et al. 2022; Kangben et al. 2024). Excessively narrow angles, however, can limit light and air penetration, predisposing plants to disease (Cai et al. 2023). Throughout the history of rice domestication, the modification of tiller angle has contributed to the development of compact plant architecture, a trait that enhances planting density and resistance to lodging in modern rice varieties (Zhang et al. 2019; Xu and Sun 2021; Tokuyama et al. 2024). This shift from wild rice prostrate growth to cultivated rice erect growth marks one of the key adaptations during domestication, driven by the selection of specific genes regulating tiller angle (Wambugu et al. 2021). Wild rice species, such as *Oryza rufipogon*, exhibit a wider tiller angle, which is characteristic of their prostrate growth habit (Zhu et al. 2013; Wang, Lu, et al. 2022). In contrast, cultivated rice has been selected for a more compact tiller angle, which aids in higher planting densities and resistance to lodging, traits crucial for modern agricultural practices (Reinhardt and Kuhlemeier 2002; Yang and Hwa 2008). Thus, rice cultivars and wild rice species significantly differ in terms of their architecture. To better understand the genetic basis of the unique plant architecture of wild rice species, researchers have mainly focused on *Oryza rufipogon*, which is the ancestral progenitor of *O. sativa* (Huang et al. 2012), and identified genes for architectural traits such as tiller angle, panicle shape, plant height, and leaf architecture (Jin et al. 2008; Tan et al. 2008; Zhu et al. 2013; Zhou et al. 2021). These studies have not only highlighted the genetic basis for the architecture of wild rice species, but they have also provided clues about domestication trends and dynamics in *O. sativa*.

Cluster of genes such as *PROG1*, *PROG7* and *RPAD* and genes like *TIG1*, have been cloned and characterized, shedding light on the evolutionary dynamics shaping rice architecture, while BTA8 is currently defined as a locus associated with basal tiller angle in wild rice (*Oryza minuta*), rather than a fully cloned and functionally validated gene. Its precise molecular function and regulatory pathway remain largely unresolved. Moreover, no direct genetic or molecular interactions have yet been demonstrated between BTA8 and key regulators such as *PROG1*, the RPAD locus, or *TIG1*. Further studies are required to elucidate its role in the regulatory network controlling tiller angle and plant architecture (Jin et al. 2008; Tan et al. 2008; Hu et al. 2018; Wu et al. 2018; Zhang et al. 2019). Furthermore, recently, important progress has been made in the molecular interactions between the genes, such as *PROG1* with *LA1*, in regulating tiller angles in rice (Wang, Huang, et al. 2023; Zhang et al. 2023). In parallel, critical domestication genes, regulating tiller angle have been identified, such as *sd1* (Semidewarf1) gene, which encode protein gibberelline 20 oxidase (GA20ox2) has historically been linked to semidwarf stature and reduced tiller angle in domesticated rice (Ashikari et al. 2002; Hedden 2003). Moreover, the gene *IPA1* has been associated with ideal plant architecture, encoding the protein SQUAMOSA promoter-binding protein-like 14 (*SPL14*), influencing both tiller number and angle, thus contributing to the high-yield potential of modern varieties (Jiao et al. 2010). Therefore, the *IPA1* gene has become a crucial component of rice breeding, with ideal plant architecture representing a novel strategy for developing extremely high-yield varieties (Wang et al. 2017; Zhang et al. 2017; Gao et al. 2021; Kong et al. 2022). Understanding the role of such genes in controlling tiller angle as well as plant architecture provides insight into the genetic foundation of rice domestication and offers pathways for future breeding programs. Mutations in the sequences of individual genes are the strongest contributors to evolutionary change (Hershberg et al. 2007), and that mutations at the genomic level accelerate the evolution of rice during domestication and modern breeding (Wang, Wang, et al. 2022). Furthermore, plant architecture, resource efficiency, and yield potential are all directly impacted by growth habit (Inagaki et al. 2021; Wang, Gao, et al. 2022). An upright growth habit with modest tiller angles has long been favored by breeders due to its advantages for high-density planting and ease of mechanization (Chen et al. 2024). In addition to direct genetic control, phytohormonal regulation, particularly involving cytokinins and auxin, plays a significant role in modulating tiller development and spatial orientation (Li et al. 2007; Zhang et al. 2018; Wu et al. 2024). Interactions between these hormonal pathways coordinate the balance between vegetative and reproductive growth, directly impacting overall plant architecture (Albacete et al. 2014). While tiller angle remains a central focus, it is important to note that domestication also involved other critical traits such as seed shattering, flowering time, and grain size, which collectively contributed to the evolution of modern rice varieties. Furthermore, ecological factors such as drought and photoperiodic responses have indirectly influenced tiller architecture, emphasizing the complex interplay between genetic, environmental, and human-mediated selection pressures (Wambugu et al. 2021). Mutations in key regulatory genes have been major drivers of evolutionary change during domestication (Wang, Wang, et al. 2022). New technologies such as CRISPR-Cas9 genome editing and multiomics approaches, advance opportunities now exist to further dissect and manipulate tiller angle-related traits for future rice improvement (Yin et al. 2025). However, caution is warranted, as over-compaction of plant architecture could negatively impact disease resistance and canopy ventilation. Recent advances in genomics and integrative databases have further accelerated the understanding of rice plant architecture and provide comprehensive genomic maps and integrated information on plant architecture-related genes, enabling systematic exploration of gene networks involved in tiller angle regulation (Wei et al. 2021). Moreover, several recent reviews have summarized the molecular basis of rice plant architecture and tiller angle regulation (Bai et al. 2018; Huang et al. 2021). But most of these studies primarily focus on individual genes or pathways without integrating domestication genetics, physiological mechanisms, and emerging genome editing technologies. In this review, we aim to provide a more integrative perspective by linking genetic regulation, physiological processes, and modern biotechnological approaches to better understand and manipulate tiller angle in rice. Furthermore, in this review, we summarize recent advances in understanding the genetic basis of prostrate growth and tiller angle development in wild and cultivated rice species. We particularly focus on key cloned genes, their functional mechanisms during domestication, and future directions for breeding high-yield, resource-efficient rice varieties. We also highlight current limitations, knowledge gaps, and the potential of emerging technologies to accelerate the genetic

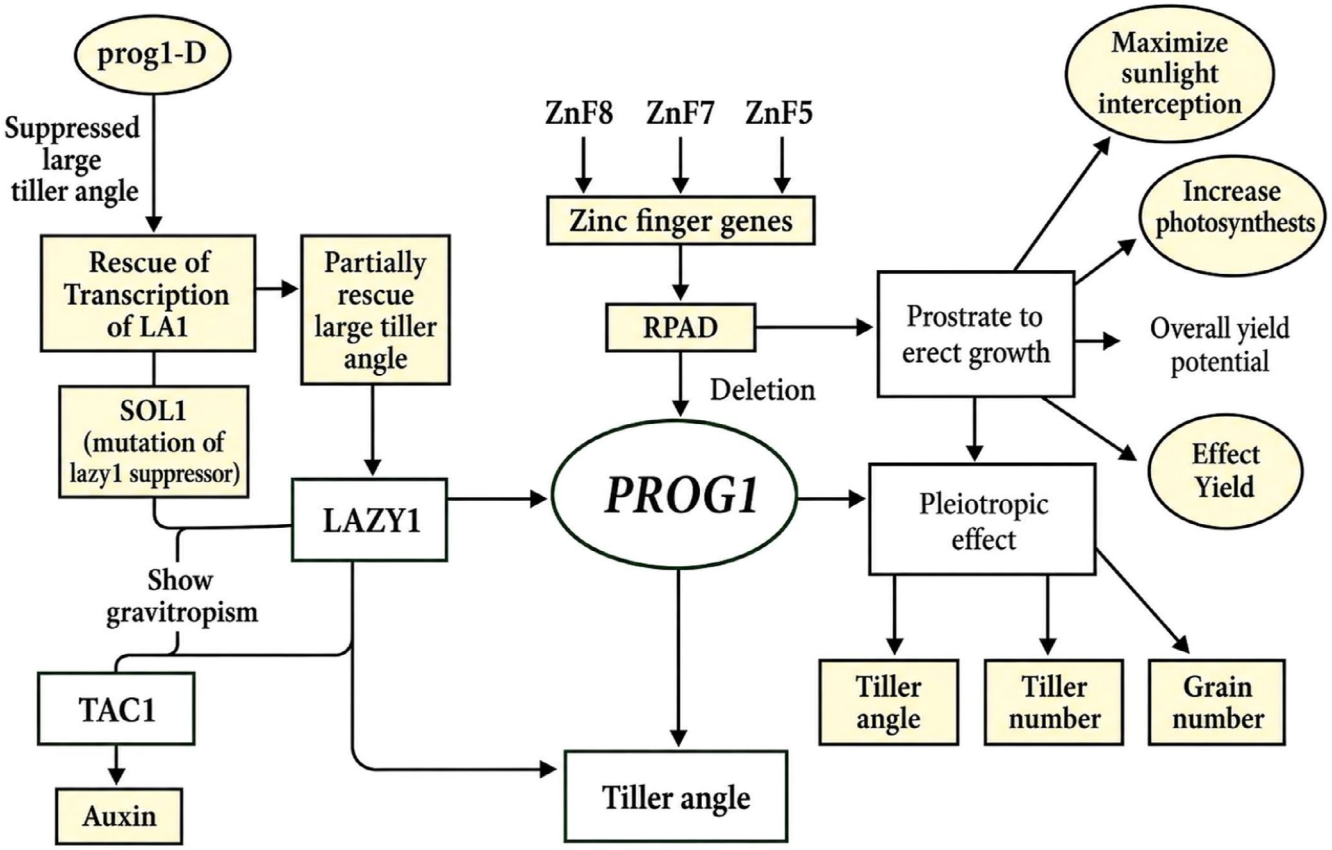


FIGURE 1 | Schematic molecular and physiological illustration of tiller angle in rice. *PROG1* acts as a central regulator, repressing *LAZY1*, which governs shoot gravitropism through auxin signaling. *TAC1* also contributes to auxin-mediated control of tiller angle. *RPAD*, influenced by zinc finger genes (*Znf5*, *Znf7*, *Znf8*), promotes erect growth through deletion of *PROG1*. Changes in tiller angle affect light interception, photosynthesis, and yield traits such as tiller and grain number via *PROG1* pleiotropic effects. Further, Prostrate Growth 1 indicates PROG1, LAZY1 to LA1, Rice Plant Architecture Domestication to RPAD, Tiller Angle Control 1 to TAC1. Arrows indicate the direction of physiological processes and developmental transitions, while different colored components represent distinct processes, including growth stages, resource allocation, and regulatory mechanisms influencing tiller angle.

improvement of rice plant architecture. In addition, systematic analysis of plant architecture genes provides new opportunities for understanding complex regulatory networks and guiding breeding strategies. Extracted information will also improve our understanding about the mechanisms of erect growth in domesticated *Oryza* species and can identify the additional genes regulating important traits in wild rice species, which could be proven beneficial for breeding high-yield varieties.

