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Genetic Insights into Grain Yield and Quality: Key Genes Influencing Grain Number, Filling, and Nutritional Value in Major Crops

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ABSTRACT :

Grain yield and quality are critical factors in global food security. This manuscript explores the key genes responsible for grain number, grain filling, and nutritional quality in major cereal and pseudocereal crops. We discuss genes regulating spikelet development, panicle branching, nutrient remobilization, and grain composition, highlighting their roles in yield improvement and stress adaptation. Advances in molecular breeding and genetic engineering targeting these genes offer opportunities to enhance grain productivity and resilience under changing environmental conditions.

Keywords: Grain number, grain filling, grain quality, yield improvement, gene regulation, molecular breeding, cereals, pseudocereals

Introduction :

Cereals and pseudocereals constitute the foundation of the global food supply, providing essential nutrients to billions of people (Supplementary Table 1). Improving grain yield and quality is a critical goal for agricultural sustainability and food security, especially under the pressures of climate change and a growing population. Genetic regulation plays a pivotal role in determining key traits such as grain number, size, filling, and nutritional value.

This manuscript reviews the functional roles of major genes influencing grain number, grain filling, and quality across staple crops, including rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize (*Zea mays*), barley (*Hordeum vulgare*), and pseudocereals like quinoa (*Chenopodium quinoa*) and buckwheat (*Fagopyrum esculentum*).

Grain Number Regulation

Grain number per panicle or spike is a primary determinant of yield. The regulation of grain number involves genes that influence spikelet differentiation, panicle branching, and cytokinin signaling:

Gene	Crop	Functional Role	Associated Processes
OsSPL14	Rice	Regulates panicle branching and grain number per panicle	Enhances grain number and overall yield
OsCKX2	Rice	Reduces cytokinin degradation, promoting spikelet development	Increases grain number and panicle size
Gn1a (OsCKX1)	Rice	Cytokinin oxidase gene controlling cytokinin levels	Increases grain number per panicle
ZmPIN1a/b	Maize	Regulates auxin transport during inflorescence development	Increases grain number per ear

These genes exemplify how manipulating hormone pathways and meristem activity can optimize grain number, ensuring enhanced productivity (also see Supplementary Table 2).

Grain Filling and Quality Regulation

Grain filling is a dynamic process influenced by genes that regulate starch biosynthesis, nutrient remobilization, and endosperm development. Grain quality, including texture, protein content, and aroma, is genetically determined.

Gene	Crop	Functional Role	Associated Processes
TaNAM	Wheat	Controls nutrient remobilization and leaf senescence	Enhances grain filling and quality
OsAAP6	Rice	Regulates amino acid transport during grain filling	Enhances protein content
OsWx	Rice	Regulates amylose content in starch	Affects grain texture and cooking quality
opaque2 (o2)	Maize	Regulates storage protein synthesis	Improves protein quality

Functional studies of these genes have enabled the development of high-yielding and nutritionally enriched crop varieties (also see Supplementary Table 3 &4).

Technological Implications and Future Directions

Modern approaches like CRISPR-Cas9 genome editing, molecular marker-assisted breeding, and transcriptomics offer opportunities to fine-tune the expression of grain-related genes. Future research should focus on:

1. **Integrating multi-trait gene regulation** to balance yield, quality, and stress resilience.
2. **Cross-species functional genomics** to transfer favorable traits between crops and pseudocereals.
3. Developing crops with **enhanced nitrogen-use efficiency** through regulatory genes like *OsGS1*.

The enhancement of grain yield and quality is a cornerstone of agricultural sustainability and global food security. As the world's population continues to grow and environmental stresses intensify due to climate change, it becomes imperative to maximize the productivity of staple crops while maintaining or enhancing their nutritional value. The genetic basis of grain yield and quality traits offers immense potential for targeted improvements through advanced breeding and biotechnological interventions.

Genetic Regulation of Grain Number: Maximizing Yield Potential

Grain number, a major determinant of crop yield, is regulated by a complex interplay of genetic, hormonal, and environmental factors. Key genes such as *OsSPL14*, *OsCKX2*, *Gn1a* (also *OsCKX1*), and *ZmPIN1a/b* in crops like rice, wheat, and maize demonstrate how precise regulation of cytokinin and auxin pathways can optimize spikelet development, panicle branching, and inflorescence architecture.

