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Cereal protein biofortification at the interface of nutrition, yield and sustainability

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Protein malnutrition remains a major global health challenge, particularly in regions where cereal grains dominate daily diets and access to diverse protein sources is limited. Cereals such as rice, wheat and maize provide most of the world's calories, yet their grain proteins are often low in essential amino acids and poorly balanced for human nutrition. Improving both the quantity and quality of cereal protein therefore represents a critical opportunity to enhance human health while reducing reliance on environmentally intensive animal-based foods. In this Review, we synthesize recent advances in understanding how grain protein content and composition are regulated in cereals, and why protein enhancement has historically been constrained by trade-offs with starch accumulation and yield. We discuss how domestication and modern breeding reshaped carbon and nitrogen allocation in cereal grains, creating a starch-dominant optimum that limits protein concentration. Drawing on genetic studies from rice, maize and wheat, we highlight emerging strategies that improve nitrogen acquisition, amino acid transport, storage protein composition and endosperm buffering capacity, enabling partial decoupling of protein accumulation from yield penalties. Finally, we place cereal protein biofortification within a broader nutritional and environmental context. Enhancing protein density and amino acid balance in staple cereals can improve dietary adequacy for vulnerable populations while lowering greenhouse gas emissions per unit of nutrition. Together, these insights position cereal protein biofortification as a scalable and equitable pathway towards healthier diets and more sustainable food systems under global climate and population pressures.

Protein is an indispensable macronutrient essential for human growth, cellular maintenance, immune function and enzymatic activity. Despite its critical biological role, more than one billion individuals, particularly in sub-Saharan Africa, South Asia and parts of Southeast Asia, fail to meet the minimum dietary protein requirement of 0.83 g per kg body weight[1]. Beyond considering protein malnutrition, meeting the recommended daily intake of essential amino acids (EAAs) is critical for public health[2]. A complete amino acid profile is biologically important given the inability of humans to synthesize the EAAs[3]. Although animal-based proteins provide complete amino acid profiles, they are not always accessible or sustainable due to economic constraints, land-use pressures and their disproportionately high environmental impact. Moreover, higher levels of red meat consumption are associated with increased risk of heart disease and cancer[4]. Increasing the protein content of cereals can strengthen the EAT–*Lancet* planetary health diet framework, which advocates shifting protein intake away from red

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Table 1 | Protein quality, environmental footprint, agricultural yield and global production values for major cereals, legumes, animal protein sources and dairy, including GHG emissions, water use, global average yield and global production

Category	Food source	Protein percentage (typical)	PDCAAS	DIAAS (numeric value)	Percentage of protein RDA met for women (46 g per day) per 100 g food[a]	Percentage of protein RDA met for men (56 g per day) per 100 g food[a]	GHG emissions (kg CO_2-eq per kg protein)[b]	Water use (l per kg protein)[c]	Global average yield (t ha^{-1}, ~2020–2022)[d]	Global production (Mt yr^{-1}, ~2023–2024)[d,e]
Cereals	Rice	6–9%	0.55–0.65	0.37–0.60	13.0–19.6%	10.7–16.1%	6.27	~3,000–4,000	4.6–4.7	523
Cereals	Wheat	10–14%	0.40–0.50	0.40–0.45	21.7–30.4%	17.9–25.0%	1.29	~1,800–2,400	3.5	788
Cereals	Maize (corn)	8–10%	0.40–0.50	0.35–0.50	17.4–21.7%	14.3–17.9%	1.79	~1,000–2,000	5.8	1,220
Legumes	Pulses (general)	20–25%	0.55–0.70	0.65–0.75	43.5–54.3%	35.7–44.6%	0.44	~1,000–1,500	0.6–1.4 (aggregate)	96 (aggregate)
Legumes	Beans (kidney, black, mung)	20–23%	0.55–0.65	0.55–0.70	43.5–50.0%	35.7–41.1%	~2–5	~1,500–2,000		
Legumes	Peas	22–25%	0.60–0.70	0.64–0.82	47.8–54.3%	39.3–44.6%	~2–4	~1,000–1,500		
Legumes	Lentils	23–26%	0.55–0.65	0.60–0.70	50.0–56.5%	41.1–46.4%	1–2	500–1,000		
Animal protein	Beef	20–24%	1	0.82–1.10	43.5–52.2%	35.7–42.9%	70–105	15,000–20,000	NA	60–70
Animal protein	Chicken	20–23%	1	1.08–1.10	43.5–50.0%	35.7–41.1%	15–25	4,000–5,000	NA	125–140
Animal protein	Pork	20–22%	1	0.90–1.00	43.5–47.8%	35.7–39.3%	20–30	~5,000	NA	110–120
Animal protein	Eggs	12–13%	1	1.18–1.21	26.1–28.3%	21.4–23.2%	12–20	3,000–4,000	NA	75–85
Dairy	Milk	3–4%	1	1.10–1.20	6.5–8.7%	5.4–7.1%	30–40	1,000–2,000	NA	920–960
Dairy	Whey protein (isolate)	80–90%	1	1.09–1.25	173.9–195.7%	142.9–160.7%	(Depends on milk source)	NA	NA	NA
Dairy	Casein	80–90%	1	~1.10–1.20	173.9–195.7%	142.9–160.7%	NA	NA	NA	NA
Aquatic protein	Farmed fish (for example, tilapia, salmon and pangasius)	~18–22%	1	~1.0	~32–48%	~25–39%	5.98	NA	NA	~200–220