1.1 | Physiological Bases of Tiller Angle Contributing to Resource Use Efficiency

A key component of efficient resource utilization in rice is the tiller angle, which affects light interception, photosynthetic efficiency, and crop output (Figure 1; Mubarak et al. 2022). It is crucial to comprehend the physiological and genetic processes underlying tiller angle in order to optimize plant architecture and to obtain highest productivity. Effective resource use is made possible by the dynamic variations in the tiller angle that occur over the plant's life cycle. In the beginning, a broader angle during the tillering stage aids in the space occupation of young plants and prevents the growth of weeds (Wang et al. 2021). As the plant matures, the angle decreases to lessen leaf shadowing and increase photosynthetic efficiency (Alam et al. 2014; Dong et al. 2016). Larger plants can minimize soil water evaporation and boost competition for resources, but they may have worse photosynthetic efficiency because of more leaf shade (Tao et al. 2024). Furthermore, at the physiological level, gravitropism represents the central mechanism regulating tiller angle, enabling plants to maintain appropriate shoot orientation relative to gravity (Wang, Gao, et al. 2022). This process is primarily mediated by the asymmetric distribution of auxin, which generates differential cell elongation at the base of tillers (Zhang et al. 2018). Upon gravistimulation, auxin is redistributed toward the lower side of the tiller base, leading to enhanced cell elongation on that side and bending of the tiller toward a specific orientation (Rehman et al. 2022). This auxin-driven differential growth establishes and maintains the angle between the main culm and lateral tillers (Wang 2019). Disruption of this asymmetric auxin distribution leads to altered tiller orientation and impaired gravitropic responses (Zhang et al. 2018). Consequently, breeding programs that integrate knowledge of tiller angle and crop physiology can develop rice varieties combining high planting density with efficient light capture. It is illustrated in Figure 1, to summarize the physiological and molecular mechanisms underlying tiller angle regulation through gravitropism and auxin-mediated processes.

1.2 | Genetic Basis for Prostrate Growth/Large Tiller Angle of Wild Rice Species

One of the earliest domestication traits in cultivated rice (*Oryza sativa*) was the selection for erect growth from prostrate wild ancestors. Wild rice species within the *Oryza* genus exhibit diverse growth habits, namely prostrate (> 60°), semiprostrate, or erect adapted to a range of ecological niches (Vaughan 1989, 1994; Samal et al. 2018). For example, in *Oryza rufipogon*, tiller angles exceeding 60° typically characterize prostrate growth (Lizhi et al. 2000). In the early 2000s, the molecular basis of prostrate growth remained largely unknown. However, recent studies have uncovered several genes that regulate tiller angle and directly or indirectly contribute to domestication of rice (Table 1). These genes reveal that tiller angle is a complex, genetically controlled trait shaped by selection for improved resource use efficiency and agronomic performance.

Furthermore, the detailed explanation of some genes involved in tiller angle regulation such as the *PROG7* (*PROSTRATE GROWTH 7*) and *YABBY5* gene, which encodes a protein located on chromosome 7, cloned into another AA-genome wild rice species i.e., *Oryza barthii* are discussed here. This species is the progenitor of African cultivated rice, *Oryza glaberrima* (Hu et al. 2018; Zheng et al. 2024). The *PROG7* allele regulates prostrate growth in *O. barthii*, which is characterized by a larger tiller angle and numerous additional tillers, whereas *O. glaberrima* carrying a *prog7* allele exhibits upright growth. *PROG7* is a zinc-finger transcription factor, and mutations in the promoter region of *prog7* reduced its expression level and induced the transition of prostrate growth in African wild rice to erect growth in *O. glaberrima* (Hu et al. 2018). Moreover, the gene sequences of *prog1* and *prog7* were conserved, with *prog7* in *O. glaberrima* being identical to *prog1* in *O. sativa*. This serves as a strong indication of parallel domestication of plant architecture between the two cultivated rice species.

Another locus involved in plant architecture, *RPAD* (*RICE PLANT ARCHITECTURE DOMESTICATION*) contains a cluster of genes and is closely linked to *PROG1*, was cloned in *O. rufipogon* (Wu et al. 2018). In *O. sativa*, however, there is a 110-kb deletion at the *RPAD* locus. It was found that a tandem repeat of seven zinc-finger genes occurred in this 110-kb region of wild rice, with *ZnF5*, *ZnF7*, and *ZnF8* functioning in regulating the semiprostrate growth phenotype in wild rice species, as well as plant height, panicle number per plant, grain number per panicle, and grain yield per plant (Wu et al. 2018). Alleles of the zinc-finger gene at the *RPAD* locus in the Asian wild rice species *O. rufipogon* and *Oryza nivara*, along with the African wild rice *O. barthii*, played similar roles in the development of large tiller angles. The locus of *RPAD* in *Oryza glaberrima* indicated convergent selection with O. sativa (Wu et al. 2018). Similar to the gene *prog1* in *O. sativa* and *prog7* in *O. glaberrima*, the *RPAD* locus is also involved in the parallel domestication of plant architecture in both Asian and African rice species (Wu et al. 2018). Furthermore, targeted editing of the *RPAD* gene cluster offers a promising strategy to modify tiller angle and plant stature for breeding compact, high-yielding varieties (Wu et al. 2018; Zhang et al. 2023). This suggests that the evolution of wild rice species into cultivated varieties is primarily driven by positive selection; specifically, during the domestication process, cultivated rice varieties were largely formed through the loss of certain genes or the deletion of specific gene sequences.

TILLER INCLINED GROWTH 1 (TIG1), a single dominant gene on chromosome 8 that controls the natural inclination of tillers in the wild rice species *O. rufipogon*, was recently cloned. In wild rice, elevated *TIG1* activity leads to an inclined growth habit (Zhang et al. 2019). The TCP family transcription factor protein OsTCP15 is encoded by the *TIG1* gene. The OsTCP15 protein consists of 266 amino acids and is a class II TCP protein. *TIG1* stimulates cell elongation, increases the tiller angle, and is primarily expressed along the adaxial side of tillers in wild rice. During rice domestication, transition of the inclined tiller angle in *O. rufipogon* to fully erect growth in cultivated rice was induced by variations in the promoter region of the *tig1* allele of cultivars, which resulted in lower expression of *TIG1* at the tiller base on the adaxial side and decreased tiller angle and cell length. *TIG1* promotes cell elongation on the far-land side of the tiller base and increases the tiller angle. Furthermore, as a transcription factor, *TIG1* can bind to the TCP-binding sites in *EXPA3*, *EXPB5*, and *SAUR39* promoters to activate their expression (Zhang et al. 2019). In addition, *Aux/IAA* repressors and *ARF* activators are pivotal in auxin signaling (Yan et al. 2020), while *GRAS* and *HD-ZIP* transcription factors modulate developmental plasticity in shoot branching and tiller angle adjustment under stress (Zhang et al. 2022). Additionally, *TIG1* shares a significant degree of similarity with several well-known proteins, including OsTB1 and REP1 in rice, TB1 and BAD1 in maize, and BRC1 in *Arabidopsis* (Luo et al. 1996; Doebley et al. 1997; Takeda et al. 2003; Costa et al. 2005; Aguilar-Martínez et al. 2007; Yuan et al. 2009; Bai et al. 2012). Moreover, editing *TIG1* expression through promoter engineering has also been proposed as a means to fine-tune tiller inclination without adversely affecting other agronomic traits (Guo et al. 2020).

1.3 | *PROG1* Interacts With Other Genes in Regulating Rice Tiller and Panicle Architecture

PROG1 (PROSTRATE GROWTH 1) was the first gene identified and cloned that regulates prostrate growth in *Oryza rufipogon*. Through map-based cloning technique, Jin et al. (2008) and Tan et al. (2008) cloned *PROG1* simultaneously using the genomes of *O. rufipogon* and the indica cultivar, Teqing (*O. sativa*). *PROG1* is located on the short arm of chromosome 7 and encodes a 167-residue polypeptide containing a C_2H_2-type zinc-finger motif; mutations in the *prog1* coding region induce amino acid variation and cause the loss of protein function, resulting in erect growth with small tiller angles (Jin et al. 2008; Tan et al. 2008). Whole-genome sequencing of 163 *O. glaberrima* and 83 *O. barthii* accessions from the African Sahel and East Africa revealed convergent selection of *PROG1* during independent domestication events. Full deletion of *PROG1* was consistently associated with erect growth in both domesticated African rice and wild individuals carrying the deletion, while wild individuals retained an intact *PROG1* exhibited a prostrate phenotype (Cubry et al. 2018). Comparative analyses of *PROG1* sequence and expression, together with the widespread distribution of tiller angle variation across *Oryza* species, suggested that prostrate growth is a derived trait shaped by strong natural selection, conferred or enhanced by *PROG1*

TABLE 1 | A list of key genes affecting the angle of tillers and playing a role in domestication of rice.

