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Review

Advances in Genetics and Breeding of Grain Shape in Rice

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Abstract

Grain shape is a critical determinant of rice yield, quality, and market value. Recent advances in molecular biology, genomics, and systems biology have revealed a complex regulatory network governing grain development, integrating genetic loci, plant hormone signaling, transcriptional regulation, protein ubiquitination, epigenetic modifications, and environmental cues. This review summarizes key genetic components such as QTLs, transcription factors, and hormone pathways—including auxin, cytokinin, gibberellin, brassinosteroids, and abscisic acid—that influence seed size through regulation of cell division, expansion, and nutrient allocation. The roles of the ubiquitin–proteasome system, miRNAs, lncRNAs, and chromatin remodeling are also discussed, highlighting their importance in fine-tuning grain development. Furthermore, we examine environmental factors that impact grain filling and size, including temperature, light, and nutrient availability. We also explore cutting-edge breeding strategies such as gene editing, functional marker development, and wild germplasm utilization, along with the integration of multi-omics platforms like RiceAtlas to enable intelligent and ecological zone-specific precision breeding. Finally, challenges such as pleiotropy and non-additive gene interactions are discussed, and future directions are proposed to enhance grain shape improvement for yield stability and food security.

Keywords: rice; grain shape; hormone signaling; ubiquitin–proteasome system; precision breeding

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1. Introduction

Competition in the global rice market has become increasingly intense, driving producers and breeders to focus on improving grain shape to meet consumer preferences. For example, slender grains are generally considered more appealing due to their superior cooking qualities [1]. Consequently, grain shape improvement has emerged as a crucial factor for enhancing rice market value. Modern consumers are also more conscious of nutritional and health benefits. Improving grain shape not only affects rice appearance and taste but also influences nutritional content, including starch type and concentration. Research indicates that grain shape significantly correlates with starch composition and digestibility [2]. Advances in molecular biology and genomics have enabled breeders to identify genes associated with grain shape more effectively, using techniques like gene editing and marker-assisted selection to achieve desired traits [3,4]. These technological advancements help breeders to quickly respond to evolving market demands for high-quality rice. Additionally, agricultural policies in various countries actively encourage the production of premium rice. Governments may provide subsidies or establish support programs to motivate farmers, thus promoting research and practical implementation of grain shape improvements [5]. In summary, growing global demand for high-quality rice directly drives research and practices aimed at enhancing grain shape, helping breeders to satisfy consumer preferences, boost market competitiveness, and improve nutritional value. This trend significantly benefits rice production efficiency, economic returns, global food security, and nutritional improvement.

Grain shape in rice refers to the integrated traits of mature kernels, including length, width, thickness, and the degree of chalkiness, which not only serve as key determinants of yield components but also strongly influence grain appearance and market quality. According to the internationally accepted classification based on length-to-width ratio (L/W), grains can be categorized as extra-long slender (length $\geq$ 7.5 mm, L/W $\geq$ 3.0), long (6.6–7.5 mm, L/W 2.5–3.0), medium (5.5–6.6 mm, L/W 2.0–2.5), and short/bold (4.0–5.5 mm, L/W $\leq$ 2.0) [6]. Based on the chalkiness pattern, five types are commonly distinguished: milky-white, white-core, white-belly, white-based, and white-back [7]. Regardless of grain type, nutrient distribution within rice kernels is highly heterogeneous. At the macroscopic level, brown rice can be divided into the hull, bran layer (pericarp + aleurone), embryo (mainly the scutellum), and endosperm. The bran layer and embryo are enriched in proteins, lipids, ash, and B vitamins, whereas the endosperm consists predominantly of starch and contains the lowest concentrations of other nutrients. Spatially, mineral elements such as P, K, Ca, Mn, Fe, and Zn are preferentially accumulated in the aleurone layer and embryo (especially the scutellum), while their concentrations are lowest in the central endosperm [8,9]. Elemental distribution also shows distinct patterns: Zn is concentrated in the plumule and radicle of the embryo; Fe is most abundant in the scutellum and aleurone layer; K exhibits high intensity in the scutellum; Ca is preferentially distributed in the hull and scutellum; and Mn is localized in both the hull and embryo. During grain filling, a substantial proportion of minerals is remobilized from vegetative tissues, with approximately 60% of grain K and 20% of P derived from remobilization, while Fe and Zn can also be redistributed from the culm and sheath to the grain under flag leaf deficiency [6]. Ultimately, rice grain shape is shaped by the combined action of major negative regulators, polygenic networks, maternal genetic background, and environmental factors. Dissecting these genes and their interaction networks not only provides insights into the evolutionary and domestication history of grain morphology but also offers precise targets for modern molecular design breeding.

Grain size significantly influences plant adaptability and agricultural yield. In agricultural contexts, optimal grain size directly contributes to reproductive success, nutritional value, and market appeal [10]. In natural environments, grain size impacts plant dispersal capabilities, germination rates, and seedling survival, collectively influencing plant population dynamics and evolutionary paths [11]. While larger grains generally correlate with higher planting efficiency and yield, excessively large grains may result in nutritional imbalances and decreased quality [12]. Thus, the development of grain size is governed by a complex interplay of genetic and environmental factors. Understanding these molecular mechanisms is essential for enhancing crop yield and adaptation.

The entire life cycle of rice comprises five distinct stages: seedling, tillering, heading, flowering, and maturity (Figure 1). Seed germination is a critical stage initiating plant life, requiring appropriate conditions such as adequate moisture, temperature, and oxygen. Upon water absorption, seeds swell and rupture their coats, activating stored nutrients in the endosperm to support embryonic growth. Increased enzyme activity stimulates cell division and elongation; embryonic roots extend downward, establishing the root system, while shoots grow upward to form stems and leaves. After early growth, rice seedlings enter the tillering phase, increasing plant numbers and yield potential. Subsequently, plants transition to reproductive growth, marked by heading—a pivotal developmental stage. Following heading, rice enters the grain-filling period, during which grains accumulate vital nutrients such as starch and proteins, directly influencing rice quality and yield. Grain filling is regulated by internal genetic factors and external environmental conditions until grain maturity, signaling the completion of the rice lifecycle and the beginning of harvest [13]. During grain filling, cell wall invertases, SWEETs, and SUTs function coordinately to mediate sucrose unloading and allocation to the endosperm. Invertases hydrolyze transported sucrose into monosaccharides, SWEETs facilitate their efflux along concentration gradients, and SUTs actively import residual sugars. This coordinated "source–flow–sink" mechanism is critical for sustaining assimilate flux, thereby determining starch deposition and final grain yield [14,15].

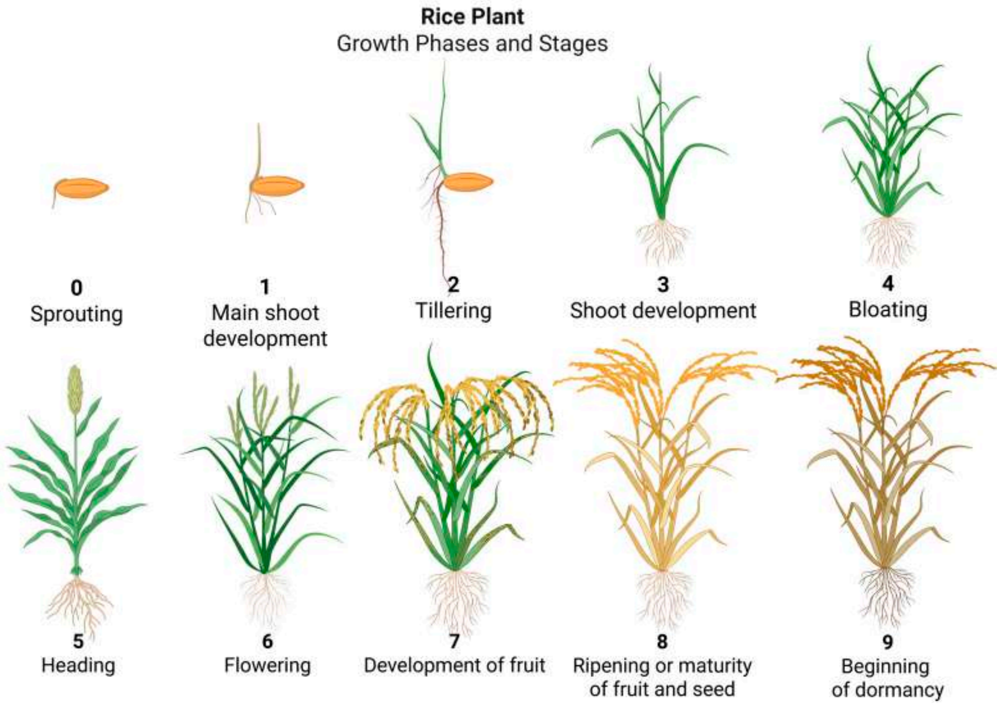

Figure 1. Growth stages of rice. The rice life cycle consists of five main stages: seedling, tillering, heading, flowering, and maturity. The figure illustrates the key developmental changes occurring at each stage in most rice varieties.

Grain size formation in rice is a complex biological process intricately regulated by genetic factors, hormone signaling pathways, epigenetic modifications, and environmental cues [16], offering valuable insights for the advancement of modern rice breeding technologies. This review comprehensively examines the roles of quantitative trait loci (QTLs), non-coding RNAs (including miRNAs and lncRNAs), plant hormones (such as auxin and gibberellin), the ubiquitin–proteasome system, and environmental variables (including temperature, light, and nutrient availability) in controlling grain development and final grain size. These factors collectively determine grain size through mechanisms involving cell division, cell expansion, and nutrient accumulation and transport. Future research integrating multi-omics and systems biology approaches will further clarify these regulatory networks, providing a robust scientific foundation for crop improvement.

2. Genetic Regulation Mechanisms of Rice Grain Shape

2.1. Hormone Signaling Pathways

Hormone signaling pathways play critical regulatory roles in rice growth and development, influencing cell division, cell expansion, and nutrient accumulation (Figure 2, Table 1), all processes directly affecting grain size [17,18].

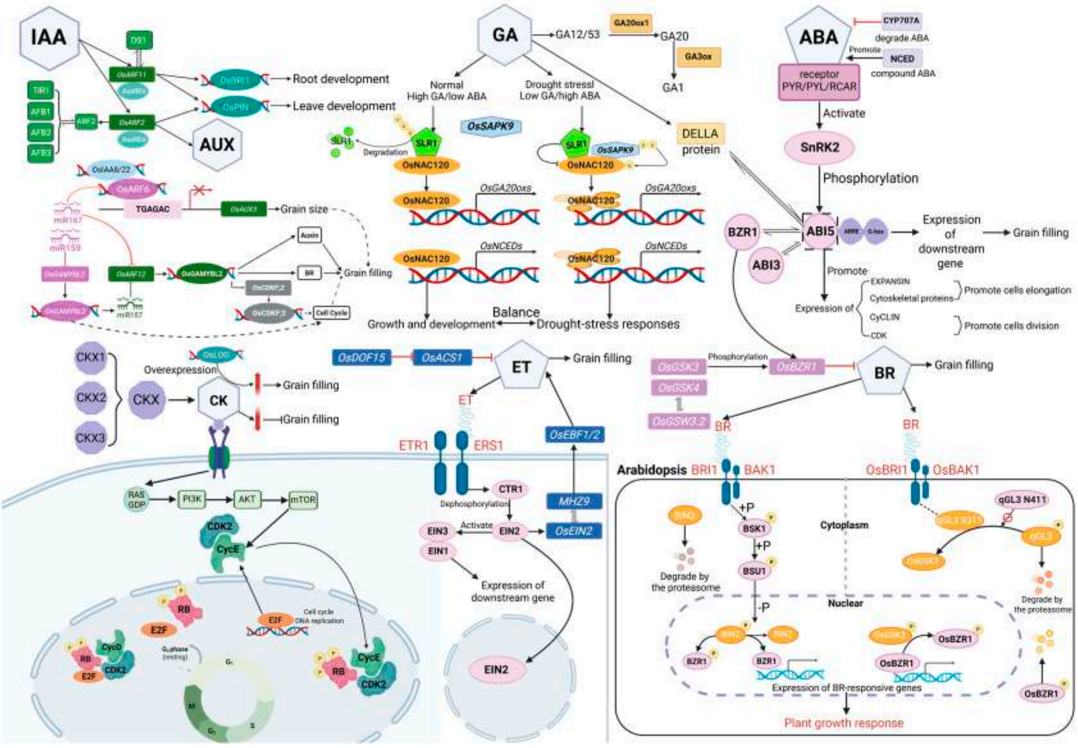

Figure 2. Plant hormone signaling pathways influencing seed size in rice. The signaling mechanisms of various hormones, including auxin (IAA), gibberellin (GA), abscisic acid (ABA), ethylene (ET), cytokinin (CK), and brassinosteroids (BR). It highlights how these hormonal pathways interact with environmental cues and internal physiological processes to coordinately regulate the plant's responses and seed size development.

2.1.1. Auxin

Auxin is one of the most critical plant hormones, playing a central role in cell division and expansion through its response factors, Auxin Response Factors (*ARFs*) [19]. The functions of auxin during plant development are mediated by complex signaling pathways. Particularly in crops such as rice, auxin signaling pathways regulate grain size via various genes and molecular mechanisms. These genes indirectly or directly influence grain size through their involvement in cell division, cell expansion, and endosperm development [20].

In rice, the genes *OsARF11* and *OsARF6* have been extensively studied and shown to positively regulate grain size. Activated ARF transcription factors bind to the promoters of target genes, promoting the expression of genes associated with cell wall synthesis and expansion, consequently increasing cell volume, grain filling rate, and final grain size [21–24]. Research indicates that *OsARF11* mutants exhibit reduced cell proliferation and inhibited cell expansion during grain development, resulting in smaller grain size and weight [21,25].

OsIAA1 is an auxin-responsive factor in rice, whose expression is regulated by auxin concentration. Auxin binds to the intracellular receptor *TIR1*, which facilitates the degradation of *OsIAA1*, enabling ARF transcription factors to function [26]. Studies demonstrate that *OsIAA1* negatively regulates the auxin signaling pathway, controlling cell division and expansion [27,28]. *OsARF2*, another member of the *ARF* family, also plays an essential role in auxin signaling. Knockout studies have shown that *OsARF2* mutants produce smaller and developmentally limited grains, highlighting its crucial role in grain development and cellular expansion [29,30]. *OsPIN1*, a key auxin transporter in rice, regulates auxin distribution between different cellular regions, significantly influencing plant morphology, including grain size. Research has revealed that *OsPIN1* plays essential roles during embryo, endosperm, and seed coat development, affecting final grain size [31].

Additionally, grain development in rice relies on auxin signaling and cell cycle regulation genes. Auxin increases grain size by upregulating the expression of *OsCyclinD1* and *OsCDKA*, significantly enhancing cell division rates and cell numbers during grain development [20,32].

2.1.2. Cytokinin

Cytokinins are essential phytohormones that govern various aspects of plant development, notably influencing the cell division cycle and cellular proliferation [27–30]. The homeostasis of cytokinins is tightly regulated by cytokinin oxidase/dehydrogenase (CKX) enzymes, which catalyze the irreversible degradation of active cytokinins [31]. Through modulating cytokinin levels, CKXs indirectly affect grain development by influencing the rate and extent of cell division. A reduction in cytokinin concentration is generally associated with decreased cell proliferation, often resulting in smaller grain size, whereas elevated cytokinin levels tend to enhance cell division and expansion, thereby contributing to increased grain size [32–34].

Rice possesses several *OsCKX* genes, including *OsCKX1*, *OsCKX2*, and *OsCKX3*. The genes *OsCKX1* and *OsCKX2* are involved in cytokinin degradation in rice, regulating grain development by reducing cytokinin levels. Studies indicate that overexpression of *OsCKX1* or *OsCKX2* results in smaller grains, whereas suppression of these genes enhances grain size. *OsCKX3* also participates in cytokinin degradation and plays a significant role in rice growth and development. Its expression is modulated by environmental factors, consequently affecting grain size and yield [33].

