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Review

Bridging Genes and Sensory Characteristics in Legumes: Multi-Omics for Sensory Trait Improvement

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Abstract

Legumes are vital sources of protein, dietary fibre and nutrients, making them crucial for global food security and sustainable agriculture. However, their widespread acceptance and consumption are often limited by undesirable sensory characteristics, such as “a beany flavour”, bitterness or variable textures. Addressing these challenges requires a comprehensive understanding of the complex molecular mechanisms governing appearance, aroma, taste, flavour, texture and palatability in legumes, aiming to enhance their sensory appeal. This review highlights the transformative power of multi-omics approaches in dissecting these intricate biological pathways and facilitating the targeted enhancement of legume sensory qualities. By integrating data from genomics, transcriptomics, proteomics and metabolomics, the genetic and biochemical networks that directly dictate sensory perception can be comprehensively unveiled. The insights gained from these integrated multi-omics studies are proving instrumental in developing strategies for sensory enhancement. They enable the identification of key biomarkers for desirable traits, facilitating more efficient marker-assisted selection (MAS) and genomic selection (GS) in breeding programs. Furthermore, a molecular understanding of sensory pathways opens avenues for precise gene editing (e.g., using CRISPR-Cas9) to modify specific genes, reduce off-flavour compounds or optimise texture. Beyond genetic improvements, multi-omics data also inform the optimisation of post-harvest handling and processing methods (e.g., germination and fermentation) to enhance desirable sensory profiles and mitigate undesirable ones. This holistic approach, spanning from the genetic blueprint to the final sensory experience, will accelerate the development of new legume cultivars and products with enhanced palatability, thereby fostering increased consumption and ultimately contributing to healthier diets and more resilient food systems worldwide.

Keywords: sensory traits; aroma; taste and flavour; texture; seed size and shape; seed-coat colour; legumes; omics

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1. Introduction

Legumes are important crops from a diverse family (*Fabaceae*), including beans, lentils and peas, which are primarily harvested for their grains, thus playing a role in improving human and livestock health [1]. They are rich in proteins, essential minerals, vitamins, fibre and antioxidants, and they are low in fat with no cholesterol. Therefore, they are considered a healthy and cost-effective alternative to animal-based proteins and a vital source of diverse nutrients [2]. Most importantly, legumes are a key component of many traditional dishes and recipes worldwide and are often incorporated into everyday meals due to their unique sensory properties. A broad range of legumes, such as chickpeas, kidney beans, lentils, peas and soybeans, are considered cornerstones of many ancient diet patterns, including the Mediterranean diet [3]. Legumes are naturally gluten-free, making them an excellent choice for consumers with coeliac disease [4]. They are eaten in various ways, such as being soaked, cooked, baked, or raw (freshly harvested) and can be used in salads, soups and pasta dishes. Legumes represent an excellent choice for sustainable food production as they are relatively resilient to climate change, can grow in various environments, improve soil quality and enhance soil carbon content by fixing nitrogen from the atmosphere [5,6].

Persistent demand for legume crops exists to fulfil the food requirements of an ever-growing human population. Moreover, legumes are predominantly self-pollinated crops with a narrow genetic base that poses a challenge to crop improvement programs. To overcome this constraint, legume breeders and geneticists employ both conventional and modern breeding approaches, which have significantly enhanced the agronomic traits, stress tolerance and nutritional qualities of legume crops, as well as their sensory traits [7]. Modern breeding techniques leverage germplasm diversity and high-throughput omics approaches, such as transcriptomics, metabolomics, proteomics, genome sequencing, marker-assisted backcross (MAB) breeding, genome-wide association studies (GWAS), genome editing and machine learning algorithms to contribute to sustainable agriculture and food security.

While traditional phenotypic selection and single-omics studies have yielded considerable progress, they often provide only a partial view of complex biological systems. Phenotypic selection, though effective, can be slow and resource-intensive, particularly for traits that are environmentally influenced or expressed late in the plant developmental stages. Similarly, relying on a single omics layer, such as genomics, reveals the potential but not the active expression or functional consequences of genes. This is where the true power of multi-omics approaches emerges. By integrating data across multiple biological levels—from the genome (what genes are present), to the transcriptome (which genes are active), the proteome (which proteins are produced and functional) and the metabolome (what small molecules are being made)—multi-omics provides an unparalleled holistic understanding. This comprehensive insight enables researchers to not only identify candidate genes but also decipher the intricate regulatory networks, metabolic pathways, and gene–environment interactions that underpin complex traits such as yield, stress response and sensory qualities. Recent advances in multi-omics approaches offer hope for future genetic improvements in domesticated and underutilised legumes. The availability of complete genome assemblies and high-throughput resequencing of diverse germplasm collections has facilitated the discovery of key genomic loci and candidate genes underlying critical agronomic traits. This knowledge is crucial for boosting genetic gain and breeding climate-resilient, nutrient-rich and locally adapted cultivars [1,8,9].

Sensory traits are fundamental to the widespread adoption, nutritional impact and economic success of legumes [10]. Often, appearance, colour and shape are the first initial criteria consumers use to judge food quality, thus influencing food consumption and purchases [11]. Legumes come in various colours and sizes. Seed colour, shape and size are significant agronomic traits in legumes and have been studied in detail [12,13]. The aroma in legumes is primarily derived from organic compounds and is released during the cooking process. These compounds, influenced by genetic diversity and processing techniques, can range from desirable earthy and nutty notes to less appealing grassy or beany characteristics [14]. Flavour, a more complex perception that incorporates both taste and aroma, is equally variable. While some legumes offer sweet and subtle flavours, others possess more pronounced bitter, astringent or even sulphurous notes. Taste involves the perception of basic sensations, including sweet, sour, bitter, salty and umami, which contribute to the overall palatability. Bitterness is often a significant concern in certain legumes, such as chickpeas [15,16]. Texture, determined by cell structure, moisture content and the presence of components, such as starch and fibre, plays a vital role in consumer preference [17]. Legumes exhibit a spectrum of textures, from firm and intact to soft and mashed, each influencing mouthfeel. Finally, aftertaste, the residual sensory experience following ingestion, can significantly impact overall satisfaction. Undesirable aftertastes, described as bitter or astringent, can detract from the experience.

The nutritional benefits of legumes are clear, yet their widespread consumption is hindered due to the presence of undesirable organoleptic characteristics, such as off-flavours (contributing to the bitter aftertaste), suboptimal digestibility and complex post-harvest processing demands [18]. Therefore, to increase the consumption of legumes worldwide, it would be essential to design new products or develop technologies to modify existing products, thus improving their flavour, digestibility and consumer acceptance [19]. Additionally, established methods are needed to measure the sensory impact of compounds that increase the overall flavour of legume-based food products and eliminate off-flavours. Thus, a detailed understanding of the sensory characteristics of legumes, such as their appearance, aroma, flavour, taste, texture and aftertaste, is crucial for effectively using legumes in diverse food applications (Figure 1).

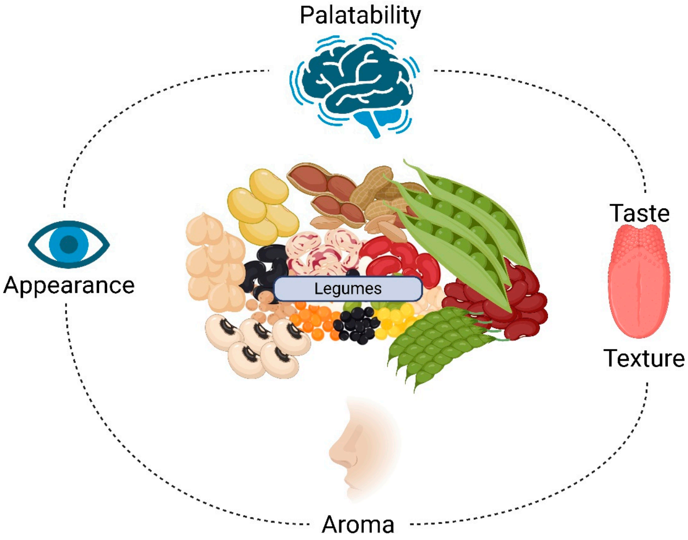

Figure 1. Schematic representation of key sensory traits in legumes, highlighting the factors affecting consumer acceptance. Visual and tactile qualities, such as texture and appearance, alongside the crucial impact of aroma and flavour profiles, significantly drive legume consumer acceptance. These traits collectively influence consumer preferences for legume-based food choices.

The genetics of sensory characteristics in legumes are vital for enhancing food quality, increasing consumer acceptance and promoting the broader utilisation of these important crops. Additionally, this knowledge can facilitate the development of new or improved food products with tailored sensory profiles. Therefore, by understanding the genetic underpinnings of these traits, researchers and breeders can develop improved legume varieties that contribute to a healthier and more sustainable food system. This review paper explores the intricate world of sensory perception to elucidate the genetic and molecular mechanisms that govern sensory characteristics in legumes. The outcomes will be a foundation for future research and breeding programs to develop more palatable and consumer-accepted varieties. This will ultimately contribute to increased legume consumption and their role in a healthy and sustainable diet for the world's growing population.

2. Appearance

Often, appearance is the first and one of the most crucial sensory traits significantly influencing consumer perception and acceptance of legumes. It encompasses various visual attributes that can be assessed, such as colour, size, shape and texture of seeds. Legumes exhibit various seed-coat colours, including white, red, black, brown, green and speckled. The colour of legumes can indicate their freshness and quality. For instance, bright, uniform colours are associated with freshness and high nutritional value, while dull or uneven colours may suggest ageing or poor quality [20]. Seed size, shape and colour in legumes vary when harvested fresh compared to when they are dried and dehydrated for storage. For example, the wrinkled seed coat of certain legumes (such as chickpeas, red kidney beans, pigeonpeas and lentils) changes when soaked in water or pre-processed before cooking. Furthermore, colour changes during cooking can affect consumer acceptance. For example, the darkening of beans during cooking can be perceived negatively, even though it does not necessarily affect the nutritional value [10]. Apart from colour, legumes also come in various shapes and sizes, such as round, oval, kidney-shaped and elongated, and they vary in size, ranging from small (lentils) to large (lima beans). Irregularly shaped or sized legumes may be perceived as lower quality or less appealing, as lentils of uniform size and shape are more likely to be chosen by consumers over irregular ones [21]. Also, the size of legume seeds can influence their cooking time and texture. The visual appeal of legumes is important for direct consumption and their incorporation into various food products. Often, consumers make quick judgments about the appearance of food at the point of purchase, which are related to their expectations about the product's quality and satisfaction. For example, the market value of chickpeas is mainly determined by grain phenotypic traits, including colour, shape and size. Recent consumer and industry trends have shown increasing demand for large-seeded desi chickpea varieties. Even most Kabuli breeding programmes have emphasised larger seed sizes to attain higher premiums [22].