Gene	Function	Effect on tiller angle	Domestication significance	Mode of regulation	Genome editing and breeding application	Regulatory pathway/ mechanism	Recent advances/ future potential	References
TAC1	Regulates tiller angle by controlling asymmetric growth	Wider tiller angle in wild rice; reduced angle in domesticated varieties	Selection for erect tillers to improve planting density	Direct	CRISPR/Cas9-mediated editing of *TAC1* can further reduce tiller angle for high-density planting	Auxin-mediated asymmetric growth regulating tiller inclination	CRISPR-based fine-tuning of TAC1 expression enables optimization of planting density and climate-resilient architecture	Yu et al. (2007); Wang, Tu, et al. (2022); Yin et al. (2025)
LAZY1	Mediates gravity signaling in tiller orientation.	Erect tiller phenotype in mutants.	Contributed to compact plant architecture	Direct	Targeted mutation of *LAZY1* can create desirable compactness for mechanized farming	Auxin transport and gravitropic signaling controlling shoot orientation	Identified as part of *PROG1–LAZY1* regulatory module; potential target for precise control of tiller angle via gene network engineering	Yoshihara and Iino (2007); Yoshihara and Spalding (2017); Sun et al. (2023)
OsIAA6	*Auxin-responsive gene influencing tiller growth.*	Affects auxin distribution, altering the tiller angle.	Auxin signaling fine-tunes tiller angle.	Indirect	Overexpression or editing of OsIAA6 offers precise control of tiller angle for customized plant types	Auxin signaling pathway regulating tiller development and orientation	Promising target for precision breeding to modulate auxin distribution and adaptive plant architecture under stress conditions	Jung et al. (2015)
PROG1	Promotes prostrate growth in wild rice.	Prostrate growth in wild species with large tiller angles of approximately 45°–60°; erect growth in domesticated rice.	Loss-of-function by mutation can favor the domestication	Direct	Knockout of *PROG1* by gene editing replicates domestication traits, improving yield potential	Transcriptional repression of LAZY1 and regulation of auxin-mediated gravitropism	Central domestication gene; CRISPR-mediated knockout replicates erect growth and serves as a model for ideotype breeding	Tan et al. (2008)
PROG7	Regulates prostrate growth in African wild rice	Large tiller angle and spreading growth habit	Demonstrates parallel domestication in African rice	Indirect	Promoter editing can modify growth habit and plant architecture	YABBY transcription factor regulating plant architecture	Provides evidence for convergent evolution; useful for comparative genomics and breeding	Hu et al. (2018)

(Continues)

TABLE 1 | (Continued)

Gene	Function	Effect on tiller angle	Domestication significance	Mode of regulation	Genome editing and breeding application	Regulatory pathway/ mechanism	Recent advances/ future potential	References
TIG1	Promotes cell elongation at the tiller base	Increased tiller inclination	Reduced expression selected for erect growth in cultivated rice	Direct	Promoter engineering enables fine-tuning of tiller angle without affecting yield	TCP transcription factor regulating cell elongation	Useful for ideotype breeding and optimizing the canopy structure	Zhang et al. (2019)
D53	Downstream repressor in strigolactone signaling.	Strigolactone signaling reduces tiller angle	Erect tiller phenotype improves crop management	Indirect	Target for manipulating tiller number and optimizing plant architecture; modulation of D53 activity can help balance branching and yield under different planting densities	Acts downstream of the strigolactone receptor D14 and F-box protein D3; in the absence of strigolactones, D53 represses downstream signaling, while in the presence of strigolactones, D53 is degraded via the ubiquitin–proteasome pathway, leading to inhibition of shoot branching	Understanding D53 degradation dynamics provides opportunities for fine-tuning strigolactone signaling to coordinate tiller number and plant architecture, enabling precision breeding strategies	Song et al. (2017)
D3	Encodes an F-box protein that adversely affects shoot branching through its involvement in the strigolactone signaling pathway	Due to impaired strigolactone sensing, a loss-of-function mutation causes an increase in tiller angle and excessive tillering.	Spreading tillers, a primitive characteristic caused by mutation in D3, are essential for developing compact plant architecture during rice domestication	Indirect	Target for manipulating tiller number and canopy structure to optimize yield under different planting densities	Acts as an F-box component of the SCF (SKP1–Cullin–F-box) complex in the strigolactone signaling pathway	Integration of strigolactone signaling with auxin and other hormonal pathways provides opportunities to coordinate tiller number and plant architecture for improved crop performance	Zhao et al. (2022); Chen et al. (2024)

(Continues)

TABLE 1 | (Continued)

Gene	Function	Effect on tiller angle	Domestication significance	Mode of regulation	Genome editing and breeding application	Regulatory pathway/ mechanism	Recent advances/ future potential	References
D14	Encodes an α/β hydrolase that functions as a strigolactone receptor, preventing shoot branching by mediating the breakdown of repressors in strigolactone signaling	Strigulate sensing and downstream signaling are impaired in *D14*, there is an increase in tiller angle and excessive tillering	In order to suppress the ancestral spreading tiller characteristic and promote the erect growth habit that was chosen during rice domestication for effective planting and increased yield, D14 is necessary	Indirect	Target for manipulating tiller number and improving plant architecture to enhance yield and adaptability under high-density planting conditions	Acts as a strigolactone receptor that interacts with D3 (MAX2 ortholog) to promote degradation of D53 repressors, thereby inhibiting shoot branching through the strigolactone signaling pathway	Fine-tuning D14-mediated strigolactone signaling offers potential to balance tiller number and plant architecture, enabling development of high-yield and climate-resilient rice varieties	Arite et al. (2009); Stanic et al. (2021)
LPA1	Encodes a transcription factor with an indeterminate domain (IDD) that controls the development of lamina joints	Overexpression of *LPA1* increases the tiller angle	During domestication, varieties that contributed to decreased expression were chosen to support high-density planting and tall growth	Indirect	Target for modifying plant architecture to improve light distribution, canopy structure, and yield potential in high-density planting systems.	Regulates plant architecture through interaction with auxin and brassinosteroid signaling pathways, influencing lamina joint development and shoot orientation	Fine-tuning of LPA1 expression offers the potential to optimize plant architecture for enhanced photosynthetic efficiency and yield under varying environmental conditions	Liu et al. (2016); Zegeye et al. (2022)
BTA8 (locus)	Locus associated with basal tiller angle and prostrate growth in wild rice (*Oryza minuta*)	Promotes wider tiller angle and prostrate growth habit	Represents genetic basis of prostrate growth in wild rice species	Direct	Potential target for modifying tiller angle and plant architecture in breeding programs	Mechanism not fully characterized; likely involved in regulation of shoot orientation	Requires further functional validation; promising candidate for dissecting wild rice architecture traits	Zhang et al. (2019); Liu et al. (2024)
sd1	Encodes GA20 oxidase (GA20ox2) involved in gibberellin biosynthesis	Indirect reduction in tiller angle due to shortened plant height and compact architecture	Key "Green Revolution" gene contributing to semidwarf, lodging-resistant varieties	Indirect	Widely used in breeding for semidwarfism; genome editing can fine-tune the plant height and architecture	Gibberellin biosynthesis pathway controlling internode elongation	Fine-tuning GA levels via gene editing may optimize plant architecture without yield penalty	Ashikari et al. (2002); Hedden (2003)

(Continues)

TABLE 1 | (Continued)

Gene	Function	Effect on tiller angle	Domestication significance	Mode of regulation	Genome editing and breeding application	Regulatory pathway/ mechanism	Recent advances/ future potential	References
RPAD locus (gene cluster)	Genomic region containing multiple zinc-finger genes (e.g., ZnF5, ZnF7, ZnF8) regulating plant architecture	Promotes prostrate or semiprostrate growth with larger tiller angle in wild rice	Deletion of RPAD locus associated with erect growth in cultivated rice; key domestication event	Direct	Genome editing of individual zinc-finger genes or locus regions may allow fine-tuning of plant architecture	Zinc-finger transcription factors regulating growth habits and tiller orientation	Provides insight into polygenic control of architecture; useful for studying gene cluster domestication	Wu et al. (2018)
MOC1	Encodes a GRAS family transcription factor controlling axillary bud initiation and tiller formation	Indirect effect on tiller angle through regulation of tiller number and branching pattern	Essential for tiller formation; mutations result in single culm phenotype, influencing plant architecture during domestication and breeding	Indirect	Target for modifying tiller number and optimizing plant architecture; genome editing can balance branching and yield	Interacts with gibberellin signaling via SLR1; regulates the axillary meristem initiation and tiller bud outgrowth	Potential target for balancing tiller number and plant architecture in high-density planting systems	Sun et al. (2010)

in *O. rufipogon* (Huang et al. 2020). Furthermore, CRISPR-based knockouts of *PROG1* have been successfully utilized to reproduce the erect growth phenotype, confirming their critical roles in architecture regulation. *PROG1* was the first dominant gene to be cloned that controls prostrate growth in wild rice species, marking a pivotal step in understanding tiller angle regulation during domestication. Subsequently, *LA1* encodes the protein LA1, which is a putative transcription factor, and was the first cloned gene that plays a key role in tiller angle and shoot gravitropism in cultivated rice; this gene regulates tiller angle through asymmetric distribution of auxin (Luo et al. 1996; Li et al. 2007, 2019; Yoshihara and Iino 2007; Zhang et al. 2018). Exploring *PROG1* interaction with other architectural genes thus presents a promising avenue for deeper mechanistic understanding and genetic improvement. Recent studies have proposed a *PROG1-LA1* transcriptional regulatory module regulating rice tiller and panicle architecture (Zhang et al. 2023). Phenotypic variations were clearly observed in several constructed genetic materials related to the alleles of *PROG1* and *LA1*. Mutant *la1* and *PROG1* complementation transgenic plants (*prog1-D*) exhibited phenotypes featuring a larger tiller angle and reduced shoot gravitropism. Expression of the auxin-responsive gene *OsIAA20* was greatly reduced in *prog1-D* upon gravistimulation for 6 h, a response similar to that of the *la1* mutant, indicating that in rice both *LA1* and *PROG1* are involved in regulating tiller angle and shoot gravitropism via lateral auxin transport-mediated asymmetric distribution. Moreover, expression of *LA1* was significantly reduced in *prog1-D*, and *PROG1* inhibited the luciferase activity of pLA1-LUC, suggesting that *PROG1* inhibited *LA1* expression (Zhang et al. 2018, 2023). In plants overexpressing *LA1* in the background of ZH11 or *prog1-D*, plant tiller angle was reduced; however, the tiller angle of the two gene aggregation lines (*prog1-D la1*) was similar to that of *la1* and significantly larger than that of *prog1-D*. Additionally, suppressor of lazy1 (sol1) restored the defective shoot gravitropism and larger tiller angle of *prog1-D* by alleviating the transcriptional repression of *LA1* in *prog1-D*. Based on these results, *PROG1* appears to function as a transcriptional repressor upstream of *LA1*, regulating both shoot gravitropism and tiller angle in rice (Zhang et al. 2023).