Rice Response Regulators (*OsRR*s) are pivotal factors in cytokinin signaling, representing one of the most important transcription factor families within the cytokinin signaling pathway. *OsRR* genes regulate grain development through cytokinin signaling interactions, activating downstream gene expression and thus promoting cell division and expansion, ultimately impacting grain size [30,34,35]. In rice, the *OsRR* family includes several members such as *OsRR1*, *OsRR2*, and *OsRR3*. *OsRR1* negatively regulates cytokinin signaling; its overexpression leads to smaller grains, whereas knockout mutants enhance cytokinin signaling, resulting in larger grains [30]. *OsRR2* and *OsRR3* also participate in cytokinin response and signaling, activating downstream target gene expression to influence grain development and size [36]. Additionally, *OsLOG* encodes a cytokinin synthesis enzyme, contributing to cytokinin synthesis and affecting grain growth and size [37].

In interactions between cytokinin and auxin, cytokinin typically dominates the early stages of cell division, while auxin primarily regulates later stages, such as cell expansion and grain filling. The coordination of these hormones is vital for normal grain development [38–40].

2.1.3. Gibberellin

Gibberellins (GAs) are pivotal regulators of plant growth and development, with pronounced roles during seed development. One of their key functions is to modulate cell elongation by promoting cell wall loosening and extensibility [41–43]. During the grain filling stage, GAs facilitate the expression of genes encoding cell wall-modifying proteins, such as expansins and xyloglucan endotransglucosylase/hydrolases, which enhance cell wall plasticity. This, in turn, promotes cellular expansion and contributes to the determination of final grain size [44].

OsGA20ox1 is a critical gene in the gibberellin biosynthesis pathway. Negative regulatory factors in the GA signaling pathway, such as *OsSLR1*, are also essential for regulating grain expansion. Overexpression of *OsGA20ox1* inhibits these negative regulatory factors, enhancing cell expansion and influencing final grain size [41,45,46]. The *OsGA3ox2* gene is also involved in GA biosynthesis, regulating GA activity, which affects rice grain development. Elevated *OsGA3ox2* expression enhances GA activity, resulting in increased grain size [42]. DELLA proteins, negative regulators within the GA signaling pathway, typically restrict cell division and expansion by suppressing plant growth. Multiple *DELLA* genes in rice are regulated by GA. GA promotes DELLA protein degradation, removing restrictions on grain size [43–45,47,48].

The synergistic interaction among auxin, cytokinin, and gibberellin forms a complex regulatory network, promoting seed development at different growth stages [49].

2.1.4. Abscisic Acid

Abscisic acid (ABA) is one of the primary plant hormones, extensively involved in regulating rice growth, particularly playing essential roles in seed development, germination, and drought responses [45,50–52]. *OsABI5* is a crucial gene within the ABA signaling pathway, significantly influencing the ABA response. Studies have found that *OsABI5* regulates hormone balance within seeds, affecting their final size [52–54]. *OsNCED* is a key enzyme in ABA biosynthesis in rice, responsible for ABA synthesis. Modulating *OsNCED* expression can alter ABA production levels, thus influencing rice grain size [55]. *OsCYP707A*, involved in ABA metabolism, facilitates ABA degradation. Research indicates that ABA levels are closely related to *OsCYP707A* activity, thereby affecting grain development and size [56].

2.1.5. Brassinosteroids

Brassinosteroids (BRs) are a class of plant hormones that play crucial roles in plant growth and development. Recent studies have demonstrated that brassinosteroids significantly influence not only the development of plant roots, stems, and leaves but also regulate seed size, shape, and quality [57–59]. Particularly in rice, brassinosteroids significantly affect grain size and weight by regulating processes such as cell division, cell expansion, and endosperm development [60–62].

BRI1 is a key receptor in the BR signaling pathway, responsible for perceiving brassinosteroids and initiating downstream signaling, thus influencing plant growth and development. *BRI1* directly regulates grain size by modulating cell division and expansion. Studies have shown that rice grains are significantly smaller in *BRI1* mutants, highlighting *BRI1*'s critical role in controlling grain size in rice [63,64]. *OsBZR1*, a transcription factor within the BR signaling pathway, enters the nucleus after activation by *BRI1*, where it regulates genes involved in seed development. Overexpression of *OsBZR1* increases grain size, while its suppression significantly reduces grain size. These findings suggest that brassinosteroids promote rice grain development through *OsBZR1* regulation [65,66]. *OsGSK3*, a kinase within the BR signaling pathway, regulates the cell cycle and proliferation. During BR signaling, *OsGSK3* directly influences rice grain development by modulating cell growth and division. Functional loss of *OsGSK3* leads to smaller rice grains and impaired embryo development [67]. Studies further indicate that *OsGSK3* expression correlates closely with BR signaling strength. When the BR signaling pathway is activated, *OsGSK3* enhances cell division and expansion, thereby promoting grain enlargement [68–70]. *OsGSW3.2* controls grain size by inhibiting cell proliferation in rice husks. Knockout mutants of *OsGSW3.2* exhibit significantly shortened and narrowed husk cells, resulting in increased cell numbers and larger grains. *OsGSW3.2* interacts with *OsGSK4*, an important component of the BR signaling pathway. This interaction may regulate grain size by influencing cell cycles and proliferation through modulation of BR signaling [71].

2.1.6. Ethylene

Ethylene is another critical hormone involved in plant growth and development, regulating various physiological processes, especially those related to grain size development [72–75]. The action of ethylene in plants begins with its binding to ethylene receptors.

OsACS1 is a key enzyme gene responsible for ethylene biosynthesis in rice, catalyzing the synthesis of 1-aminocyclopropane-1-carboxylate (ACC) and promoting ethylene production. Ethylene, a gaseous hormone, is vital for plant growth and development. Overexpression of *OsACS1* can lead to excessive ethylene production, promoting seed maturation and development, potentially increasing grain size. Studies show enhanced ethylene synthesis promotes rice grain cell expansion, thereby increasing grain size [76,77]. *OsETR1* is an ethylene receptor gene in rice, part of the ethylene receptor family. Ethylene binding to *OsETR1* initiates downstream signaling pathways. *OsETR1* perceives ethylene molecules and activates signaling cascades, leading to expression of downstream regulatory factors. Excessive ethylene through *OsETR1* accelerates seed aging, affecting grain quality and size. Mutants exhibit incomplete seed development and smaller grains. Similarly, *OsERS1*, another member of the ethylene receptor family, participates in ethylene perception and signaling. Studies demonstrate *OsERS1* impacts rice grain size by influencing cell division and expansion via ethylene signaling [78]. *OsEIN2* serves as a mediator between ethylene receptors and downstream effector genes in ethylene signaling pathways. After ethylene binds to receptors, *OsEIN2* transmits signals to nuclear transcription factors, activating or repressing downstream gene expression. Overexpression of *OsEIN2* in rice enhances grain cell expansion, increasing overall grain size, whereas its mutants produce smaller grains [79,80]. *OsCTR1*, a negative regulator within the ethylene signaling pathway, suppresses excessive ethylene responses. By interacting with ethylene receptors, *OsCTR1* moderates ethylene signaling. Studies indicate that loss of *OsCTR1* function leads to exaggerated ethylene signaling, promoting cell expansion and resulting in larger grains [81,82].

Table 1. Hormone-related genes in rice and their functions.

Gene	Type	Function	Reference
OsARF2	Transcription factor	An auxin response factor that positively regulates grain size	[29,30]
OsARF11	Transcription factor	An auxin response factor that positively regulates grain size	[21,25]
OsIAA1	Member of the rice Aux/IAA family	An auxin response factor that negatively regulates the auxin signaling pathway	[26]
OsPIN1	Auxin transport protein	Determines rice grain size by "establishing and maintaining the auxin (IAA) concentration gradient between vascular bundles and endosperm"	[31]
OsCyclinD1	Cell cycle regulatory protein	Positively regulates grain size	[20,32]

Table 1. *Cont.*

Gene	Type	Function	Reference
OsCDKA	Cell cycle regulatory protein	Positively regulates grain size	[20,32]
OsCKX1	Member of the cytokinin oxidase/dehydrogenase gene family	Negatively regulates grain length and width by degrading active cytokinins	[33]
OsCKX2	Member of the cytokinin oxidase/dehydrogenase gene family	Negatively regulates grain length and width by degrading active cytokinins	[33]
OsCKX3	Member of the cytokinin oxidase/dehydrogenase gene family	Negatively regulates grain length and width by degrading active cytokinins	[33]
OsRR1	Member of the type-A cytokinin response regulator family	Negatively regulates grain size by repressing cytokinin signaling	[30]
OsRR2	Member of the type-A cytokinin response regulator family	Negatively regulates grain size by repressing cytokinin signaling	[36]
OsRR3	Member of the type-A cytokinin response regulator family	Negatively regulates grain size by repressing cytokinin signaling	[36]
OsLOG	Cytokinin activation/biosynthesis gene	Promotes cytokinin biosynthesis, thereby positively regulating grain size	[37]
OsGA20ox1	Key late-stage enzyme gene in gibberellin biosynthesis	Negatively regulates grain size by reducing gibberellin activity	[41,45,46]
OsGA3ox2	Key late-stage enzyme gene in gibberellin biosynthesis	Positively regulates grain size by enhancing gibberellin activity	[42]
OsABI5	bZIP transcription factor gene in the ABA signaling pathway	Negatively determines grain size by repressing the cell cycle, expansins, and sugar transport	[52–54]
OsNCED	Member of the 9-cis-epoxycarotenoid dioxygenase gene family	Positively regulates ABA biosynthesis, promoting cell differentiation and early grain filling	[55]
OsCYP707A	Member of the cytochrome P450 monooxygenase A-type family	Negatively regulates ABA biosynthesis, preventing premature termination of grain filling	[56]
OsBRI1	Key receptor in the brassinosteroid (BR) signaling pathway	Perceives brassinosteroids and initiates downstream signaling, thereby positively regulating grain size	[63,64]
OsBZR1	Core transcription factor in the BR signaling pathway	Functions with OsBRI1 to positively regulate grain size	[65,66]
OsGSK3	Key kinase in the BR signaling pathway	Positively regulates grain size by controlling cell growth and division	[67]
OsACS1	Key enzyme gene in ethylene biosynthesis	Positively regulates ethylene biosynthesis, thereby influencing grain size	[76,77]
OsETR1	Member of the ethylene receptor gene family	Perceives ethylene and activates signaling cascades, inducing downstream regulatory factors to control grain size	[78]
OsERS1	Member of the ethylene receptor gene family	Regulates cell division and expansion via ethylene signaling, thereby influencing grain size	[78]

Table 1. *Cont.*

Gene	Type	Function	Reference
OsEIN2	Core transducer in the ethylene signaling pathway	Transmits signals to nuclear transcription factors, activating or repressing downstream genes, thus positively regulating grain size	[79,80]
OsCTR1	Negative regulator RAF-like serine/threonine protein kinase gene in the ethylene signaling pathway	Suppresses abnormal responses triggered by excessive ethylene, thereby negatively regulating grain size	[81,82]

2.2. Transcriptional Regulatory Pathways

Transcription factors play central roles in plant growth and development, particularly in regulating grain size. Research indicates that transcription factors regulate grain size primarily through several pathways, including the *SPL* family, *WRKY* family, and *NAC* family, among others (Figure 3).

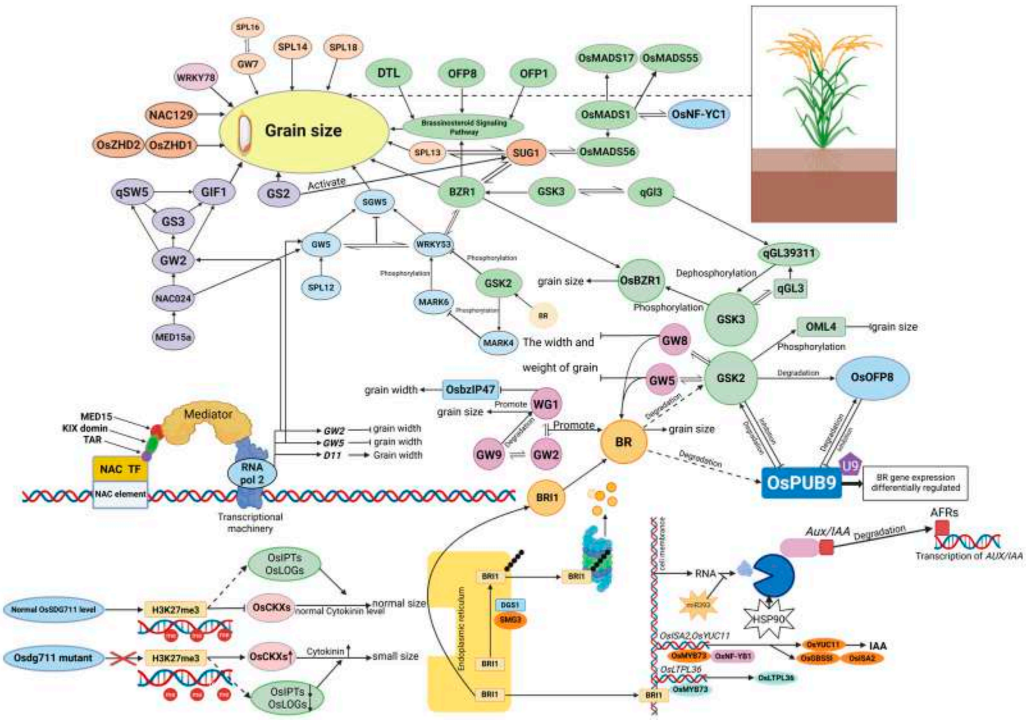

Figure 3. Multigene regulatory networks controlling seed size in rice. This figure presents the complex gene networks involved in the regulation of seed size in rice, including key signaling pathways mediated by plant hormones such as auxin, gibberellin, and cytokinin. It illustrates how multiple genes interact within and across these pathways to coordinately influence grain development and final seed size.

The *SPL* family, a class of plant-specific transcription factors, plays key roles in plant growth and development, particularly in regulating grain size [83]. *OsSPL12* regulates grain width in rice by binding to the promoter region of the *GW5* gene [84]. *OsSPL13*, another plant-specific transcription factor, positively regulates rice hull width by increasing hull cell size, thereby positively impacting grain length and yield [85]. *OsSPL14* is a key transcription factor in rice, negatively regulating grain size by influencing cell division and expansion through auxin-related metabolism and signaling pathways, affecting grain length and weight [86–88]. *OsSPL16*, an SBP-domain transcription factor, regulates grain width in rice. Increased expression of the *GW7* gene is associated with more slender grains, while OsSPL16 directly binds to and suppresses *GW7* promoter expression, thus modulating hull width [89,90]. *OsSPL18* influences grain width and thickness by directly affecting cell proliferation during rice hull development [91].

The *WRKY* family is another highly conserved transcription factor family in plants, extensively involved in responses to environmental stress and developmental regulation [92]. Specifically, *WRKY53* plays crucial roles in regulating grain size and plant structure by interacting with the brassinosteroid (BR) and mitogen-activated protein kinase (MAPK) signaling pathways [93]. *OsWRKY78*, specifically in rice, promotes grain enlargement by regulating genes associated with cell division and expansion. Studies suggest OsWRKY78 interacts with auxin signaling pathways, regulating early cell proliferation and differentiation [94].

The *NAC* family is another plant-specific transcription factor family involved in stress responses and developmental processes [95,96]. OsNAC23 indirectly regulates plant growth and development, including grain filling and yield formation, by influencing sugar utilization and allocation [97]. OsNAC024 and OsNAC025 directly bind to the promoters of the *GW2*, *GW5*, and *D11* genes, known regulators of rice grain weight. *OsMED15a* enhances OsNAC024 binding to these promoters through its KIX domain, potentially boosting transcriptional activity. In *OsMED15a* RNAi transgenic rice, expression of *GW2*, *GW5*, and *D11* is downregulated, resulting in shorter and wider seeds [98]. *SS1/ONAC025*, an ER- and nucleus-localized transcriptional repressor, regulates seed size by influencing cell elongation [99]. Compared to the wild-type, *osnac129* mutants exhibit increased grain length, grain weight, and plant height, while overexpression lines show reduced grain width, grain weight, and plant height, indicating *OsNAC129* negatively regulates these traits. *OsNAC129* modulates rice grain size and starch synthesis by repressing expression of genes like *OsPGL1* and *OsPGL2*; its functional loss alters starch content, affecting grain quality [100].