2.1. Seed-Coat Colour

Seed-coat colour is a significant agronomic trait in legumes, influencing their marketability, nutritional value, functional properties and adaptability to environmental stresses. Various seed-coat colours exist within and among legume species [23]. This trait is closely associated with various pigments (polyphenolic substances), primarily flavonoids and anthocyanins, contributing to legume seeds' wide range of colours. Flavonoids and anthocyanins exhibit potent antioxidant properties, which can help mitigate oxidative stress at the cellular level, thereby contributing to the prevention and management of various chronic diseases. Adzuki beans have over a dozen seed-coat colours with pigment compositions closely related to the combination of proanthocyanidins and anthocyanins [24].

2.1.1. Genetics of Legume Seed-Coat Pigmentation

Seed-coat colour is genetically regulated through a complex network of genes that modulate the biosynthetic pathways of anthocyanins and flavonoids. The variation in seed-coat colour can be attributed to different combinations and expressions of these genes, resulting in a spectrum of colours ranging from white and yellow to red, brown and black. The stay-green seed-coat colour in chickpeas, for example, results from a loss of function in the *CaStGR1* (*stay-green gene 1*) gene, which impairs the chlorophyll degradation pathway and promotes prolonged chlorophyll retention [25]. Biochemical investigations in chickpeas indicated that the downregulation of two genes encoding a basic helix–loop–helix (CabHLH) protein and a tonoplast-localised multidrug and toxic compound extrusion transporter (CaMATE1) reduced the accumulation of anthocyanins and proanthocyanidins, resulting in altered flower and seed-coat colours [26]. The colour of common beans (*Phaseolus vulgaris*) is controlled by a set of genes that influence the flavonoid and anthocyanin pathways [27]. Moreover, the *T* gene (a MYB transcription factor (TF) gene) and *Z* (a WD40 repeat protein) gene are found to be crucial for seed-coat patterning in common beans [28,29]; both are components of the MBW complex (a ternary complex of MYB, bHLH, and WD40 proteins). In the case of seed-coat patterning, the MBW complex activates the expression of late flavonoid biosynthesis pathway genes, leading to pigment production and defining seed-coat colour [30]. Soybean seed colour is linked to the *I* locus, which controls the chalcone synthase gene expression and flavonoid biosynthesis, resulting in black seeds in wild types and yellow in domesticated varieties [31,32]. Similarly, homologous genes in various legumes, such as the *P* locus in common bean, the *A* locus in pea, the *B* locus in chickpeas and the *Tan* gene in lentils, are crucial for anthocyanin and flavonol biosynthesis [33–35]. In addition, two homologous genes contributing to seed-coat colour have been identified in the faba bean [36,37]. Flavonoid biosynthesis is also responsible for the diverse seed-coat colours seen in adzuki beans, including red, black, ivory, black mottle on red, beige, greenish-yellow, light brown, brown, green, golden (strong orange-yellow), black mottle on grey and others [27,38].

A study on genotyping by sequencing (GbS) and genetic map construction in common beans indicated three independent genes, one controlling a white colour, and two genes (with epistatic interaction) controlling a black colour [39], were involved in the anthocyanin biosynthetic pathway, encoding a flavonoid $3',5'$-hydroxylase and MYB113 TF. Researchers have identified candidate genes for a red seed-coat colour in cowpea (*Vigna unguiculata*), mapping to two loci. *Red-1* (*R-1*) encodes a dihydroflavonol 4-reductase, a homolog of anthocyanidin reductase 1, which drives the synthesis of epicatechin from cyanidin. The *Red-2* (*R-2*) gene, which is predicted to have a nucleolar function, also exhibited high expression in developing seeds [40]. Another GWAS study on cowpeas involved accessions exhibiting red, green and blue seed coats, highlighting the polygenic nature of the seed-coat colour trait [41]. Various candidate genes were identified, including pentatricopeptide repeat family (PPR), Lupus La-related protein/La-related protein 1, UDP-glycosyltransferase 71b2-related and MYB-like DNA-binding genes, which are implicated in anthocyanin biosynthesis. On the other hand, BSA-Seq (Bulked Segregant Analysis by deep sequencing) and genetic analysis indicated that red testa in peanuts was controlled by a single recessive gene *AhRt2* (*Red testa gene 2*), encoding anthocyanin reductase and a SNP in the third exon of *AhRt2* was also associated with red testa [42]. By comparing red and pink-seeded peanut cultivars using bulk RNA-sequencing (BR-seq), researchers identified differentially expressed genes (DEGs) involved in flavonoid biosynthesis, transportation and key TFs, including MYB and bHLH proteins. These DEGs regulated the expression of structural genes in the flavonoid pathway, resulting in the accumulation of anthocyanins that confer red pigmentation [43]. A GWAS study on common beans identified 31 significant SNP-trait associations for flavonoid synthesis, including regions for phenolic metabolites and seed-coat colour. The study proposed candidate genes involved in the phenylpropanoid pathway, as well as some anthocyanin genes [44]. Another research identified significant genotype × environment interactions affecting the seed-coat colour in yellow beans, and SNPs associated with seed-coat colour traits were found near the *J* gene and the *P* gene [12]. These reports are indicative of the complexity of gene networks involved in the genetic control of pigment compounds that govern the seed colour in various legumes. Another study investigates genetic diversity and seed-coat colour variation in common bean composite populations using genomic insights. It revealed significant genetic diversity within and among these populations, with specific populations exhibiting high variability. The research identifies selective sweeps and enriched pathways related to phosphatidylinositol signalling, which are crucial for understanding the change in seed-coat colour in common beans [45].

2.1.2. Unveiling the Seed-Coat Colour Using a Multi-Omics Lens

Recent advancements in omics technologies have provided more profound insights into the genetics and molecular mechanisms underlying seed-coat colour variation in legumes. Researchers used an untargeted metabolomics approach to link the antioxidant and iron-chelating properties of various seed-coat types from five key pulse crops: common bean, lentil, pea, chickpea and faba bean [46]. The highest antioxidant capacities were found in black bean seed coats; regardless of pulse crop, proanthocyanidins were the primary contributors to antioxidant capacity. Another study employed liquid chromatography coupled with mass spectrometry (LC-MS) to compare the polyphenolic profiles of pea seed components between speckled and dun seed-coat types, revealing differences in gallic acid content [47]. An MS-based untargeted metabolomics approach investigated polyphenol differences among lentil seed-coat patterns and discovered that patterned green lentils showed a significant upregulation of flavones, which were absent in non-patterned lentils [48]. Studies on mungbean (*Vigna radiata* L.) have demonstrated that different seed-coat colours are associated with distinct metabolic profiles. Specifically, researchers found significant variations in polyphenol content, including flavonoids, phenylpropanoids and anthocyanins, across genotypes. Interestingly, green and yellow mungbeans had higher levels of anthocyanins compared to black mungbeans [49]. Soybean germplasm (from America, China, Japan and Korea) exhibiting different seed-coat colours was analysed, and Korean accessions displayed the highest isoflavone content. In contrast, black soybeans were found to be dominant in terms of antioxidant activities [50]. Using UPLC-MS/MS, another study profiled metabolites in four peanut lines distinguished by their testa (seed coat) colours: pink, purple, red and white. This research revealed that proanthocyanidins were most abundant in pink peanuts, whereas the red testa accumulated more isoflavones, flavonols and anthocyanidins than the pink testa [51].

A comparative transcriptomics study of soybean seeds with black and yellow seed-coat colours discovered DEGs involved in ethylene, lipid, brassinosteroid, lignin and amino acid biosynthesis in cultivars with black seed-coat pigmentation [52]. Another soybean transcriptomics study identified differential expression of two candidate genes, one encoding a CAAX amino-terminal protease protein and a chalcone and stilbene synthase family protein, between wild and cultivated soybean accessions and identified the allelic differences contributing to seed-coat colour [53]. A comparative transcriptomic analysis, combined with Weighted Gene Co-expression Network Analysis (WGCNA), was used to identify the regulatory network underlying anthocyanin biosynthesis in black and green-seeded mungbean cultivars [54]. Researchers identified key TFs, structural genes in the anthocyanin biosynthetic pathway and regulatory genes encoding the ternary complex of MYB-bHLH-WD40 as being differentially expressed in the two mungbean varieties and suggested roles of VrMYB3 and VrMYB90 in enhancing anthocyanin content.

One of the recent studies conducted in 2023 integrated results from metabolomics and transcriptomics of two mungbean genotypes with different seed-coat colours to clarify the composition of anthocyanins and identify TFs regulating anthocyanin biosynthesis [55]. Black mungbeans had significantly higher anthocyanin content, with differential expression of most of the structural genes involved in anthocyanin biosynthesis. Through BSA-seq and fine mapping, the candidate genes for mungbean seed-coat colour were identified, and three out of eight candidate genes were differentially expressed between black and green seed-coat colour accessions [56], with their expression levels positively correlated with the metabolites of the flavonoid biosynthesis pathway. Another study employed a multi-omics approach (BSA and transcriptomics analysis) to investigate the formation of seed-coat colour in soybean seeds. Results revealed QTLs for seed-coat colour and DEGs were found to be involved in flavonoid biosynthesis, TF regulation, gibberellin and terpenoid metabolism, photosynthesis, ascorbate and aldarate metabolism and lipid metabolism [57]. Another combined metabolomics and transcriptomics analysis delineated the regulatory mechanisms of seed-coat pigmentation in peanuts and identified flavonoids in the seed-coat of four peanut cultivars with different testa (seed coat) colours [58]. Black peanut skin had substantially higher levels of cyanidin-based anthocyanins, contributing to its testa colouration. Another integrative analysis of the transcriptome and metabolome in a *wsc* mutant and its wild-type peanut revealed the mutant's influence on flavonoid biosynthesis and suberin formation, accompanied by enhanced hormone synthesis and signalling [59]. Three testa-specific genes, *Araip.M7RY3*, *Aradu.R8PMF* and *Araip.MHR6K*, were identified as governing the white testa phenotype.

Proteomic analyses complement genomic and transcriptomic data by identifying proteins involved in pigment biosynthesis and regulation. The proteomic analysis of the testa from developing soybean seeds revealed that proteins in the soybean seed-coat were primarily involved in primary and secondary metabolism, cellular structure, stress responses, nucleic acid metabolism, protein synthesis, folding and targeting, hormone synthesis, signalling and the biogenesis of seed storage proteins [60]. Comparative proteomics analysis of two black soybean cultivars revealed distinct protein profiles during seed development, particularly in proteins related to flavonoid biosynthesis and transport [61]. These differences, while both leading to black seed coats, likely contribute to variations in pigmentation intensity, chemical composition and potential functional properties of the seed coats. A comparative proteomics and metabolomics analysis of brown and yellow soybean seeds revealed that brown-seeded soybeans showed increased levels of proanthocyanidins, a class of flavonoids responsible for pigmentation [62]. This was accompanied by downregulation of proteins involved in primary metabolism, suggesting a diversion of energy towards proanthocyanidin biosynthesis.

Omics technologies have significantly advanced our understanding of the genetic and molecular bases of seed-coat colour in legumes. These studies elucidate the complex biosynthetic pathways and provide valuable genetic markers for breeding programs to improve seed quality and marketability.