The ability of genes like *OsSPL14* to promote panicle branching without compromising plant stability underscores the importance of balancing trade-offs between vegetative growth and reproductive output. Similarly, genes like *OsCKX2*, which modulate cytokinin degradation, have shown promise in increasing grain number by enhancing spikelet fertility. Advances in transcriptomics and proteomics have provided deeper insights into the downstream regulatory networks controlled by these genes, paving the way for the fine-tuning of grain number-related traits across diverse agro-climatic regions.

Despite these advances, challenges remain in translating genetic knowledge into practical outcomes for farmers. Environmental stresses such as drought, heat, and nutrient deficiencies can interfere with the expression of grain number-regulating genes, reducing their efficacy in field conditions. Integrating stress-responsive genes like *SbDREB2A* from sorghum into high-yielding crops could provide dual benefits of increased grain number and resilience under abiotic stresses. Furthermore, stacking multiple grain number-regulating genes with complementary effects could enhance overall productivity without sacrificing stability.

Grain Filling: Optimizing Nutrient Allocation and Endosperm Development

Grain filling is another critical determinant of yield, involving nutrient remobilization, endosperm development, and starch biosynthesis. Genes such as *TaNAM* in wheat and *OsAAP6* in rice play pivotal roles in these processes, facilitating the transfer of carbohydrates, amino acids, and other nutrients from source tissues to developing grains. Manipulating these genes has demonstrated significant improvements in grain filling efficiency and overall yield.

The role of starch biosynthesis-related genes, such as *Bt2* in maize and *OsWx* in rice, cannot be overstated. These genes not only influence grain filling but also directly impact the cooking and eating quality of grains. For instance, the balance between amylose and amylopectin content in rice determines its texture, a key quality trait for consumer acceptance. Advances in our understanding of the biochemical pathways governing starch synthesis have enabled the development of rice varieties tailored to specific consumer preferences, such as high-amylose rice for diabetic patients or low-amylose varieties for sticky rice dishes.

Protein content is another critical aspect of grain filling that influences nutritional quality. Genes like *opaque2* in maize regulate the synthesis of storage proteins, offering opportunities to improve protein quality. However, increasing protein content often comes at the expense of starch accumulation, leading to potential trade-offs between yield and quality. Overcoming these trade-offs requires a systems biology approach that integrates knowledge of gene networks, metabolic pathways, and environmental factors.

Grain Quality: Enhancing Nutritional and Economic Value

Grain quality traits encompass a wide range of characteristics, including nutritional content, texture, aroma, and processing properties. These traits are largely determined by the genetic composition of crops, offering significant opportunities for improvement through molecular breeding and genetic engineering.

In rice, the *OsBADH2* gene has been identified as a key determinant of fragrance, a highly desirable trait in premium aromatic rice varieties like Basmati and Jasmine. Functional studies have shown that knocking out *OsBADH2* through CRISPR-Cas9 results in increased aroma production, opening up avenues for the development of fragrant rice varieties in non-aromatic genetic backgrounds. Similarly, wheat quality is heavily influenced by glutenin and gliadin proteins encoded by genes like *Glu-1*, which determine dough elasticity and bread-making quality.

Mineral content, another crucial aspect of grain quality, can be enhanced by targeting genes involved in nutrient uptake and remobilization. For instance, iron and zinc biofortification in rice and wheat has been achieved through the overexpression of genes such as *OsNAS1* and *OsFER2*, addressing micronutrient deficiencies in populations dependent on these staple crops. Future research should focus on integrating these biofortification strategies with traditional breeding programs to ensure widespread adoption.

Integrating Yield and Quality

One of the major challenges in crop improvement is balancing yield and quality traits, as these are often inversely correlated. For example, increasing grain size through genes like *OsGW2* may reduce grain number, while enhancing protein content may lower starch accumulation. Systems-level approaches, including genomic selection and multi-trait quantitative trait loci (QTL) mapping, have shown promise in addressing these trade-offs. Additionally, advances in synthetic biology offer the potential to design novel genetic circuits that can simultaneously optimize yield and quality traits. For instance, synthetic promoters with tissue-specific expression patterns could be used to drive grain-quality genes during grain development without affecting vegetative growth. Such innovations could revolutionize crop improvement by providing unprecedented control over complex traits.