Additionally, numerous other transcription factors significantly influence grain size. GS2 (OsGRF4) directly binds to the *SUG1* promoter, activating its expression. SUG1 interacts with transcription factors such as OsBZR1, OsMADS56, and OsSPL13, integrating gibberellin (GA) and brassinosteroid (BR) signaling pathways to promote cell expansion and regulate grain size [101]. GS2 interacts directly with IPA1 to co-regulate downstream *DEP1* expression, affecting rice panicle type and grain number [102]. *DWARF AND LOW-TILLERING* (*DLT*), a *GRAS* family member, acts as a positive regulator in the BR signaling pathway, interacting with WG3 to influence plant architecture and grain size [103]. OVATE family proteins, including OFP3 and OFP8, are transcription factors in the BR signaling pathway, regulating leaf angle and grain size [104,105].

In rice, editing *OsSPL16* resulted in mutant plants exhibiting abnormal carbohydrate allocation, poor grain filling, and reduced grain size [106]. *RGA1* regulates rice grain size through multiple mechanisms, including involvement in G-protein signaling, regulation of cell proliferation and expansion, interactions with other grain-size-related genes, influencing grain filling, and responding to environmental and hormonal signals. *RGA1* controls grain size, rice quality, and seed germination in minimal rice plants [107,108]. *OsbZIP47*, a bZIP transcription factor, has its transcriptional activation inhibited by *WG1*. *GW2*-mediated WG1 degradation relieves *WG1*'s repression, activating *OsbZIP47* and restricting grain growth [109]. *OsMYB73* regulates rice grain size by controlling endosperm storage substance accumulation and auxin biosynthesis signaling pathways. In cooperation with OsNF-YB1, OsMYB73 binds promoters of downstream genes (e.g., *OsISA2*, *OsLTPL36*, *OsYUC11*), regulating starch, lipid biosynthesis, and auxin synthesis, thus impacting endosperm development and grain chalkiness. *OsMYB73* mutations increase grain length but cause chalkiness, while its overexpression reduces grain size and increases chalkiness, highlighting its crucial role in regulating grain size and quality [110]. *OsZHD1* and *OsZHD2*, zinc finger homeodomain transcription factors in rice, may influence grain shape by directly binding to promoters of target genes [111].

These transcription factor families are involved in complex regulatory networks controlling rice grain size through various signaling pathways and interactions. They finely tune multiple aspects of grain development in response to plant hormones, environmental factors, and developmental signals [81].

2.3. Multigenic Interactions and Regulatory Networks

2.3.1. Multigenic Regulatory Networks

Seed size is a critical agronomic trait in plant growth and development, intricately regulated by numerous quantitative trait loci (QTL). Extensive QTL studies have demonstrated that seed size across various crops results from the collaborative actions of multiple genetic loci (Figure 3) [112–114]. In rice, several key genes such as *GW2*, *GS3*, *qGL3*, and *GW5* significantly influence seed development and grain shape [115].

GW2 functions as a negative regulator through ubiquitination, affecting cell division and expansion by reducing cellular proliferation, consequently decreasing grain width and weight [109,116]. *GS3* regulates grain shape by modulating glume cell morphology, with specific alleles leading to elongated but narrower glume cells [117,118]. *qGL3*, an essential QTL in rice, encodes a putative protein phosphatase containing kelch-repeat domains homologous to *BSU1*, a positive regulator of brassinosteroid (BR) signaling in Arabidopsis [68]. *GW5* negatively regulates rice grain width, with loss-of-function mutations causing increased grain width and weight [119]. qSW5 and GW2 positively regulate *GS3* expression, although *qSW5* expression can be suppressed by *GW2*-mediated transcriptional inhibition [120]. *GIF1* expression is positively regulated by qSW5 and negatively regulated by GW2 and GS3. In natural rice populations, an epistatic interaction exists between qSW5 and GS3, where *qSW5*'s effect on seed length is masked by *GS3* alleles, and conversely, *GS3*'s effect on seed width is masked by *qSW5* alleles. In the Kasalath cultivar, reduced *ORF1* expression at the *qSW5* locus increases grain width [121]. Variations in *qGL3* alleles influence its capacity to dephosphorylate *OsGSK3*, thus regulating grain length and yield. Loss-of-function mutations in *GS3* and *qGL3* markedly enhance grain length, with *qGL3* exerting a stronger effect [122].

OsMADS1 affects grain size by regulating glume cell proliferation; loss of *OsMADS1* function reduces cell numbers and sizes, leading to smaller grains. *OsMADS1* directly controls several downstream genes, such as *OsMADS17* and *OsMADS55*, pivotal in grain development. Additionally, interaction with *OsNF-YC1* significantly enhances the transcriptional activation activity of *OsMADS1*. GS3 and DEP1, both Gγ subunits, directly interact with the conserved keratin-like domain of OsMADS1, acting as co-factors to enhance its transcriptional activity, thereby synergistically regulating grain size and shape [123].

GW5 interacts with WRKY53, potentially suppressing *WRKY53*-induced activation of *SGW5*, negatively regulating grain width. *SGW5* positively regulates grain width by influencing spikelet hull cell division and size. The WRKY53 transcription factor binds to the W-box motif in the *SGW5* promoter, modulating its expression and grain width. *GW5*, *WRKY53*, and *SGW5* form a regulatory module affecting grain width, with GW5 suppressing *SGW5* expression and consequently reducing grain width. Conversely, deletion of the *WRKY53* binding site enhances *SGW5* expression and grain width [124].

qGL3 interacts with OsGSK3, modulating its phosphorylation state and influencing *OsBZR1* phosphorylation and subcellular localization. Variations among *qGL3* alleles alter their ability to dephosphorylate *OsGSK3*, thereby impacting grain length and yield [68].

Moreover, *GW5* promotes seed length and width by regulating grain expansion and increasing cell volume [119].

The *TGW2* gene encodes *CELL NUMBER REGULATOR 1* (*OsCNR1*). Overexpression of *TGW2* results in reduced grain width and thousand-grain weight, whereas CRISPR/Cas9-mediated knockout of *TGW2* enhances these traits. TGW2 interacts with KRP1, a cell cycle regulatory protein, whose overexpression similarly reduces grain width and thousand-grain weight [125].

Integrating QTL models with genome-wide association studies (GWAS) has further elucidated the complex regulatory networks between QTLs and genes, providing fundamental insights essential for crop yield and quality improvement [126].

2.3.2. Conservation and Functional Divergence of Genes Across Species

Although genes regulating seed size vary across crops, there is notable genetic conservation. For instance, similar genes such as *GS3* and *GW2* control comparable processes of cell proliferation and expansion in both rice and wheat [116,118]. In rice, *GS3* negatively regulates cell division rates and endosperm development, and its function is conserved across other cereal crops [127]. *GW2* in rice and wheat modulates cell wall formation, influencing grain size in both species [128,129].

Despite this conservation, gene expression patterns and functional mechanisms may differ among species. For example, *TaSPL13* in wheat predominantly regulates carbohydrate allocation, whereas *SPL* genes in rice primarily control endosperm expansion [85,130]. Cross-species analyses of gene function provide valuable insights for breeding strategies, especially the identification and utilization of conserved genes. These findings lay theoretical foundations for gene editing and molecular marker-assisted breeding [131,132]. Advancements in genomics will further clarify functional divergences of conserved genes across species, offering promising opportunities for enhancing seed size and crop productivity.

2.4. Mechanisms of Protein Metabolism and Ubiquitination Regulation

2.4.1. Functions of the Ubiquitin–Proteasome System (UPS) in Seed Development

The ubiquitin–proteasome system (UPS) plays a central role in maintaining protein homeostasis in plant cells by selectively degrading misfolded, damaged, or regulatory proteins [133]. This tightly controlled proteolytic pathway is especially important during seed development, where it modulates key signaling and metabolic pathways that ultimately affect seed size and growth dynamics [134,135]. Ubiquitination proceeds through a sequential cascade involving E1 activating enzymes, E2 conjugating enzymes, and E3 ubiquitin ligases, the latter conferring substrate specificity by recognizing and tagging target proteins for degradation via the 26S proteasome [136]. The functional diversity and large number of E3 ligases in plants allow for highly selective and dynamic regulation of protein turnover during developmental processes.

In rice, the E3 ligase *GW2* negatively regulates seed size by ubiquitinating proteins involved in cell division and expansion. Mutations in *GW2* enhance cellular proliferation rates, resulting in increased grain size, highlighting its negative regulatory role [116]. *GW2* directly influences endosperm cell proliferation through the targeted degradation of proteins involved in cellular expansion processes [137]. *GW9* has been identified as a ubiquitination target of *GW2*; together, they regulate rice grain dimensions [138]. Another E3 ligase, *OsPUB9*, interacts with *GSK2*, preventing its own degradation while promoting degradation of *GSK2*. Additionally, *OsPUB9* interacts with *OsOFP8*, stabilizing itself but inducing degradation of *OsOFP8*, collaboratively influencing rice grain size [139]. Furthermore, *OsDA1*, an E3 ligase family member, significantly impacts seed development by regulating endosperm cell size and proliferation during grain filling [140]. A similar *DA1*

E3 ligase identified in Arabidopsis also controls seed development through ubiquitination-mediated protein turnover [133,140]. This regulatory mechanism shows high conservation across various crops, including rice, wheat, and soybean, indicating the broad applicability of ubiquitination systems in controlling seed size [134,135]. Moreover, ubiquitination enables plants to adapt to environmental stresses, such as elevated temperatures or nutrient deficiencies, by accelerating the degradation of stress-responsive proteins, thus stabilizing seed development and yield under adverse conditions [136].

2.4.2. Molecular Mechanisms Linking Protein Degradation and Signal Transduction

Beyond its canonical role in protein turnover, ubiquitination serves as a key regulatory mechanism in hormone signaling pathways that govern seed development. By modulating the stability and activity of signaling components, the ubiquitin–proteasome system (UPS) enables precise temporal and spatial control of hormone responses. In the brassinosteroid (BR) signaling pathway, for example, the transcription factor OsBZR1, which regulates endosperm and embryonic cell expansion, is subject to ubiquitin-mediated degradation. This regulation prevents excessive cell enlargement and contributes to energy homeostasis during seed development [71]. In rice, OsUBC13, a ubiquitin-conjugating enzyme, has been shown to influence cytokinin signaling by modulating the turnover of key pathway components, thereby coordinating endosperm cell proliferation and optimizing grain filling processes [141,142].

In auxin signaling, the UPS precisely regulates the activity of Auxin Response Factors (*ARFs*), orchestrating cell division and differentiation [29]. TIR1 and AFB proteins function as auxin receptors, interacting with ubiquitin ligases to rapidly degrade AUX/IAA repressors, thereby activating *ARFs* and promoting dynamic adjustments of auxin signaling during different stages of seed development [26,143]. This ensures precise modulation of cell proliferation and expansion, tailored to the developmental needs of seeds.

Moreover, ubiquitination is crucial in plant responses to environmental stress. Under drought or saline conditions, plants rapidly degrade non-essential stress-response proteins via ubiquitination, conserving energy and improving survival chances [144]. Studies in rice seeds demonstrate that the UPS facilitates degradation of negative regulators in stress response pathways, optimizing energy utilization efficiency, enhancing seed viability, and increasing final yields [145,146]. These adaptive responses illustrate the versatile roles of the UPS during seed development under fluctuating environmental conditions.

In summary, protein metabolism and ubiquitination significantly influence seed size regulation. Selective protein degradation mediated by the ubiquitin–proteasome system (UPS) precisely modulates essential proteins involved in cell proliferation, division, and expansion, integrated with hormone signaling pathways to form complex, multi-layered regulatory networks [136]. Exploiting the adaptability and specificity of UPS pathways presents promising avenues for crop improvement, potentially leading to enhanced seed yield and quality through targeted modifications of ubiquitination mechanisms.

2.5. Epigenetic and Non-Coding RNA Regulatory Mechanisms

2.5.1. Epigenetic Modifications in Seed Development

Epigenetic modifications, including DNA methylation, histone modification, and chromatin remodeling, are among the most critical molecular mechanisms influencing seed size and development in plants (Table 2). DNA methylation, a chemical modification of DNA, alters gene expression without changing the underlying DNA sequence [147]. As a pivotal epigenetic regulatory mechanism, DNA methylation influences the expression of genes essential for plant growth and development. In rice, the gene *OsDDM1b* modulates gene activation and silencing by regulating genomic DNA methylation status. Loss-of-function mutations in *OsDDM1b* significantly reduce overall DNA methylation levels, leading to activation of several genes that negatively regulate cell division, ultimately resulting in reduced seed size [148]. Moreover, DNA methylation is closely associated with environmental adaptability and seed development. Under adverse environmental conditions, changes in methylation patterns can rebalance gene expression to ensure proper seed development despite environmental stress [148].

Histone modification represents another crucial epigenetic mechanism, with histone acetylation and methylation playing particularly important roles in regulating gene expression [141,149]. Histone modifications, mediated by specific enzymes, include methylation, acetylation, phosphorylation, adenylation, ubiquitination, and ADP-ribosylation [149]. *OsHDT701*, an important histone deacetylase in rice, regulates gene acetylation levels during grain development to synchronize cell division and germination. Loss of *OsHDT701* activity leads to premature endosperm cell expansion and division, resulting in poor grain filling, highlighting the significance of histone deacetylation in grain development [142].

Epigenetic modifications are critically involved during the seed filling phase, especially the histone marks *H3K27me3* and *H3K4me3*, commonly associated with gene activation states, significantly influencing transcription of grain development genes. Genes closely associated with grain development exhibit elevated *H3K27me3* modification levels during seed filling [150,151]. *H3K4me3*, an activating histone methylation mark, enhances transcriptional activity, thereby promoting grain growth and filling. Activation of these genes ensures both grain expansion and nutrient accumulation, substantially impacting crop yield and quality [152]. A deeper understanding of the regulatory roles of *H3K27me3* and *H3K4me3* in grain development will facilitate genetic improvement and molecular breeding strategies aimed at producing higher-yielding and superior-quality crop varieties.

2.5.2. Regulatory Roles and Biological Significance of miRNAs and lncRNAs

Non-coding RNAs, particularly microRNAs (miRNAs) and long non-coding RNAs (lncRNAs), significantly contribute to gene expression regulation and phenotypic determination during seed development in plants [23,153–155]. miRNAs finely regulate gene expression at the post-transcriptional level by binding target mRNAs and inhibiting their translation [156]. For example, the *miRNA156* family regulates seed size by targeting members of the *SPL* gene family, influencing cell division and expansion [88,157]. *SPL* genes play critical roles in auxin signaling pathways, and *miRNA156* controls plant responses to auxin by modulating *SPL* expression, thereby regulating the rate of cell expansion [87,88].

Compared to miRNAs, lncRNAs exhibit greater structural complexity and employ diverse regulatory mechanisms, including transcriptional, pre-transcriptional, post-transcriptional, and epigenetic controls. They interact with protein complexes and modulate chromatin structures, thereby regulating gene expression at multiple levels [158,159]. For instance, in rice, the lncRNA TCONS_00023703 is highly expressed at crucial stages of seed development, precisely regulating transcriptional activity of specific genes involved in cell division and proliferation during grain filling by interacting with chromatin remodeling proteins [155]. This precise control mechanism decisively impacts seed development, influencing seed size, shape, and nutrient accumulation, thereby significantly affecting crop yield and quality [159]. Understanding lncRNA-mediated regulation provides valuable insights and potential strategies for crop improvement and enhanced adaptability.

2.5.3. Synergistic Effects of Non-Coding RNAs and Epigenetic Modifications

Non-coding RNAs, including miRNAs and lncRNAs, act synergistically with epigenetic modifications to regulate gene expression. Specific lncRNAs can interact with histone-modifying enzymes, such as H3K27 methyltransferases, to regulate chromatin states in particular genomic regions at specific developmental stages, thereby determining gene activation or silencing [160]. This mechanism is crucial for regulating gene expression during cellular differentiation and tissue development. Similarly, miRNAs indirectly influence traits like seed size by targeting the expression of epigenetic regulators. By binding and destabilizing or inhibiting translation of specific mRNAs, miRNAs reduce the levels of epigenetic factors, thus adding complexity to their regulatory roles [156,161–163].

2.5.4. Role of Chromatin Remodeling in Seed Size Regulation

Chromatin remodeling is a fundamental epigenetic mechanism controlling gene expression by altering chromatin accessibility and openness. Chromatin remodelers, such as the SWI/SNF complex, play essential roles in seed development by modifying chromatin states at targeted genomic regions, thereby regulating the expression of seed-specific genes [164]. An open chromatin structure facilitates the transcription of genes related to grain filling and cell division, whereas a condensed chromatin state suppresses unnecessary gene activation [165–167].

Table 2. Epigenetic and non-coding RNA factors in rice and their roles in grain size regulation.