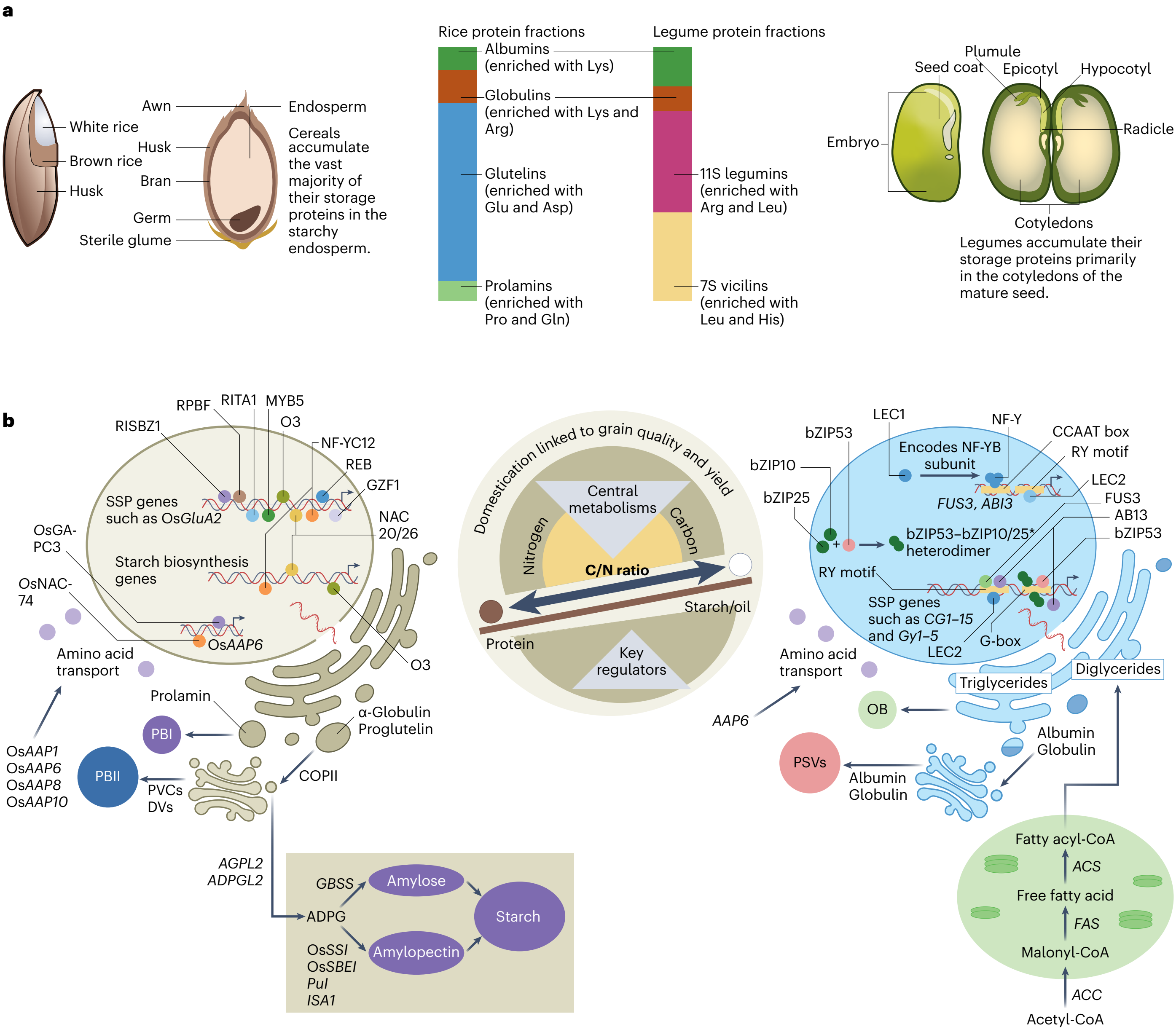
DIAAS, digestible indispensable amino acid score; NA, not available; PDCAAS, protein digestibility-corrected amino acid score; RDA, recommended dietary allowance. [a]Data from ref. 58. Women (≥19 years old) have a reference weight of 57 kg whereas men (≥19 years old) have a reference weight of 70 kg. [b]Data from ref. 59. They can also be accessed at https://ourworldindata.org/environmental-impacts-of-food. [c]Data from refs. 60,61. [d]Data from ref. 62. [e]Data from ref. 63.

and processed meats towards plant-based sources. Recent evidence suggests that replacing animal meat with legume and cereal proteins is adequate to meet the adult requirements of protein and EAAs[5]. Such a dietary transition could reduce global greenhouse gas (GHG) emissions by up to 32.4% while improving long-term health outcomes[6].

Plant-based proteins derived from legumes and cereal grains produce far lower emissions at both the farm and processing stages with enriched EAAs (Supplementary Fig. 1). While legumes are naturally rich in protein (20–45% dry weight) and serve as a vital dietary complement, overcoming their yield barrier is essential (Table 1). Increasing protein in cereals remains critical owing to their dominant role in global caloric intake, as well as their high-yielding capability to meet the food and nutritional security targets of raising the global population to 9.8 billion by 2050 (ref. 7). In many regions, especially among vulnerable populations, cereals are consumed in much higher quantities than legumes, which may be seasonally scarce or economically inaccessible. Whereas higher consumption of refined cereals has been shown to increase type 2 diabetes[8], replacing carbohydrates with 5% protein is associated with a reduction in non-communicable disease incidences[9]. In this context, enhancing protein quality and content in cereals ensures that even populations with limited dietary diversity can obtain sustainable, nutritionally dense staple foods. This does not replace the value of legumes but rather strengthens overall dietary resilience.

Grain protein content (GPC) accumulation is a multi-tiered system encompassing nitrogen acquisition, amino acid biosynthesis, source–sink transport, storage-protein gene transcription and protein body biogenesis, which differs between cereals and legumes (Fig. 1). Legumes inherently possess nitrogen-fixing mechanisms, with GPC accumulating in the range of 20–45% in cotyledons and a balanced composition of EAAs, such as lysine. Cereals rely on external nitrogen application, with GPC of 5–8% dry weight in endosperm. Natural variation between wild and cultivated pools contributes to the broad protein diversity observed across cereals. In domesticated rice cultivars, GPC varies about threefold[10]. However, wild rice has over 20% higher protein content than the cultivated rice varieties[11]; hence, rewilding the rare alleles to increase GPC with enriched EAAs while maintaining a higher rate of starch and thousand-grain weight in cereal grains such as maize, rice and wheat would be a desirable strategy.

The wheat endosperm preferentially accumulates gliadins and glutenin (including high-molecular-weight and low-molecular-weight glutenin subunits). In maize, the majority (60–70%) of seed storage proteins (SSPs) are prolamins (also named zeins in maize, gliadins in wheat or hordeins in barley), which are devoid of the EAAs lysine and tryptophan, resulting in poor nutritional quality of cereal seed protein[12] (Supplementary Figs. 2 and 3). Breeding or engineering cereals with balanced EAA profiles can thus help deliver more complete nutrition from the foods people already consume daily. Such biofortification strategies, when aligned with agronomic performance and farmer acceptance, can transform staple crops into vehicles of improved health and resilience against malnutrition.



Regulatory pathways controlling storage protein accumulation in cereal grains

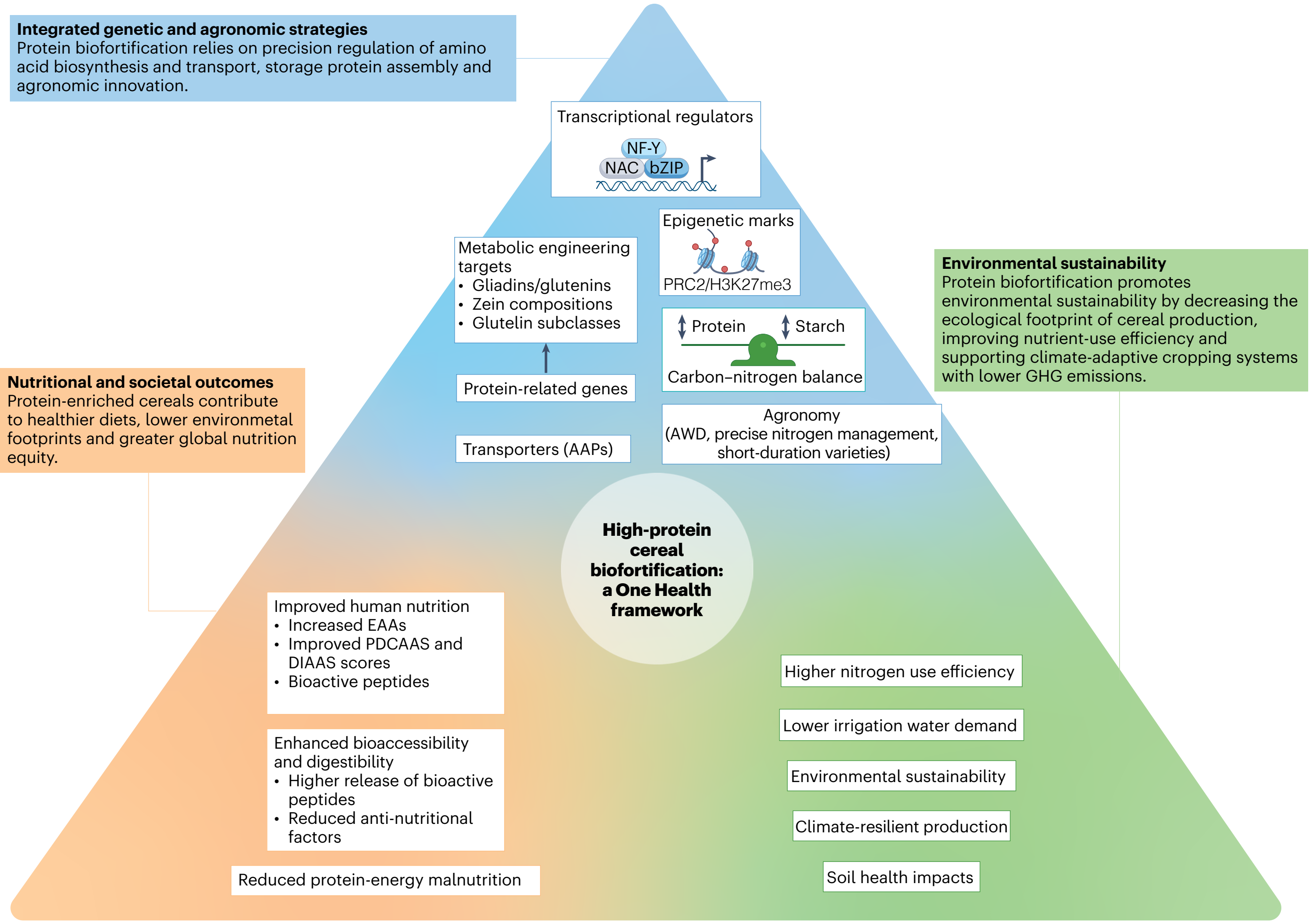
Regulatory pathways controlling storage protein accumulation in legumes