2.1.3. Other Factors Affecting Seed-Coat Colour

Crop domestication processes have led to the loss of seed-coat pigmentation, possibly as a trade-off for protection from foragers [63,64]. The seed-coat pigmentation of wild chickpea progenitors, which often matches the surrounding soil, highlights the evolutionary significance of seed-coat colour [65]. Resequencing of 302 wild and domesticated soybean accessions and GWAS detected the contribution of structural variants towards selection during domestication and improvement of traits [66]. Another recent combined omics approach (published in 2024) was used to compare DEGs and altered metabolite/protein profiles between wild and domesticated pea genotypes [67] and showed that domestication prioritised proteins for photosynthesis and protein metabolism while reducing those involved in seed defence. The depigmentation of cultivated bean seed coats clearly illustrates the effects of domestication [33]. It remains unclear whether people's preferences directly selected seed colour, or if it was indirectly selected as being associated with seed dormancy [68]. Wild soybeans with the stay-green genotype also had dormant seeds, a trait that disappeared during domestication, as evidenced by the mutant allele found in yellow soybean varieties [69]. Also, pigmentation loss was linked to bitter-tasting compounds [70].

Furthermore, the effect of seed-coat colour on legume nodulation has been established at the molecular level [5,71], but the mechanisms by which seed-coat colour influences a legume's choice of rhizobia for symbiotic partnership, root nodulation and nitrogen (N2) fixation remain unclear. Darker seed-coat colours contain more significant flavonoids, anthocyanins and anthocyanidins that promote superior symbiotic functioning [71–73]. The success of rhizobia in forming a nitrogen-fixing relationship with legumes depends on specific symbiotic signals that enable molecular communication during nodule development [74]. Usually, plants produce the first signals in the form of flavonoids, which interact with *nodD* proteins of compatible rhizobia, resulting in a *nodD*–flavonoid complex. This complex then leads to the activation of *nod* boxes, causing the formation of deformed root hairs that facilitate the entry of rhizobia into plant roots. Flavonoids released from legume seed coats and young roots serve as powerful signals for symbiotic rhizobia, acting as chemoattractants, cell growth enhancers and *nod* gene inducers [75,76]. Thus, the same flavonoid molecule can elicit different responses in different rhizobia [77]. Understanding these pathways will provide a molecular framework for comprehending the functional role of seed-coat pigmentation in nitrogen-fixing symbioses.

2.2. Seed Size and Shape

Seed weight, shape and size are complex and polygenic yield traits in legumes and they are essential in determining seed quality and appearance. Thus, selecting uniform-sized large seeds has been key in crop domestication and breeding. Additionally, seed size and shape have a significant impact on industrial production and play a crucial role in influencing consumer and farmer choices. However, these traits have low heritability and are highly influenced by the environment and genotype × environment interaction [78]. The chemical composition of the cell wall directly regulates seed size and has been well documented in the literature [79,80]. Thus, deciphering how cell-wall dynamics influence seed size regulation will shed light on their respective roles throughout seed development.

2.2.1. Genes Regulating Seed Size and Shape in Legumes

Genetic and environmental factors play a complex role in governing legume seed size and shape. Genetic factors include specific regions of the genome that control seed size, like quantitative trait loci (QTLs); hormones, such as auxin and gibberellic acid, play crucial roles in regulating cell division and expansion, ultimately affecting seed size and TFs, regulating gene expression during seed development [81–83]. Environmental factors, such as nutrient and water availability, temperature and light intensity, can indirectly impact seed size. In legumes, these factors collectively control the diverse shapes and sizes of seeds within each pod. By understanding the interplay between cell-wall components, genetic factors and hormonal signalling, researchers can develop strategies to improve seed size and yield in crop plants. Furthermore, larger, uniformly sized and shaped seeds can hold more food reserves and nutrients than smaller, uneven ones. This quality has led to increased demand from both consumers and farmers for pods containing these consistent, larger seeds [84]. Table 1 lists genes involved in regulating seed size in legumes.

Table 1. A compilation of genes related to seed size regulation in legumes.

No.	*Gene Name*	*Plant*	Role	Reference
1.	*BIG SEEDS1* (*BS1*)—transcriptional regulator	*Medicago truncatula*, Soybean	Deletion/downregulation of *BS1* in *Medicago/Soybean* significantly increases seed size, weight and amino acid content.	[85]
2.	Subtilase gene (*SBT1.1*)	*Medicago truncatula*, *Pisum sativum*	Controls seed size in legumes through the regulation of embryo cell division. Co-located at a chromosomal position coinciding with a seed weight QTL.	[86]
3.	*USP* (Unknown Seed Protein) and *ANT* (*AINTEGUMENTA*)	*Medicago truncatula*	Specific expression of *ANT* in seeds resulted in larger seeds. The gene driven by the seed-specific promoter *USP* leads to the expansion of storage parenchyma cells in the cotyledon and a significant increase in vacuole size, resulting in a large-seeded phenotype.	[87]
4.	*ABCC3*-type transporter gene	Chickpea	Regulates seed weight by transcriptional regulation and modulation of the transport of glutathione conjugates in seeds.	[88]
5.	*Ca4_TIFY4B*	Chickpea	Determines leaf and seed size.	[89]
6.	*Glyma.19G151900*—gene encoding a histidine phosphor transfer protein	Soybean	Known to regulate seed weight.	[90]
7.	*PP2C-1*	Soybean	Regulates the brassinosteroid (BR) signalling pathway and controls the seed size.	[91]
8.	*GA20OX* and *NFYA*	Soybean	Overexpression of genes enhanced seed size/weight and oil content in seeds of transgenic plants.	[92]
9.	*Isopentenyladenine* (*iPR*)	*Medicago truncatula*	Associated with cell proliferation during seed development.	[93]
10.	*GmJAZ3* (*JASMONATE-ZIM DOMAIN 3*)	Soybean	Promotes increased cell proliferation and enhanced seed size/weight	[94]
11.	*GmAP2-1*, *GmAP2-4* and *GmAP2-6*	Soybean	Play crucial roles in regulating seed size in soybeans by positively influencing seed weight and size.	[95]

Detailed reports on the molecular regulatory networks of seed size in soybeans [78,96] and the regulatory landscape of seed development in peanuts [97] have already been published.

Seed shape is a lesser-explored trait, and its potential for use in applied breeding programs remains to be fully understood. A 2024 study on chickpeas primarily focused on classifying seed shapes and understanding their relationship to seed quality. Seed shapes in chickpeas were classified into distinct classes, such as angular, globular and owl-headed types, using a set of genotypes that constituted all three seed shapes [98]. Research has identified several genes that influence seed shape in legumes. For example, the *GmPDIL5-1* gene is involved in regulating seed shape by affecting the development of the seed-coat [99]. The wrinkled seed pea trait is rooted in the mutation of a gene encoding starch-branching enzyme I (*SBEI*), which disrupts the normal process of starch synthesis, resulting in the accumulation of sugars in the developing seed [100]. This increased sugar concentration draws in more water, causing the seed to swell and wrinkle as it dries.

For optimal growth and yield, pods need to contain seeds that are equal in size, uniformly shaped and larger [101]. Previously, QTL mapping was used to identify genomic regions linked to seed size traits in *Medicago truncatula* [102], *Vigna radiata* L. [103], *Vigna unguiculata* L. [104], *Cajanus cajan* [105] and *Cicer arietinum* [89]. Using sequenced data from 162 accessions in the *Medicago* HAPMAP collection, GWAS was performed on 32 seed size-related traits. This analysis identified candidate genes, such as *MtrunA17 Chr1_35506650* and *MtrunA17 Chr4_56801315*, which could help explain the connection between seed size and protein content [82]. Researchers in another study also utilised the sequencing data from 162 accessions of *M. truncatula* to identify an RNA-binding domain protein as a central regulator determining both seed size and composition [82]. A GWAS study on common bean dissected the genetic architecture and identified genomic loci associated with seed weight, size and shape and some candidate genes, such as those encoding an AT-hook motif nuclear-localized protein 8, type 2C protein phosphatases and a protein Mei2-like 4 isoform [106], revealing that the Andean gene pool produced larger, heavier seeds than the Mesoamerican gene pool. Also, researchers indicated that soybean seed size and shape may be controlled independently by performing a genetic analysis via linkage and association analyses [107]. Hence, these examples suggest multiple or independent genes can regulate seed size and shape traits in different crop cultivars.

A multi-environment study in soybeans, utilising deep re-sequencing and GWAS, identified SNPs strongly linked to seed length, width, diameter, circumference, area and length-to-width ratio across six different environments [108]. Some candidate genes related to seed size and shape were also identified, including *Glyma.10G035200* (Sn1-specific diacylglycerol lipase), *Glyma.10G035400* (transcription factor) and *Glyma.10G058200* (phenylalanine ammonia-lyase). A similar study was conducted on field peas to identify loci associated with seed yield and seed weight, seed morphology (shape and dimpling) and seed quality (protein, starch and fibre concentrations) and identified candidate genes as *Chr1LG6_57305683* and *Chr1LG6_366513463* for grain yield, *Chr1LG6_176606388*, *Chr2LG1_457185*, *Chr3LG5_234519042* and *Chr7LG7_8229439* for seed starch concentration (SSC) and *Chr3LG5_194530376* for seed protein concentration (SPC) [109]. Another GWAS study identified novel candidate genes and SNPs putatively linked with seed size in *Pisum sativum* L. [101]. Researchers conducted association analyses on 240 Pea Single Plant Plus Collection (PSPPC) panels of pea germplasm, measuring allometric seed traits including length, width, thickness, volume, biomass and seed biomass by volume (SBV). This work successfully identified candidate genes for each of these traits.

Also, two stable QTL regions for seed weight and size were identified in peanuts using Specific locus amplified fragment sequencing (SLAF-seq) for high-density genetic map (HDGM) construction and QTL mapping [110]. Additionally, researchers applied SNP genotyping and legume synteny knowledge to characterise cowpea genome regions associated with seed size [111]. Co-localisation of the genomic regions related to seed morphology (seed shape, size, colour, composition and weight) and composition in a desi chickpea population varying in SPC was also reported [112]. Further, three QTLs for shrivelled seed and one QTL for seed size were identified in pigeonpea using the genotyping data from the Axiom Cajanus SNP Array [113].

Researchers used high-resolution mapping in two soybean recombinant inbred line (RIL) populations to pinpoint four major QTL hotspots/clusters controlling seed size and shape across multiple environments [114]. By integrating gene annotation, gene ontology enrichment analysis and RNA-seq data, potential candidate genes within these QTL hotspots were identified, providing valuable insights into the genetic mechanisms underlying seed size and shape variation in soybeans. Another study in common beans combined association studies and differential expression analyses to pinpoint consistent genomic regions and candidate genes controlling seed traits [115]. Five QTL regions revealed three main clusters that were significantly associated with seed weight. Additionally, DEGs related to cell growth, signalling pathways, and transcription factors were also identified.

Furthermore, many QTLs related to soybean seed size and shape were identified using Changjiang Chun 2 × JiYu 166 and Changjiang Chun 2 × Yushuxian 2 crosses, resulting in a genetic linkage map, QTLs and candidate genes with significant overlaps between hundred-grain weight and seed width [116,117]. In common beans, a 240-SNP linkage map was used to identify 39 QTLs associated with seed size and yield traits, with most seed size alleles originating from the Andean parent and pod traits from the Mesoamerican parent [118]. In soybeans, 42 QTLs were related to seed weight and shape, with 29 novel QTLs, 17 of which were major QTLs. Additionally, 66 genes within the stable QTL regions were predicted as potential candidates for regulating seed shape and weight [119]. Conclusively, high-throughput omics studies have significantly advanced our understanding of the complex genetic and molecular mechanisms that govern seed size and shape in legumes. This knowledge is crucial for developing improved legume varieties with enhanced yield and quality.