1.4 | Molecular Regulation of Tiller Angle Genes for Rice Improvement

Previous studies have also identified several other regulator genes of tiller angle in rice, including *TAC1* (*TILLER ANGLE CONTROL 1*), *LAZY1* (*LA1*), *D3* (*DWARF3*), *D14* (*DWARF14*), and *LPA1* (*LOOSE PLANT ARCHITECTURE1*) (Li et al. 2007; Yu et al. 2007; Arite et al. 2009; Wu et al. 2013; Zhang et al. 2017). These genes participate in hormonal signaling pathways such as auxin and strigolactone, and their manipulation has demonstrated significant phenotypic effects on plant architecture (tiller angle). For instance, mutations in *LAZY1* and *D3* lead to altered gravitropism and tillering, respectively, underscoring their crucial role in shoot orientation (Sang et al. 2014). Moreover, it has been reported that *LA1* and *LPA1* use shoot gravitropism to control tiller angle. The *la1* mutant disrupts the auxin asymmetry distribution in the shoot base and, consequently, the tiller-spreading phenotype

of rice plants by increasing polar auxin transport (PAT) and decreasing lateral auxin transport (Li et al. 2007). In addition, another important regulator gene that governs the development of rice tiller buds is *MONOCULM1* (*MOC1*). Because of abnormalities in the production of tiller buds, mutants without functional *MOC1* only generate a main culm without tillers (Sun et al. 2010). *MOC1* is shielded from degradation by its interaction with the DELLA protein SLENDER RICE 1 (SLR1). Gibberellin (GA) signaling causes *SLR1* to degrade, which in turn degrades *MOC1*, lowering the number of tillers and encouraging stem elongation. This system balances branching and upright development by coordinating the quantity of tillers and plant height.

However, three genes *PROG1*, *PROG7*, *TIG1* and one locus *RPAD* containing cluster of genes are known to regulate prostrate growth in wild rice species, have now been successfully cloned. As shown in Figure 2, collectively, *PROG1*, *PROG7*, *RPAD*, and *TIG1* regulate prostrate growth habits in wild rice species and have been integral to the domestication process through targeted selection. In parallel, the emergence of CRISPR/Cas9 genome editing technology has opened new avenues for precise functional validation and targeted improvement of these key genes (Figure 3; Pacesa et al. 2024). Despite recent advances, most studies focus heavily on a few gene families (Zinc-finger transcription factors and TCPs (Viola and Gonzalez 2023)), potentially overlooking other regulatory mechanisms, such as epigenetic control (Gibney and Nolan 2010), small RNAs (Mitarai et al. 2009), or hormonal cross-talk (Liu et al. 2010). Likewise, much of the current functional validation relies on overexpression or knockout approaches in model backgrounds (e.g., Zhonghua11 (Liu et al. 2020; Xie et al. 2025)), which may not fully represent the field conditions. However, these advances deepen our understanding of the genetic control of plant and provide powerful tools for accelerating rice domestication and future crop improvement.

1.5 | Gene Interactions and Precision Editing in the Regulation of Rice Tiller Angle

Recent studies have highlighted the complex regulatory network governing tiller angle and panicle architecture in rice, involving multiple key genes such as *PROG1*, *LA1*, *OsGI*, *TAC1*, *MOC1*, and *LA1* (Figure 3). *PROG1* interacts with both LA1 and OsGI to negatively regulate tiller angle and panicle traits (Wang, Tu, et al. 2023). Interestingly, *PROG1* and *LA1* act as mutual repressors in the gene network: *PROG1* directly binds to the promoter of *LA1* to inhibit its expression, whereas *LA1* can bind to the *PROG1* promoter and suppress its transcription (Wang, Tu et al. 2023; Tan et al. 2008). Overexpression of *LA1* in near-isogenic lines (NILs) carrying active *PROG1* alleles (associated with larger tiller angles) resulted in a compact plant architecture with reduced tiller angle and tiller number. Conversely, in *PROG1* overexpression lines, *LA1* expression was significantly downregulated in the tiller base. This mutual antagonism demonstrates that both genes play critical and opposing roles in controlling tiller number and orientation (Wang, Tu et al. 2023; Tan et al. 2008). Functionally, *PROG1* and *LA1* influence lateral auxin transport at the shoot base, a key determinant of tiller angle (Tan et al. 2008). Downstream of *PROG1*, *OsGI* mediates panicle architecture; knockout of *OsGI* in *PROG1* overexpression backgrounds led to significant increases in panicle length and grain number. Similarly, double knockouts of *OsGI* and *LA1* produced comparable effects, reinforcing the role of *OsGI* as a downstream effector positively regulated by *PROG1*, which binds to its intragenic region to activate expression (Wang et al. 2023). Integration of additional regulators such as *TAC1*, *MOC1*, and

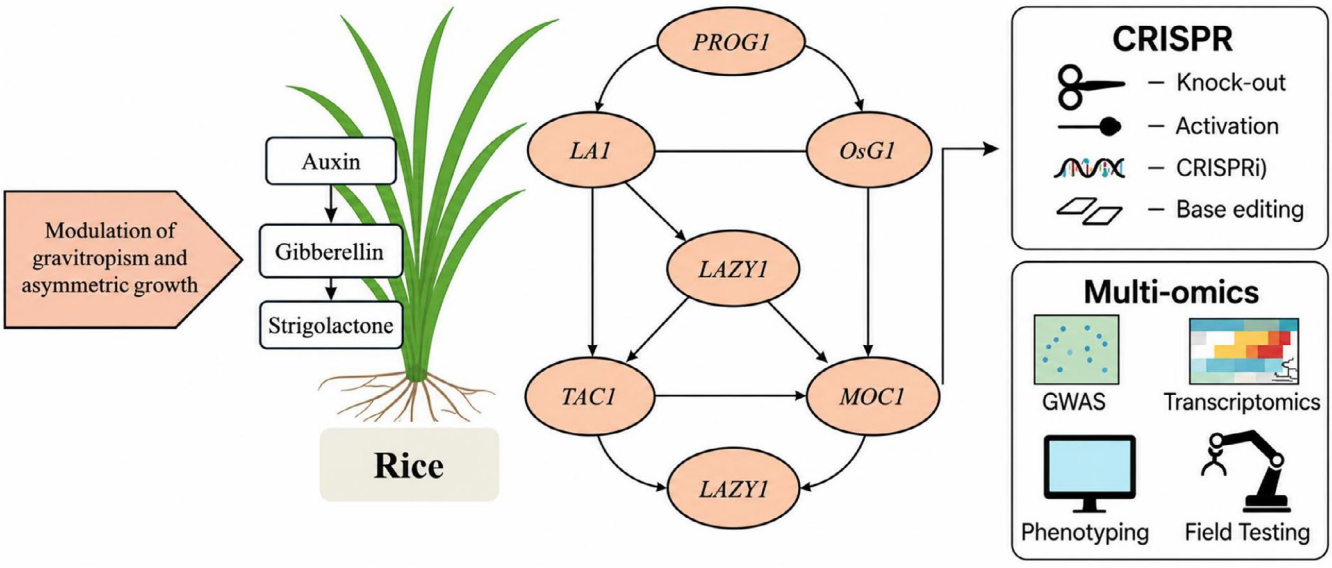


FIGURE 2 | It represents the summarized information of key genes involved in regulating tiller angle during rice domestication. *PROG7* (from *Oryza barthi*) is an ortholog of *PROG1*, while *TIG1* was identified from *Oryza rufipogon*. Loss-of-function by mutations or reduced expression of these genes contributed to the transition from prostrate to erect growth in cultivated rice. Haplotype analysis and GUS reporter assays were used to characterize gene variation and expression. *PROG1* represses *LA1* (*LAZY1*) by binding to its promoter region, while LA1 can also bind to the *PROG1* promoter, indicating mutual regulation. *PROG1* further regulates panicle architecture via interaction with the intragenic region of *OsGI*. Further Or, Os, Ob, Og are indicating *Oryza rufipogon*, *Oryza sativa*, *Oryza barthi* and *Oryza glaberrima* respectively. Moreover, arrows indicate regulatory relationships.

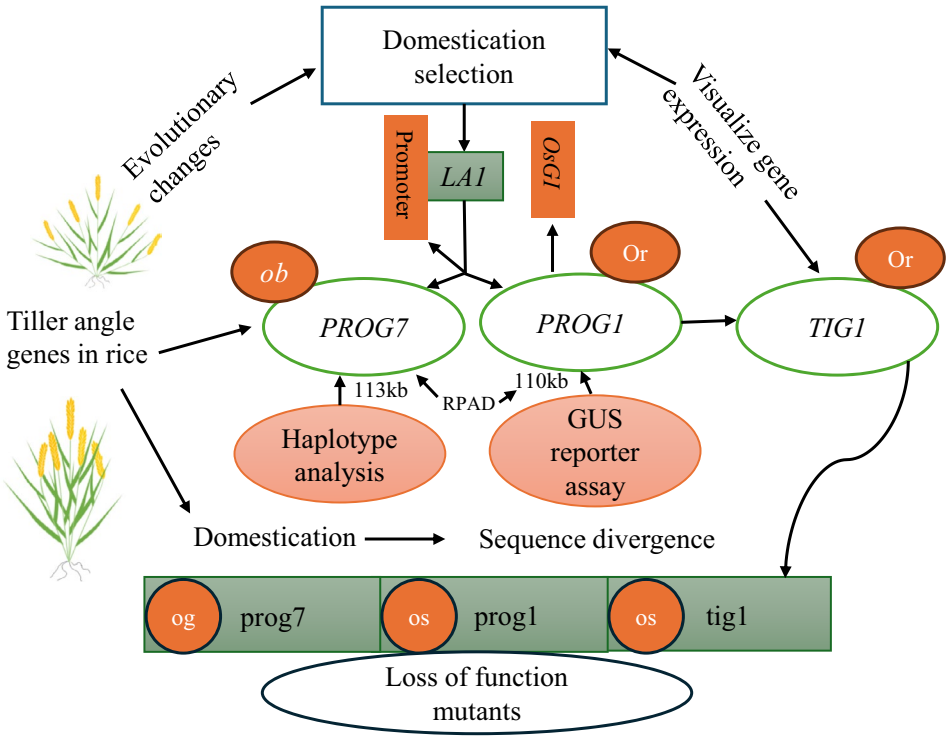


FIGURE 3 | A schematic diagram is illustrating the molecular regulation of rice tiller angle. It presents a regulatory network of key genes involved in tiller angle control, including *PROG1* (PROSTRATE GROWTH 1), *LA1* (LATERAL AXES 1), *OsGI* (*Oryza sativa GIGANTEA*), *TAC1* (TILLER ANGLE CONTROL 1), *MOC1* (MONOCULM 1), and *LAZY1*. These genes collectively coordinate shoot orientation, tiller angle formation, and plant architecture. Connections between genes represent regulatory or functional relationships within the network (directionality is simplified for clarity). On the left, key phytohormones auxin, gibberellin, and strigolactone are shown as major regulators influencing tiller angle through modulation of gravitropism and asymmetric growth. On the right, modern biotechnological tools, including CRISPR-based genome editing (knock-out, activation, CRISPRi, and base editing) and multiomics approaches such as genome-wide association studies (GWAS), transcriptomics, phenotyping and field testing are highlighted as strategies for dissecting and improving tiller angle traits in rice. Further, GWAS and CRISPRi represent Genome-Wide Association Study and Clustered Regularly Interspaced Short Palindromic Repeats interference, respectively.