Fig. 1 | Storage protein localization and regulatory control in cereals and legumes. a, In cereals, exemplified by rice, storage proteins accumulate mainly in the starchy endosperm and are dominated by glutelins and prolamins, with smaller contributions from albumins and globulins, whereas in legumes, storage proteins are deposited primarily in the cotyledons and consist largely of 7S vicilins and 11S legumins with a more balanced EAA composition. **b**, Schematic comparison of the regulatory pathways governing storage protein accumulation. In cereals (left), endosperm-specific transcriptional networks (including bZIP, Dof, NAC, MYB and NF-Y factors) co-ordinate amino acid transport, storage protein synthesis and starch metabolism, creating trade-offs between protein content and yield that are influenced by carbon–nitrogen balance and domestication. In legumes (right), conserved seed regulators (LEC1, LEC2, ABI3, FUS3 and NF-Y) control storage protein deposition predominantly into protein storage vacuoles, with comparatively weaker coupling to starch metabolism. COPII, coat protein complex II; DVs, dense vesicles; PSVs, protein storage vacuoles; PVCs, prevacuolar compartments.

This Review synthesizes recent advances in characterizing and manipulating amino acid composition and grain protein accumulation in cereals through genetics. We propose a conceptual framework that positions cereal protein biofortification at the intersection of nutrition, metabolism and sustainability. Within this framework, we highlight (a) molecular and regulatory networks conferring increased protein and EAA content in cereals; (b) emerging strategies designed to mitigate the yield, quality and sensory penalties that often accompany enhanced protein traits; and (c) translational strategies that integrate environmental footprint and climate-resilience considerations to inform the development of cereal varieties that are nutritionally enriched, agronomically robust and aligned with the broader goals of sustainable global food and nutrition security (Fig. 2 and Box 1).

Genetic and molecular mechanisms underlying GPC, its trade-off with yield and strategies for overcoming yield penalty

Cereal protein-enhancing genes are in the process of being domesticated, but frequently in intricate and perhaps unexpected ways. Increased yield has historically been achieved by selecting against



Integrated genetic and agronomic strategies
Protein biofortification relies on precision regulation of amino acid biosynthesis and transport, storage protein assembly and agronomic innovation.

Environmental sustainability
Protein biofortification promotes environmental sustainability by decreasing the ecological footprint of cereal production, improving nutrient-use efficiency and supporting climate-adaptive cropping systems with lower GHG emissions.

Nutritional and societal outcomes
Protein-enriched cereals contribute to healthier diets, lower environmetal footprints and greater global nutrition equity.

Fig. 2 | High-protein cereal biofortification as a One Health framework linking molecular innovation, improved nutrition and environmental sustainability. Conceptual framework illustrating how genetic and metabolic innovations that enhance amino acid biosynthesis and transport as well as storage protein accumulation in cereals translate into improved nutritional outcomes and reduced environmental impacts. Molecular and breeding targets, including regulators of amino acid metabolism, storage protein composition and transporter activity, are integrated with agronomic strategies to improve EAA content, protein digestibility and grain nutritional quality. These improvements enhance human nutrition by increasing protein availability and bioaccessibility while reducing anti-nutritional factors. At the systems level, protein-enriched cereals can reduce protein-energy malnutrition, support healthier diets and lower the GHG footprint of protein production, aligning crop improvement with the broader One Health goals of human health, environmental sustainability and global food security. AWD, alternate wetting and drying.

non-shattering grains and for larger seed size with elevated starch content during artificial selection. However, these processes have also unintentionally and negatively influenced the protein content and quality of cereals. Efforts to enhance EAA and overall protein content in cereals often trigger phenotypic trade-offs that complicate the balance between nutritional improvement and agronomic performance. As illustrated in Fig. 3a, protein-enhancing alleles and mutants across rice, maize and wheat fall into distinct 'safe', 'transition' and 'penalty' zones, reflecting how increases in protein content frequently coincide with penalties in texture or yield. These examples visually illustrate the domestication constraints and physiological trade-offs that breeding programmes must consider when enhancing GPC.

A well-documented example is the inverse relationship between protein and starch content in the grain, classically explained through carbon–nitrogen partitioning. When carbon assimilation is high relative to nitrogen availability, crops allocate more carbon towards the synthesis of carbon-rich storage compounds such as starch in the grains, leaving less glucose available for the carbon skeletons required for amino acid synthesis. Conversely, when nitrogen supply is greater than carbon availability, plants channel more nitrogen towards protein synthesis. A well-established negative correlation between GPC and grain yield in wheat was observed at Rothamsted Research Station trials, exhibiting a 'dilution effect'[13]. This protein–yield trade-off is more pronounced in wheat because it relies heavily on post-anthesis nitrogen remobilization from vegetative tissues to grains, accounting for up to 66.7% in Chinese winter wheat[14], which is readily diluted by increased starch deposition. As shown in Supplementary Fig. 4, linear regression analysis reveals a strong negative correlation in wheat ($R^2 = 0.57$), whereas rice and maize display only weak positive correlations ($R^2 = 0.07$ and 0.04, respectively). In contrast to wheat, rice and maize maintain both nitrogen remobilization and active nitrogen uptake during grain filling, with post-anthesis uptake contributing substantially to grain nitrogen content[15]. Thus, rice and maize possess a more flexible nitrogen supply, making them less sensitive to dilution effects. The factors of nitrogen use efficiency (NUE) and stay-green, which impact maintaining GPC with optimum grain yield, need to be unravelled in future studies.