Significant morphological changes occurred during domestication for seed size and shape traits. For example, wild soybeans have smaller seeds, twisted stems, breakable pods, and impermeable seed coats compared to cultivated soybeans; whereas cultivated soybeans have larger seeds [120].

2.2.2. A Multi-Omics Exploration of Legume Seed Size and Shape

In lentils, a study unfolded the pathways regulating seed size by employing a transcriptomics approach using large-seeded (L4602) and small-seeded (L830) genotypes. Various genes linked to hormone signalling, cell division pathways, TFs and kinases were found to play a role in cell expansion and seed growth, thereby influencing lentil seed size [121]. RNA-Seq analysis in soybeans revealed two genes: *Glyma.17G202700* (encoding an E3 ligase zinc finger protein), highly expressed in the seed-coat of large seeds and *Glyma.07G196500* (encoding an E2-conjugating enzyme phosphatase 2), which showed a seven-fold higher expression in the seed-coat of large seeds compared to small ones [122]. Further findings suggested a potential role of the ubiquitin-mediated protein degradation pathway in regulating soybean seed size. A comparative proteomics and metabolomics study revealed that larger grains were associated with the overproduction of proteins involved in starch, lipid and amino acid metabolism, along with an accumulation of gibberellin. In contrast, smaller grains exhibited an excess of proteins associated with water deprivation, alongside various phenolics (including vanillin, salicylic acid, protocatechuic acid, 4-coumaric acid, 4-hydroxybenzoic acid, vanillic acid, ferulic acid and kaempferol 3-O-glucoside), as well as the amino acid L-phenylalanine. This suggests that the activated phenolic pathway contributed to the higher antioxidant capacity of small grains [123]. However, there have been limited studies in this area, and future research can be targeted at legume species such as pigeonpeas and groundnuts.

Multi-omics approaches are proving instrumental in dissecting seed-coat colour, size and shape traits in legumes, from identifying key regulatory genes to mapping the precise accumulation of pigments. This integrated understanding is crucial for breeding new legume varieties with the desired seed aesthetics and functional properties, which in turn impact market acceptance and nutritional value in legumes.

3. Aroma

Comprehensive knowledge about aroma in legumes is essential for optimising their sensory quality and developing new and appealing food products. Aroma is composed of volatiles and is nasally perceived, while taste is caused by non-volatiles and perceived in the oral cavity by the tongue. The flavour is multifaceted and involves both taste and aroma. Off-flavours in legumes and pulses are the perception of an unpleasant taste, aroma, and/or other effects such as beany, grassy and astringency, which were reviewed in detail [124]. Aroma in legumes is a highly complex sensory trait, primarily driven by the intricate interplay of numerous volatile organic compounds (VOCs). These VOCs, present in trace amounts, are derived from multiple biochemical pathways (including lipid oxidation, amino acid metabolism and carbohydrate breakdown) occurring within the legume seed, particularly during processing, storage and cooking. Legumes contain a wide array of VOCs, including aldehydes, alcohols, ketones, pyrazines and sulphur compounds, which contribute to their smell and aroma. Also, the types and levels of volatile compounds produced or present during cooking, roasting and other processing or storage methods can significantly alter the aroma profile of legumes.

Legumes are rich in unsaturated fatty acids, which are highly susceptible to enzymatic (lipoxygenase activity) and non-enzymatic oxidation. This process generates a variety of volatile aldehydes (hexanal, responsible for “grassy” or “beany” notes), ketones and alcohols that contribute significantly to the overall aroma profile, often associated with both desirable and undesirable characteristics [125]. Amino acids serve as precursors for a diverse range of volatile compounds through pathways like Strecker degradation and enzymatic conversions. For instance, branched-chain amino acids (leucine, isoleucine and valine) and aromatic amino acids (phenylalanine, tyrosine and tryptophan) can be metabolised into aldehydes, alcohols and sulphur-containing compounds, contributing to nutty, roasted, or sometimes sulphurous notes [126]. The breakdown of carbohydrates, particularly during processing methods such as fermentation or cooking, contributes to the formation of aroma. This can occur through caramelisation, Maillard reactions (which involve reducing sugars and amino acids) and microbial fermentation. These processes generate various aldehydes, furans, pyrazines and other heterocyclic compounds that impart sweet, caramel-like, or roasted aromas [127,128].

Information on odour-active compounds in pulses is limited, with existing studies focusing primarily on peas and lupins [129]. Various small compounds have been identified in pulses, including aromatic hydrocarbons, aldehydes, alkanes, alkenes, alcohols, ketones, acids, esters, pyrazines, terpenes, furans and lactones [124]. While each of these molecules has its own distinct scent, the aroma we perceive is usually a blend of different notes from several molecules [130]. Furthermore, to boost consumer acceptance of legume-based foods and beverages, the distinctive “beany” aroma needs to be either eliminated or altered [131].

Volatile compounds are the primary source of aroma in legumes. Depending on their concentration and how they interact with other substances, some of these compounds, such as hexanal and 1-octen-3-ol, can create unpleasant odours in uncooked legumes [124]. Other chemicals with beany odour characteristics are 3-methyl-1-butanol, 1-pentanol, (*E*,*E*)-2,4-heptadienal, acetophenone, 1-octen-3-one and 3-isopropyl-2-methoxypyrazine [132]. While hexanal can contribute to an undesirable off-flavour, it does not have a “beany” scent on its own. However, its presence can intensify the beany odour [132]. Additionally, previous research has also documented how different binary mixtures of molecules can alter aroma perception when their concentrations vary [133]. Also, the characteristic smell of protein isolates originates from a mixture of odourants rather than any single one; for example, 2-pentylfuran is known to suppress the odour perception of dimethyltrisulfide [134]. Therefore, determining the roles of individual compounds and developing targeted removal strategies is challenging. This is because the concentrations and ratios of odourants, as well as the complex way mixtures of molecules affect our flavour perception, all play a part. The beany aroma found in extruded and commercial navy bean powders comes from the volatile compounds hexanal, 3,5-octadien-2-one and benzaldehyde [135], which are considered definitive volatile markers for dry beans [136].

Also, the enzymatic and non-enzymatic oxidation of lipids and fatty acids, such as linoleic acid and linolenic acid, is a major contributor to the volatile profiles in legumes [132]. Enzymes involved in the breakdown of compounds that contribute to aroma, such as lipases, lipoxygenases, lyases, peroxygenases and proteases, also play a role [137,138]. The decomposition of fatty acids, either through auto-oxidation or enzymatic degradation, leads to the formation of primary (hydroperoxides) and secondary oxidation products. Many alkanals, alkenals and alcohols originate from unsaturated fatty acids. Odour-active molecules such as 1-pentanol, hexanal, 2-heptanone, 1-octen-3-ol, 2-pentylfuran, (E)-2-octenal, octanoic acid, (E,E)-2,4-nonadienal, (E,E)-2,4-decadienal, (E,E)-2,4-heptadienal and (E,E)-3,5-octadione are typically formed through the autooxidation of linoleic and linolenic acid [139].

Other potent odourants, not derived from fatty acids, also contribute to the aroma of peas, including pyrazines, such as 3-alkyl-2-methoxypyrazines [139]. Pyrazines and pyranones contributed to the aroma of roasted peas, giving them a nutty flavour [140]. 2-Isopropyl-3-methoxypyrazine and 2,5-dimethylpyrazine are known to have "pea-like" and "malty, nutty" attributes, as perceived by sensory panellists [141]. Apart from pyrazines, 2-acetyl-1-pyrroline, methional and *p*-vinylguaiacol are other reported odourants from pea extracts [142].

Furthermore, thermal processing can trigger reactions such as the Maillard reaction and Strecker degradation, as well as other heat-induced breakdowns. These processes form various odour-active volatile compounds, such as furans, Strecker aldehydes and sulphur compounds [143]. During cooking, red kidney beans show a notable decrease in aldehydes, alcohols and terpene hydrocarbons. Conversely, an increase in sulphurous compounds, terpene alcohols, ketones and pyrazines was noted [144]. In cooked red kidney beans, *p*-vinyl guaiacol was identified as the primary contributor to the smoky smell. The sulphury note primarily came from diethyl sulphide and 2-ethyl-3-methyl pyrazine was responsible for the earthy aroma [145]. Therefore, by observing changes in volatile compounds, we can understand how processing affects these complex reactions and, ultimately, the overall flavour and aroma profile. A comprehensive characterisation of legume-seed volatile and fatty acid profiles revealed that soybean, chickpea and lentil had distinct volatiles, including lactones, esters and ketones, respectively. While the *Phaseolus* cultivars had similar volatile profiles, 3-methyl-1-butanol was the only volatile compound that set them apart from the other legumes [146].

3.1. Genetic Regulation of Aroma in Legumes

It is essential to recognise that the genetic regulation of aroma in legumes is a highly complex research area, highlighting the potential of aroma traits to be introduced in legume breeding programs [147]. Genes that can be targeted include those regulating the production of volatile compounds, lipoxygenase genes and genes involved in the breakdown of amino acids, mainly through processes such as Strecker degradation, which produce aroma-active compounds.

2-Acetyl-1-pyrroline (2AP) is a volatile compound that imparts a 'popcorn-like' aroma in many cereal and food products, presenting an appropriate example for aroma studies in legumes. Previously, a deficiency in amino aldehyde dehydrogenase (AMADH) was reported to be responsible for 2AP biosynthesis in rice (*Oryza sativa* L.) [148]. This mechanism was also investigated in soybeans. An assay of AMADH activity in aromatic soybeans with 2AP showed the lack of AMADH enzyme activity. Homologs of the rice *Os2AP* gene in soybean: *GmAMADH1* and *GmAMADH2* that encode AMADH were characterised. Aromatic soybean varieties were reported to have a lower transcription level of *GmAMADH2* and a double-nucleotide (TT) deletion. This variation resulted in a frame-shift mutation and a premature stop codon, which in turn inhibited AMADH synthesis and induced 2AP biosynthesis [149]. In another study, researchers developed a codominant PCR-based marker for the aroma trait in soybeans, leveraging the 2-bp deletion in the *GmAMADH2* gene. This marker was successfully validated in five aromatic and five non-aromatic soybean varieties as well as in an F_2 soybean population exhibiting aroma segregation [150]. Furthermore, a sequence comparison of *GmBADH1/2* (aminoaldehyde dehydrogenase) between aromatic and non-aromatic soybean varieties uncovered a mutation in exon 1 of *GmBADH2,* consisting of 10 SNPs and an 11-nucleotide deletion. Genetic analyses revealed that the aromatic trait in soybeans is inherited as a single recessive gene. Notably, *GmBADH2* has been identified as enhancing soybean aroma and serving as a functional marker for improving soybean flavour [151].