LA11 further refines tiller orientation. *MOC1*, which regulates tiller bud initiation, interacts with *LA1*, a key mediator of auxin redistribution necessary for shoot gravitropism (Yu et al. 2007; Hollender et al. 2020; Jiao et al. 2021). Together, these interactions form a foundational developmental axis governing tiller emergence and angle. Modern genome editing tools offer new avenues for manipulating these genetic networks (Figure 3). Loss-of-function editing of *PROG1* via CRISPR/Cas9 promotes more erect plant architecture, ideal for high-density planting (Chen et al. 2021; Kumar et al. 2022). However, over-compact phenotypes may increase susceptibility to diseases such as blast under high humidity (Zhao et al. 2022). Therefore, fine-tuning gene expression through CRISPR activation (CRISPRa), interference (CRISPRi), or base editing can provide more nuanced control over tiller angle, preserving genetic diversity and minimizing trade-offs in plant health (Chaudhary et al. 2024; Yin et al. 2025). Furthermore, multiplex genome-editing (MGE) technologies are advanced bioengineering tools designed to precisely modify two or more specific DNA loci within a genome. These tools have significantly enhanced the ability to introduce targeted changes at multiple nucleotide sites, making genome modification more efficient and versatile (Abdelrahman et al. 2021). Beyond single-gene editing, gene pyramiding offers a robust strategy to enhance tiller architecture. For example, pyramiding favorable alleles of *TIG1*/*PROG1* and *TIG1*/*TAC1* led to lines with significantly wider tiller angles compared to individual NILs (Zhang et al. 2019; Mao et al. 2022). This suggests that allele stacking can be tailored to specific agroecological environments. Yet, the molecular basis of such additive interactions remains unclear. To address this, future studies should incorporate multiomics approaches including transcriptomics, proteomics, and epigenomics, along with virus-induced gene silencing (VIGS) to dissect the cooperative effects of pyramided genes. Moreover, high-resolution phenotyping platforms are essential to evaluate gene functions under real-world field conditions, since most functional studies have been limited to early growth stages or controlled environments. Recent advances in GWAS and RNA-seq analyses have led to the identification of novel candidate genes regulating tiller angle in rice (Dong et al. 2016). These genes are implicated in key hormonal signaling pathways, including auxin and gibberellin, which are known to influence plant architecture. Although their precise functions remain to be validated, these candidates represent promising targets for functional studies and potential integration into the genetic network controlling tiller angle.

1.6 | Genomic and Biotechnological Approaches to Tiller Angle Regulation

Tiller angle is a fundamental trait influencing plant architecture, photosynthetic efficiency, lodging resistance, and yield

potential in cereal crops such as rice (Zhang et al. 2018; Wang, Tu, et al. 2022). Recent advancements in single-cell omics technologies, including single-cell RNA sequencing (scRNA-seq) and ATAC-seq, have made it possible to examine gene expression and chromatin accessibility at cellular resolution (Buenrostro et al. 2015; Lu et al. 2024). These (scRNA-seq) and ATAC-seq tools can help to identify key regulators of tiller angle in specific tissues, such as axillary buds, and provide insights into cell fate determination and developmental trajectories during tiller bud formation (Denyer et al. 2019; Hamrud et al. 2025). Gene editing tools, particularly CRISPR-Cas systems, have facilitated precise modifications of genes associated with tiller angle (Romero and Gatica-Arias 2019), these technologies allow functional validation through targeted knockouts or allele replacements, and advanced systems such as base and prime editing enable subtle alterations of regulatory elements or single nucleotides without inducing double-strand breaks (Kantor et al. 2020; Saber Sichani et al. 2023). Multiplex editing further enables simultaneous modification of multiple targets, accelerating the development of rice varieties with optimal architecture (Gupta et al. 2024).

In addition to single-cell and genome editing approaches, multiomics technologies have become essential in uncovering the complex regulatory networks underlying tiller angle control (Chachar et al. 2025). Transcriptomic analyses have been used to compare rice genotypes with contrasting tiller angles, enabling the identification of differentially expressed genes associated with gravitropism, auxin transport, and cell elongation pathways (Zhang et al. 2018; Chen et al. 2024). Metabolomics offers insights into the hormonal dynamics particularly of auxins, cytokinins, and strigolactones that drive tiller bud outgrowth and orientation (Chachar et al. 2025). Integration of multiomics datasets has enabled systems biology approaches to model tiller angle regulation in conjunction with other agronomic traits, facilitating the identification of key genetic hubs and signaling cascades (Figure 4; Table 2). The application of machine learning and artificial intelligence to large omics datasets further enhances the ability to predict gene functions, regulatory elements, and genotype-to-phenotype relationships (Cembrowska-Lech et al. 2023). Furthermore, gene pyramiding strategies, combining favorable alleles of multiple regulators, together with

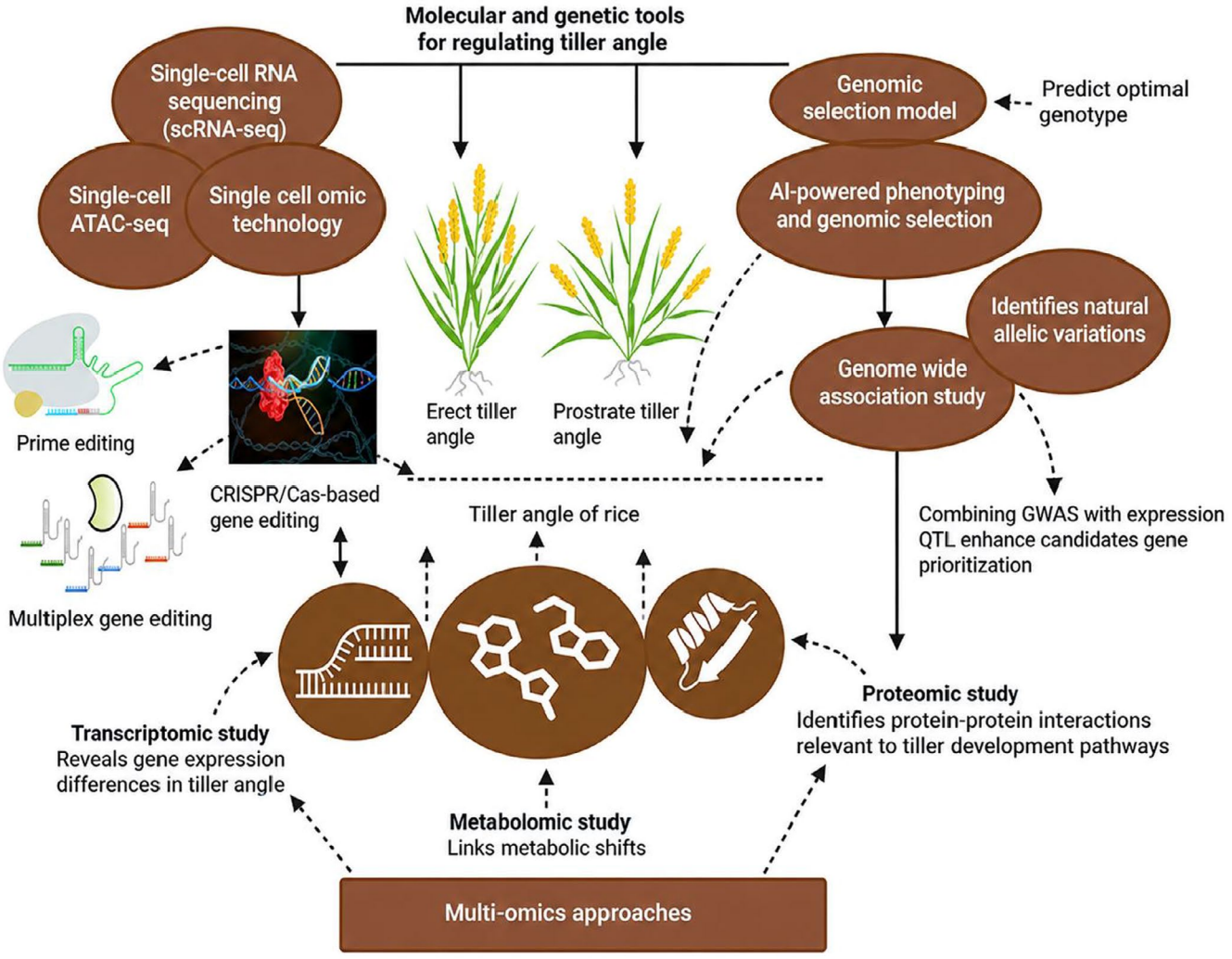


FIGURE 4 | Integration of multiomics approaches explaining the tiller angle for different growth habits of rice. Further, this figure illustrates that advanced tools such as single-cell omics, gene editing, and multiomics technologies including transcriptomics (gene expression profiling), proteomics (identification of tiller angle-related proteins), and metabolomics (metabolite analysis) can contribute to improving the tiller angle in modern rice cultivars. Moreover, GWAS, QTL, and CRISPR are the abbreviations of genome-wide association study, quantitative trait loci, and clustered regularly interspaced short palindromic repeats.

TABLE 2 | Integrative tools and strategies for understanding and modifying tiller angle in rice.

Approach	Description	Application	References
QTL Mapping	Identifies genomic regions associated with phenotypic traits	Locates major loci controlling tiller angle across diverse populations	Wang et al. (2011)
GWAS	Associates SNP markers with natural phenotypic variation in populations	Detects natural allelic variation linked to tiller angle in diverse rice accessions	Bai et al. (2022)
Gene Cloning	Isolates and functionally characterizes specific genes	Enables functional analysis of key regulators genes regarding tiller angle in rice	Yan et al. (2023)
Transcriptomics	Analyzes gene expression patterns across tissues and conditions	Reveals expression changes in tiller angle regulatory pathways in rice	Zhang et al. (2018)
Proteomics	Identifies and quantify proteins involved in trait development	Detects differentially expressed proteins involved in shoot orientation in rice	Xu et al. (2015)
Metabolomics	Profiles metabolites that influence physiological pathways	Links hormone levels and metabolic shifts to tiller angle formation in rice	Li et al. (2022)
Single-Cell Omics	Resolves gene expression at cellular resolution in specific tissues	Maps developmental trajectories in axillary buds regulating tiller outgrowth in rice	Lian et al. (2024)
CRISPR/Cas Genome Editing	Precisely edits specific gene sequences to alter function	Validates gene function and introduces beneficial alleles from wild relatives of rice	Shan et al. (2014)

high-throughput field phenotyping, provide promising avenues for validating gene function under realistic agronomic conditions and accelerating the development of climate-resilient, high-yielding rice varieties (Abdelrahman, Wei et al. 2021, Wei et al. 2021, Mao et al. 2022, Cembrowska-Lech et al. 2023). Collectively, these genomics and biotechnological tools are transforming our capacity to dissect, understand, and engineer tiller angle traits for improved crop productivity.