The GS/GOGAT cycle, which converts ammonium into glutamine and glutamate, constitutes a central metabolic bottleneck and supplies nitrogen for nearly all amino acids. In parallel, carbon metabolic pathways such as glycolysis, the citric acid cycle and the pentose phosphate pathway supply the carbon skeleton for amino acid biosynthesis. Nitrogen assimilation processes are thus tightly linked with carbon metabolism in determining seed protein accumulation. Once synthesized, amino

BOX 1

Protein sources across nutrition, productivity and environmental cost

Comparative analysis of major protein sources highlights pronounced trade-offs between nutritional quality, agronomic productivity and environmental impact (Table 1). Cereals such as rice, wheat and maize dominate the global protein supply because of their high yields and massive production volumes, particularly in low and middle-income regions. However, their protein quality is intrinsically limited, with low PDCAAS and DIAAS values (~0.35–0.65) driven by lysine-poor amino acid profiles and reduced digestibility of storage proteins. Consequently, even large cereal servings meet only a modest fraction of daily protein requirements, leaving cereal-dependent populations nutritionally vulnerable.

Legumes provide substantially higher protein density and improved amino acid balance, often achieving DIAAS values above 0.70, while maintaining markedly lower GHG emissions than livestock systems. Although yields are lower than those for cereals, legumes can supply a large share of daily protein requirements and represent a critical, environmentally efficient complement in diets affected by protein-energy malnutrition.

Animal-derived proteins offer near-complete amino acid profiles (DIAAS ≈ 0.9–1.2) and high bioavailability but impose disproportionately high environmental costs. Beef production, in particular, exhibits the highest GHG emissions per unit protein, while dairy systems demand extensive water and land resources. Poultry, eggs and aquatic proteins occupy an intermediate position, combining high protein quality with more moderate environmental footprints, although their global availability remains uneven.

These contrasts underscore a central premise of this Review: enhancing protein content, amino acid balance and digestibility of cereals represents one of the most scalable and equitable strategies to close global protein gaps while reducing reliance on environmentally intensive livestock systems.

acids must be efficiently translocated from leaves to developing grains. Amino acid permeases (AAPs), UMAMIT exporters and GDU–LOG2 ubiquitination modules collaboratively regulate long-distance transport and phloem unloading. Variants of these transporters strongly modulate GPC. For instance, the maize Zm*AAP6* and rice Os*AAP6* enhance sink strength by increasing amino acid flux into the developing endosperm[16], whereas Os*AAP1* adjusts the valine/proline balance and influences both protein composition and yield-related traits[17]. Os*AAP6* remains one of the most intensively characterized transporters, with loss or gain-of-function lines clearly demonstrating its central role in controlling grain protein deposition (Fig. 3). Emerging evidence indicates that these transporters act in tissue-specific domains such as the nucellar projection and aleurone layer, suggesting that spatial regulation of amino acid unloading is integral to determining the protein density of the mature grain[18]. Upon arrival in the developing kernel, amino acids are incorporated into the major SSP classes (namely, prolamins, glutelins, globulins and albumins), whose accumulation depends on both transcriptional activation and efficient protein processing.

It is important to note that enhancing nitrogen uptake and assimilation through amino acid transporter manipulation does not automatically improve NUE. The specific transporter and its expression pattern are critical determinants. For example, overexpressing Os*AAP3* and Os*AAP5* in rice reduces tillering and yield. These transporters have high affinity for basic amino acids, especially lysine and arginine, facilitating their movement to basal nodes and tiller buds. Excess lysine and arginine in these tissues inhibit bud elongation via the cytokinin pathway, ultimately lowering NUE and reducing yield. Conversely, Os*AAP1* and Os*AAP4* preferentially transport neutral amino acids that promote growth, and their overexpression reduces lysine and arginine concentrations while improving co-ordination between nitrogen and phytohormone signalling. Additionally, overexpression of Os*AAP6* increases total amino acid content and enhances the accumulation of individual storage proteins, resulting in higher total grain protein (12.15–14.56% relative to the wild type) and larger protein bodies[16]. Further analyses confirmed enhanced amino acid uptake by the roots and increased deposition into the hulls. Consequently, these overexpression lines show substantially reduced starch content (by 3.91–5.05%) and more spherical starch granules. Subsequent studies revealed upregulation of storage-protein-encoding genes and downregulation of starch-branching genes. Similar trends have been observed for other amino acid transporters, including Os*AAP8* and Os*AAP10* in rice[19], Zm*AAP6* in maize[18] and Ta*AAP13* in wheat[20], as well as their upstream regulators, such as Os*NAC74* and Os*GAPC3* (ref. 21).

Elevating GPC while maintaining optimum yield

Natural diversity across cereals reveals multiple evolutionary solutions to enhancing protein content (Fig. 4a). These natural variants demonstrate that high GPC is not intrinsically incompatible with yield but instead reflects alternative configurations of nitrogen allocation and endosperm buffering capacity (Fig. 4b). Teosinte (*Zea mays* ssp. *parviglumis*), the wild progenitor of modern maize, contains nearly three times more protein than modern maize but exhibits substantially lower yield[22,23]. Importantly, genetic dissection of a teosinte × B73 hybrid population revealed that high protein accumulation can be uncoupled from yield penalties in an elite background. In this population, *TEOSINTE HIGH PROTEIN 9* (*THP9*), encoding an asparagine synthetase 4 enzyme that catalyses asparagine biosynthesis, was mapped to chromosome 9. The teosinte-derived *THP9* allele conferred a 25–30% increase in GPC relative to modern inbred lines by improving NUE[24]. These findings are supported by overexpressing Os*ASN1* in rice, with overexpression lines showing improved nitrogen uptake and assimilation, leading to higher GPC without yield penalties under normal paddy conditions[25].

These examples highlight nitrogen acquisition and allocation as recurrent evolutionary targets for protein enhancement. In rice and maize, the dual-affinity nitrate transporter–sensor *NRT1.1B* integrates external nitrogen availability with systemic regulation of the nitrogen response[26,27]. Beyond transporting nitrate, *NRT1.1B* activates NIN-like protein (NLP) family transcription factors (TFs), which co-ordinately upregulate nitrogen-responsive genes involved in nitrate reduction, ammonium assimilation and amino acid biosynthesis[27]. Os*NLP3* and Os*NLP4* confer NUE with increased grain yield[28,29]. Genes involved in nitrogen uptake have undergone strong selection during rice domestication. A marked reduction in nucleotide diversity surrounding Os*AMT1;1*, which encodes a high-affinity ammonium transporter, reflects a prominent domestication sweep probably driven by selection for efficient ammonium acquisition in flooded paddy systems[30]. In the IndI subgroup, Os*AMT1;1* carries clear signatures of selection, whereas in IndII, selective pressure appears to have targeted genes associated with high-affinity nitrate uptake and assimilation, including Os*NRT2.3*, Os*NAR2.2* and Os*NiR1* (ref. 31).

In wheat, selective sweeps associated with GPC encompass both domestication and improvement-related events. The clearest domestication sweep involves the NAC TF NAM-B1, whose functional allele, responsible for accelerated senescence and enhanced nitrogen remobilization[32,33], was largely lost during early domestication. By contrast, several storage-protein loci, including *Glu-D1* and the *Gli-1/2* clusters, exhibit strong improvement sweeps linked to selection for gluten quality[34]. Additional genes involved in nitrogen assimilation (for