Also, aromatic mungbeans possess a unique, desirable aroma, often described as popcorn-like or pandan-like, which is primarily attributed to 2AP. Thus, identifying the specific volatile compounds responsible for this aroma, especially 2AP, enables the selection and breeding of mungbean varieties with enhanced sensory qualities. Researchers identified 26 volatiles in aromatic mungbean seeds and 20 in non-scented mungbean seeds. Among these, 3,7-dimethyl-6-octenal, (2E)-2-decen-1-ol, 2-ethyl-1-dodecanol and 3,5,5-trimethyl-2-cyclohexene-1-one were reported for the first time. Statistical analysis revealed that 2AP, octanal, 1-pentanol, decanal, phenylmethanol and 2-nonen-1-ol were the main contributors to mungbean aroma. A significantly higher level of proline and methylglyoxal, coupled with a lower level of *BADH2* transcripts, was found in aromatic mungbeans compared to non-scented ones. This suggests that the 2AP biosynthesis mechanism in aromatic mungbeans is similar to that reported in scented rice, sorghum and soybean [152].

Freshly harvested lablab bean pods have a unique fragrance that fetches a premium price. A lablab bean homolog (*LpBADH2*) of soybean *GmBADH2* with a high degree of similarity contains one and three non-synonymous and synonymous SNPs, respectively. The substitution of tyrosine (found in fragrant lablab bean accessions) with phenylalanine (found in non-fragrant accessions) in the LpBADH2 protein suggests its involvement in fragrance. This finding could be used in breeding programs to develop lablab bean cultivars with strong fragrance [153].

3.2. Omics Studies to Decode Aromatic Traits in Legumes

A study has reported the use of combined metabolomic and quantitative RT-PCR analyses in the two developmental stages of vegetable soybean grains in a non-aromatic and aromatic variety [154]. To understand the pathways of aroma formation, researchers conducted a targeted metabolome analysis measuring both metabolite and gene expression levels. Differentially accumulated metabolites (DAMs) in two varieties were grouped into nine categories, including flavonoids, lipids, amino acids and derivatives, saccharides and alcohols, organic acids, nucleotides and derivatives, phenolic acids, alkaloids and vitamins. These metabolite categories essentially explained the observed phenotypic differences between the soybean varieties. When focusing on the 2AP synthesis pathway, they discovered that differences in amino acids and their derivatives were primarily involved in 2AP synthesis. Further analysis of 2AP precursors indicated that 1-pyrroline-5-carboxylate (P5C), rather than 4-aminobutyraldehyde (GABald), was the main source of 2AP accumulation. Quantitative RT-PCR confirmed this synthetic pathway for 2AP, showing that the associated genes were 1-pyrroline-5-carboxylate dehydrogenase (*P5CDH*), Δ1-pyrroline-5-carboxylate synthetase (*P5CS*), proline dehydrogenase (*PRODH*) and pyrroline-5-carboxylate reductase

(*P5CR*). Additionally, the betaine aldehyde dehydrogenase 2 (*GmBADH2*) mutant proved crucial for synthesising both 2AP and 4-aminobutyric acid (GABA) in vegetable soybeans. Ultimately, this study illuminated the reasons behind the different 2AP accumulation levels in aromatic and non-aromatic vegetable soybeans, providing a critical theoretical foundation for breeding aromatic vegetable soybean varieties.

A multi-omics analysis (involving genomics, transcriptomics, and metabolomics) of genes related to oil traits in soybeans provides insights into lipid metabolism and how these genes influence oil content. Results indicate that gene family expansions and contractions, especially in triacylglycerol (TAG) biosynthesis and degradation pathways, play a crucial role in determining oil richness. Additionally, the study identified key TFs that act as regulators of lipid metabolism, potentially offering targets for enhancing oil production in soybean [155]. Such studies will play a pivotal role in deciphering other molecular mechanisms involved in regulating aroma and the production of odour-active compounds in legumes and pulses.

To date, various omics approaches have been employed to unravel the intricate genetic and biochemical pathways governing legume aroma, providing a comprehensive understanding of the volatile organic compounds and their origins. This holistic insight is crucial for precisely manipulating and enhancing desirable aroma profiles in legumes, thereby increasing their consumer appeal and expanding their culinary applications.

4. Taste and Flavour

Legumes, such as lentils, can be consumed in various forms, including dry seeds, fresh sprouts, flours, protein isolates, and concentrates. They are also used as the main ingredients in many traditional and modern food products. Different tastes and flavours are attributed to each form in which legumes are consumed and are influenced by genetic, biochemical and environmental elements. The growing conditions, including soil type, climate and agricultural practices, can influence the taste of legumes. Even environmental factors such as drought or high temperatures can affect the concentration of taste-related compounds [156]. Taste is a basic chemical sense perceived solely by the taste buds on our tongue and refers explicitly to sensations of sweet, salty, sour, bitter and umami. In contrast, flavour is a complex, multi-sensory experience that integrates aroma, texture, mouthfeel and taste. The primary taste compounds in legumes are influenced by the presence of volatile and non-volatile compounds, including saponins, phenolic compounds and alkaloids. These volatile and sapid compounds also contribute to the undesirable or off-flavours in legumes and pulses [124,157].

Additionally, several compounds contribute to the bitterness and astringency of pulses. Saponins, alkaloids, isoflavones, peptides and free amino acids are linked to bitterness, while phenolic compounds primarily cause astringent sensations [158]. Also, some lipids and lipid oxidation products contribute to the bitterness of pea protein isolates [159]. While vicine and convicine are linked to bitterness, other compounds, such as free phenolic compounds and amino acids (including phenylalanine, tryptophan and histidine), also play a role in this taste [157]. Another source of bitterness is the high protein content in lupins and faba beans, where proteins are enzymatically degraded, and bitter peptides can form during food processing [160]. The bitter impact of different peptides varies significantly and can be reduced by enzymatic degradation to shorter peptides and amino acids [161]. The bitter taste can also be masked or suppressed by adding sweet-, salty-, sour-, or umami-tasting components [162].

Volatile compounds primarily result from the oxidation of unsaturated fatty acids, degradation of amino acids and carotenoids and processes like storage and transformation (e.g., dehulling, milling, and starch or protein production) [130]. Some volatile compounds, such as pyrazines and alkylated pyrazines, are produced during roasting and might be important for masking the beany flavour in raw pulses [163]. However, we know little about the non-volatile compounds that cause these off-flavours in pulses. Also, the presence or absence of tannins, phytic acid and lectins can affect taste perception.

While lentils are valued for their nutritional and health benefits, their ingredients and products often have off-flavours described as beany, green or grassy, which limits their consumer acceptance [164]. Off-flavours in legumes and legume-based foods are a well-documented phenomenon [14,165]. Consumers particularly notice the beany off-flavour, which stems from a combination of aldehydes, alcohols, ketones and furans. These compounds are either naturally present in the seeds or developed through chemical reactions during processing. Several molecules that are responsible for a beany off-flavour are 3-methyl-1-butanol, 1-pentanol, 1-octen-3-ol, (E,E)-2,4-heptadienal, acetophenone, 1-octen-3-one, and 3-isopropyl-2-methoxypyrazine [133,166]. In addition, lentils have high lipoxygenase (LOX) activity, responsible for the oxidation of polyunsaturated fatty acids [167], resulting in off-flavours and adversely affecting the sensory quality of lentil derivatives [168]. Additionally, seed starch content (SSC) affects the taste, flavour and processing properties of soy-based foods.

Different processing and storage methods produce distinct appearances and aromas, assigning distinguishable tastes, mouthfeels, flavours and aftertastes. For example, bean snacks exceed the minimum flavour requirements for acceptability, but many panellists reported an undesirable beany flavour [169]. Also, crackers made from unprocessed navy beans were unacceptable to consumers due to the same beany flavour [170]. Boiled dry beans were disliked due to their bitter taste and soapy and metallic aftertastes [171]. However, roasted legumes were characterised by unique flavours, enhancing their sensory appeal [172]. Similarly, porridge produced from bean extrudates did not have a beany flavour, as determined by a consumer panel, due to the reduced availability of lipids for oxidation [173]. However, bean flour is prone to developing off-flavours due to the breakdown or alteration of naturally occurring phytochemicals and odour-active chemicals [158], such as furans resulting from Maillard reaction products and aliphatic aldehydes from lipid degradation [169]. The mashed potato flavour of legumes can be attributed to methional, which is formed when methionine undergoes the Strecker degradation reaction [174], and is further oxidised into potent aroma compounds, such as methanethiol and dimethyl sulphide.

Furthermore, lentils contain antinutritional compounds, such as trypsin inhibitors, phytates, raffinose-family oligosaccharides and tannins, that reduce nutrient digestibility or cause gastrointestinal discomfort and flatulence [175]. However, cooking or fermentation can reduce the presence of these antinutritional compounds [176]. Raffinose family oligosaccharides (RFOs), which are abundant in legumes like chickpeas, cause flatulence in both humans and animals [177]. Also, tannin extract from the lentil seed-coat increased the phenolic compounds in lentils [178]. Trypsin inhibitors, phytohemagglutinins and allergens in peanuts are some other antinutritional compounds reported in legumes [179]. To fully understand the metabolic pathways that produce antinutritional compounds and to ultimately remove these factors from plants, it is essential to integrate results from multi-omics approaches.

4.1. Genetic Determinants of Taste and Flavour in Legumes

Breeding may offer an alternative to mitigate the beany flavour of legumes and lentil-based products, involving genetic selection and the utilisation of varieties with low contents of the compound precursors responsible for off-flavours and/or low enzymatic activity, compared to expensive and energy-intensive post-harvest treatments (e.g., thermal, chemical or enzymatic). Varietal differences in lipid content and fatty acid composition have been reported among faba beans and lentils [180,181]. Therefore, to optimise the content of desired metabolites in legume cultivars, it is crucial to identify key genes or alleles linked to various secondary metabolite pathways, particularly those producing volatile organic compounds that impact taste and flavour.

Moreover, the availability of genomic resources accelerates efforts to enhance the quality of seed legumes, such as the intention to breed out the bitter taste caused by alkaloids in legumes. In yellow lupin (*Lupinus luteus*), the domesticated variety is reported to have much lower alkaloid content than the wild form [182]. In lupins, efforts are focused on identifying and manipulating genes involved in the quinolizidine alkaloid (QA) biosynthetic pathway to breed “sweet” (low-alkaloid) varieties [183]. Likewise, the saponin biosynthesis pathways can be targeted by involving enzymes such as oxidosqualene cyclases and various glycosyltransferases, as the genes encoding these enzymes would influence the type and quantity of saponins produced. Similarly, genes like *zero-tannin* (*zt*) are targets for reducing undesirable compounds in faba bean [184]. Significantly reduced off-flavour notes have been reported in varieties with low LOX and lipid content for soybeans and peas [164]. Clustered Regularly Interspaced Short Palindromic Repeat-associated protein 9 (CRISPR-Cas9) technology was used to edit LOX-related genes in soybeans and peas [185,186]. Additionally, genomic approaches have facilitated the development of molecular markers associated with the low-raffinose phenotype in soybeans [187]. Faba bean breeding efforts have focused on reducing off-flavours by targeting specific marker compounds, including volatile (e.g., hexanal) and non-volatile (e.g., 1-linoleoyl glycerol) lipid-oxidation products, phenolic acids (e.g., p-coumaric acid and ferulic acid), flavonoids (e.g., quercetin) and tannins (e.g., epicatechin and procyanidin B2) [188]. Additionally, sweet lupins with low alkaloid content [187] and low-tannin cultivars of faba beans [188] have been developed.