Gene	Type	Function	Reference
OsDDM1b	Chromatin remodeling enzyme gene of the WI2/SNF2 family	Loss-of-function mutation significantly reduces overall DNA methylation, activating multiple genes that negatively regulate cell division, ultimately leading to smaller grain size	[148]
OsHDT701	Histone deacetylase	Loss of activity causes premature expansion and division of endosperm cells, resulting in poor grain filling	[142]
H3K27me3	Trimethylation of lysine 27 on histone H3	Acts as an epigenetic “brake”; its level and distribution determine the balance between cell proliferation and grain filling, directly regulating grain size	[150,151]
H3K4me3	Trimethylation of lysine 4 on histone H3	Enhances transcriptional activity, promoting grain growth and filling	[152]
miRNA156	MicroRNA (miRNA)	Regulates SPL expression to control plant responses to auxin, thereby influencing grain size	[87,88]
lncRNA	Long non-coding RNA	Interacts with chromatin remodeling proteins to precisely regulate the transcription of specific genes involved in cell division and proliferation during grain filling	[155]
SWI/SNF complex	Chromatin remodeling factor	Open chromatin structure promotes transcription of genes related to grain filling and cell division	[164]

2.6. Environmental Influences on Seed Development and Adaptive Mechanisms

2.6.1. Impact of High-Temperature Stress, Light, and Nutrients on Seed Size

External environmental factors, such as temperature, light conditions, and nutrient availability, significantly influence plant growth and development, directly affecting seed filling rates and ultimate seed size. High-temperature stress, especially during grain filling, notably hampers seed development, often resulting in poorly developed grains [168]. Elevated temperatures accelerate water evaporation from leaves and seeds, disrupting overall plant water balance. Studies indicate that temperatures exceeding 35 °C inhibit starch synthesis in rice grains, significantly slowing endosperm cell expansion, reducing grain filling, and consequently decreasing seed size [169]. Additionally, oxidative stress induced by high temperature leads to lipid peroxidation and cellular membrane damage, inhibiting endosperm cell division and enlargement [168–170]. To mitigate high-temperature stress, plants activate protective mechanisms such as synthesizing heat-shock proteins (HSPs) to stabilize protein structures and maintain cellular functions [171]. These proteins improve plant tolerance to heat stress, maintaining seed size under challenging conditions.

Light and photoperiod are key environmental cues that profoundly influence seed development by modulating hormonal balance and metabolic activity. Variations in day length and light intensity affect the biosynthesis and signaling of plant hormones such as auxin, gibberellins, and cytokinins, thereby shaping developmental outcomes in response to light stimuli [34,172,173]. Under favorable photoperiodic conditions, enhanced photosynthetic activity leads to increased carbohydrate production, which supports seed growth and filling. For example, extended day lengths have been shown to promote carbohydrate accumulation, contributing to improved grain filling and increased seed size and weight [174]. In addition, light regulates the expression of transcription factors involved in seed development, including members of the phytochrome-interacting factor (OsPIF) family. Under long-day conditions, OsPIFs activate downstream genes associated with endosperm development and nutrient accumulation, ultimately enhancing seed filling efficiency and grain enlargement [175].

Nutrient availability, particularly of nitrogen (N), phosphorus (P), and potassium (K), also plays a critical role in regulating seed development and grain filling [176]. Nitrogen is central to protein synthesis and cellular proliferation and is known to stimulate cytokinin production, which accelerates cell division and expansion during seed filling, thereby increasing final seed size [177,178]. Phosphorus, essential for nucleic acid synthesis and energy transfer, is a key component of ATP and phospholipids. Its deficiency leads to impaired metabolic activity and reduced seed filling, often resulting in smaller seeds [179]. Potassium contributes to osmotic regulation, enzyme activation, and the maintenance of photosynthetic and assimilate transport processes. Adequate potassium supply has been associated with improved endosperm development and higher grain weight due to its role in facilitating water and nutrient movement within the developing seed [180,181].

2.6.2. Effects of Local Environmental Conditions on Seed Development

In addition to broad environmental factors such as temperature, light, and nutrients, localized micro-environmental conditions, including soil moisture and plant density, significantly influence seed development. Localized soil moisture profoundly affects plant water and nutrient absorption. Adequate moisture supply is essential for cell expansion and grain filling, particularly during periods of high-temperature stress or drought, when water deficits cause cellular dehydration and impede seed enlargement [182,183]. Studies have shown that moderate irrigation significantly increases grain filling rates and seed plumpness in crops such as rice and wheat, whereas drought stress severely restricts endosperm cell expansion and decreases grain filling [184,185]. Additionally, localized moisture availability impacts enzymatic activities and protein synthesis efficiency, further influencing seed development quality and size [182].

Plant density and competition from neighboring vegetation also indirectly influence seed size. Higher planting densities intensify competition among plants for limited resources, especially light and nutrients, reducing photosynthetic efficiency and limiting seed filling [172,186]. Increased planting density lowers light availability and air circulation, reducing leaf photosynthesis and thus constraining seed expansion [187]. Furthermore, dense neighboring vegetation can restrict root growth and nutrient uptake, indirectly impacting seed size [188]. Adjusting plant spacing and density can improve the local growth environment, thus enhancing seed development potential and optimizing seed size [189].

2.6.3. Agricultural Implications of Regulating Seed Size

In modern agriculture, seed size significantly influences crop yield, seedling vigor, and market value. Understanding molecular mechanisms controlling seed size enhances germination rates and seedling vitality, thereby directly improving plant stress tolerance and disease resistance. Larger seeds typically store greater reserves of nutrients, including carbohydrates, proteins, and lipids, providing essential energy and structural materials for seedlings to better cope with adverse conditions such as drought, salinity, and poor soil fertility during early growth stages [173]. For instance, seed size directly affects germination and emergence rates in rice, while larger seeds in legumes boost seedling growth rates and resilience to early environmental stressors [10,174].

Genetic regulation of seed size can improve yield per unit area and enhance nutritional and commercial value. Key genes such as *OsGS3* and *OsGW2* significantly influence seed size traits in rice and other crops. *OsGS3* primarily controls seed length, whereas *OsGW2* modulates seed width and thickness through regulation of cell division [174]. Mutants of these genes are widely employed in crop breeding programs to substantially enhance seed size and productivity. Furthermore, gene-editing technologies such as CRISPR enable precise modification of seed size-regulating genes, accelerating the selection of superior crop varieties. For example, mutating or knocking out *OsGS3* significantly increases grain length, thereby boosting grain weight and yield per area [3].

Understanding molecular control of seed size also facilitates optimization of seed nutritional composition. Adjusting carbohydrate, protein, and lipid metabolism during seed filling significantly enhances nutritional value, such as increased protein content, improved starch quality, and elevated micronutrient concentrations [175]. In high-protein crops like soybean, increased seed size boosts protein content and essential amino acid profiles. In cereals, modulating endosperm development enhances starch accumulation and nutritional quality [176,177]. Moreover, regulating genes associated with seed size and related metabolic pathways increases mineral nutrients (e.g., iron, zinc) in seeds, enhancing nutritional quality, food security, and market adaptability [178,179].

Amid global climate change, knowledge of seed size regulation provides potential solutions to environmental challenges such as extreme climates and resource scarcity. Increasing seed size enhances crop resilience, significantly boosting yields per unit area and reducing dependence on fertilizers and irrigation [10,179]. Under drought or saline conditions, larger seeds exhibit enhanced drought and salt tolerance at seedling stages, substantially improving survival rates and productivity, especially under limited water or nutrient availability [10,180] (Figure 4). Looking ahead, integrating genomic editing and conventional breeding strategies to optimize seed size will increasingly support agricultural productivity and global food security.

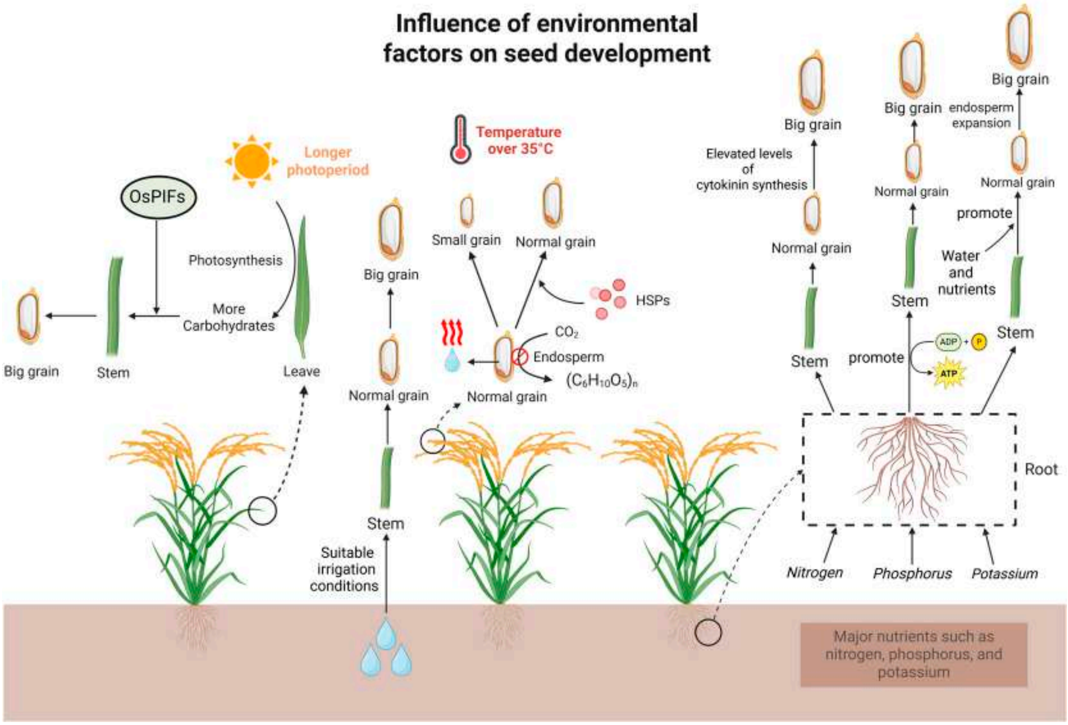

Figure 4. Environmental factors influencing grain size in rice. This figure illustrates how various environmental factors—such as light, water availability, soil nutrients, and temperature—affect the growth and development of rice grains by modulating plant hormone signaling and nutrient uptake. It also highlights the crucial roles of key macronutrients, including nitrogen, phosphorus, and potassium, in determining final grain size.

3. Application of Grain Shape Research in Rice Breeding

3.1. Molecular Regulatory Networks Lay the Foundation for Precision Breeding

Major progress in rice grain shape research has come from the elucidation of several key regulatory pathways, particularly BR signaling, the ubiquitin–proteasome system, and cell cycle regulation. In 2025, Wan Jianmin's team identified *SRG*, a gene encoding a kinesin-domain protein, as a positive regulator of grain size through the BR pathway. *OsWRKY53* activates *SRG* transcription under BR induction, while *OsBSK3* interacts with and phosphorylates the SRG protein, enhancing its stability and promoting microtubule organization. This leads to increased spikelet cell proliferation and extended grain length. Overexpression of SRG significantly increased thousand-grain weight, demonstrating its potential in yield improvement [181].

Additionally, Li Yunhai's group proposed a GS2–SUG1 module involved in the integration of multiple hormonal pathways. The transcription factor *GS2/OsGRF4* not only regulates grain size but also activates *SUG1*, a plant-specific DEP2/SRS1/EP2/OsRELA-like protein. *SUG1* functions as a molecular hub by interacting with *OsBZR1* (BR receptor), *OsMADS56* (flowering regulator), and *OsSPL13* (panicle development), thus coordinating BR, GA, and auxin signaling to regulate grain development. Introduction of the *SUG1Hap2* allele from indica rice into japonica backgrounds led to significant improvement in grain size and yield [101]. This result offers insight into inter-subspecific differences and provides a valuable allele for breeding programs.

3.2. Gene-Based Breeding Strategies and Germplasm Innovation

Functional characterization of grain shape genes has enabled various breeding strategies, including gene editing, use of wild germplasm, and marker-assisted selection (MAS).

In 2025, Wang Lan and Liu Xiangdong's team cloned *OsGSW3.2* from a wild rice accession in Suixi, Guangdong. *OsGSW3.2* exhibits pleiotropic effects, regulating grain size, awn development, and chlorophyll biosynthesis. It interacts with *OsGSK4*, a negative regulator of BR signaling. CRISPR/Cas9 knockout lines exhibited larger grains, while overexpression lines showed reduced grain size. Importantly, natural variation in wild rice for this gene includes favorable alleles that enhance grain weight [71]. This finding emphasizes the value of wild rice for modern molecular breeding and offers new insight into grain shape selection during domestication.

Although gene editing is a powerful tool for grain shape improvement, balancing yield and grain quality remains a challenge. Recent studies on *OsANK3*, encoding an ankyrin repeat protein, revealed dual roles in grain development. *OsANK3* regulates spikelet cell proliferation via cell cycle genes and also modulates starch metabolism by affecting both biosynthetic (e.g., *OsGBSSI*, *OsAGPL1*) and hydrolytic (e.g., *OsAmy1A*, *OsAmy3B*) genes. Knockout mutants showed increased plant height, grain size, and thousand-grain weight, but also higher chalkiness and reduced starch quality [190]. This highlights the need to optimize grain filling traits, possibly through spatiotemporal regulation or targeted editing.

Marker-assisted breeding based on functional polymorphisms has also made notable progress. Wan Jianmin's group identified *SMG4*, a MATE family transporter affecting grain shape by regulating spikelet cell division. Multiple alleles of *SMG4* were found, some strongly associated with grain size. Functional markers developed from these variants have been implemented in high-yielding japonica breeding programs. Similarly, molecular markers for *SUG1Hap2* and *WLGhap.B* have shown strong application potential in enhancing grain selection efficiency [191].

4. Perspectives

4.1. Multi-Omics Platforms Promote Intelligent Breeding of Grain Shape

As functional genomics advances, multi-omics integration and smart breeding platforms are becoming central to modern rice breeding. In 2025, the Crop Science Institute of the Chinese Academy of Agricultural Sciences released RiceAtlas, an integrated omics platform covering 6044 rice varieties from five major ecological regions. The platform includes high-depth resequencing data and phenotypic data from 212 trials across 19 locations. Using RiceAtlas, researchers have identified 3131 loci associated with traits such as heading date, yield, and stress response [192].

RiceAtlas has driven significant progress in grain shape research by providing a high-density variant map that enables tracking of grain shape-related alleles across different ecological regions, supporting the online design of trait-associated modules, and facilitating rapid gene mapping and functional validation. Leveraging this platform, researchers successfully improved the grain size of the japonica variety "Suijing 4" through precise introgression of favorable alleles, achieving enhancement of grain traits without compromising stress resistance [192]. Furthermore, RiceAtlas revealed ecotypic variation in grain shape preferences—long slender grains (L/W > 3.0) in indica regions and short round grains (L/W ~1.8–2.2) in japonica areas—reflecting both consumer preferences and environmental adaptations. Based on these patterns, RiceAtlas enables ecological zone-specific gene combination recommendations, supporting regionally optimized precision breeding [192].

4.2. Challenges and Future Outlook

4.2.1. Challenges

Despite substantial advances in elucidating the genetic control of grain traits, several challenges persist in the practical application of these genes in breeding programs. One of the major obstacles is the pleiotropic nature of many key regulatory genes. For example, *OsGSW3.2* simultaneously influences grain size, awn development, and chlorophyll content, complicating targeted trait improvement [76]. Similarly, mutations in *OsANK3* have been reported to enhance yield potential, but at the cost of reduced grain quality [190]. These examples highlight the difficulty of uncoupling desirable and undesirable phenotypes. To overcome this, refined genetic strategies—such as the use of tissue-specific or inducible promoters, as well as temporally controlled gene-editing tools like conditionally activated CRISPR/Cas systems—are increasingly being explored to achieve precise trait regulation while minimizing adverse trade-offs.

Another limitation is the lack of understanding of non-additive effects. For example, the OsMAPK6–GW6a and CLG1–GW6a modules exhibit complex interactions that are difficult to model [193]. Predictive tools integrating structural biology and artificial intelligence will be necessary to improve the reliability of multigene design.