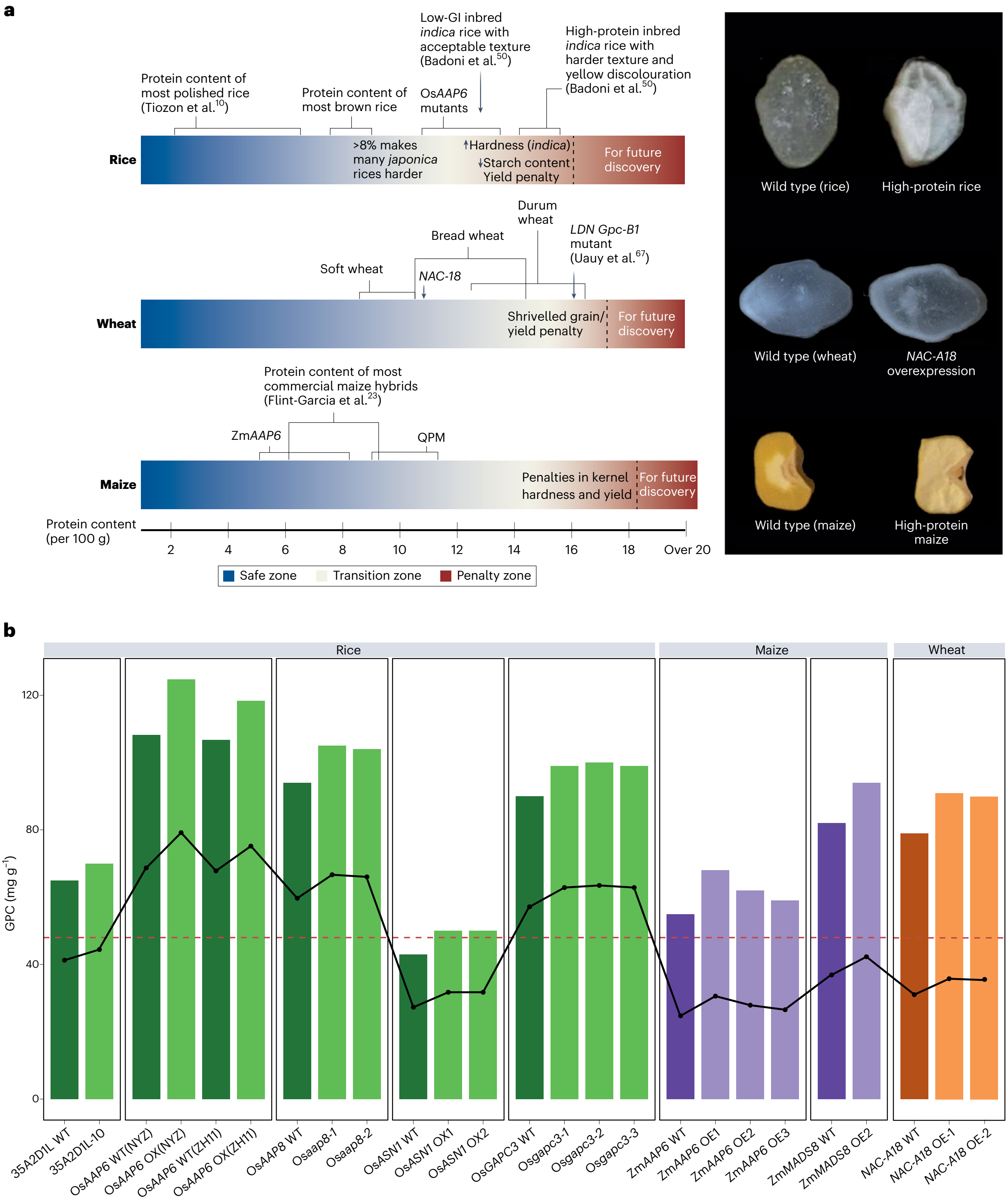


Fig. 3 | Protein–yield trade-offs define safe, transition and penalty zones for cereal protein enhancement. a, Conceptual mapping of GPC in rice, wheat and maize, highlighting safe, transition and penalty zones. Moderate increases in protein content can be achieved without major penalties to grain quality or yield (safe zone), whereas higher protein levels are increasingly associated with altered endosperm texture, reduced starch content or yield penalties (transition and penalty zones). Representative genetic interventions and breeding outcomes are indicated, together with illustrative grain phenotypes. **b**, GPC of selected rice, maize and wheat genotypes carrying protein-enhancing alleles or transgenes. The bars indicate total grain protein concentration, and the black line denotes estimated protein intake per typical serving (630 g of rice, 450 g of maize, or 394 g of wheat). The red dashed line marks the recommended dietary intake reference, illustrating how genetic gains in cereal protein translate into nutritional relevance while revealing crop and genotype-specific trade-offs. The consumption intake for rice[64], maize[65] and wheat[66] in Asia and Africa were considered. OE, overexpression; WT, wild type.