Recently, a GWAS study (conducted in 2025) in 245 faba bean accessions identified several SNP loci and key regulators as candidate genes involved in lipid biosynthesis (*ATS2*, *KAS*, *LPP*), amino acid transport (*CAT4*) for protein storage, *zero tannins locus-1* (*zt-1*) and regulators of the phenylpropanoid pathway, such as a *shikimate kinase* gene and TFs bHLH137-like and MYB [189]. In common beans, six SNPs were found to be associated with total flavour intensity, five SNPs with beany flavour, three SNPs with earthy flavour, one SNP with starchy flavour, one SNP with bitter flavour, three SNPs with seed-coat perception and two SNPs with cotyledon texture [190]. In soybean, nine QTLs associated with SSC were identified using 169 recombinant inbred lines; however, no stable QTL was observed across three years, highlighting the strong influence of environmental factors. Two QTLs (*qSTR11_1* and *qSTR20_1*) overlapped with sucrose-related QTL, suggesting a connection between starch and sucrose biosynthesis in soybean [191]. Some studies have mapped QTLs for lipid and protein content in faba beans but could not identify any candidate genes [192,193]. A GWAS study identified 48 SNPs for all the targeted sugar types and nine genes as potential candidate genes for sugar metabolism and transport in chickpeas [194]. Faba bean breeding has largely focused on developing cultivars that are anti-nutritional-free (such as tannins and low vicine and convicine) cultivars [195]. Through an integrative analysis of transcriptomics and metabolomics, the key regulatory gene implicated in vicine and convicine pathways was identified in faba beans [196].

4.2. Omics Studies Exploring Taste and Flavour Profiles in Legumes

A recent metabolomics study examined the impact of thermal processing (baking and cooking) on mungbean flavour and the changes that occur during storage. Researchers identified a total of 131 flavour precursors and 45 volatile substances. Thermal processing increased the levels of volatile substances, including ketones, aldehydes, esters, pyridine and pyrazines, as well as compounds from the Maillard reaction, such as 2-hydroxypyridine, 2-methoxy-3-isobutylpyrazine, 1,2-hexanedione and 2,3-butanedione. Both baking and cooking inhibited linoleic acid oxidation, significantly reducing the content of hexanal, a major contributor to the beany odour. However, storage had the opposite effect, accelerating the conversion of linoleic acid to C_{13} peroxides. This led to an increase in hexanal content and a more pronounced bean odour. Additionally, storage caused a decrease in precursor substances, such as glucose-1-phosphate and led to the accumulation of pyruvic acid intermediates in the pentose phosphate and pyruvate/amino acid metabolism pathways. These changes ultimately resulted in a reduced taste richness in mungbeans [197]. Another study explored the flavour of green beans and its connection to volatile compounds, including 1-octen-3-ol, 3-hexen-1-ol (both from fatty acid metabolism) and linalool (from the terpenoid pathway). Metabolomic measurements showed a correlation between linalool and the floral descriptor and 1-octen-3-ol and the nutty descriptor. Interestingly, a negative correlation was observed between linalool and 1-octen-3-ol. The study identified six QTLs for linalool, three for 1-octen-3-ol and three for 3-hexen-1-ol. Furthermore, a GWAS analysis on 201 diverse green bean varieties revealed 27 significant associations for eight volatile compounds and a cluster of alcohol dehydrogenase genes was also identified [198]. Researchers analysed metabolites in two broad bean (*Vicia faba* L.) genotypes that show significant differences in taste, flavour and nutritional content. Results identified a total of 149 DAMs, with most of them closely linked to the antioxidant and anti-cancer properties of beans, while others belonging to the flavone and flavonol biosynthesis pathways, contributed to taste formation. Furthermore, the variations in key secondary metabolites, including flavonoids, terpenoids, amino acid derivatives and alkaloids, likely contribute to a higher nutritional value and improved taste [199]. Another study used NMR-based metabolomics to analyse 14 different cultivars of four types of pulses (pea, lentil, faba bean and lupin). Lupin had a higher content of carbohydrates and a lower content of free amino acids than the other species. Differences among cultivars related to carbohydrates were observed in peas and lentils. Faba beans had the highest concentrations of phenolic compounds. By correlating with descriptive sensory profiling, researchers were able to identify several amino acids and organic acids that explained the differences in perceived smell and taste among the various cultivars [200]. Additionally, metabolomics revealed the potential bitter, non-volatile compounds in faba beans. The fractions from high-alkaloid cultivars and the protein fractions showed a more intense bitter taste. These compounds mainly consisted of alkaloids, amino acids, phenolic compounds, organic acids, and terpenoids [201]. Furthermore, metabolomics is currently combined with sensory studies to better understand the origins of taste perceptions, such as bitterness in faba beans [202].

While pulse proteins offer excellent nutritional benefits, their use in food is limited by their poor functionality and unpleasant flavour. Protein structure modification was proven useful in improving the functionality and flavour profile of pulse proteins. Comprehensive reviews were published detailing current techniques for improving pulse protein structure and functionality/flavour, including chemical and enzymatic modifications, as well as molecular breeding [14,203]. Some pea protein-based foods were analysed in detail, including their chemical composition and mechanisms behind perceptions of beany, bitterness, and astringency, resulting in comprehensive volatile molecule profiles. The beany and bitterness notes depended mainly on the protein and gellan content type, while the formulation can limit highly persistent astringency [204].

Such omics approaches are crucial for understanding the complex interplay of taste and flavour in legumes, by aiding in the identification of both volatile and non-volatile compounds. This comprehensive insight allows for targeted breeding and processing strategies, ultimately enhancing the overall palatability and consumer acceptance of these vital crops.

5. Texture

The texture of legume seeds is determined primarily by their starch composition, especially the balance between amylose and amylopectin. Starch, a key carbohydrate in legumes, comprises two polysaccharides: amylose with a linear structure and branched amylopectin [205]. The ratio of these two components influences the functional properties of starch, affecting the texture of foods derived from legumes. Generally, legumes contain a higher proportion of amylose compared to cereals. For example, cereals typically have around 25–28% amylose and 72–75% amylopectin, whereas legumes contain about 5–10% more amylose [206]. This higher amylose content produces a firmer and less sticky texture in cooked legume products [207]. The starch content in legumes influences their culinary uses, affecting the texture, consistency and thickening properties of legume-based dishes, making them versatile ingredients in a wide range of foods.

Seed-coat thickness also significantly impacts the texture of legume seeds, primarily by influencing their water absorption rate and consequently, their cooking time and final cooked firmness [208]. Some legumes exhibit "hard-to-cook" (HTC) phenomenon, which can be exacerbated by thick, impermeable seed coats, resulting in hard seeds even after extended cooking [209]. Thus, seed-coat thickness is a critical breeding target for improving the textural quality and reducing cooking time of legumes, which directly affects their convenience and consumer acceptance.

Additionally, understanding the seed cell-wall structure is crucial for legume breeding programs, as cell-wall biosynthesis contributes to texture by influencing cell size, shape and thickness [210,211]. Identifying key genes involved in cell-wall biosynthesis and accumulation of storage compounds makes it possible to develop legume varieties with specific textural properties, thereby improving their overall suitability [212]. Cellulose is the primary structural component of the cell wall and is synthesised by cellulose synthase enzymes. Cellulose is composed of linear chains of β-(1→4)-linked D-glucose units, which assemble into microfibrils (produced by cellulose synthase complexes embedded in the plasma membrane), thereby giving structural support to the cell wall. In legumes, the arrangement and density of cellulose microfibrils affect cell-wall rigidity, thereby influencing seed hardness and texture. Generally, a higher cellulose content leads to firmer seed coats, which in turn impact the overall seed texture [213,214]. Hemicelluloses are branched polysaccharides that interact with cellulose microfibrils and contribute to the structural integrity of the cell wall. In legumes, hemicelluloses, such as xyloglucans and xylans, are abundant and play a crucial role in cell-wall flexibility and porosity, thereby affecting cell expansion, size and shape [215]. The synthesis and arrangement of cellulose and hemicellulose in legume seeds are crucial for determining cell-wall properties, which in turn influence seed size, shape, and texture. Variations in cellulose and hemicellulose biosynthesis or relative abundance can modify cell-wall thickness, elasticity, and strength. For instance, a higher cellulose-to-hemicellulose ratio may increase seed hardness, while changes in hemicellulose composition can alter cell-wall flexibility, thereby affecting seed shape and size [216,217].

Also, the quantity and types of proteins in seeds impact seed texture by affecting water binding capacity and gel formation. Proteins form gels, which are three-dimensional networks that trap water, contributing to the firmness and elasticity of foods. For instance, gelatin, derived from collagen, forms a gel when dissolved in hot water and cooled, a property utilised in various food products [218]. Similarly, plant-based proteins, such as those from soy, can form heat-induced gels, enhancing the texture of plant-based foods.

The specific amino acid composition and structure of proteins determine their gelation behaviour and water-binding abilities, which affect the final product's texture [219,220]. The protein content and composition of legume seeds are controlled by intricate genetic mechanisms that play a key role in determining their texture [17,221]. Gaining insight into these genetic factors is essential for enhancing legume quality and breeding varieties with optimal textural properties.

5.1. Genetic Basis of Seed Texture

Seed texture is a multifaceted trait that encompasses hardness, roundness and surface smoothness, all of which are shaped by various genetic factors. There is a regional specificity for a rough or smooth seed coat of cowpeas in Africa and parts of South America [222]. This study discovered that a rough seed-coat texture in cowpeas is inherited through two pairs of independent recessive genes. Conversely, a smooth seed coat results when at least one dominant gene is present at each of these two loci. Another study examined eight cowpea varieties and found that seed-coat texture was controlled by two gene pairs exhibiting dominance and recessive epistasis, resulting in four distinct textures. The smooth seed-coat texture was completely dominant over wrinkle, rough and loose textures. Similarly, wrinkle seed-coat texture showed complete dominance over both rough and loose textures. However, recessive epistasis was observed between the rough and loose seed-coat textures [223]. Two biparental crosses in cowpea (TVu 4669 × Vita 7 and Ife Brown × TVu 2723), each pair exhibiting rough and smooth seed-coat textures, revealed monogenic inheritance, indicating that a pair of single genes controls seed-coat texture [224].