1.7 | Critical Perspectives and Future Research Directions

Although substantial progress has been made in identifying key genes regulating tiller angle in rice, several important limitations and knowledge gaps remain. Most current studies focus on a limited number of gene families, particularly zinc-finger transcription factors and TCP proteins, while other regulatory layers such as epigenetic modifications, small RNAs, and chromatin remodeling (Mitarai et al. 2009; Gibney and Nolan 2010; Viola and Gonzalez 2023) remain insufficiently explored. In addition, functional validation of tiller angle-related genes has largely been conducted under controlled experimental conditions, which may not fully capture gene performance under field environments. Single-gene studies also overlook the complex regulatory networks governing plant architecture. Tiller angle is a quantitative trait influenced by gene–gene interactions, hormonal crosstalk, and environmental factors (Albacete et al. 2014; Zhang et al. 2018; Wu et al. 2024). Therefore, future research should prioritize system-level approaches integrating genomics, transcriptomics, proteomics, and phenomics to identify regulatory hubs and interaction networks (Chachar et al. 2025).

Furthermore, despite advances in genome editing technologies, precise fine-tuning of tiller angle remains a challenge due to trade-offs between compact architecture and disease susceptibility or reduced canopy ventilation. Emerging approaches such as CRISPR activation (CRISPRa), interference (CRISPRi), and multiplex genome editing offer promising strategies to overcome these limitations by enabling more nuanced regulation of gene expression (Abdelrahman et al. 2021; Chaudhary et al. 2024; Yin et al. 2025). Recent resources such as RiceNavi (Wei et al. 2021) provide integrated platforms for exploring plant architecture genes and facilitate network-based analysis. Incorporating such databases into future studies will accelerate the identification of novel regulatory pathways and enhance breeding efficiency. Overall, future research should move beyond descriptive gene identification toward predictive and integrative models that combine genetic, physiological, and environmental data. This shift will be essential for developing climate-resilient, high-yielding rice varieties with optimized plant architecture.

2 | Conclusions and Prospects

The domestication and transformation of wild rice species into modern cultivars have been shaped by both natural and artificial selection, resulting in desirable traits such as erect growth and compact tiller architecture. These traits are particularly advantageous for dense planting and high yield potential, aligning with the urgent need to meet global food demand. Importantly, many wild rice species continue to grow in natural ecosystems, offering a rich repository of untapped genetic diversity that can be leveraged to improve cultivated varieties, especially in enhancing environmental adaptability and resilience. A hallmark

of rice domestication has been the architectural shift from prostrate to upright growth. This transformation not only improves harvestability but also contributes significantly to yield enhancement. Several key regulatory genes have been identified in this process, including *PROG1*, *RPAD*, *TIG1*, *PROG7*, *D3*, *D14*, *LPA1*, *LAZY1*, and *MOC1*, which are known to control tiller angle and shoot orientation. However, many functional alleles residing in wild germplasm remain unexplored due to limitations in genetic mapping resolution, insufficient phenotyping tools, and the complex polygenic nature of plant architecture traits. Studying the tiller angle presents both challenges and opportunities. A major challenge lies in the quantitative and environmentally sensitive nature of the trait, making it difficult to dissect traditional methods. Moreover, pleiotropy and genetic redundancy often complicate functional validation of candidate genes. Despite these hurdles, modern tools such as high-throughput phenotyping, multiomics integration, single-cell analysis, and CRISPR/Cas-based genome editing offer unprecedented opportunities to decode the molecular basis of tiller angle with high precision. The strategic integration of genome editing with traditional breeding opens new avenues for directly introducing beneficial alleles from wild rice into elite cultivars without linkage drag. These cutting-edge technologies hold the potential to fine-tune the tiller angle for optimal light interception, lodging resistance, and resource use efficiency. As global agriculture confronts climate uncertainty and increasing population pressure, optimizing tiller angle through advanced biotechnological and genomic approaches offers a promising pathway to develop climate-smart, high-yielding rice varieties for sustainable production.

Author Contributions

The idea to write this review was conceived by H.A. it was drafted by H.A. with the technical inputs of Y.L., S.S., M.Z.A., S.A. All authors read and approved the final manuscript.

Acknowledgments

The authors are thankful to lab members for their assistance.

Funding

This work was supported by Overseas Renowned Teacher Project of Guangdong Province (2022-232-48). More information can be found here: http://gdstc.gd.gov.cn/zwgk_n/tzgg/mindex.html.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No new data were generated or analyzed in this study. This article is based on previously published data and all the relevant publications are duly cited within the manuscript.

References

Abdelrahman, M., Z. Wei, J. S. Rohila, and K. Zhao. 2021. "Multiplex Genome-Editing Technologies for Revolutionizing Plant Biology and Crop Improvement." *Frontiers in Plant Science* 12: 721203.

Aguilar-Martínez, J. A., C. Poza-Carrión, and P. Cubas. 2007. "Arabidopsis BRANCHED1 Acts as an Integrator of Branching Signals Within Axillary Buds." *Plant Cell* 19, no. 2: 458–472.

Alam, M. M., G. L. Hammer, E. J. Van Oosterom, A. W. Cruickshank, C. H. Hunt, and D. R. Jordan. 2014. "A Physiological Framework to Explain Genetic and Environmental Regulation of Tillering in Sorghum." *New Phytologist* 203, no. 1: 155–167.

Albacete, A. A., C. Martínez-Andújar, and F. Pérez-Alfocea. 2014. "Hormonal and Metabolic Regulation of Source–Sink Relations Under Salinity and Drought: From Plant Survival to Crop Yield Stability." *Biotechnology Advances* 32, no. 1: 12–30.

Arite, T., M. Umehara, S. Ishikawa, et al. 2009. "d14, a Strigolactone-Insensitive Mutant of Rice, Shows an Accelerated Outgrowth of Tillers." *Plant and Cell Physiology* 50, no. 8: 1416–1424.

Ashikari, M., A. Sasaki, M. Ueguchi-Tanaka, et al. 2002. "Loss-Of-Function of a Rice Gibberellin Biosynthetic Gene, GA20 Oxidase (GA20ox-2), Led to the Rice 'Green Revolution'." *Breeding Science* 52, no. 2: 143–150.

Bai, F., R. Reinheimer, D. Durantini, E. A. Kellogg, and R. J. Schmidt. 2012. "TCP Transcription Factor, Branch Angle Defective 1 (BAD1), is Required for Normal Tassel Branch Angle Formation in Maize." *Proceedings of the National Academy of Sciences* 109, no. 30: 12225–12230.

Bai, S., J. Hong, S. Su, et al. 2022. "Genetic Basis Underlying Tiller Angle in Rice (*Oryza sativa* L.) by Genome-Wide Association Study." *Plant Cell Reports* 41, no. 8: 1707–1720.

Bai, S., S. M. Smith, and J. Li. 2018. "Rice Plant Architecture: Molecular Basis and Application in Breeding." In *Rice Genomics, Genetics and Breeding*, 129–154. Springer.

Bandumula, N. 2018. "Rice Production in Asia: Key to Global Food Security." *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences* 88, no. 4: 1323–1328.

Buenrostro, J. D., B. Wu, H. Y. Chang, and W. J. Greenleaf. 2015. "ATAC-Seq: A Method for Assaying Chromatin Accessibility Genome-Wide." *Current Protocols in Molecular Biology* 109, no. 1: 21.29.21–21.29.29.

Cai, L., S. Cui, T. Jin, et al. 2023. "The N6-Methyladenosine Binding Proteins YTH03/05/10 Coordinately Regulate Rice Plant Height." *Plant Science* 329: 111546.

Cembrowska-Lech, D., A. Krzemińska, T. Miller, et al. 2023. "An Integrated Multi-Omics and Artificial Intelligence Framework for Advance Plant Phenotyping in Horticulture." *Biology* 12, no. 10: 1298.

Chachar, Z., X. Xue, J. Fang, et al. 2025. "Genetic and Molecular Insights Into Tiller Development and Approaches for Crop Yield Improvement." *Frontiers in Plant Science* 16: 1532180.

Chaudhary, D., N. Pal, A. Arora, B. D. Prashant, and S. Venadan. 2024. "Plant Functional Traits in Crop Breeding: Advancement and Challenges." In *Plant Functional Traits for Improving Productivity*, 169–202. Springer.

Chen, Q., W. Li, L. Tan, and F. Tian. 2021. "Harnessing Knowledge From Maize and Rice Domestication for New Crop Breeding." *Molecular Plant* 14, no. 1: 9–26.

Chen, X., T. Lei, Y. Yan, et al. 2024. "Genetic Basis of Tillering Angle From Other Plants to Wheat: Current Progress and Future Perspectives." *Plants* 13, no. 22: 3237.

Costa, M. M. R., S. Fox, A. I. Hanna, C. Baxter, and E. Coen. 2005. "Evolution of Regulatory Interactions Controlling Floral Asymmetry." *Development* 132: 5093–5101.

Cubry, P., C. Tranchant-Dubreuil, A.-C. Thuillet, et al. 2018. "The Rise and Fall of African Rice Cultivation Revealed by Analysis of 246 New Genomes." *Current Biology* 28, no. 14: 2274–2282.e6.

Denyer, T., X. Ma, S. Klesen, E. Scacchi, K. Nieselt, and M. C. Timmermans. 2019. "Spatiotemporal Developmental Trajectories in the Arabidopsis Root Revealed Using High-Throughput Single-Cell RNA Sequencing." *Developmental Cell* 48, no. 6: 840–852.e5.

Doebley, J., A. Stec, and L. Hubbard. 1997. "The Evolution of Apical Dominance in Maize." *Nature* 386, no. 6624: 485–488.

Dong, H., H. Zhao, W. Xie, et al. 2016. "A Novel Tiller Angle Gene, TAC3, Together With TAC1 and D2 Largely Determine the Natural Variation of Tiller Angle in Rice Cultivars." *PLoS Genetics* 12, no. 11: e1006412.

Gao, J., H. Liang, J. Huang, et al. 2021. "Development of the PARMS Marker of the TAC1 Gene and Its Utilization in Rice Plant Architecture Breeding." *Euphytica* 217, no. 3: 49.