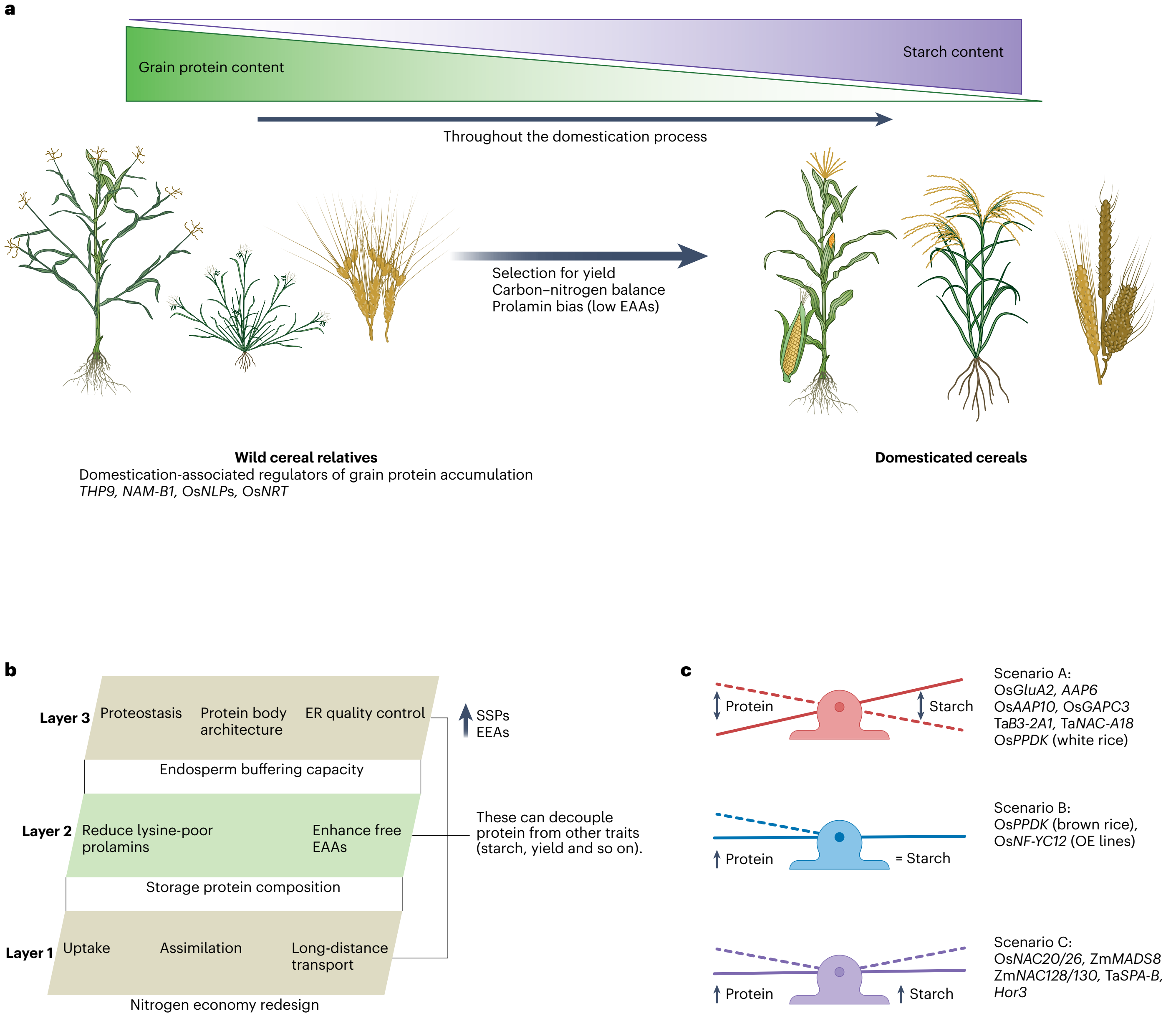


Fig. 4 | Domestication constraints and engineering trajectories for cereal grain protein biofortification. a, Conceptual model illustrating domestication-driven shifts in grain composition. Strong selection for yield and starch accumulation during cereal domestication altered carbon–nitrogen partitioning in the endosperm, leading to reduced GPC and enrichment of prolamin-rich, EAA-poor storage proteins. By contrast, wild cereal relatives retain higher protein levels and more balanced nitrogen allocation. Representative domestication-associated regulators influencing grain protein accumulation are indicated. **b**, Multi-layered framework for mitigating protein–starch trade-offs in cereals. **c**, Conceptual scenarios illustrating protein–starch trade-offs and their relaxation. Scenario A represents classical strategies that increase protein at the expense of starch. Scenario B depicts intermediate states with elevated protein and minimal starch penalty. Scenario C illustrates optimized regulatory configurations enabling concurrent increases in protein and starch through partial decoupling of carbon and nitrogen allocation. The gene examples are illustrative and not exhaustive.

example, Ta*GS1* and Ta*GS2*) and amino acid transport (for example, Ta*AAP13*) display reduced genetic diversity across elite germplasm, reflecting targeted selection for grain protein concentration and end-use quality. The allelic diversity preserved in wild cereals therefore represents not isolated high-protein genes but alternative configurations of nitrogen economy and endosperm buffering that can be reassembled using modern breeding and genome-editing approaches (Fig. 4b and Supplementary Table 1). Leveraging this diversity through modern breeding tools, including precision introgression, multiplex genome editing and de novo domestication, provides a path towards reinstating high-protein traits and superior amino acid profiles in elite cultivars while maintaining yield and adaptability[35].

Gene regulatory networks at the crossroads of grain protein and starch metabolism alter protein-to-starch ratio in cereals

The TF network bZIP–DOF–NAC, acting through *cis*-regulatory control via motifs such as the GCN4-like element, O2-box and prolamin-box, establishes the fundamental architecture for endosperm-specific expression of storage proteins (glutelins, horedeins and prolamins) in cereals, whereas LEC1–ABI3–FUS3–LEC2 TFs regulate SSPs such as albumins and globulin in the embryos of dicots[36,37]. Comparative analyses of motif composition and domain architecture across rice, maize and wheat further underscore the evolutionary conservation of this regulatory framework (Supplementary Fig. 5). Phylogenetic

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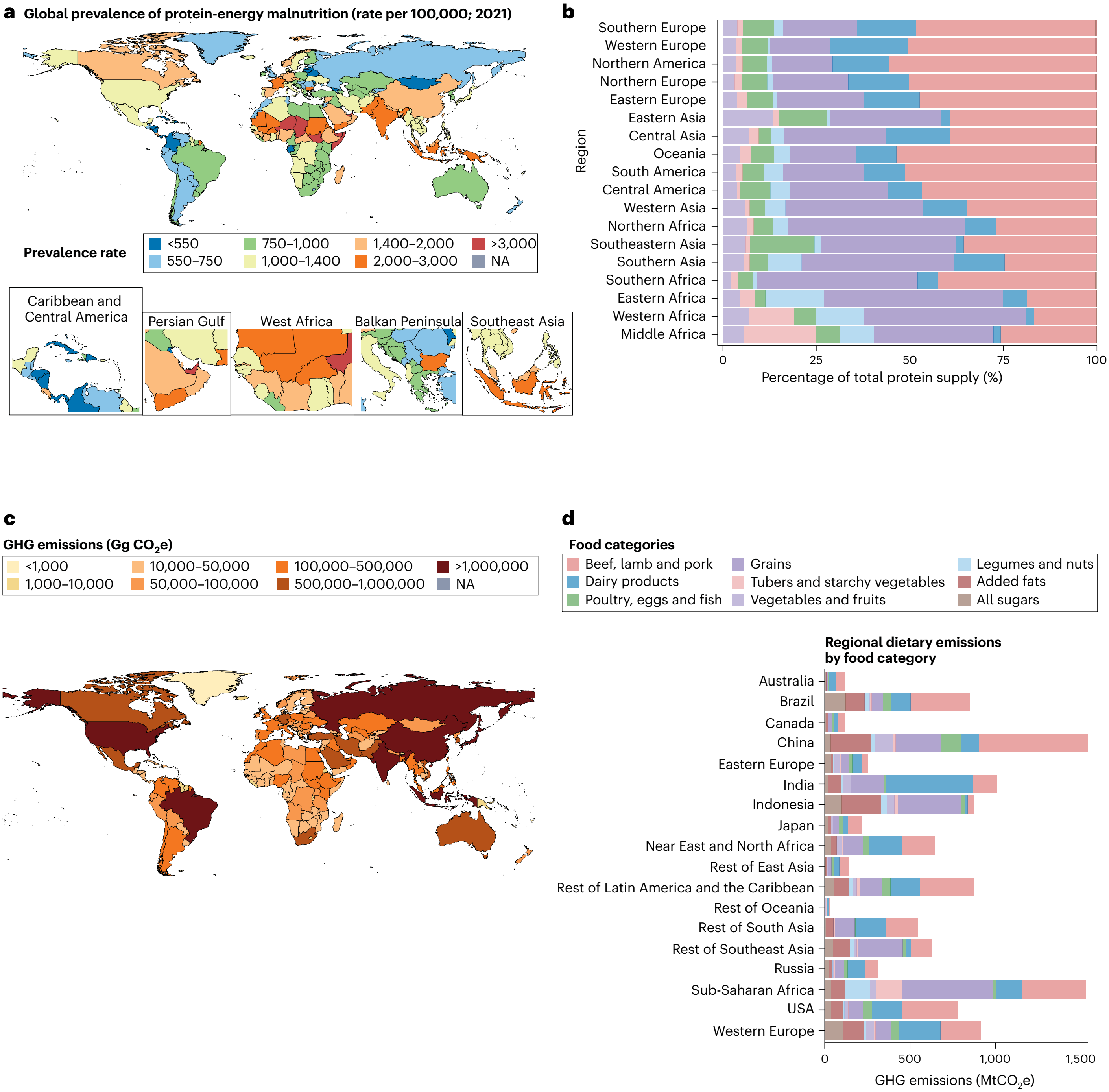

Fig. 5 | Global burden of protein malnutrition, dietary patterns and food-system GHG emissions. a, Global prevalence of protein-energy malnutrition (cases per 100,000 population, 2021) (ref. 67), highlighting regions with the highest nutritional vulnerability, particularly across sub-Saharan Africa, South Asia, Southeast Asia and parts of the Caribbean. Insets show regional detail for selected hotspots. **b**, Regional contributions of major food groups to the total dietary protein supply, illustrating strong reliance on cereals in nutritionally vulnerable regions and higher dependence on animal-source foods in high-income regions. **c**, Country-level agricultural GHG emissions (Gg CO$_2$e), showing the global distribution of emissions associated with food production[68]. **d**, Regional dietary GHG emissions partitioned by food category, revealing the disproportionate climate footprint of animal-source foods compared with cereals and legumes[69].