4.2.2. Future Outlook

Future directions in grain shape research are expected to focus on the deep mining of wild rice resources to uncover novel alleles and broaden the genetic base [194], the development of epigenetic tools for stable and heritable trait regulation such as grain shape "memory" systems derived from modules like GW6a–HDR3 [195], and the integration of intelligent breeding platforms such as RiceAtlas with machine learning algorithms to achieve holistic optimization of yield, grain shape, and quality traits across diverse environments [192].

5. Conclusions

In conclusion, rice grain shape research has transitioned from single-gene analysis to complex regulatory networks and from empirical breeding to precision design. Building on this foundation, 726 cutting-edge technologies are being systematically incorporated into breeding pipelines: CRISPR/Cas9-based editors enable single-base precise substitutions and multiplexed site stacking; molecular module design platforms allow functional modules such as *GL7*, *GW8*, and *GW5* to be combined in a "Lego-like" manner according to yield–quality–resistance requirements; over 3000 wild and local rice accessions have been deeply analyzed through pan-genomics and phenomics, providing a vast reservoir of allelic variation to broaden the genetic base; and AI-driven phenotype–genotype–environment big data prediction systems compress the traditional 8–10-year breeding cycle into just 3–4 years. Through integration of gene editing, molecular modules, wild germplasm, and omics platforms, grain shape breeding is progressing toward coordinated improvement of yield and quality. As functional genomics and synthetic biology converge, precision grain design will play a crucial role in ensuring global food security.

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References

1. Fu, Y.; Zhao, H.; Xiao, M.; Zhang, G.; Wang, S. Research progress on elongation of cooked rice. *J. South China Agric. Univ.* **2023**, *44*, 670–678.
2. Shoukat, R.; Cappai, M.; Pilia, L.; Pia, G. Rice Starch Chemistry, Functional Properties, and Industrial Applications: A Review. *Polymers* **2025**, *17*, 110. [CrossRef] [PubMed]
3. Zhang, T.; Wang, Z.; Liu, Q.; Zhao, D. Genetic Improvement of rice Grain size Using the CRISPR/Cas9 System. *Rice* **2025**, *18*, 3. [CrossRef]
4. Jamil, M.; Ahmad, W.; Sanwal, M.; Maqsood, M.F. Gene editing and GWAS for digital imaging analysis of wheat grain weight, size and shape are inevitable to enhance the yield. *Cereal Res. Commun.* **2025**, *53*, 1199–1218. [CrossRef]
5. Li, T.; Cao, H.; Xiong, L.; Wang, F.; Li, S.; Gu, H.; Luo, W.; He, G.; Liang, S. Research Progress on the Function of Rice Grain Type Genes. *Guangdong Agric. Sci.* **2023**, *50*, 12–28.
6. Khush, G.S. Origin, dispersal, cultivation and variation of rice. *Plant Mol. Biol.* **1997**, *35*, 25–34. [CrossRef]
7. Juliano, B.O.; Villareal, C.P. *Grain Quality Evaluation of World Rices*; International Rice Research Institute: Los Baños, Philippines, 1993.
8. Heinemann, R.J.B.; Fagundes, P.L.; Pinto, E.A.; Penteado, M.V.C.; Lanfer-Marquez, U.M. Comparative study of nutrient composition of commercial brown, parboiled and milled rice from Brazil. *J. Food Compos. Anal.* **2005**, *18*, 287–296. [CrossRef]
9. Díaz-Benito, P.; Banakar, R.; Rodríguez-Menéndez, S.; Capell, T.; Pereiro, R.; Christou, P.; Abadía, J.; Fernández, B.; Álvarez-Fernández, A. Iron and Zinc in the Embryo and Endosperm of Rice (*Oryza sativa* L.) Seeds in Contrasting 2′-Deoxymugineic Acid/Nicotianamine Scenarios. *Front. Plant Sci.* **2018**, *9*, 1190. [CrossRef]
10. Wang, X.; Sun, J.; Yi, Z.; Dong, S. Effects of seed size on soybean performance: Germination, growth, stress resistance, photosynthesis, and yield. *BMC Plant Biol.* **2025**, *25*, 219. [CrossRef] [PubMed]
11. Li, W.W.; Wang, L.; Xue, H.; Zhang, M.M.; Song, H.; Qin, M.; Dong, Q.Z. Molecular and genetic basis of plant architecture in soybean. *Front. Plant Sci.* **2024**, *15*, 1477616. [CrossRef] [PubMed]
12. Gao, Y.; Peng, J.Z.; Qiao, Y.C.; Wang, G.P. Natural Allelic Variations of *Bch10G006400* Controlling Seed Size in Chieh-qua (*Benincasa hispida Cogn*. var. *Chieh-qua How*). *Int. J. Mol. Sci.* **2024**, *25*, 4236. [CrossRef] [PubMed]
13. Zhao, J.; He, Y.Q.; Huang, S.L.; Wang, Z.F. Advances in the Identification of Quantitative Trait Loci and Genes Involved in Seed Vigor in Rice. *Front. Plant Sci.* **2021**, *12*, 659307. [CrossRef] [PubMed]
14. Ren, Z.W.; Kopittke, P.M.; Zhao, F.J.; Wang, P. Nutrient accumulation and transcriptome patterns during grain development in rice. *J. Exp. Bot.* **2023**, *74*, 909–930. [CrossRef] [PubMed]
15. Ji, J.; Yang, L.; Fang, Z.; Zhang, Y.; Zhuang, M.; Lv, H.; Wang, Y. Plant SWEET Family of Sugar Transporters: Structure, Evolution and Biological Functions. *Biomolecules* **2022**, *12*, 205. [CrossRef]
16. Barreda, L.; Boutet, S.; De Vos, D.; Boulard, C.; Grain, D.; Lepiniec, L.; Corso, M. Specialized metabolome and transcriptome atlas of developing Arabidopsis thaliana seed under warm temperatures. *Sci. Data* **2025**, *12*, 306. [CrossRef]
17. Pankaj, R.; Lima, R.B.; Figueiredo, D.D. Hormonal regulation and crosstalk during early endosperm and seed coat development. *Plant Reprod.* **2024**, *38*, 5. [CrossRef]
18. Zhang, Z.; Han, H.; Zhao, J.; Liu, Z.; Deng, L.; Wu, L.; Niu, J.; Guo, Y.; Wang, G.; Gou, X.; et al. Peptide hormones in plants. *Mol. Hortic.* **2025**, *5*, 7. [CrossRef]
19. Lorenzo-Manzanarez, J.L.; Enríquez-Valencia, A.J.; Olivares-García, C.A.; Ibarra-Laclette, E.; Velázquez-López, O.; Ruiz-May, E.; Loyola-Vargas, V.M.; Kú-González, A.F.; Arteaga-Vázquez, M.A.; Mata-Rosas, M. Genome-wide analysis of ARF gene family and miR160 in avocado (*Persea americana* Mill.) and their roles in somatic embryogenesis from zygotic embryos. *Planta* **2025**, *261*, 61. [CrossRef]
20. Choudhary, P.; Aggarwal, P.R.; Salvi, P.; Muthamilarasan, M. Molecular insight into auxin signaling and associated network modulating stress responses in rice. *Plant Physiol. Biochem.* **2025**, *219*, 109452. [CrossRef]
21. Sims, K.; Abedi-Samakush, F.; Szulc, N.; Honti, M.G.M.; Mattsson, J. OsARF11 Promotes Growth, Meristem, Seed, and Vein Formation during Rice Plant Development. *Int. J. Mol. Sci.* **2021**, *22*, 4089. [CrossRef]
22. Wang, F.; Lin, J.; Yang, F.; Chen, X.; Liu, Y.; Yan, L.; Chen, J.; Wang, Z.; Xie, H.; Zhang, J.; et al. The OsMAPK5-OsWRKY72 module negatively regulates grain length and grain weight in rice. *J. Integr. Plant Biol.* **2024**, *66*, 2648–2663. [CrossRef]
23. Qiao, J.; Jiang, H.; Lin, Y.; Shang, L.; Wang, M.; Li, D.; Fu, X.; Geisler, M.; Qi, Y.; Gao, Z.; et al. A novel miR167a-OsARF6-OsAUX3 module regulates grain length and weight in rice. *Mol. Plant* **2021**, *14*, 1683–1698. [CrossRef]
24. Huang, G.; Hu, H.; van de Meene, A.; Zhang, J.; Dong, L.; Zheng, S.; Zhang, F.; Betts, N.S.; Liang, W.; Bennett, M.J.; et al. AUXIN RESPONSE FACTORS 6 and 17 control the flag leaf angle in rice by regulating secondary cell wall biosynthesis of lamina joints. *Plant Cell* **2021**, *33*, 3120–3133. [CrossRef] [PubMed]

25. Liu, X.; Yang, C.Y.; Miao, R.; Zhou, C.L.; Cao, P.H.; Lan, J.; Zhu, X.J.; Mou, C.L.; Huang, Y.S.; Liu, S.J.; et al. DS1/OsEMF1 interacts with OsARF11 to control rice architecture by regulation of brassinosteroid signaling. *Rice* **2018**, *11*, 46. [CrossRef]
26. Parry, G.; Calderon-Villalobos, L.I.; Prigge, M.; Peret, B.; Dharmasiri, S.; Itoh, H.; Lechner, E.; Gray, W.M.; Bennett, M.; Estelle, M. Complex regulation of the TIR1/AFB family of auxin receptors. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 22540–22545. [CrossRef] [PubMed]
27. Thakur, J.K.; Tyagi, A.K.; Khurana, J.P. OsIAA1, an Aux/IAA cDNA from rice, and changes in its expression as influenced by auxin and light. *DNA Res.* **2001**, *8*, 193–203. [CrossRef]
28. Zhou, Y.; Ma, B.; Tao, J.J.; Yin, C.C.; Hu, Y.; Huang, Y.H.; Wei, W.; Xin, P.Y.; Chu, J.F.; Zhang, W.K.; et al. Rice EIL1 interacts with OsIAAs to regulate auxin biosynthesis mediated by the tryptophan aminotransferase MHZ10/OsTAR2 during root ethylene responses. *Plant Cell* **2022**, *34*, 4366–4387. [CrossRef] [PubMed]
29. Hernández-García, J.; Carrillo-Carrasco, V.P.; Rienstra, J.; Tanaka, K.; de Roij, M.; Dipp-Álvarez, M.; Freire-Ríos, A.; Crespo, I.; Boer, R.; van den Berg, W.A.M.; et al. Evolutionary origins and functional diversification of Auxin Response Factors. *Nat. Commun.* **2024**, *15*, 10909. [CrossRef]
30. Huang, S.; Zhou, B.; Gao, Z.; Li, H.; Ding, Z. Increased expression of OsSAUR23 and OsRR9 regulates rice plant and organ size. *Crop J.* **2025**, *13*, 350–359. [CrossRef]
31. Li, Y.; Ren, M.; Wu, Y.; Wang, L.; Zhao, K.; Gao, H.; Li, M.; Liu, Y.; Zhu, J.; Xu, J.; et al. A root system architecture regulator modulates OsPIN2 polar localization in rice. *Nat. Commun.* **2025**, *16*, 15. [CrossRef]
32. Jiang, J.Z.; Kuo, C.H.; Chen, B.H.; Chen, M.K.; Lin, C.S.; Ho, S.L. Effects of OsCDPK1 on the Structure and Physicochemical Properties of Starch in Developing Rice Seeds. *Int. J. Mol. Sci.* **2018**, *19*, 3247. [CrossRef]
33. Hou, M.; Zhang, Y.; Xu, X.; Ai, H. Advances in auxin synthesis, transport, and signaling in rice: Implications for stress resilience and crop improvement. *Front. Plant Sci.* **2025**, *15*, 1516884. [CrossRef]
34. Saha, S.R.; Islam, S.M.S.; Itoh, K. Identification of abiotic stress-responsive genes: A genome-wide analysis of the cytokinin response regulator gene family in rice. *Genes Genet. Syst.* **2024**, *99*, 24-00068. [CrossRef]
35. Liu, Y.; Peng, X.; Ma, A.; Liu, W.; Liu, B.; Yun, D.J.; Xu, Z.Y. Type-B response regulator OsRR22 forms a transcriptional activation complex with OsSLR1 to modulate OsHKT2;1 expression in rice. *Sci. China Life Sci.* **2023**, *66*, 2922–2934. [CrossRef]
36. Pellarin, I.; Dall'Acqua, A.; Favero, A.; Segatto, I.; Rossi, V.; Crestan, N.; Karimbayli, J.; Belletti, B.; Baldassarre, G. Cyclin-dependent protein kinases and cell cycle regulation in biology and disease. *Signal Transduct. Target. Ther.* **2025**, *10*, 11. [CrossRef] [PubMed]
37. Rathore, R.S.; Mishra, M.; Pareek, A.; Singla-Pareek, S.L. Concurrent improvement of rice grain yield and abiotic stress tolerance by overexpression of cytokinin activating enzyme LONELY GUY (OsLOG). *Plant Physiol. Biochem.* **2024**, *211*, 108635. [CrossRef]
38. Sosnowski, J.; Truba, M.; Vasileva, V. The Impact of Auxin and Cytokinin on the Growth and Development of Selected Crops. *Agriculture* **2023**, *13*, 724. [CrossRef]
39. Kotov, A.A.; Kotova, L.M. Auxin/cytokinin antagonism in shoot development: From moss to seed plants. *J. Exp. Bot.* **2023**, *74*, 6391–6395. [CrossRef] [PubMed]
40. Amiri, S.; Mohammadi, R. The Effects of Culture Media and Plant Growth Regulators on Micropropagation of Cornelian Cherry (*Cornus mas* L.). *Proc. Natl. Acad. Sci. India Sect. B Biol. Sci.* **2025**, *95*, 439–445. [CrossRef]
41. Oikawa, T.; Koshioka, M.; Kojima, K.; Yoshida, H.; Kawata, M. A role of OsGA20ox1, encoding an isoform of gibberellin 20-oxidase, for regulation of plant stature in rice. *Plant Mol. Biol.* **2004**, *55*, 687–700. [CrossRef]
42. Hao, X.H.; Hu, S.; Zhao, D.; Tian, L.F.; Xie, Z.J.; Wu, S.; Hu, W.L.; Lei, H.; Li, D.P. OsGA3ox genes regulate rice fertility and plant height by synthesizing diverse active GA. *Yi Chuan* **2023**, *45*, 845–855. [PubMed]
43. Hu, J.; Su, H.; Cao, H.; Wei, H.; Fu, X.; Jiang, X.; Song, Q.; He, X.; Xu, C.; Luo, K. AUXIN RESPONSE FACTOR7 integrates gibberellin and auxin signaling via interactions between DELLA and AUX/IAA proteins to regulate cambial activity in poplar. *Plant Cell* **2022**, *34*, 2688–2707. [CrossRef] [PubMed]
44. Ito, T.; Okada, K.; Fukazawa, J.; Takahashi, Y. DELLA-dependent and -independent gibberellin signaling. *Plant Signal Behav.* **2018**, *13*, e1445933. [CrossRef]
45. Xie, Z.; Jin, L.; Sun, Y.; Zhan, C.; Tang, S.; Qin, T.; Liu, N.; Huang, J. OsNAC120 balances plant growth and drought tolerance by integrating GA and ABA signaling in rice. *Plant Commun.* **2024**, *5*, 100782. [CrossRef]
46. Abe, A.; Takagi, H.; Fujibe, T.; Aya, K.; Kojima, M.; Sakakibara, H.; Uemura, A.; Matsuoka, M.; Terauchi, R. OsGA20ox1, a candidate gene for a major QTL controlling seedling vigor in rice. *Theor. Appl. Genet.* **2012**, *125*, 647–657. [CrossRef]
47. Wang, Y.; Deng, D. Molecular basis and evolutionary pattern of GA-GID1-DELLA regulatory module. *Mol. Genet. Genom.* **2014**, *289*, 1–9. [CrossRef] [PubMed]
48. Sun, T.P. The molecular mechanism and evolution of the GA-GID1-DELLA signaling module in plants. *Curr. Biol.* **2011**, *21*, R338–R345. [CrossRef]
49. Liu, X.; Chen, Y.; Yuan, B.; Peng, M.; Zhao, Y.; Chen, T.; Lu, J.; Li, F.; Lu, X.; Yang, J. Identification of the citrus GRF gene family and its expression in fruit peel thickening mediated by gibberellin. *BMC Plant Biol.* **2025**, *25*, 216. [CrossRef]