Gibney, E., and C. Nolan. 2010. "Epigenetics and Gene Expression." *Heredity* 105, no. 1: 4–13.

Guo, W., L. Chen, L. Herrera-Estrella, D. Cao, and L.-S. P. Tran. 2020. "Altering Plant Architecture to Improve Performance and Resistance." *Trends in Plant Science* 25, no. 11: 1154–1170.

Gupta, A., B. Liu, S. Raza, Q.-J. Chen, and B. Yang. 2024. "Modularly Assembled Multiplex Prime Editors for Simultaneous Editing of Agronomically Important Genes in Rice." *Plant Communications* 5, no. 2: 100741.

Hamrud, E., J. Leese, A. P. Thiery, et al. 2025. "A Single Cell ATAC-Seq Atlas Uncovers Dynamic Changes in Chromatin Accessibility During Cell Fate Specification at the Neural Plate Border." Preprint, bioRxiv, May 5. https://doi.org/10.1101/2025.05.03.652017.

Hedden, P. 2003. "The Genes of the Green Revolution." *Trends in Genetics* 19, no. 1: 5–9.

Hershberg, R., H. Tang, and D. A. Petrov. 2007. "Reduced Selection Leads to Accelerated Gene Loss in Shigella." *Genome Biology* 8, no. 8: R164.

Hollender, C. A., J. L. Hill Jr., J. Waite, and C. Dardick. 2020. "Opposing Influences of TAC1 and LAZY1 on Lateral Shoot Orientation in Arabidopsis." *Scientific Reports* 10, no. 1: 6051.

Hu, M., S. Lv, W. Wu, et al. 2018. "The Domestication of Plant Architecture in African Rice." *Plant Journal* 94, no. 4: 661–669.

Huang, L., H. Liu, J. Wu, et al. 2020. "Evolution of Plant Architecture in Oryza Driven by the PROG1 Locus." *Frontiers in Plant Science* 11: 876.

Huang, X., N. Kurata, X. Wei, et al. 2012. "A Map of Rice Genome Variation Reveals the Origin of Cultivated Rice." *Nature* 490, no. 7421: 497–501.

Huang, Y., H. Dong, M. Shang, and K. Wang. 2021. "CRISPR/Cas Systems: The Link Between Functional Genes and Genetic Improvement." *Crop Journal* 9, no. 3: 678–687.

Inagaki, N., H. Asami, H. Hirabayashi, A. Uchino, T. Imaizumi, and K. J. F. i. P. S. Ishimaru. 2021. "A Rice Ancestral Genetic Resource Conferring Ideal Plant Shapes for Vegetative Growth and Weed Suppression." 12: 748531.

Jiao, Y., Y. Wang, D. Xue, et al. 2010. "Regulation of OsSPL14 by OsmiR156 Defines Ideal Plant Architecture in Rice." *Nature Genetics* 42, no. 6: 541–544.

Jiao, Z., H. Du, S. Chen, W. Huang, and L. Ge. 2021. "LAZY Gene Family in Plant Gravitropism." *Frontiers in Plant Science* 11: 606241.

Jin, J., W. Huang, J.-P. Gao, et al. 2008. "Genetic Control of Rice Plant Architecture Under Domestication." *Nature Genetics* 40, no. 11: 1365–1369.

Jung, H., D.-K. Lee, Y. Do Choi, and J.-K. J. P. S. Kim. 2015. "OsIAA6, a Member of the Rice Aux/IAA Gene Family, Is Involved in Drought Tolerance and Tiller Outgrowth." 236: 304–312.

Kangben, F., S. Kumar, Z. Li, et al. 2024. "Phylogenetic and Functional Analysis of Tiller Angle Control Homeologs in Allotetraploid Cotton." *Frontiers in Plant Science* 14: 1320638.

Kantor, A., M. E. McClements, and R. E. MacLaren. 2020. "CRISPR-Cas9 DNA Base-Editing and Prime-Editing." *International Journal of Molecular Sciences* 21, no. 17: 6240.

Kong, W., X. Deng, J. Yang, et al. 2022. "High-Resolution Bin-Based Linkage Mapping Uncovers the Genetic Architecture and Heterosis-Related Loci of Plant Height in Indica–Japonica Derived Populations." *Plant Journal* 110, no. 3: 814–827.

Kumar, K., S. N. Mandal, B. Pradhan, P. Kaur, K. Kaur, and K. Neelam. 2022. "From Evolution to Revolution: Accelerating Crop Domestication Through Genome Editing." *Plant and Cell Physiology* 63, no. 11: 1607–1623.

Li, F., Y. Liu, X. Zhang, et al. 2022. "Transcriptome and Metabolome Analyses Reveals the Pathway and Metabolites of Grain Quality Under Phytochrome B in Rice (*Oryza sativa* L.)." *Rice* 15, no. 1: 52.

Li, P., Y. Wang, Q. Qian, et al. 2007. "LAZY1 Controls Rice Shoot Gravitropism Through Regulating Polar Auxin Transport." *Cell Research* 17, no. 5: 402–410.

Li, Z., Y. Liang, Y. Yuan, et al. 2019. "OsBRXL4 Regulates Shoot Gravitropism and Rice Tiller Angle Through Affecting LAZY1 Nuclear Localization." *Molecular Plant* 12, no. 8: 1143–1156.

Lian, X., L. Zhong, Y. Bai, et al. 2024. "Spatiotemporal Transcriptomic Atlas of Rhizome Formation in *Oryza longistaminata*." *Plant Biotechnology Journal* 22, no. 6: 1652–1668.

Liu, H., X. Zhou, Q. Li, L. Wang, and Y. Xing. 2020. "CCT Domain-Containing Genes in Cereal Crops: Flowering Time and Beyond." *Theoretical and Applied Genetics* 133, no. 5: 1385–1396.

Liu, J., S. Mehdi, J. Topping, P. Tarkowski, and K. Lindsey. 2010. "Modelling and Experimental Analysis of Hormonal Crosstalk in Arabidopsis." *Molecular Systems Biology* 6, no. 1: 373.

Liu, J., X. Wang, J. Wang, et al. 2024. "Identification of the BTA8 Gene Reveals the Contribution of Natural Variation to Tiller Angle in Rice." *Journal of Integrative Agriculture* 23, no. 8: 2868–2871.

Liu, J. M., S. J. Park, J. Huang, et al. 2016. "Loose Plant Architecture1 (LPA1) Determines Lamina Joint Bending by Suppressing Auxin Signalling That Interacts With C-22-Hydroxylated and 6-Deoxo Brassinosteroids in Rice." *Journal of Experimental Botany* 67, no. 6: 1883–1895.

Lizhi, G., G. Song, and H. Deyuan. 2000. "A Preliminary Study on Ecological Differentiation Within the Common Wild Rice *Oryza rufipogon* Griff." *Zuo Wu Xue Bao* 26, no. 2: 210–213.

Lu, C., Y. Wei, M. Abbas, et al. 2024. "Application of Single-Cell Assay for Transposase-Accessible Chromatin With High Throughput Sequencing in Plant Science: Advances, Technical Challenges, and Prospects." *International Journal of Molecular Sciences* 25, no. 3: 1479.

Luo, D., R. Carpenter, C. Vincent, L. Copsey, and E. Coen. 1996. "Origin of Floral Asymmetry in Antirrhinum." *Nature* 383, no. 6603: 794–799.

Mao, Z., X. Di, S. Xia, et al. 2022. "Detecting and Pyramiding Target QTL for Plant-And Grain-Related Traits via Chromosomal Segment Substitution Line of Rice." *Frontiers in Plant Science* 13: 1020847.

Marone, D., M. Rodriguez, S. Saia, et al. 2020. "Genome-Wide Association Mapping of Prostrate/Erect Growth Habit in Winter Durum Wheat." *International Journal of Molecular Sciences* 21, no. 2: 394.

Mitarai, N., J.-A. M. Benjamin, S. Krishna, et al. 2009. "Dynamic Features of Gene Expression Control by Small Regulatory RNAs." *Proceedings of the National Academy of Sciences* 106, no. 26: 10655–10659.

Mubarak, A., M. Musthapha, M. Roshana, and A. Kumara. 2022. "Influence of Canopy Architecture on the Light Interception,

Photosynthetic and Biomass Productivity in Irrigated Elite Sri Lankan Rice Varieties." *Journal of Agricultural Sciences—Sri Lanka* 17: 148–160.

Pacesa, M., O. Pelea, and M. Jinek. 2024. "Past, Present, and Future of CRISPR Genome Editing Technologies." *Cell* 187, no. 5: 1076–1100.

Rehman, R. S., A. N. Pasha, S. A. Zafar, et al. 2022. "Molecular Mechanisms Behind the Regulation of Rice Tiller Angle: An Update." *Asian Journal of Biology* 14, no. 4: 37–50.

Reinhardt, D., and C. Kuhlemeier. 2002. "Plant Architecture." *EMBO Reports* 3, no. 9: 846–851.

Romero, F. M., and A. Gatica-Arias. 2019. "CRISPR/Cas9: Development and Application in Rice Breeding." *Rice Science* 26, no. 5: 265–281.

Saber Sichani, A., M. Ranjbar, M. Baneshi, F. Torabi Zadeh, and J. Fallahi. 2023. "A Review on Advanced CRISPR-Based Genome-Editing Tools: Base Editing and Prime Editing." *Molecular Biotechnology* 65, no. 6: 849–860.

Samal, R., P. S. Roy, A. Sahoo, et al. 2018. "Morphological and Molecular Dissection of Wild Rices From Eastern India Suggests Distinct Speciation Between *O. rufipogon* and *O. nivara* Populations." *Scientific Reports* 8, no. 1: 2773.

Sang, D., D. Chen, G. Liu, et al. 2014. "Strigolactones Regulate Rice Tiller Angle by Attenuating Shoot Gravitropism Through Inhibiting Auxin Biosynthesis." *Proceedings of the National Academy of Sciences* 111, no. 30: 11199–11204.

Shan, Q., Y. Wang, J. Li, and C. Gao. 2014. "Genome Editing in Rice and Wheat Using the CRISPR/Cas System." *Nature Protocols* 9, no. 10: 2395–2410.

Song, X., Z. Lu, H. Yu, et al. 2017. "IPA1 Functions as a Downstream Transcription Factor Repressed by D53 in Strigolactone Signaling in Rice." *Cell Research* 27, no. 9: 1128–1141.

Stanic, M., N. M. Hickerson, R. Arunraj, and M. A. Samuel. 2021. "Gene-Editing of the Strigolactone Receptor BnD14 Confers Promising Shoot Architectural Changes in *Brassica napus* (Canola)." *Plant Biotechnology Journal* 19, no. 4: 639.