clustering reveals that bZIP, Dof and NAC proteins group primarily by TF family rather than by species (Supplementary Fig. 6), indicating that the core architecture of the storage-protein regulatory network predates cereal diversification. Although DNA-binding domains, such as the NAC domain (PF02365), bZIP domain (PF00170) and Dof zinc-finger (PF02701), are highly conserved, the carboxy-terminal activation regions exhibit substantial divergence. This pattern suggests that whereas promoter recognition and binding are deeply conserved, the downstream transcriptional activation potential has undergone lineage-specific rewiring. Notably, the conserved motifs shared between RPBF/PBF/WPBF or RISBZ1/O2/BLZ2 reinforce the existence of an ancient bZIP–Dof regulatory module governing storage protein biosynthesis, whereas the broader motif diversity observed in NAC proteins reflects their expanded functional roles in nutrient remobilization and endosperm development in cereals. This divergence probably contributes to species-specific responsiveness to environmental triggers such as heat or nitrogen scarcity. Indeed, NAC TFs show the strongest induction under abiotic stress among the major SSP regulators, implying an adaptive rewiring of endosperm proteostasis pathways in response to climate pressures.

While TF-based engineering of GPC and quality could be a promising strategy, these TFs probably reinforce trade-offs among GPC, starch content and yield. Because TFs are often embedded in broader gene regulatory networks that influence growth, development and metabolic allocation, improving protein content through TF manipulation frequently risks unintended pleiotropic effects. For example, the endosperm-specific NAC-type TFs *Zm*NAC128 and *Zm*NAC130, which act as regulators of all zein gene families, also regulate the transcription of *Bt2*, which encodes the small subunit of the endosperm-specific ADP-glucose pyrophosphorylase, a key enzyme in starch biosynthesis, as well as additional genes involved in this pathway[38,39]. In wheat, several NAC-type TFs have similarly been shown to enhance the promoter activities of storage-protein-encoding genes, supporting the notion that TFs are entwined in larger regulatory networks that complicate TF-based GPC engineering[40–43].

To date, negative trade-offs associated with increasing protein content have largely been addressed through allele pyramiding—stacking multiple beneficial alleles within a single genetic background (Fig. 4c). In wheat, a multi-institutional effort successfully pyramided genes for protein accumulation (*Gpc-B1*), gluten strength (*Glu-D1*) and rust resistance (*Yr36*, *Yr15*, *Lr24* and *Sr24*), generating lines with higher protein content, increased thousand-grain weight and improved overall yield. In rice, appearance-quality genes (*GS3* and *qSW5*) have been combined with eating and cooking-quality genes (*Wx* and *ALK*) in a super-high-yielding background, producing crosses with superior nutritional quality and agronomic performance[44]. See Supplementary Note 1 for further discussion.

Regulators controlling EAAs and protein content in cereals

Recent evidence points to the importance of TFs of the bZIP (O2 and RISBZ1), DOF (RPBF), WRKY (*Os*WRKY78) and MYB (*Os*MYB55) families in regulating EAA accumulation (including isoleucine, leucine, phenylalanine, threonine, tryptophan and valine) in cereal grains. *Os*WRKY78 has been shown to bind to the W-box *cis* motifs in Os*Aux5*, which encodes an amino acid transporter, thereby increasing EAA levels in rice grains. Natural variation at this locus has been differentially selected between the *indica* and *japonica* subspecies. Reduced binding affinity of *Os*WRKY78 to the W-box motifs in the Os*AUX5* promoter results from an 18-bp insertion in *Pro*::Os*AUX5Hap1*, destroying the structure of W-box2 and decreasing Os*AUX5* expression and EAA content in rice grains[45]. The suppression of Os*WRKY78* through RNA interference further results in reduced grain size and altered starch crystalline structure[46].

In maize and wheat, recent efforts to improve protein content and composition have largely focused on TF-based engineering. The quintessential high-lysine quality protein maize (QPM) line was developed on the basis of genetic modifiers of the *o2* mutant. The *O2* gene encodes a bZIP TF that directly activates zein gene expression[47]. The high-lysine mutants reported in maize (*o2* and *o16*) exhibit several pleiotropic effects with reduced starch content and grain weight. QPM lines display elevated lysine and tryptophan content as a result of reduced α-zein accumulation and proteome rebalancing. The translation and maturation of these proteins rely on a robust endoplasmic reticulum (ER) quality-control system, including protein disulfide isomerases, BiP chaperones and components of the unfolded protein response, which collectively facilitate proper folding, sorting and protein body biogenesis. Disruption of ER proteostasis, as observed in the maize *opaque* and *floury* mutants, reduces zein deposition while increasing free EAAs such as lysine, alters protein body structure and results in chalky or opaque kernels, highlighting the contribution of post-translational processing to grain quality. Supplementary Table 2 shows the alteration in EAAs in different strategies.

First-generation QPM kernels are soft and starchy, making them vulnerable to physical and insect damage. Scanning electron microscopy images of *o2* mutant kernels show smaller and fewer protein bodies, although earlier work argued that protein bodies and their zein compositions are not solely responsible for kernel hardness[47]. Accordingly, substantial effort has been directed towards developing high-lysine maize with vitreous endosperm deploying alleles of 'endosperm hardness modifier genes' with three hardness quantitative trait loci (QTLs)—*1.06*, *7.02* and *9.03*. Notably, the increased accumulation of 27-kDa γ-zein in vitreous kernels was attributed to QTL *1.06* and a 15.26-kb duplication in QTL *7.02*. Vitreous kernels also contain higher amylose levels, which are associated with QTL *9.03*, located near starch biosynthesis genes. Supplementary Note 2 comprehensively describes the QTLs conferring enhanced GPC. This genetic system transformed soft kernels into hard, vitreous ones by restoring the polygonal, compact starch granule architecture, without compromising protein quality[48,49].

Through traditional and marker-assisted selection breeding strategies, the high-lysine trait has been combined with a vitamin-A-rich background, as well as the introgression of this QPM trait into high-yielding backgrounds with early maturity, leading to the release of more than 39 QPM varieties in Africa, Asia and Latin America[49]. Recent multiplex CRISPR editing of 19-kDa α-zein gene families has further shown that selectively attenuating a subset of lysine-poor prolamins can raise kernel lysine without altering total protein or compromising grain hardness. These genome-edited lines provide a modular blueprint for reshaping prolamin repertoires in rice and wheat. Although lysine is relatively inexpensive and widely available as an industrial feed additive, such genetic strategies remain highly relevant for low-input smallholder systems and for human diets where post-harvest fortification is not feasible, and they underscore the broader principle that EAA profiles can be remodelled in situ. Recently, by deploying the recessive IR36 amylose extender (*IR36ae*) allele, researchers developed a high-lysine, elevated-protein rice variety in a high-yielding background with early maturity[50].

Further research identified Zm*DeSI2*, encoding a deSUMOylating isopeptidase, as a negative regulator of kernel methionine content through its deSUMOylation of sulfite reductase Zm*SIR*[51,52]. Natural variation in the Zm*DeSI2* promoter, particularly a deletion removing a Zm*WRKY105* binding site in the elite haplotype Zm*DeSI2*$^{\mathrm{Hap2}}$, reduces its expression and increases methionine accumulation. This variation has been successfully used in marker-assisted selection to develop high-methionine lines without yield penalty. It is important to infer the epigenetic, alternative splicing and post-transcriptional control mechanisms influencing GPC in cereals (Supplementary Note 3 and Supplementary Fig. 7).