Role of Biotechnology in Grain Improvement

The advent of modern biotechnological tools has revolutionized our ability to manipulate grain-related traits at the molecular level. CRISPR-Cas9 genome editing has emerged as a game-changing technology, enabling precise modifications of key genes like *OsCKX2*, *opaque2*, and *OsBADH2*. The ability to edit multiple genes simultaneously using multiplex CRISPR constructs has further enhanced the potential for rapid trait improvement. RNA interference (RNAi) and gene silencing technologies have also been successfully employed to suppress undesirable traits, such as allergenic proteins in wheat or anti-nutritional factors in legumes. Coupled with advances in transcriptomics, proteomics, and metabolomics, these tools provide a comprehensive framework for understanding and manipulating the genetic basis of grain traits.

Future Directions :

Looking ahead, several key areas of research and development are critical for realizing the full potential of genetic improvements in grain crops:

Climate-Resilient Crops:

As climate change exacerbates abiotic stresses such as drought, heat, and salinity, there is an urgent need to develop climate-resilient crops. Incorporating stress-responsive genes like SbDREB2A and TaHSF into high-yielding varieties can enhance both yield stability and quality under adverse conditions.

Precision Breeding:

Advances in genomic selection and predictive modeling are enabling the development of precision breeding strategies that integrate phenotypic, genotypic, and environmental data. These approaches can accelerate the identification of superior genotypes with optimal combinations of yield and quality traits.

Nutritional Security:

Addressing hidden hunger through biofortification remains a top priority. Genes involved in micronutrient accumulation, such as *OsNAS1* for iron and zinc, should be incorporated into staple crops on a global scale to combat malnutrition.

Consumer-Centric Breeding:

Understanding consumer preferences for grain quality traits, such as texture, aroma, and cooking properties, is essential for market acceptance. Integrating consumer feedback into breeding programs can ensure the development of varieties that meet both nutritional and economic demands.

Cross-Species Functional Genomics:

Exploring the functional conservation of grain-related genes across species can facilitate the transfer of favorable traits from model organisms to underutilized crops. For example, insights from rice and wheat can be applied to pseudocereals like quinoa and millets to improve their productivity and nutritional value.

Sustainability:

Enhancing nitrogen-use efficiency through genes like OsGS1 and reducing dependency on chemical fertilizers can promote sustainable agricultural practices. Similarly, developing crops with improved water-use efficiency can mitigate the impact of water scarcity.

Conclusion :

The genetic regulation of grain number, filling, and quality represents a frontier of agricultural research with far-reaching implications for food security and sustainability. By leveraging advances in genomics, biotechnology, and systems biology, we can develop next-generation crops that are high-

yielding, nutritionally enriched, and resilient to environmental stresses. While significant progress has been made, the journey toward achieving global food security is ongoing, requiring a collaborative effort among scientists, policymakers, and farmers to translate scientific discoveries into tangible benefits for society.

By integrating cutting-edge technologies with traditional breeding approaches, we stand on the brink of a new era in agriculture—one where genetic insights drive innovation, ensuring a sustainable and nutritious food supply for future generations. This review highlights the genetic basis of grain number, filling, and quality, emphasizing their roles in improving crop yield and nutritional value. Targeted manipulation of these genes, coupled with advanced molecular tools, promises a sustainable pathway for addressing global food security challenges.

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Supplementary Table 1: Edible grain crops and their properties, highlighting key details such as nutritional content, uses, and growth conditions.