Sun, F., W. Zhang, G. Xiong, et al. 2010. "Identification and Functional Analysis of the MOC1 Interacting Protein 1." *Journal of Genetics and Genomics* 37, no. 1: 69–77.

Sun, Z., T. Mei, T. Feng, et al. 2023. "Deletion of the OsLA1 Gene Leads to Multi-Tillering and Lazy Phenotypes in Rice." 13, no. 11: 2166.

Takeda, T., Y. Suwa, M. Suzuki, et al. 2003. "The OsTB1 Gene Negatively Regulates Lateral Branching in Rice." *Plant Journal* 33, no. 3: 513–520.

Tan, L., X. Li, F. Liu, et al. 2008. "Control of a Key Transition From Prostrate to Erect Growth in Rice Domestication." 40, no. 11: 1360–1364.

Tao, Y., Y. Zhang, K. Dittert, L. Guo, M. Liu, and S. Lin. 2024. "Rice Shoot 13C Abundance at Maximum Tillering Stage Is Well Suited to Distinguish Differences in Water Use Efficiency for Water-Saving Rice Technologies." *Agronomy* 14, no. 12: 2918.

Tokuyama, Y., M. Omachi, S. Kushida, et al. 2024. "Different Contributions of PROG1 and TAC1 to the Angular Kinematics of the Main Culm and Tillers of Wild Rice (*Oryza rufipogon*)." *Planta* 259, no. 1: 19.

Vaughan, D. A. 1989. *The Genus Oryza L. Current Status of Taxonomy*. International Rice Germplasm Center, International Rice Research Institute, Manila, Philippines.

Vaughan, D. A. 1994. *The Wild Relatives of Rice: A Genetic Resources Handbook*. International Rice Research Institute.

Viola, I. L., and D. H. Gonzalez. 2023. "TCP Transcription Factors in Plant Reproductive Development: Juggling Multiple Roles." *Biomolecules* 13, no. 5: 750.

Wambugu, P. W., M.-N. Ndjiondjop, and R. Henry. 2021. "Genetics and Genomics of African Rice (*Oryza glaberrima* Steud) Domestication." *Rice* 14, no. 1: 6.

Wang, F., C. Lu, J. Wan, et al. 2022. "Genetic Dissection of Stem Branch Trait and Envisioning of Fixing Heterosis by Vegetative Reproduction in *Oryza rufipogon*." *Agronomy* 12, no. 7: 1503.

Wang, H., R. Tu, Z. Ruan, et al. 2023. "Photoperiod and Gravistimulation-Associated Tiller Angle Control 1 Modulates Dynamic Changes in Rice Plant Architecture." *Theoretical and Applied Genetics* 136, no. 7: 160.

Wang, H., R. Tu, L. Sun, et al. 2022. "Tiller Angle Control 1 Is Essential for the Dynamic Changes in Plant Architecture in Rice." *International Journal of Molecular Sciences* 23, no. 9: 4997.

Wang, J., J. Huang, J. Bao, X. Li, L. Zhu, and J. Jin. 2023. "Rice Domestication-Associated Transcription Factor PROSTRATE GROWTH 1 Controls Plant and Panicle Architecture by Regulating the Expression of LAZY 1 and OsGIGANTEA, Respectively." *Molecular Plant* 16, no. 9: 1413–1426.

Wang, J., H. Yu, G. Xiong, et al. 2017. "Tissue-Specific Ubiquitination by IPA1 INTERACTING PROTEIN1 Modulates IPA1 PROTEIN Levels to Regulate Plant Architecture in Rice." *Plant Cell* 29, no. 4: 697–707.

Wang, L., A. Wang, X. Huang, et al. 2011. "Mapping 49 Quantitative Trait Loci at High Resolution Through Sequencing-Based Genotyping of Rice Recombinant Inbred Lines." *Theoretical and Applied Genetics* 122, no. 2: 327–340.

Wang, M. 2019. *Molecular Regulatory Network of BRANCHED1 (BRC1) Expression in Axillary Bud of Rpsa sp. in Response to Sugar and Auxin*. Agrocampus Ouest.

Wang, M. X., C. Y. Jing, X. H. Wang, et al. 2021. "Genomic Landscape of Parallel Domestication of Upland Rice and Its Implications." *Journal of Systematics and Evolution* 59, no. 2: 229–239.

Wang, W., H. Gao, Y. Liang, J. Li, and Y. Wang. 2022. "Molecular Basis Underlying Rice Tiller Angle: Current Progress and Future Perspectives." *Molecular Plant* 15, no. 1: 125–137.

Wang, X., W. Wang, S. Tai, et al. 2022. "Selective and Comparative Genome Architecture of Asian Cultivated Rice (*Oryza sativa* L.) Attributed to Domestication and Modern Breeding." *Journal of Advanced Research* 42: 1–16.

Wei, X., J. Qiu, K. Yong, et al. 2021. "A Quantitative Genomics Map of Rice Provides Genetic Insights and Guides Breeding." *Nature Genetics* 53, no. 2: 243–253.

Wu, M., J. Zhou, Q. Li, D. Quan, Q. Wang, and Y. Gao. 2024. "Auxin–Brassinosteroid Crosstalk: Regulating Rice Plant Architecture and Grain Shape." *Crop Journal* 12, no. 4: 953–963.

Wu, X., D. Tang, M. Li, K. Wang, and Z. Cheng. 2013. "Loose Plant Architecture1, an INDETERMINATE DOMAIN Protein Involved in Shoot Gravitropism, Regulates Plant Architecture in Rice." *Plant Physiology* 161, no. 1: 317–329.

Wu, Y., S. Zhao, X. Li, et al. 2018. "Deletions Linked to PROG1 Gene Participate in Plant Architecture Domestication in Asian and African Rice." *Nature Communications* 9, no. 1: 4157.

Xie, L., Y. Li, W. Sun, et al. 2025. "OsPIL15-Induced Delay in Rice Heading Date via Direct Binding to the OsLF Promoter Is Dependent on Functional Phytochrome B." *Plant, Cell & Environment* 48, no. 5: 3326–3336.

Xu, J., C. Ding, Y. Ding, et al. 2015. "A Proteomic Approach to Analyze Differential Regulation of Proteins During Bud Outgrowth Under Apical Dominance Based on the Auxin Transport Canalization Model in Rice (*Oryza sativa* L.)." *Journal of Plant Growth Regulation* 34, no. 1: 122–136.

Xu, R., and C. Sun. 2021. "What Happened During Domestication of Wild to Cultivated Rice." *Crop Journal* 9, no. 3: 564–576.

Yan, Y., C. Ding, G. Zhang, et al. 2023. "Genetic and Environmental Control of Rice Tillering." *Crop Journal* 11, no. 5: 1287–1302.

Yan, Y., N. Zhao, H. Tang, B. Gong, and Q. Shi. 2020. "Shoot Branching Regulation and Signaling." *Plant Growth Regulation* 92, no. 2: 131–140.

Yang, X., and C. Hwa. 2008. "Genetic Modification of Plant Architecture and Variety Improvement in Rice." *Heredity* 101, no. 5: 396–404.

Yin, T., Y. Tai, Y. Sun, Z. Cheng, C. Wu, and Y. Sui. 2025. "Precise Tiller Angle Control by Manipulating TAC1 Expression in Rice." *Journal of Integrative Plant Biology* 67, no. 6: 1444–1446.

Yoshihara, T., and M. Iino. 2007. "Identification of the Gravitropism-Related Rice Gene LAZY1 and Elucidation of LAZY1-Dependent And-Independent Gravity Signaling Pathways." *Plant and Cell Physiology* 48, no. 5: 678–688.

Yoshihara, T., and E. P. Spalding. 2017. "LAZY Genes Mediate the Effects of Gravity on Auxin Gradients and Plant Architectured." 175, no. 2: 959–969.

Yu, B., Z. Lin, H. Li, et al. 2007. "TAC1, a Major Quantitative Trait Locus Controlling Tiller Angle in Rice." *Plant Journal* 52, no. 5: 891–898.

Yuan, Z., S. Gao, D.-W. Xue, et al. 2009. "RETARDED PALEA1 Controls PALEA Development and Floral Zygomorphy in Rice." *Plant Physiology* 149, no. 1: 235–244.

Zegeye, W. A., M. Tsegaw, Y. Zhang, and L. Cao. 2022. "CRISPR-Based Genome Editing: Advancements and Opportunities for Rice Improvement." *International Journal of Molecular Sciences* 23, no. 8: 4454.

Zhang, H., X. Li, D. Sang, et al. 2023. "PROG1 Acts Upstream of LAZY1 to Regulate Rice Tiller Angle as a Repressor." *Crop Journal* 11, no. 2: 386–393.

Zhang, L., H. Yu, B. Ma, et al. 2017. "A Natural Tandem Array Alleviates Epigenetic Repression of IPA1 and Leads to Superior Yielding Rice." *Nature Communications* 8, no. 1: 14789.

Zhang, N., H. Yu, H. Yu, et al. 2018. "A Core Regulatory Pathway Controlling Rice Tiller Angle Mediated by the LAZY1-Dependent Asymmetric Distribution of Auxin." *Plant Cell* 30, no. 7: 1461–1475.

Zhang, W., L. Tan, H. Sun, et al. 2019. "Natural Variations at TIG1 Encoding a TCP Transcription Factor Contribute to Plant Architecture Domestication in Rice." *Molecular Plant* 12, no. 8: 1075–1089.

Zhang, W., B. Zhu, H. Childs, et al. 2022. "Effects of Boiling and Steaming on the Carbohydrates of Sweet Corn." *ACS Food Science & Technology* 2, no. 5: 951–960.

Zhao, J., X. Liu, M. Wang, et al. 2022. "The miR528-D3 Module Regulates Plant Height in Rice by Modulating the Gibberellin and Abscisic Acid Metabolisms." *Rice* 15, no. 1: 27.

Zheng, X., Y. Peng, J. Qiao, R. Henry, and Q. Qian. 2024. "Wild Rice: Unlocking the Future of Rice Breeding." *Plant Biotechnology Journal* 22, no. 11: 3218–3226.

Zhou, H., M. Yang, L. Zhao, et al. 2021. "High-Tillering and Dwarf 12 Modulates Photosynthesis and Plant Architecture by Affecting Carotenoid Biosynthesis in Rice." *Journal of Experimental Botany* 72, no. 4: 1212–1224.

Zhu, Z., L. Tan, Y. Fu, et al. 2013. "Genetic Control of Inflorescence Architecture During Rice Domestication." *Nature Communications* 4, no. 1: 2200.