Impacts of environmental stress on GPC and quality

As global food systems move towards more sustainable and nutritionally balanced diets, improving both the quantity and quality of protein in staple crops under a changing climate remains a critical objective. Projections suggest that by 2050, global atmospheric CO_2 elevations may reduce cereal protein concentrations by an additional ~4%, underscoring the urgency of developing climate-resilient protein biofortification strategies[53,54]. Elevated CO_2 consistently leads to a dilution effect in C_3 cereals, where increased photosynthetic carbon assimilation stimulates starch deposition more than nitrogen assimilation. Wheat and rice experience 7–15% reductions in GPC under elevated CO_2 (~500–550 ppm)[54]. Wheat grains grown under elevated CO_2 show 4.8–9% decreases in the EAAs, with similar patterns reported for rice[53,54]. Thus, rising CO_2 does not merely lower total protein; it systematically reduces the nutritional and metabolic quality of cereal protein.

By contrast, heat stress during grain filling generally increases the percentage of grain protein because of reduced starch synthesis, with wheat and rice showing 6–21% increases in protein concentration depending on timing and severity[55]. However, this apparent enrichment masks declines in protein functionality. Heat alters storage protein composition in wheat, reducing the gliadin-to-glutenin ratio by ~5.5%, weakening dough properties. In rice, heat reduces prolamin by 12% but raises glutelin by 31%, affecting digestibility and cooking quality. Heat also increases chalkiness in rice and disrupts endosperm structure in wheat, linking temperature stress directly to protein fraction imbalance and grain textural defects[56]. Achieving this resilience will require combining alleles and pathways that enhance protein accumulation with those that safeguard grain filling and starch–protein homeostasis under abiotic stress.

Recent work has shown that thermotolerance of grain quality is genetically tractable: for example, processes by which the *NF-YA8* regulator binds to the *cis* motif of ATTGG in *QT12* to drive switch-on and switch-off expression of *QT12* cause the percentage of grain chalk to increase in sensitive genotypes at high temperatures[56]. Because the regulatory complex of *NF-YC10*, *NF-YB9* and *NF-YA8* interacts as a complex at normal temperatures, *NF-YA8* is not released to control the expression of *QT12*. As a result, milled rice is translucent and has a very low percentage of chalk. Interestingly, NF-Ys-QT10 trait regulatory haplotypes are differentially chosen between subspecies, where superior haplotypes are prevalent in selected *indica* germplasms exhibiting superior yield and grain quality, while the majority of the *japonica* germplasms adapted to temperate conditions are more sensitive to rising temperature, which affects yield quantity and quality.

Protein-enhancing strategies and environmental sustainability

Global GHG emissions from food systems vary widely across regions and are highest where livestock consumption is most intensive (Fig. 5). These patterns reflect the very large contribution of beef, lamb and dairy to national dietary footprints, underscoring how animal-source foods generate substantially higher emissions than plant-based protein alternatives[57].

The global distribution of protein malnutrition reveals a striking geographical clustering of vulnerability, with the highest prevalence concentrated across West Africa, Central Africa, parts of South Asia, Southeast Asia and the Caribbean (Fig. 5a). These regions consistently exceed 2,000–3,000 cases per 100,000, reflecting chronic deficits in both protein intake and dietary diversity. When overlaid with regional protein-source contributions, the following nutritional reliance pattern emerges (Fig. 5b):

- Sub-Saharan Africa and South Asia derive more than 50–70% of their dietary protein from cereals, primarily maize, sorghum, millet and rice, which tend to cause protein malnutrition.
- Legumes contribute meaningfully only in selected regions (for example, eastern Africa and parts of South Asia), while animal-source proteins remain low due to economic and logistical constraints.
- By contrast, North America, Western Europe and Oceania exhibit protein profiles dominated by livestock products (dairy, beef and pork) and poultry/eggs, reflecting higher dietary quality but heavier environmental footprints.

Countries with high animal-source protein consumption, notably North America, Brazil, Europe and parts of China, align with the highest agricultural emissions (>100,000 Gg of CO_2 equivalent (CO_2e) per year) (Fig. 5c). Conversely, many regions experiencing severe protein malnutrition produce far fewer total agricultural emissions, highlighting a paradox: the world's most nutritionally vulnerable populations contribute the least to climate change yet are most exposed to its impacts on crop productivity.

Diet-related emissions by food category underscore the disproportionate climate burden of animal-source foods. In virtually all high and middle-income regions, beef, lamb, pork and dairy dominate dietary emissions, often exceeding 50–70% of the total food-related CO_2e emissions (Fig. 5d). By contrast, cereals, legumes, vegetables and fruits contribute a small fraction, even in regions where they supply most of the protein. This contrast reinforces the nutritional and environmental efficiency of plant-based proteins: grains and legumes provide a high share of dietary protein while generating comparatively modest emissions.

Doubling the protein content of major cereals such as rice, wheat and maize reduces their GHG intensity per nutritional unit by about 50% (Supplementary Fig. 1), demonstrating that protein biofortification strengthens both the nutritional and environmental advantages of plant-based foods and would probably contribute to what has recently become known as 'One Health efficiency' by tackling global challenges of human health, planetary health and climate resilience. In addition, cereal varieties with higher protein density often reach physiological maturity with shorter grain-filling durations and require less time in the field, which can further reduce total season-long nitrogen losses and associated emissions. Increasing protein density per unit of edible grain enhances dietary adequacy while reducing the need for costly supplements or external fortification programmes.

Conclusion and future perspectives

The EAT–*Lancet* planetary health diet framework, which promotes switching protein intake from red and processed meats to plant-based sources, can be strengthened by (a) dietary complementarity—combining cereal and legume-based foods—as the most efficient strategy to meet EAA requirements in vulnerable populations as the immediate priority shift in the short-term and (b) increasing the protein level of cereals with elevated EAAs in the next decade. Furthermore, cereal-based protein enhancement offers a pragmatic solution in farming systems with constrained crop diversity, delivering more nutrition per unit of land while aligning with local dietary habits. A critical question is whether cereals can increase protein while maintaining—or even enhancing—starch accumulation. The emerging consensus is that this dual optimization becomes achievable only when the entire nitrogen economy of the plant is redesigned, rather than simply redistributing existing carbon and nitrogen pools within the grain.

Insights from high-lysine maize demonstrate that EAA enrichment is feasible without catastrophic yield penalties when metabolic bottlenecks, proteostasis and endosperm structure are simultaneously managed. One critical strategy is marker-assisted selection, combined with speed-breeding facilities, to target the key alleles (Os*Aux5*, Os*WRKY78*, *O2*, *O16* and lysine catabolism recessive alleles) being enriched in the breeding pools to increase EAAs while maintaining increased protein content without compromising yield and grain quality across cereals.

Moreover, the above-mentioned approaches can help ensure that protein-enhanced cereals contribute not only to improved nutrition but also to more climate-resilient and environmentally efficient food systems. Ensuring that cereal protein biofortification aligns with climate-mitigation goals therefore requires pairing nutritional improvements with agronomic and breeding interventions that lower the environmental footprint of cereal production. Agronomic interventions include intercropping of cereals and legumes to maintain soil health, planetary health and human health, as well as adopting alternate wetting and drying in rice fields or direct-seeded rice technologies, which lowers methane emissions by 30–70%. Beyond increasing total protein, future cereal biofortification must explicitly address protein bioavailability, which ultimately determines how much dietary protein is digested, absorbed and utilized.

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Competing interests

The authors declare no competing interests.

Additional information

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