The seed-coat thickness in legumes is a highly heritable trait, and several gene families and pathways have been implicated in regulating seed-coat thickness and development. Members of the AP2/ERF family (APETALA2 and Ethylene Responsive Factor) TF families are known to play crucial roles in ovule and seed-coat development across various plant species, including legumes. For example, some AP2-type TFs, such as *AINTEGUMENTA* (*ANT*), can influence seed size by regulating cell size and proliferation in the integuments (the maternal tissues that develop into the seed coat) in *Medicago truncatula* [87]. The suppression of AP2 function has been reported to increase the size of outer integument cells, affecting seed-coat dimensions [225]. MYB-bHLH-WDR (MBW) complexes are involved in regulating the biosynthesis of polyphenols (like proanthocyanidins) that accumulate in the seed coat and can influence its structure and permeability, which may indirectly affect thickness [226]. Studies on castor bean have identified genes involved in lignin biosynthesis (e.g., specific NAC members, MYB46/83, MYB58/63, and enzymes like cinnamoyl-CoA reductase (CCR) and cinnamyl alcohol dehydrogenase (CAD)), whose expression patterns correlate with seed-coat thickness and lignification [227]. Glycosyl-hydrolase genes, such as *β-glucosidase* and *β-galactosidase*, are also known to be involved in degrading complex polysaccharides in the cell wall. Their expression levels correlated with seed-coat thickness and imbibition capacity in legumes, such as lentils [228]. Phytohormones, such as auxin, gibberellins, and abscisic acid (ABA), play crucial roles in seed development, including the growth and maturation of the seed coat. Genes involved in hormone biosynthesis, transport, and signalling pathways indirectly regulate seed-coat thickness by controlling cell division, expansion, and differentiation within the developing integuments [229,230]. Additionally, genomic regions governing seed-coat permeability and thickness have been identified in common beans [231], soybeans [232] and lentils [228]. Understanding the genetic regulation of seed-coat thickness is crucial for breeding efforts aimed at improving water uptake, reducing cooking time, and enhancing the overall texture and palatability of legume seeds.

Also, the composition of storage compounds, such as starch and proteins, influences the texture of legume seeds. Genes that regulate the synthesis and accumulation of these compounds play a role in determining seed firmness and mouthfeel. For example, variations in genes responsible for starch biosynthesis can change the amylose-to-amylopectin ratio, affecting the gelatinisation properties of the seeds [233,234]. Seed starch content (SSC) in mungbean (*Vigna radiata*) is a critical trait for the starch and noodle industries due to its impact on texture and taste. The heritability of SSC was determined using an F_2 population derived from high- and low-starch genotypes (V6087AG × V5020BY). Using BSA with 123 polymorphic SSR (Simple Sequence Repeat) markers, the SSR marker CEDG092 on mungbean chromosome 8 was found to be associated with starch content. QTL mapping then identified the locus *qSSC8.1*, which contains 21 annotated genes. This locus is a target for fine mapping to precisely locate the gene responsible for controlling seed starch content in mungbean [235]. In dry beans (*Phaseolus vulgaris* L.), research has focused on understanding the inheritance of seed chemical composition, including starch, amylose and protein content, using a RIL population from Xana × Cornell 49242. Nineteen significant QTLs were identified across 11 chromosomes, displaying transgressive segregation with key loci, including *Phaseolin* (Pv07) for protein content [236]. However, in pea (*Pisum sativum*), an analysis of 50 diverse accessions revealed 132 SNPs with key associations identified for amylose, total starch and crude protein content, facilitating MAS in pea breeding [237]. In pea seeds, six well-characterised biosynthetic mutant genes located at the *r, rb, rug3, rug4, rug5* and *lam* loci have been extensively studied for their effects on seed starch production, structure, texture and granular properties [238,239]. The genes at the *r* (*SBE I, SBEI*), *rug5* (*SSII*) and *lam* (*GBSSI*) loci directly influenced polymer biosynthesis and the degree of starch branching. In contrast, the *lam* locus, which lacks starch synthase (SS) activity, reduced amylose content significantly in wild-type peas. The *rb* (ADP-Glc pyrophosphorylase L1 subunit), *rug3* (plastidial phosphoglucomutase) and *rug4* (sucrose synthase) loci primarily affect substrate availability. Additionally, mutations at other *rugosus* loci alter seed shape from round to wrinkled and exhibit pleiotropic effects on seed morphology [240].

Legume seeds exhibit significant variation in protein content and amino acid composition, which influences seed hardness and texture. Research efforts have explored QTLs linked to seed protein concentration, emphasising their polygenic nature. For example, in alfalfa (*Medicago sativa*), genetic mapping for protein content and fibre composition traits have identified multiple interacting QTLs [241]. A study identified QTLs controlling pod fibre content (cellulose, hemicellulose, lignin) and pod shattering in populations derived from a cross between yardlong bean and wild cowpea. Comparative analysis with azuki beans found *MYB83* (LG7) and *cellulose synthase A7* (*CESA7* (LG1)) as key genes involved in fibre biosynthesis and shattering, making them promising targets for further research [242]. In soybean, QTL mapping, QTL-seq and RNA-seq were performed on the high-protein variety 'Nanxiadou 25′ to reveal genes controlling seed protein content (SPC) [243]. A total of 50 QTLs across 14 chromosomes were identified, with two major QTLs, *qSPC_20–1* and *qSPC_20–2* and nine potential candidate genes associated with SPC. SNPs and indels between high- and low-protein genotypes in two genes, *Glyma.20G088000* and *Glyma.16G066600,* were identified as the causal variants for this trait, suggesting their role in protein content variation [243]. QTL-Seq and candidate gene-based association mapping approaches were employed to identify two QTLs and a tightly associated marker, *CaREN1* (*ROP1 ENHANCER1*), responsible for SPC in chickpeas. This SNP was then turned into a cost-effective, allele-specific PCR-based marker to screen SPC during marker-assisted breeding [244]. However, direct studies on QTLs specifically governing seed texture in pulses remain limited. Further research focused on seed texture is necessary to pinpoint specific QTLs and develop pulse varieties with tailored textural properties to meet end-user preferences.

5.2. The Multi-Omics Approaches in Legumes Reveal Seed Structure and Texture Properties

Transcriptomics and metabolomics studies have identified several genes and TFs essential for seed development, regulating key metabolic pathways involved in carbohydrate biosynthesis and storage [245]. High-throughput RNA-Seq during pea seed development identified several genes related to soluble sugar and starch metabolism, which were significantly activated, coinciding with the onset of sugar and starch accumulation in the seeds [246]. Similarly, chickpea seeds exhibit elevated expression of crucial genes involved in carbohydrate metabolism, including starch synthase (*SS*), debranching enzymes, starch cleavage enzymes and galactinol synthase [247]. These genes exhibited heightened expression in later stages of seed development, contrasting with their lower expression levels at 10 days after anthesis (DAA). At the early stage (10 DAA), genes involved in sucrose and starch degradation, as well as raffinose and trehalose metabolism, were significantly more active compared to later stages (40 DAA), suggesting a dynamic regulatory mechanism that meets cellular energy needs during early-stage degradation. Conversely, later-stage biosynthetic processes drove starch accumulation, which is crucial for seed maturation and quality. Transcriptomic and starch biosynthesis studies in mungbean leaves and developing seeds identified key starch-related genes, such as *PTST, SS3,* and *SBE1*, which exhibit lower expression in seeds, impacting the starch molecular structure and granule morphology. *SBE1, SS1, GBSS* and *ISA1* expression patterns correlate with starch molecular size distribution during seed development. Additionally, hormonal (ABA and IAA) and redox regulation were highlighted as potential factors influencing starch biosynthesis [248]. Hence, understanding the genetic regulation of starch composition in legumes involves identifying genes responsible for starch synthesis, such as *GBSS1* (*Granule-Bound Starch Synthase 1*), which controls amylose production and *SBE* (*Starch Branching Enzyme*) genes, which regulate amylopectin formation. Targeted manipulation of these genes enables breeders to develop legume varieties with customised starch compositions, enhancing textural properties [248,249].

Specific cellulose synthase (*CesA*) and cellulose synthase-like (*Csl*) genes were discovered in legumes. For example, in peanuts (*Arachis hypogaea*), certain *CesA* and *Csl* genes are actively expressed during shell development, contributing to cellulose and hemicellulose deposition, which influences cell-wall thickness and rigidity [250]. Global transcriptional profiling in *Medicago truncatula* has uncovered the expression of genes responsible for cellulose, hemicellulose and lignin biosynthesis, thereby influencing cell-wall composition and structural properties [251]. In 2024, a study combined GWAS and TWAS (transcriptome-wide association studies) on 421 soybean accessions. This research identified 26 loci associated with seed weight and 5276 expression quantitative trait loci (eQTLs) that regulate 3347 genes. From these, 22 candidate causal genes for seed traits were prioritised by TWAS, including *Regulator of Weight and Oil of Seed 1* (*GmRWOS1*), which encodes a sodium pump protein [252].

Also, metabolomic studies in legumes provided crucial insights into seed biochemical composition and the impact of genetic modifications on various metabolic pathways. A comparative analysis examined the relative metabolite contents of pea seeds with and without the reserve protein pea albumin-2 (PA2) by introducing a targeted deletion into a standard genetic background. This deletion resulted in significant changes in seed amino acid and polyamine levels, emphasising the role of PA2 in seed metabolism and nutrient composition [253]. This research also suggests potential benefits of the PA2-deficient mutant for improved seed quality, including enhanced digestibility and reduced allergenicity.

Additionally, metabolic profiling was used to compare genetically modified (GM) and conventional soybean lines, revealing differences in metabolite accumulation. This analysis identified 40 metabolites, including isoflavones, amino acids, carboxylic acids and peptides, in GM soybean lines and an extensive 169 metabolites in conventional lines [254]. Another metabolomic study has identified significant differences in phenolic acid and flavonoid profiles between dormant (hard seeded) and non-dormant chickpea genotypes, highlighting the direct link between specific metabolites and seed-coat impermeability [255].

The texture of legumes is shaped by factors such as starch composition, protein content and cell-wall structure, yet there is still a considerable gap in our understanding of the complex genetic factors that drive these traits. Our current knowledge of how genes influencing starch composition, protein types and cell-wall biosynthesis affect texture remains limited, with many aspects still underexplored. Without thorough research, we may overlook key insights into the interactions between these components, potentially hindering the development of effective breeding strategies for improving legume texture. Further in-depth research is crucial for understanding the genetic and molecular mechanisms that govern the texture of legume seeds, as depicted in Figure 2. Various studies have employed multi-omics approaches to elucidate legume seed texture traits, encompassing cell-wall composition and interactions between starch and protein. This comprehensive understanding is crucial for breeding and processing strategies aimed at developing legume varieties with optimised textural properties, enhancing their consumer appeal and versatility in food applications.