50. Wang, J.D.; Wang, J.; Huang, L.C.; Kan, L.J.; Wang, C.X.; Xiong, M.; Zhou, P.; Zhou, L.H.; Chen, C.; Zhao, D.S.; et al. ABA-mediated regulation of rice grain quality and seed dormancy via the NF-YB1-SLRL2-bHLH144 Module. *Nat. Commun.* **2024**, *15*, 4493. [CrossRef]
51. Zhao, F.; Ma, Q.; Li, Y.; Jiang, M.; Zhou, Z.; Meng, S.; Peng, Y.; Zhang, J.; Ye, N.; Liu, B. OsNAC2 regulates seed dormancy and germination in rice by inhibiting ABA catabolism. *Biochem. Biophys. Res. Commun.* **2023**, *682*, 335–342. [CrossRef]
52. Li, Y.; Zhou, J.; Li, Z.; Qiao, J.; Quan, R.; Wang, J.; Huang, R.; Qin, H. SALT AND ABA RESPONSE ERF1 improves seed germination and salt tolerance by repressing ABA signaling in rice. *Plant Physiol.* **2022**, *189*, 1110–1127. [CrossRef]
53. Jiang, M.; Song, Y.; Yang, R.; Zheng, C.; Zheng, Y.; Zhang, H.; Li, S.; Tan, Y.; Huang, J.; Shu, Q.; et al. Melatonin activates the OsbZIP79-OsABI5 module that orchestrates nitrogen and ROS homeostasis to alleviate nitrogen-limitation stress in rice. *Plant Commun.* **2023**, *4*, 100674. [CrossRef]
54. Zou, M.; Guan, Y.; Ren, H.; Zhang, F.; Chen, F. A bZIP transcription factor, OsABI5, is involved in rice fertility and stress tolerance. *Plant Mol. Biol.* **2008**, *66*, 675–683. [CrossRef]
55. Chen, Y.; Xiang, Z.; Liu, M.; Wang, S.; Zhang, L.; Cai, D.; Huang, Y.; Mao, D.; Fu, J.; Chen, L. ABA biosynthesis gene OsNCED3 contributes to preharvest sprouting resistance and grain development in rice. *Plant Cell Environ.* **2023**, *46*, 1384–1401. [CrossRef] [PubMed]
56. Yang, B.; Cheng, J.; Wang, J.; Cheng, Y.; He, Y.; Zhang, H.; Wang, Z. Physiological characteristics of cold stratification on seed dormancy release in rice. *Plant Growth Regul.* **2019**, *89*, 131–141. [CrossRef]
57. Yang, X.; Zhang, J.; Wang, L.; Zhang, C.; Xu, P.; Li, Y.; Yu, S.; Li, Y. BR signalling haplotypes contribute to indica-japonica differentiation for grain yield and quality in rice. *Plant Biotechnol. J.* **2025**, *23*, 1618–1636. [CrossRef] [PubMed]
58. Dong, L.; Shi, J.; Persson, S.; Huang, G.; Zhang, D. RMD and Its Suppressor MAPK6 Control Root Circumnutation and Obstacle Avoidance via BR Signaling. *Int. J. Mol. Sci.* **2024**, *25*, 10543. [CrossRef]
59. Su, X.; Liu, X.; Li, C.; Zhang, Y. 24-epibrassinolide as a multidimensional regulator of rice (*Oryza sativa*) physiological and molecular responses under isoproturon stress. *Ecotoxicol. Environ. Saf.* **2024**, *281*, 116575. [CrossRef] [PubMed]
60. Zhang, X.; Meng, W.; Liu, D.; Pan, D.; Yang, Y.; Chen, Z.; Ma, X.; Yin, W.; Niu, M.; Dong, N.; et al. Enhancing rice panicle branching and grain yield through tissue-specific brassinosteroid inhibition. *Science* **2024**, *383*, eadk8838. [CrossRef]
61. Pan, Y.H.; Gao, L.J.; Liang, Y.T.; Zhao, Y.; Liang, H.F.; Chen, W.W.; Yang, X.H.; Qing, D.J.; Gao, J.; Wu, H.; et al. OrMKK3 Influences Morphology and Grain Size in Rice. *J. Plant Biol.* **2023**, *66*, 269–282. [CrossRef]
62. Huang, J.; Chen, Z.; Lin, J.; Chen, J.; Wei, M.; Liu, L.; Yu, F.; Zhang, Z.; Chen, F.; Jiang, L.; et al. Natural variation of the BRD2 allele affects plant height and grain size in rice. *Planta* **2022**, *256*, 27. [CrossRef]
63. Blanco-Touriñán, N.; Rana, S.; Nolan, T.M.; Li, K.; Vukašinović, N.; Hsu, C.W.; Russinova, E.; Hardtke, C.S. The brassinosteroid receptor gene BRI1 safeguards cell-autonomous brassinosteroid signaling across tissues. *Sci. Adv.* **2024**, *10*, eadq3352. [CrossRef]
64. Luo, Y.; Takagi, J.; Claus, L.A.N.; Zhang, C.; Yasuda, S.; Hasegawa, Y.; Yamaguchi, J.; Shan, L.; Russinova, E.; Sato, T. Deubiquitinating enzymes UBP12 and UBP13 stabilize the brassinosteroid receptor BRI1. *EMBO Rep.* **2022**, *23*, e53354. [CrossRef] [PubMed]
65. Bai, M.Y.; Zhang, L.Y.; Gampala, S.S.; Zhu, S.W.; Song, W.Y.; Chong, K.; Wang, Z.Y. Functions of OsBZR1 and 14-3-3 proteins in brassinosteroid signaling in rice. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 13839–13844. [CrossRef]
66. Cao, X.H.; Wei, Y.N.; Shen, B.D.; Liu, L.C.; Mao, J. Interaction of the Transcription Factors BES1/BZR1 in Plant Growth and Stress Response. *Int. J. Mol. Sci.* **2024**, *25*, 6836. [CrossRef] [PubMed]
67. Pal, A.K.; Gandhivel, V.H.-S.; Nambiar, A.B.; Shivaprasad, P.V. Upstream regulator of genomic imprinting in rice endosperm is a small RNA-associated chromatin remodeler. *Nat. Commun.* **2024**, *15*, 7807. [CrossRef]
68. Gao, X.; Zhang, J.Q.; Zhang, X.; Zhou, J.; Jiang, Z.; Huang, P.; Tang, Z.; Bao, Y.; Cheng, J.; Tang, H.; et al. Rice qGL3/OsPPKL1 Functions with the GSK3/SHAGGY-Like Kinase OsGSK3 to Modulate Brassinosteroid Signaling. *Plant Cell* **2019**, *31*, 1077–1093. [CrossRef]
69. Yan, L.; Jiao, B.; Duan, P.; Guo, G.; Zhang, B.; Jiao, W.; Zhang, H.; Wu, H.; Zhang, L.; Liang, H.; et al. Control of grain size and weight by the RNA-binding protein EOG1 in rice and wheat. *Cell Rep.* **2024**, *43*, 114856. [CrossRef] [PubMed]
70. Tian, P.; Liu, J.; Yan, B.; Li, S.; Lei, B.; Shen, R.; Lei, C.; Xu, M. OsBSK3 Positively Regulates Grain Length and Weight by Inhibiting the Phosphatase Activity of OsPPKL1. *Plants* **2022**, *11*, 1586. [CrossRef]
71. Liang, X.; Liu, Y.; Tian, M.; Jiang, W.; Zheng, Y.; Chen, Z.; Liu, X.; Wang, L. The natural variation allele OsGSW3.2 in Oryza rufipogon is involved in brassinosteroid signaling and influences grain size and weight. *Plant J.* **2025**, *121*, e70110. [CrossRef]
72. Liu, C.; Ma, T.; Yuan, D.; Zhou, Y.; Long, Y.; Li, Z.; Dong, Z.; Duan, M.; Yu, D.; Jing, Y.; et al. The OsEIL1-OsERF115-target gene regulatory module controls grain size and weight in rice. *Plant Biotechnol. J.* **2022**, *20*, 1470–1486. [CrossRef]
73. Qin, H.; Xiao, M.; Li, Y.; Huang, R. Ethylene Modulates Rice Root Plasticity under Abiotic Stresses. *Plants* **2024**, *13*, 432. [CrossRef]
74. Li, Z.; Chen, H.; Yuan, P.; Jiang, X.; Li, Z.M.; Wang, S.T.; Zhou, T.G.; Zhu, H.Y.; Bian, Q.; Zhu, X.F.; et al. IDD10-NAC079 transcription factor complex regulates sheath blight resistance by inhibiting ethylene signaling in rice. *J. Adv. Res.* **2024**, *71*, 93–106. [CrossRef]

75. Xie, W.; Ding, C.; Hu, H.; Dong, G.; Zhang, G.; Qian, Q.; Ren, D. Molecular Events of Rice AP2/ERF Transcription Factors. *Int. J. Mol. Sci.* **2022**, *23*, 12013. [CrossRef]
76. Qin, H.; Wang, J.; Chen, X.; Wang, F.; Peng, P.; Zhou, Y.; Miao, Y.; Zhang, Y.; Gao, Y.; Qi, Y.; et al. Rice OsDOF15 contributes to ethylene-inhibited primary root elongation under salt stress. *New Phytol.* **2019**, *223*, 798–813. [CrossRef]
77. Lee, H.Y.; Yoon, G.M. Regulation of Ethylene Biosynthesis by Phytohormones in Etiolated Rice (*Oryza sativa* L.) Seedlings. *Mol. Cells* **2018**, *41*, 311–319.
78. Rzewuski, G.; Sauter, M. Ethylene biosynthesis and signaling in rice. *Plant Sci.* **2008**, *175*, 32–42. [CrossRef]
79. Huang, Y.H.; Han, J.Q.; Ma, B.; Cao, W.Q.; Li, X.K.; Xiong, Q.; Zhao, H.; Zhao, R.; Zhang, X.; Zhou, Y.; et al. A translational regulator MHZ9 modulates ethylene signaling in rice. *Nat. Commun.* **2023**, *14*, 4674. [CrossRef] [PubMed]
80. Ma, B.; He, S.J.; Duan, K.X.; Yin, C.C.; Chen, H.; Yang, C.; Xiong, Q.; Song, Q.X.; Lu, X.; Chen, H.W.; et al. Identification of rice ethylene-response mutants and characterization of MHZ7/OsEIN2 in distinct ethylene response and yield trait regulation. *Mol. Plant* **2013**, *6*, 1830–1848. [CrossRef]
81. Li, X.-K.; Huang, Y.-H.; Zhao, R.; Cao, W.-Q.; Lu, L.; Han, J.-Q.; Zhou, Y.; Zhang, X.; Wu, W.-A.; Tao, J.-J.; et al. Membrane protein MHZ3 regulates the on-off switch of ethylene signaling in rice. *Nat. Commun.* **2024**, *15*, 5987. [CrossRef] [PubMed]
82. Huang, S.; Wang, H.; Liu, S.; Lu, S.; Hua, J.; Zou, B. Ethylene antagonizes ABA and inhibits stomatal closure and chilling tolerance in rice. *J. Exp. Bot.* **2025**. [CrossRef]
83. Yan, Y.; Wei, M.X.; Li, Y.; Tao, H.; Wu, H.Y.; Chen, Z.F.; Li, C.; Xu, J.H. MiR529a controls plant height, tiller number, panicle architecture and grain size by regulating SPL target genes in rice (*Oryza sativa* L.). *Plant Sci.* **2021**, *302*, 110728. [CrossRef]
84. Zhang, X.F.; Yang, C.Y.; Lin, H.X.; Wang, J.W.; Xue, H.W. Rice SPL12 coevolved with GW5 to determine grain shape. *Sci Bull.* **2021**, *66*, 2353–2357. [CrossRef]
85. Si, L.; Chen, J.; Huang, X.; Gong, H.; Luo, J.; Hou, Q.; Zhou, T.; Lu, T.; Zhu, J.; Shangguan, Y.; et al. OsSPL13 controls grain size in cultivated rice. *Nat. Genet.* **2016**, *48*, 447–456. [CrossRef]
86. Guo, X.; Chen, Y.; Hu, Y.; Feng, F.; Zhu, X.; Sun, H.; Li, J.; Zhao, Q.; Sun, H. OsMADS5 interacts with OsSPL14/17 to inhibit rice root elongation by restricting cell proliferation of root meristem under ammonium supply. *Plant J.* **2023**, *116*, 87–99. [CrossRef] [PubMed]
87. Li, Y.; He, Y.; Liu, Z.; Qin, T.; Wang, L.; Chen, Z.; Zhang, B.; Zhang, H.; Li, H.; Liu, L.; et al. OsSPL14 acts upstream of OsPIN1b and PILS6b to modulate axillary bud outgrowth by fine-tuning auxin transport in rice. *Plant J.* **2022**, *111*, 1167–1182. [CrossRef]
88. Jiao, Y.; Wang, Y.; Xue, D.; Wang, J.; Yan, M.; Liu, G.; Dong, G.; Zeng, D.; Lu, Z.; Zhu, X.; et al. Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. *Nat. Genet.* **2010**, *42*, 541–544. [CrossRef]
89. Wang, S.; Li, S.; Liu, Q.; Wu, K.; Zhang, J.; Wang, S.; Wang, Y.; Chen, X.; Zhang, Y.; Gao, C.; et al. The OsSPL16-GW7 regulatory module determines grain shape and simultaneously improves rice yield and grain quality. *Nat. Genet.* **2015**, *47*, 949–954. [CrossRef] [PubMed]
90. Wang, S.; Wu, K.; Yuan, Q.; Liu, X.; Liu, Z.; Lin, X.; Zeng, R.; Zhu, H.; Dong, G.; Qian, Q.; et al. Control of grain size, shape and quality by OsSPL16 in rice. *Nat. Genet.* **2012**, *44*, 950–954. [CrossRef] [PubMed]
91. Yuan, H.; Qin, P.; Hu, L.; Zhan, S.; Wang, S.; Gao, P.; Li, J.; Jin, M.; Xu, Z.; Gao, Q.; et al. OsSPL18 controls grain weight and grain number in rice. *J. Genet. Genom.* **2019**, *46*, 41–51. [CrossRef]
92. Tang, J.; Mei, E.; He, M.; Bu, Q.; Tian, X. Functions of OsWRKY24, OsWRKY70 and OsWRKY53 in regulating grain size in rice. *Planta* **2022**, *255*, 92. [CrossRef]
93. Tian, X.; He, M.; Mei, E.; Zhang, B.; Tang, J.; Xu, M.; Liu, J.; Li, X.; Wang, Z.; Tang, W.; et al. WRKY53 integrates classic brassinosteroid signaling and the mitogen-activated protein kinase pathway to regulate rice architecture and seed size. *Plant Cell* **2021**, *33*, 2753–2775. [CrossRef]
94. Zhang, C.Q.; Xu, Y.; Lu, Y.; Yu, H.X.; Gu, M.H.; Liu, Q.Q. The WRKY transcription factor OsWRKY78 regulates stem elongation and seed development in rice. *Planta* **2011**, *234*, 541–554. [CrossRef]
95. Mathew, I.E.; Das, S.; Mahto, A.; Agarwal, P. Three Rice NAC Transcription Factors Heteromerize and Are Associated with Seed Size. *Front. Plant Sci.* **2016**, *7*, 1638. [CrossRef] [PubMed]
96. Wang, X.L.; Liu, Y.C.; Hao, C.Y.; Li, T.; Majeed, U.; Liu, H.X.; Li, H.F.; Hou, J.; Zhang, X.Y. Wheat NAC-A18 regulates grain starch and storage proteins synthesis and affects grain weight. *Theor. Appl. Genet.* **2023**, *136*, 123. [CrossRef]
97. Li, Z.; Wei, X.; Tong, X.; Zhao, J.; Liu, X.; Wang, H.; Tang, L.; Shu, Y.; Li, G.; Wang, Y.; et al. The OsNAC23-Tre6P-SnRK1a feed-forward loop regulates sugar homeostasis and grain yield in rice. *Mol. Plant* **2022**, *15*, 706–722. [CrossRef]
98. Dwivedi, N.; Maji, S.; Waseem, M.; Thakur, P.; Kumar, V.; Parida, S.K.; Thakur, J.K. The Mediator subunit OsMED15a is a transcriptional co-regulator of seed size/weight-modulating genes in rice. *Biochim. Biophys. Acta Gene Regul. Mech.* **2019**, *1862*, 194432. [CrossRef]
99. Mathew, I.E.; Priyadarshini, R.; Mahto, A.; Jaiswal, P.; Parida, S.K.; Agarwal, P. SUPER STARCHY1/ONAC025 participates in rice grain filling. *Plant Direct* **2020**, *4*, e00249. [CrossRef] [PubMed]