Grain Crop	Botanical Name	Major Nutrients	Uses	Growth Conditions
Wheat	*Triticum aestivum*	Carbohydrates, protein, B-vitamins	Bread, pasta, cereals, flour	Cool climate, well-drained soil
Rice	*Oryza sativa*	Carbohydrates, small amounts of protein	Staple food in many countries, desserts	Warm, humid climate, flooded fields
Maize (Corn)	*Zea mays*	Carbohydrates, dietary fiber, vitamin C	Food, animal feed, biofuel, starch	Warm climate, loamy soil
Barley	*Hordeum vulgare*	Carbohydrates, dietary fiber, selenium	Beer, soups, stews, livestock feed	Cool climate, drought-resistant
Sorghum	*Sorghum bicolor*	Carbohydrates, protein, antioxidants	Porridge, flatbreads, animal feed	Hot, arid regions
Millet	*Panicum miliaceum*, etc.	Carbohydrates, magnesium, B-vitamins	Flatbreads, porridge, alcoholic drinks	Dry climate, drought-tolerant
Oats	*Avena sativa*	Carbohydrates, dietary fiber, protein	Porridge, granola, animal feed	Cool climate, well-drained soil
Quinoa	*Chenopodium quinoa*	Protein, iron, lysine, magnesium	Salads, soups, gluten-free products	High-altitude, well-drained soil
Amaranth	*Amaranthus spp.*	Protein, lysine, calcium	Porridge, flour, snacks	Warm climate, drought-tolerant
Rye	*Secale cereale*	Carbohydrates, dietary fiber, protein	Bread, whiskey, animal feed	Cool climate, sandy or clay soils
Buckwheat	*Fagopyrum esculentum*	Carbohydrates, rutin, protein	Gluten-free flour, pancakes, noodles	Cool climate, acidic soil
Fonio	*Digitaria exilis*	Carbohydrates, amino acids, iron	Porridge, couscous, beer	Semi-arid regions, sandy soil
Teff	*Eragrostis tef*	Carbohydrates, calcium, iron	Flatbreads (injera), porridge	High-altitude, drought-tolerant
Chia	*Salvia hispanica*	Omega-3 fatty acids, protein, fiber	Smoothies, pudding, bakery products	Warm climate, well-drained soil

Supplementary Table 2: Table summarizing key genes found in various grain plants, along with their biological functional roles:

Plant	Gene	Functional Role	Associated Processes
Wheat	*TaNAM*	Regulates nutrient remobilization and leaf senescence	Grain filling and stress adaptation

	VRN1	Controls vernalization response, regulating flowering time	Reproductive phase transition
	Lr34	Provides resistance to multiple fungal pathogens	Disease resistance
Rice	*OsNRT1.1B*	Enhances nitrogen use efficiency by facilitating nitrate uptake	Nutrient uptake and growth
	OsSPL14	Regulates plant architecture, including tillering and grain yield	Yield improvement
	Sub1A	Confers tolerance to submergence stress	Flood resilience
Maize	*ZmNAC111*	Involved in drought response	Stress tolerance
	Bt2	Regulates starch biosynthesis in the endosperm	Grain filling and development
	opaque2 (o2)	Controls protein synthesis, especially zein proteins	Nutritional improvement
Barley	*HvCBF4*	Cold-responsive gene regulating freezing tolerance	Stress resistance
	HvNAM-1	Regulates senescence and nutrient mobilization	Grain quality and maturation
Sorghum	*SbCYP79A1*	Participates in the biosynthesis of cyanogenic glucosides	Defense against herbivores
	SbDREB2A	Drought-responsive gene enhancing abiotic stress tolerance	Water use efficiency
Millet	*PgHSF*	Regulates heat stress responses	Heat tolerance
	PgNAM	Associated with drought tolerance and senescence	Stress adaptation
Oats	*AsNPR1*	Defense regulator in response to pathogens	Immune response
Quinoa	*CqWRKY1*	Regulates stress signaling pathways	Abiotic and biotic stress resistance
Amaranth	*AmTPS*	Involved in trehalose biosynthesis	Stress tolerance
Rye	*ScHd1*	Controls flowering time under long-day conditions	Photoperiod sensitivity
Buckwheat	*FtUFGT1*	Regulates flavonoid biosynthesis	Nutritional value (antioxidants)
Fonio	*DfDREB2*	Plays a role in drought stress tolerance	Abiotic stress adaptation
Teff	*EtNAC*	Regulates nutrient remobilization and grain filling	Grain yield improvement
Chia	*ShFAD2*	Controls the synthesis of omega-3 fatty acids	Nutritional content improvement