100. Jin, S.K.; Zhang, M.Q.; Leng, Y.J.; Xu, L.N.; Jia, S.W.; Wang, S.L.; Song, T.; Wang, R.A.; Yang, Q.Q.; Tao, T.; et al. OsNAC129 Regulates Seed Development and Plant Growth and Participates in the Brassinosteroid Signaling Pathway. *Front. Plant Sci.* **2022**, *13*, 905148. [CrossRef] [PubMed]
101. Li, Y.; Huang, K.; Zhang, L.; Zhang, B.; Duan, P.; Zhang, G.; Huang, X.; Zhou, C.; Han, N.; Zheng, L.; et al. A molecular framework for the GS2-SUG1 module-mediated control of grain size and weight in rice. *Nat. Commun.* **2025**, *16*, 3944. [CrossRef]
102. Wang, Y.; Lv, Y.; Wen, Y.; Wang, J.; Hu, P.; Wu, K.; Chai, B.; Gan, S.; Liu, J.; Wu, Y.; et al. GS2 cooperates with IPA1 to control panicle architecture. *New Phytol.* **2025**, *245*, 2726–2743. [CrossRef]
103. Chen, W.; Hu, X.; Hu, L.; Hou, X.; Xu, Z.; Yang, F.; Yuan, M.; Chen, F.; Wang, Y.; Tu, B.; et al. Wide Grain 3, a GRAS Protein, Interacts with DLT to Regulate Grain Size and Brassinosteroid Signaling in Rice. *Rice* **2022**, *15*, 55. [CrossRef]
104. Xiao, Y.; Liu, D.; Zhang, G.; Tong, H.; Chu, C. Brassinosteroids Regulate OFP1, a DLT Interacting Protein, to Modulate Plant Architecture and Grain Morphology in Rice. *Front. Plant Sci.* **2017**, *8*, 1698. [CrossRef]
105. Huang, Y.; Dong, H.; Mou, C.; Wang, P.; Hao, Q.; Zhang, M.; Wu, H.; Zhang, F.; Ma, T.; Miao, R.; et al. Ribonuclease H-like gene SMALL GRAIN2 regulates grain size in rice through brassinosteroid signaling pathway. *J. Integr. Plant Biol.* **2022**, *64*, 1883–1900. [CrossRef] [PubMed]
106. Usman, B.; Nawaz, G.; Zhao, N.; Liao, S.; Qin, B.; Liu, F.; Liu, Y.; Li, R. Programmed Editing of Rice (*Oryza sativa* L.) OsSPL16 Gene Using CRISPR/Cas9 Improves Grain Yield by Modulating the Expression of Pyruvate Enzymes and Cell Cycle Proteins. *Int. J. Mol. Sci.* **2020**, *22*, 249. [CrossRef]
107. Jangam, A.P.; Pathak, R.R.; Raghuram, N. Microarray Analysis of Rice d1 (RGA1) Mutant Reveals the Potential Role of G-Protein Alpha Subunit in Regulating Multiple Abiotic Stresses Such as Drought, Salinity, Heat, and Cold. *Front. Plant Sci.* **2016**, *7*, 11. [CrossRef]
108. Yang, X.; Lu, J.; Shi, W.J.; Chen, Y.H.; Yu, J.W.; Chen, S.H.; Zhao, D.S.; Huang, L.C.; Fan, X.L.; Zhang, C.Q.; et al. RGA1 regulates grain size, rice quality and seed germination in the small and round grain mutant srg5. *BMC Plant Biol.* **2024**, *24*, 167. [CrossRef]
109. Hao, J.; Wang, D.; Wu, Y.; Huang, K.; Duan, P.; Li, N.; Xu, R.; Zeng, D.; Dong, G.; Zhang, B.; et al. The GW2-WG1-OsbZIP47 pathway controls grain size and weight in rice. *Mol. Plant* **2021**, *14*, 1266–1280. [CrossRef]
110. Liu, S.; Wu, J.; Mawia, A.M.; Wei, X.; Cao, R.; Jiao, G.; Wu, Y.; Zhang, J.; Xie, L.; Sheng, Z.; et al. A novel transcription factor OsMYB73 affects grain size and chalkiness by regulating endosperm storage substances' accumulation-mediated auxin biosynthesis signalling pathway in rice. *Plant Biotechnol. J.* **2025**, *23*, 1021–1038. [CrossRef] [PubMed]
111. Guo, M.; Zheng, C.; Shi, C.; Lu, X.; She, Z.; Jiang, S.; Tian, D.; Qin, Y. The OsZHD1 and OsZHD2, Two Zinc Finger Homeobox Transcription Factor, Redundantly Control Grain Size by Influencing Cell Proliferation in Rice. *Rice* **2025**, *18*, 20. [CrossRef] [PubMed]
112. Liang, P.; Wang, H.; Zhang, Q.; Zhou, K.; Li, M.; Li, R.; Xiang, S.; Zhang, T.; Ling, Y.; Yang, Z.; et al. Identification and Pyramiding of QTLs for Rice Grain Size Based on Short-Wide Grain CSSL-Z563 and Fine-Mapping of qGL3-2. *Rice* **2021**, *14*, 35. [CrossRef] [PubMed]
113. Luo, S.; Jia, J.; Liu, R.; Wei, R.; Guo, Z.; Cai, Z.; Chen, B.; Liang, F.; Xia, Q.; Nian, H.; et al. Identification of major QTLs for soybean seed size and seed weight traits using a RIL population in different environments. *Front. Plant Sci.* **2022**, *13*, 1094112. [CrossRef] [PubMed]
114. Arif, M.A.R.; Komyshev, E.G.; Genaev, M.A.; Koval, V.S.; Shmakov, N.A.; Börner, A.; Afonnikov, D.A. QTL Analysis for Bread Wheat Seed Size, Shape and Color Characteristics Estimated by Digital Image Processing. *Plants* **2022**, *11*, 2105. [CrossRef] [PubMed]
115. Lu, L.; Shao, D.; Qiu, X.J.; Sun, L.; Yan, W.H.; Zhou, X.C.; Yang, L.; He, Y.Q.; Yu, S.B.; Xing, Y.Z. Natural variation and artificial selection in four genes determine grain shape in rice. *New Phytol.* **2013**, *200*, 1269–1280. [CrossRef]
116. Yamaguchi, K.; Yamamoto, T.; Segami, S.; Horikawa, M.; Chaya, G.; Kitano, H.; Iwasaki, Y.; Miura, K. *gw2* mutation increases grain width and culm thickness in rice (*Oryza sativa* L.). *Breed. Sci.* **2020**, *70*, 456–461. [CrossRef]
117. Chen, Y.Y.; Zhu, A.K.; Xue, P.; Wen, X.X.; Cao, Y.R.; Wang, B.F.; Zhang, Y.; Shah, L.; Cheng, S.H.; Cao, L.Y.; et al. Effects of GS3 and GL3.1 for Grain Size Editing by CRISPR/Cas9 in Rice. *Rice Sci.* **2020**, *27*, 405–413. [CrossRef]
118. Takano-Kai, N.; Doi, K.; Yoshimura, A. GS3 participates in stigma exsertion as well as seed length in rice. *Breed. Sci.* **2011**, *61*, 244–250. [CrossRef]
119. Liu, J.F.; Chen, J.; Zheng, X.M.; Wu, F.Q.; Lin, Q.B.; Heng, Y.Q.; Tian, P.; Cheng, Z.J.; Yu, X.W.; Zhou, K.N.; et al. GW5 acts in the brassinosteroid signalling pathway to regulate grain width and weight in rice. *Nat. Plants* **2017**, *3*, 17043. [CrossRef]
120. Rasheed, H.; Fiaz, S.; Khan, M.A.; Mehmood, S.; Ullah, F.; Saeed, S.; Khan, S.U.; Yaseen, T.; Hussain, R.M.; Qayyum, A. Characterization of functional genes GS3 and GW2 and their effect on the grain size of various landraces of rice (*Oryza sativa*). *Mol. Biol. Rep.* **2022**, *49*, 5397–5403. [CrossRef]
121. Shomura, A.; Izawa, T.; Ebana, K.; Ebitani, T.; Kanegae, H.; Konishi, S.; Yano, M. Deletion in a gene associated with grain size increased yields during rice domestication. *Nat. Genet.* **2008**, *40*, 1023–1028. [CrossRef]

122. Gao, X.Y.; Zhang, X.J.; Lan, H.X.; Huang, J.; Wang, J.F.; Zhang, H.S. The additive effects of GS3 and qGL3 on rice grain length regulation revealed by genetic and transcriptome comparisons. *BMC Plant Biol.* **2015**, *15*, 156. [CrossRef]
123. Liu, R.; Zhao, D.; Li, P.; Xia, D.; Feng, Q.; Wang, L.; Wang, Y.; Shi, H.; Zhou, Y.; Chen, F.; et al. Natural variation in OsMADS1 transcript splicing affects rice grain thickness and quality by influencing monosaccharide loading to the endosperm. *Plant Commun.* **2025**, *6*, 101178. [CrossRef] [PubMed]
124. Abbas, W.; Shalmani, A.; Zhang, J.; Sun, Q.; Zhang, C.; Li, W.; Cui, Y.; Xiong, M.; Li, Y. The GW5-WRKY53-SGW5 module regulates grain size variation in rice. *New Phytol.* **2024**, *242*, 2011–2025. [CrossRef]
125. Ruan, B.; Shang, L.; Zhang, B.; Hu, J.; Wang, Y.; Lin, H.; Zhang, A.; Liu, C.; Peng, Y.; Zhu, L.; et al. Natural variation in the promoter of TGW2 determines grain width and weight in rice. *New Phytol.* **2020**, *227*, 629–640. [CrossRef] [PubMed]
126. He, J.B.; Meng, S.; Zhao, T.J.; Xing, G.N.; Yang, S.P.; Li, Y.; Guan, R.Z.; Lu, J.J.; Wang, Y.F.; Xia, Q.J.; et al. An innovative procedure of genome-wide association analysis fits studies on germplasm population and plant breeding. *Theor. Appl. Genet.* **2017**, *130*, 2327–2343. [CrossRef]
127. Zhu, L.; Shen, Y.; Dai, Z.; Miao, X.; Shi, Z. Gγ-protein GS3 Function in Tight Genetic Relation with OsmiR396/GS2 to Regulate Grain Size in Rice. *Rice* **2024**, *17*, 59. [CrossRef]
128. Ma, S.; Sun, Y.; Chen, X.; Guo, J.; Wu, S.; Wu, G.; Huang, G.; Kabore, M.A.F.; Woldegiorgis, S.T.; Ai, Y.; et al. Gα Solicits OsNYC4 and GW2-WG1-OsbZIP47 Modules to Regulate Grain Size in Rice (*Oryza sativa* L.). *Agronomy* **2024**, *14*, 1514. [CrossRef]
129. Liu, H.; Li, H.; Hao, C.; Wang, K.; Wang, Y.; Qin, L.; An, D.; Li, T.; Zhang, X. TaDA1, a conserved negative regulator of kernel size, has an additive effect with TaGW2 in common wheat (*Triticum aestivum* L.). *Plant Biotechnol. J.* **2020**, *18*, 1330–1342. [CrossRef]
130. Li, L.; Shi, F.; Wang, Y.Q.; Yu, X.F.; Zhi, J.J.; Guan, Y.B.; Zhao, H.Y.; Chang, J.L.; Chen, M.J.; Yang, G.X.; et al. TaSPL13 regulates inflorescence architecture and development in transgenic wheat (*Triticum aestivum* L.). *Plant Sci.* **2020**, *296*, 110516. [CrossRef]
131. Jin, T.; Zhang, K.; Hao, X.; Zhang, X.; Wang, S.; Long, W. Genome-Wide Analysis of Soybean GS3-Family Genes and Functional Characterization of GmGS3-1 Responses to Saline and Drought Stresses. *Agriculture* **2025**, *15*, 443. [CrossRef]
132. Peng, Y.-B.; Du, C.-Y.; He, Y.-N.; Zheng, C.-K.; Sun, W.; Zhou, J.-J.; Xie, L.-X.; Jiang, C.-H.; Xu, J.-D.; Wang, F.; et al. Natural variation of Grain size 3 allele differentially functions in regulating grain length in xian/indica and geng/japonica rice. *Euphytica* **2024**, *220*, 44. [CrossRef]
133. Wang, J.L.; Tang, M.Q.; Chen, S.; Zheng, X.F.; Mo, H.X.; Li, S.J.; Wang, Z.; Zhu, K.M.; Ding, L.N.; Liu, S.Y.; et al. Down-regulation of BnDA1, whose gene locus is associated with the seeds weight, improves the seeds weight and organ size in Brassica napus. *Plant Biotechnol. J.* **2017**, *15*, 1024–1033. [CrossRef]
134. Wei, B.; Jiao, Y. Grain size control in wheat: Toward a molecular understanding. *Seed Biol.* **2024**, *3*, e007. [CrossRef]
135. Liang, S.; Duan, Z.; He, X.; Yang, X.; Yuan, Y.; Liang, Q.; Pan, Y.; Zhou, G.; Zhang, M.; Liu, S.; et al. Natural variation in GmSW17 controls seed size in soybean. *Nat. Commun.* **2024**, *15*, 7417. [CrossRef] [PubMed]
136. Xu, J.; Liu, H.J.; Zhou, C.; Wang, J.X.; Wang, J.Q.; Han, Y.H.; Zheng, N.; Zhang, M.; Li, X.M. The ubiquitin-proteasome system in the plant response to abiotic stress: Potential role in crop resilience improvement. *Plant Sci.* **2024**, *342*, 112035. [CrossRef]
137. Verma, A.; Prakash, G.; Ranjan, R.; Tyagi, A.K.; Agarwal, P. Silencing of an Ubiquitin Ligase Increases Grain Width and Weight in indica Rice. *Front. Genet.* **2020**, *11*, 600378. [CrossRef]
138. Wen, Y.; Hu, P.; Fang, Y.; Tan, Y.; Wang, Y.; Wu, H.; Wang, J.; Wu, K.; Chai, B.; Zhu, L.; et al. GW9 determines grain size and floral organ identity in rice. *Plant Biotechnol. J.* **2024**, *22*, 915–928. [CrossRef]
139. Xie, Y.H.; Fan, Z.P.; Liang, X.Y.; Teng, K.C.; Huang, Z.J.; Huang, M.Y.; Zhao, H.; Xu, K.Z.; Li, J.X. OsPUB9 modulates leaf angle and grain size through the brassinosteroid signaling pathway in rice. *Plant J.* **2025**, *121*, e17230. [CrossRef] [PubMed]
140. Shi, C.; Ren, Y.; Liu, L.; Wang, F.; Zhang, H.; Tian, P.; Pan, T.; Wang, Y.; Jing, R.; Liu, T.; et al. Ubiquitin Specific Protease 15 Has an Important Role in Regulating Grain Width and Size in Rice. *Plant Physiol.* **2019**, *180*, 381–391. [CrossRef]
141. Wang, Z.; Liu, Z.; Lv, M.; Luan, Z.; Li, T.; Hu, J. Novel histone modifications and liver cancer: Emerging frontiers in epigenetic regulation. *Clin. Epigenet.* **2025**, *17*, 30. [CrossRef]
142. Sarki, Y.N.; Singh, H.B.; Keot, A.K.; Marwein, R.; Singha, D.L.; Dehury, B.; Chikkaputtaiah, C. Investigating the Role of OsHDT701 and Other Blast-Associated Negative Regulatory Genes in Indica Rice Cultivar Ranjit Using Combined Wet Lab and Computational Approaches. *Mol. Biotechnol.* **2024**. [CrossRef] [PubMed]
143. Du, W.; Lu, Y.; Li, Q.; Luo, S.; Shen, S.; Li, N.; Chen, X. TIR1/AFB proteins: Active players in abiotic and biotic stress signaling. *Front. Plant Sci.* **2022**, *13*, 1083409. [CrossRef] [PubMed]
144. Nawaz, M.; Sun, J.; Shabbir, S.; Khattak, W.A.; Ren, G.; Nie, X.; Bo, Y.; Javed, Q.; Du, D.; Sonne, C. A review of plants strategies to resist biotic and abiotic environmental stressors. *Sci. Total Environ.* **2023**, *900*, 165832. [CrossRef]
145. Wang, X.; Liu, X.; Su, Y.; Shen, H. Rice Responses to Abiotic Stress: Key Proteins and Molecular Mechanisms. *Int. J. Mol. Sci.* **2025**, *26*, 896. [CrossRef]
146. Li, Y.; Yin, M.; Wang, J.; Zhao, X.; Xu, J.; Wang, W.; Fu, B. Epitranscriptome profiles reveal participation of the RNA methyltransferase gene OsMTA1 in rice seed germination and salt stress response. *BMC Plant Biol.* **2025**, *25*, 115. [CrossRef]

147. Nau, T.; Cutts, S.; Naidoo, N. DNA methylation and its influence on the pathogenesis of osteoarthritis: A systematic literature review. *EFORT Open Rev.* **2025**, *10*, 66–74. [CrossRef]
148. Guo, M.; Zhang, W.; Mohammadi, M.A.; He, Z.; She, Z.; Yan, M.; Shi, C.; Lin, L.; Wang, A.; Liu, J.; et al. OsDDM1b Controls Grain Size by Influencing Cell Cycling and Regulating Homeostasis and Signaling of Brassinosteroid in Rice. *Front. Plant Sci.* **2022**, *13*, 873993. [CrossRef]
149. Wang, M.; He, Y.; Zhong, Z.; Papikian, A.; Wang, S.; Gardiner, J.; Ghoshal, B.; Feng, S.; Jami-Alahmadi, Y.; Wohlschlegel, J.A.; et al. Histone H3 lysine 4 methylation recruits DNA demethylases to enforce gene expression in Arabidopsis. *Nat. Plants* **2025**, *11*, 206–217. [CrossRef] [PubMed]
150. Lu, J.Q.; Jiang, Z.J.; Chen, J.Y.; Xie, M.Y.; Huang, W.D.; Li, J.; Zhuang, C.X.; Liu, Z.L.; Zheng, S.Y. SET DOMAIN GROUP 711-mediated H3K27me3 methylation of cytokinin metabolism genes regulates organ size in rice. *Plant Physiol.* **2024**, *194*, 2069–2085. [CrossRef]
151. Wang, H.; Tong, X.; Tang, L.; Wang, Y.; Zhao, J.; Li, Z.; Liu, X.; Shu, Y.; Yin, M.; Adegoke, T.V.; et al. RLB (RICE LATERAL BRANCH) recruits PRC2-mediated H3K27 tri-methylation on OsCKX4 to regulate lateral branching. *Plant Physiol.* **2022**, *188*, 460–476. [CrossRef]
152. Huang, Y.; Bai, X.; Cheng, N.; Xiao, J.; Li, X.; Xing, Y. Wide Grain 7 increases grain width by enhancing H3K4me3 enrichment in the OsMADS1 promoter in rice (*Oryza sativa* L.). *Plant J.* **2020**, *102*, 517–528. [CrossRef] [PubMed]
153. Li, X.; Huang, X.; Wen, M.; Yin, W.; Chen, Y.; Liu, Y.; Liu, X. Cytological observation and RNA-seq analysis reveal novel miRNAs high expression associated with the pollen fertility of neo-tetraploid rice. *BMC Plant Biol.* **2023**, *23*, 434. [CrossRef]
154. Jiang, C.; Wang, Y.; He, Y.; Peng, Y.; Xie, L.; Li, Y.; Sun, W.; Zhou, J.; Zheng, C.; Xie, X. Identification and Characterization of miRNAs and lncRNAs Associated with Salinity Stress in Rice Panicles. *Int. J. Mol. Sci.* **2024**, *25*, 8247. [CrossRef]
155. Xue, Y.; Muhammad, S.; Yang, J.; Wang, X.; Zhao, N.; Qin, B.; Qiu, Y.; Du, Z.; Ulhassan, Z.; Zhou, W.; et al. Comparative transcriptome-wide identification and differential expression of genes and lncRNAs in rice near-isogenic line (KW-Bph36-NIL) in response to BPH feeding. *Front. Plant Sci.* **2022**, *13*, 1095602. [CrossRef]
156. Nalbant, E.; Akkaya-Ulum, Y.Z. Exploring regulatory mechanisms on miRNAs and their implications in inflammation-related diseases. *Clin. Exp. Med.* **2024**, *24*, 142. [CrossRef]
157. Arshad, M.; Feyissa, B.A.; Amyot, L.; Aung, B.; Hannoufa, A. MicroRNA156 improves drought stress tolerance in alfalfa (*Medicago sativa*) by silencing SPL13. *Plant Sci.* **2017**, *258*, 122–136. [CrossRef]
158. Much, C.; Lasda, E.L.; Pereira, I.T.; Vallery, T.K.; Ramirez, D.; Lewandowski, J.P.; Dowell, R.D.; Smallegan, M.J.; Rinn, J.L. The temporal dynamics of lncRNA Firre-mediated epigenetic and transcriptional regulation. *Nat. Commun.* **2024**, *15*, 6821. [CrossRef]
159. Lone, J.K.; Bhardwaj, R. Posttranscriptional Gene Regulation: The Role of Noncoding RNAs. In *Non-Coding RNAs for Crop Improvement: Concepts and Applications*; Goswami, K., Gelaw, T.A., Sanan-Mishra, N., Eds.; Springer Nature: Singapore, 2025; pp. 41–56.
160. Ferrer, J.; Dimitrova, N. Transcription regulation by long non-coding RNAs: Mechanisms and disease relevance. *Nat. Rev. Mol. Cell Biol.* **2024**, *25*, 396–415. [CrossRef]
161. Pawłasek, N.; Sokołowska, A.; Koter, M.; Oracz, K. The interaction between miR165/166 and miR160 regulates Arabidopsis thaliana seed size, weight, and number in a ROS-dependent manner. *Planta* **2024**, *260*, 72. [CrossRef] [PubMed]
162. Liao, D.; Zhang, Y.; Li, S.; Tang, H.; Bai, X. miRNAs in neurodegenerative diseases: From target screening to precision therapy. *Neurol. Sci.* **2025**, *46*, 2393–2399. [CrossRef] [PubMed]
163. Choi, D.K. Epigenetic regulation of angiogenesis and its therapeutics. *Genom. Inform.* **2025**, *23*, 4. [CrossRef]
164. Lu, Y.; Zeng, J.; Liu, Q. The Rice miR396-GRF-GIF-SWI/SNF Module: A Player in GA Signaling. *Front. Plant Sci.* **2021**, *12*, 786641. [CrossRef]
165. Huang, F.; He, Y. Epigenetic control of gene expression by cellular metabolisms in plants. *Curr. Opin. Plant Biol.* **2024**, *81*, 102572. [CrossRef]
166. Tremblay, B.J.; Qüesta, J.I. Non-coding and epigenetic mechanisms in the regulation of seed germination in *Arabidopsis thaliana*. *J. Exp. Bot.* **2025**, *76*, 2455–2467. [CrossRef]
167. Luo, L.; Yang, M.; Zhou, Y. BMI1s interact with condensin complexes to regulate chromatin 3D structure and gene expression in Arabidopsis. *aBIOTECH* **2025**. [CrossRef]
168. Yu, J.; Du, T.; Zhang, P.; Ma, Z.; Chen, X.; Cao, J.; Li, H.; Li, T.; Zhu, Y.; Xu, F.; et al. Impacts of High Temperatures on the Growth and Development of Rice and Measures for Heat Tolerance Regulation: A Review. *Agronomy* **2024**, *14*, 2811. [CrossRef]
169. Xing, Y.-H.; Lu, H.; Zhu, X.; Deng, Y.; Xie, Y.; Luo, Q.; Yu, J. How Rice Responds to Temperature Changes and Defeats Heat Stress. *Rice* **2024**, *17*, 73. [CrossRef] [PubMed]
170. Pant, K.K.; Naik, J.; Barthakur, S.; Chandra, V. High-temperature stress in wheat (*Triticum aestivum* L.): Unfolding the impacts, tolerance and methods to mitigate the detrimental effects. *Cereal Res. Commun.* **2025**, *53*, 1171–1197. [CrossRef]
171. Wang, H.; Charagh, S.; Dong, N.; Lu, F.; Wang, Y.; Cao, R.; Ma, L.; Wang, S.; Jiao, G.; Xie, L.; et al. Genome-Wide Analysis of Heat Shock Protein Family and Identification of Their Functions in Rice Quality and Yield. *Int. J. Mol. Sci.* **2024**, *25*, 11931. [CrossRef]

172. Shen, Q.; Xiao, J.; Wang, L.; Feng, J.; Chen, Y.; Zhu, B.; Li, H.; Lambers, H. Maize shows intraspecific facilitation under phosphorus deficiency but competition under nitrogen deficiency when grown under increased plant densities in alkaline soil. *Plant Soil* **2025**. [CrossRef]
173. Lin, G.; Wang, L.; Li, Y.; Li, J.; Qian, C.; Zhang, X.; Zuo, Q. Optimal Planting Density Increases the Seed Yield by Improving Biomass Accumulation and Regulating the Canopy Structure in Rapeseed. *Plants* **2024**, *13*, 1986. [CrossRef]
174. Mathan, J.; Dwivedi, A.; Ranjan, A. Revisiting development and physiology of wild rice relatives for crop improvement and climate resilience. *Plant Cell Rep.* **2025**, *44*, 55. [CrossRef]
175. Gann, P.J.I.; Nandy, S.; Botelho, F.B.S.; Vinzant, K.; Khodakovskaya, M.; Srivastava, V. A vacuolar proton pump controls the post-germinative growth of rice (*Oryza sativa* ssp. japonica). *Plant Growth Regul.* **2025**, *105*, 675–686. [CrossRef]
176. Wu, C.; Acuña, A.; Florez-Palacios, L.; Harrison, D.; Rogers, D.; Mozzoni, L.; Mian, R.; Vieira, C.C. Across-environment seed protein stability and genetic architecture of seed components in soybean. *Sci. Rep.* **2024**, *14*, 16452. [CrossRef] [PubMed]
177. Zarea, M.J. The Regulatory Roles of Phytohormones in the Wheat Grain-Filling Process. *J. Plant Growth Regul.* **2025**, *44*, 2609–2626. [CrossRef]
178. Kannababu, N.; Nanjundappa, S.; Narayanan, N.; Vetriventhan, M.; Venkateswarlu, R.; Das, I.K.; Srikanth, A.; Viswanath, A.; Singh, S.; Malipatil, R.; et al. Role of functional genes for seed vigor related traits through genome-wide association mapping in finger millet (*Eleusine coracana* L. Gaertn.). *Sci. Rep.* **2025**, *15*, 5569.
179. Whisnant, E.D.; Keith, C.; Smieska, L.; Chia, J.-C.; Bekele-Alemu, A.; Vatamaniuk, O.K.; VanBuren, R.; Ligaba-Osena, A. Biggest of tinies: Natural variation in seed size and mineral distribution in the ancient crop tef [*Eragrostis tef* (Zucc.) Trotter]. *Front. Plant Sci.* **2024**, *15*, 1485819. [CrossRef]
180. Weng, Y.; Wang, Y.; Wang, K.; Wu, F.; Wei, Y.; Jiang, J.; Zhu, Y.; Wang, F.; Xie, H.; Xiao, Y.; et al. OsLOX1 positively regulates seed vigor and drought tolerance in rice. *Plant Mol. Biol.* **2025**, *115*, 16. [CrossRef] [PubMed]
181. Miao, R.; Lin, Q.; Cao, P.; Zhou, C.; Feng, M.; Lan, J.; Luo, S.; Zhang, F.; Wu, H.; Hao, Q.; et al. SMALL AND ROUND GRAIN is involved in the brassinosteroid signaling pathway which regulates grain size in rice. *J. Integr. Plant Biol.* **2025**, *67*, 1290–1306. [CrossRef] [PubMed]
182. Pell, C.J.; King, S.L.; Hawkins, T.; Symmank, M. Determining the effects of reduced water availability on seed germination of five bottomland hardwood tree species. *For. Ecol. Manag.* **2025**, *577*, 122410. [CrossRef]
183. Upretee, P.; Bandara, M.S.; Tanino, K.K. The Role of Seed Characteristics on Water Uptake Preceding Germination. *Seeds* **2024**, *3*, 559–574. [CrossRef]
184. Awasthi, R.; Devi, P.; Jha, U.C.; Sharma, K.D.; Roorkiwal, M.; Kumar, S.; Pareek, A.; Siddique, K.H.M.; Prasad, P.V.V.; Parida, S.K.; et al. Exploring the synergistic effects of drought and heat stress on chickpea seed development: Insights into nutritional quality and seed yield. *Plant Stress* **2024**, *14*, 100635. [CrossRef]
185. Zhuang, T.; Ata-Ui-Karim, S.T.; Zhao, B.; Liu, X.; Tian, Y.; Zhu, Y.; Cao, W.; Cao, Q. Investigating the impacts of different degrees of deficit irrigation and nitrogen interactions on assimilate translocation, yield, and resource use efficiencies in winter wheat. *Agric. Water Manag.* **2024**, *304*, 109089. [CrossRef]
186. Zhai, M.; Wei, X.; Pan, Z.; Xu, Q.; Qin, D.; Li, J.; Zhang, J.; Wang, L.; Wang, K.; Duan, X.; et al. Optimizing plant density and canopy structure to improve light use efficiency and cotton productivity: Two years of field evidence from two locations. *Ind. Crops Prod.* **2024**, *222*, 119946. [CrossRef]
187. Tao, Y.; Li, Z.; Shah, F.; Wu, W. Optimizing biomass allocation for optimum balance of seed yield and lodging resistance in rapeseed. *Field Crops Res.* **2024**, *316*, 109493. [CrossRef]
188. Gong, H.; Duan, D.; Suo, Y.; Jia, N.; Hu, K.; Chen, J.; Hu, N.; Zhao, G.; Wang, Z. Conservative allocation strategy of nitrogen and phosphorus among leaves, stems and roots of Artemisia species. *BMC Plant Biol.* **2025**, *25*, 182. [CrossRef]
189. Li, R.; Xu, C.; Wu, Z.; Xu, Y.; Sun, S.; Song, W.; Wu, C. Optimizing canopy-spacing configuration increases soybean yield under high planting density. *Crop J.* **2024**, *13*, 233–245. [CrossRef]
190. Zhao, J.; Xin, Y.; Cui, W.; Li, P.; Su, J.; Zhao, L.; Wang, Q. The ankyrin repeat-containing protein OsANK3 affects grain size and quality in rice. *Planta* **2025**, *262*, 21. [CrossRef]
191. Zhou, C.; Lin, Q.; Ren, Y.; Lan, J.; Miao, R.; Feng, M.; Wang, X.; Liu, X.; Zhang, S.; Pan, T.; et al. A CYP78As-small grain4-coat protein complex II pathway promotes grain size in rice. *Plant Cell* **2023**, *35*, 4325–4346. [CrossRef]
192. Ma, X.; Wang, H.; Yan, S.; Zhou, C.; Zhou, K.; Zhang, Q.; Li, M.; Yang, Y.; Li, D.; Song, P.; et al. Large-scale genomic and phenomic analyses of modern cultivars empower future rice breeding design. *Mol. Plant* **2025**, *18*, 651–668. [CrossRef]
193. Bai, C.; Wang, G.J.; Feng, X.H.; Gao, Q.; Wang, W.Q.; Xu, R.; Guo, S.J.; Shen, S.Y.; Ma, M.; Lin, W.H.; et al. OsMAPK6 phosphorylation and CLG1 ubiquitylation of GW6a non-additively enhance rice grain size through stabilization of the substrate. *Nat. Commun.* **2024**, *15*, 4300. [CrossRef] [PubMed]

194. Bai, F.; Ma, H.; Cai, Y.; Shahid, M.Q.; Zheng, Y.; Lang, C.; Chen, Z.; Wu, J.; Liu, X.; Wang, L. Natural allelic variation in GRAIN SIZE AND WEIGHT 3 of wild rice regulates the grain size and weight. *Plant Physiol.* **2023**, *193*, 502–518. [CrossRef] [PubMed]
195. Gao, Q.; Zhang, N.; Wang, W.Q.; Shen, S.Y.; Bai, C.; Song, X.J. The ubiquitin-interacting motif-type ubiquitin receptor HDR3 interacts with and stabilizes the histone acetyltransferase GW6a to control the grain size in rice. *Plant Cell* **2021**, *33*, 3331–3347. [CrossRef] [PubMed]