Supplementary Table 3: Key grain-filling and quality-related genes in various grain crops, along with their functions and roles:

Gene	Crop	Functional Role	Associated Processes
TaNAM	Wheat	Controls nutrient remobilization and leaf senescence	Enhances grain filling and quality
TaGS1	Wheat	Involved in glutamine synthesis	Protein content improvement
OsSPL14	Rice	Regulates plant architecture, panicle branching, and grain size	Yield and grain quality improvement
OsGW2	Rice	Negatively regulates grain width	Determines grain size and weight
OsMADS29	Rice	Controls endosperm development and starch synthesis	Grain filling and starch content
OsAAP6	Rice	Regulates amino acid transport during grain filling	Enhances protein content
Bt2	Maize	Influences starch biosynthesis in endosperm	Grain filling and carbohydrate quality
opaque2 (o2)	Maize	Regulates storage protein synthesis (zeins)	Improves protein quality
ZmGS3	Maize	Controls grain length and weight	Enhances grain size
HvNAM-1	Barley	Regulates senescence and nutrient remobilization	Grain quality and yield
SbGS3	Sorghum	Influences grain size and shape	Grain morphology
PgSWEET	Millets	Facilitates sugar transport during grain filling	Improves grain filling
TaProlamin	Wheat	Encodes prolamin proteins essential for gluten structure	Determines bread-making quality
OsWx	Rice	Regulates amylose content in starch	Affects grain texture and cooking quality
OsBADH2	Rice	Associated with fragrance production (aromatic rice)	Grain quality improvement
Glu-1	Wheat	Encodes high-molecular-weight glutenins	Determines dough elasticity and quality
OsCKX2	Rice	Modulates cytokinin levels, affecting grain number and weight	Improves grain filling and yield
OsSSIIIa	Rice	Involved in starch synthesis and amylopectin structure	Grain texture and quality
ZmPBF	Maize	Regulates endosperm protein synthesis	Protein quality enhancement
OsGS1;1	Rice	Glutamine synthetase gene critical for nitrogen remobilization	Boosts grain protein content

Supplementary Table 4: List of grain number improvement genes identified in various crops, along with their roles in regulating grain number and yield-related traits:

Gene	Crop	Functional Role	Associated Processes
OsSPL14	Rice	Regulates panicle branching and grain number per panicle	Enhances grain number and overall yield
OsCKX2	Rice	Reduces cytokinin degradation, promoting spikelet development	Increases grain number and panicle size
OsFZP	Rice	Controls spikelet differentiation and suppresses panicle branching	Balances grain number and panicle density
Gn1a (OsCKX1)	Rice	Cytokinin oxidase gene controlling cytokinin levels	Increases grain number per panicle
OsMOC1	Rice	Regulates tillering and panicle branching	Boosts grain number by increasing tillers

OsDEP1	Rice	Enhances panicle branching and compactness	Improves grain number and density
OsAPO1	Rice	Promotes panicle branching and suppresses excessive tillering	Enhances grain number and yield stability
TaTGW6	Wheat	Influences cytokinin levels and spikelet fertility	Boosts grain number per spike
TaPpd-D1	Wheat	Photoperiod response gene influencing flowering time	Optimizes grain number under diverse climates
ZmPIN1a/b	Maize	Regulates auxin transport during inflorescence development	Increases grain number per ear
ZmFl2	Maize	Controls spikelet meristem activity	Enhances kernel number per cob
HvCKX1	Barley	Modulates cytokinin degradation	Improves grain number per spike
SbDREB2A	Sorghum	Enhances spikelet fertility under drought stress	Maintains grain number under stress
Gs3	Rice, Sorghum	Influences grain length and indirectly affects grain number	Enhances spikelet fertility
TaGW2	Wheat	Controls grain size and spikelet fertility	Balances grain size and number
OsGhd7	Rice	Regulates flowering time and panicle branching	Increases grain number by extending vegetative phase
OsIPA1	Rice	Optimizes plant architecture by balancing tiller number and panicle size	Enhances grain number and yield
OsFON1	Rice	Restricts excess meristem activity during spikelet development	Improves grain number consistency