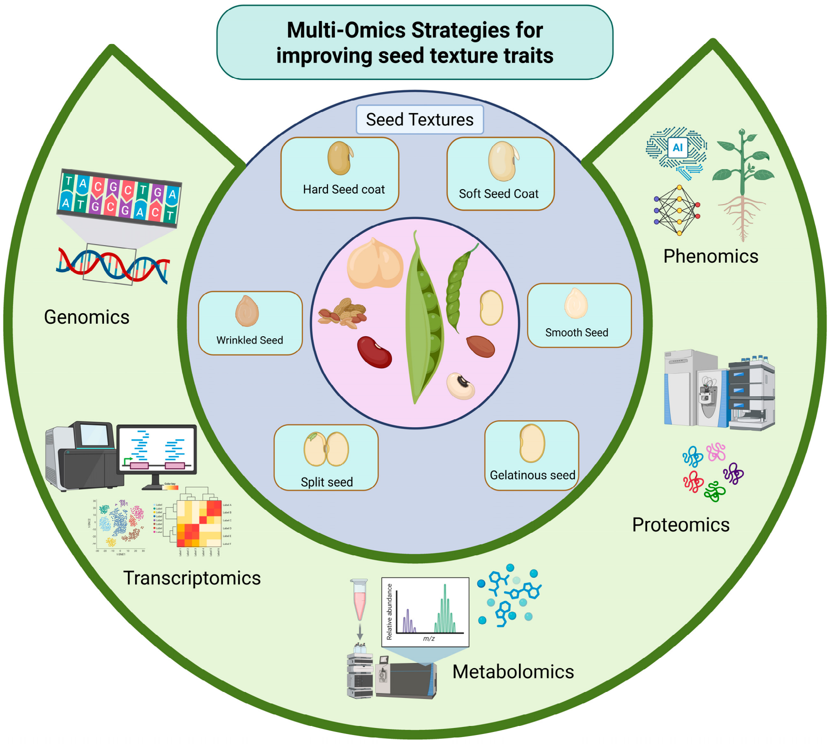

Figure 2. Highlights of the multi-omics approach for studying seed texture traits. The depicted different seed textures (hard and soft seed coats, wrinkled and smooth surfaces, split seeds and gelatinous seeds) represent different phenotypes influenced by genetic and biochemical factors, which uncover the molecular mechanisms underlying seed texture traits.

6. Palatability

Palatability is broadly defined as the degree to which a food is agreeable to the taste and readily consumed. Palatability in forage legumes for livestock has a direct impact on animal intake, nutrient utilisation, and overall productivity [256]. If forage legumes are unpalatable, animals will restrict their consumption, even if the nutritional content is high, leading to reduced weight gain, milk production, or reproductive performance. Factors influencing forage legume palatability include texture, chemical composition, aroma, moisture content and anti-nutritional factors [257]. Palatability in grain legumes for human consumption is mainly influenced by texture, taste, flavour, aroma, cooking time and visual appeal [258], thereby affecting the extent to which legume grains, after cooking, are acceptable in terms of mouthfeel and aftertaste. Or how appealing legumes are to a person's sense of taste and other sensory perceptions. Palatability determines how readily legumes are consumed in human diets, influencing nutritional intake. Palatability is a complex characteristic influenced by various factors, such as texture, aroma, flavour, chemical composition, preparation, processing and maturity of legume grains.

Evaluating the palatability of grain legumes for human consumption involves a combination of sensory analysis, instrumental measurements and chemical profiling. Sensory evaluation directly assesses human perception. It commonly involves a trained panel of 8–15 individuals evaluating cooked legume samples based on their sensory attributes using standardised scales [171,259]. Additionally, a larger panel of untrained consumers (typically 50–100 or more) assesses the overall liking of the cooked legumes using hedonic scales (e.g., a 9-point scale ranging from "dislike extremely" to "like extremely"). Or specific attributes for food pleasantness might also be rated [171]. The physical measurements, such as hardness, chewability or springiness of cooked grains, are taken using a texture analyser to provide a basic assessment of the mouthfeel. However, to predict mouthfeel more meaningfully, rheological and tribological qualities [260], such as sliminess, creaminess or dryness of cooked and mashed grains, must also be measured. Instrumental texture analysis methods include cooking time determination, texture profile analysis and shear tests [261,262]. By combining omics approaches with sensory and instrumental data, a more comprehensive understanding of the complex genetic and molecular basis of legume palatability can be achieved, facilitating targeted breeding for improved varieties. Evaluating palatability is crucial for breeding programs, food processing optimisation, and ultimately, increasing the consumption of nutritious grain legumes. Additionally, the palatability of legume grains can be enhanced by removing undesirable flavours [124,157,158] and developing more desirable umami flavours [263].

Genetic Factors and Multi-Omics Approaches to Characterise Palatability

The genetic factors determining palatability are the same that influence seed texture and flavour. The seed coat, cell-wall thickness and rigidity, as well as the molecular makeup and structural arrangement of the starch, fibre, and storage proteins, all affect palatability in legumes. Genes that control the chemical composition and production of cell-wall components, starches, and proteins influence the texture of legumes [70]. Variations in these genes can lead to differences in firmness, mealiness, and overall mouthfeel. Genes involved in the biosynthesis of secondary metabolites, such as tannins and alkaloids, impart bitter or astringent tastes or contribute to aroma and flavour in legumes [146], directly affecting palatability.

Texture is a major determinant of palatability, with the "hard-to-cook" (HTC) phenomenon being a significant issue [209]. GWAS and QTL mapping have identified SNPs and genomic regions associated with specific sensory attributes of cooked beans, including total flavour, beany, earthy, starchy, bitter, seed-coat perception and cotyledon texture [190]. Another study on yellow dry bean population identified QTLs for water uptake, cooking time and numerous sensory attribute intensities (including starchy, sweet, seed-coat perception, total flavour, beany, earthy, bitter, and cotyledon texture) [263].

The application of different multi-omics approaches, combined with quantitative RT-PCR, to investigate the biosynthesis of aroma, taste and flavour-imparting compounds is well-documented [154]. Recently, a comprehensive review [125] described the use of flavouromics, a multi-omics approach to qualitatively and quantitatively determine flavour compounds and elucidate the mechanism for the formation of compounds responsible for beany flavours in peas. From a crop breeding perspective, a comparative flavouromics of raw and fermented seeds can be useful in quantifying the remnants of off-flavours in the fermented grains and precursors in the raw grains, resulting in desirable flavours in the fermented seeds and in identifying suitable gene-editing targets.

The genetic control of palatability in legumes is complex and polygenic, involving genes that impact seed-coat structure, cell-wall integrity and the biosynthesis of diverse secondary metabolites. Advances in genomics and phenotyping are continually enhancing our ability to identify and manipulate these genes for the breeding of more palatable and consumer-friendly legume varieties.

However, phenotypic traits, such as the thickness and rigidity of the seed coat and cell walls, control the efficacy of enzyme treatment and microbial fermentation in improving legume palatability. No direct evidence is available to support this hypothesis; however, digestibility studies suggest that cell walls control nutrient bio-accessibility and digestibility and particle size controls enzyme access to the substrate [264,265]. Therefore, it is reasonable to hypothesise that cell-wall thickness or permeability in legume seed controls the efficacy of enzyme treatment and fermentation. The time required to ferment legume grains or their isolated proteins is up to three days [266–268]; hence, it is commercially expensive to adopt fermentation as a large-scale treatment to remove off-flavour or improve palatability. Recent studies investigating the effect of fermentation on legumes or isolated protein fractions have examined the impact of fermentation time [267] or different microbial strains [268]. However, limited or no research has been undertaken to examine the role of legume grain composition and structure on the rate and efficacy of fermentation. It is essential to investigate the impact of grain factors, such as cell-wall thickness and porosity, on microbial fermentation kinetics to breed legume crops that require shorter fermentation times to eliminate off-flavours and enhance more desirable flavours and overall palatability.

7. Current Challenges

Enhancing the sensory characteristics of legumes is crucial for boosting their consumption and market value, but faces several persistent challenges. Sensory attributes, such as texture, flavour and palatability, are polygenic, i.e., many genes contribute to their expression. This complexity makes traditional breeding difficult. While QTLs for some sensory traits are identified, many of these effects are minor, making precise genetic manipulation challenging. Even when a QTL is identified, determining the exact causative gene(s) within that region and understanding their precise mechanism of action remains a significant challenge, thereby limiting the avenues for targeted gene editing. While pangenomics offers immense potential to capture the full genetic diversity relevant to sensory traits, its application is still in its early stages for many legume species due to computational demands and the need for extensive sequencing of diverse germplasm.

A major challenge in breeding for improved sensory qualities is the negative correlation or trade-offs with other essential agronomic traits, particularly yield [269]. Breeders face the dilemma of balancing yield, which directly impacts farmer profitability, with quality traits that drive consumer acceptance. Many compounds that contribute to undesirable flavours (e.g., tannins, saponins and certain alkaloids) also play roles in plant defence mechanisms against pests and diseases. Eliminating or drastically reducing these compounds for palatability might compromise the plant’s natural resistance, requiring increased reliance on chemical inputs [188,270]. Thus, targeting all these undesirable compounds simultaneously without adverse pleiotropic effects is difficult.

The hard-to-cook (HTC) phenomenon, where seeds remain hard even after prolonged cooking, is a major barrier to legume consumption. While linked to changes in pectin and phytate metabolism, the precise biochemical pathways and their genetic control contributing to HTC are not yet fully elucidated, hindering targeted breeding efforts [271].

Despite advancements, the sensory evaluation of legumes still faces challenges in consistency and efficiency. There's a need for a universally standardised lexicon of sensory descriptors for legumes and legume-derived ingredients to enable consistent communication and comparison across studies and breeding programs [272]. Traditional descriptive sensory analysis, while comprehensive, is expensive and time-consuming, limiting the number of samples that can be evaluated in high-throughput breeding pipelines. While rapid methods are emerging, their widespread adoption and validation across diverse legume types are ongoing [273]. Developing robust, predictive models that accurately correlate objective instrumental measurements with subjective human sensory perception for all relevant palatability attributes is an ongoing challenge [274]. Even genetically improved legumes can suffer sensory degradation due to improper post-harvest handling and processing. Additionally, climate change poses emerging threats to the sensory quality of legumes. Greater climate variability can lead to more inconsistent sensory quality from year to year and region to region, making it harder to ensure a consistent product for consumers. Addressing these challenges requires an integrated approach that combines advanced genomic tools (pangenomics and gene editing), high-throughput phenotyping, standardised sensory evaluation and a deeper understanding of the biochemical pathways underlying palatability [275]. Balancing these quality traits with yield and stress resilience will be key to increasing legume consumption globally.

8. Conclusions and Future Perspective

Understanding the molecular mechanisms governing the sensory traits in legumes and pulses has significant implications for agricultural research. Multi-omics approaches combined with QTL mapping studies offer transformative potential for advancing our understanding and enhancing the sensory characteristics of legumes, aligning with evolving consumer preferences for nutritious, flavourful and sustainable food. By integrating diverse biological data, including genomics, transcriptomics, proteomics and metabolomics, in addition to employing advanced analytical tools (artificial intelligence and machine learning), researchers can unravel the complex molecular mechanisms underlying appearance, flavour, aroma, texture and palatability (Figure 3). QTL mapping further complements this by identifying genetic regions associated with key sensory traits, enabling the precise selection of desirable characteristics for breeding programs.

Various studies have employed omics approaches to comprehensively dissect the genetic and biochemical pathways that dictate traits such as seed-coat colour, seed size and shape, identifying the genes and regulatory networks responsible for the visual appeal and physical properties of legume seeds. Crucially, this holistic perspective illuminates the intricate molecular basis of aroma, taste, and overall flavour, pinpointing the specific volatile compounds, sugars, amino acids, and other metabolites, along with the enzymes and genes involved in their biosynthesis or degradation. Furthermore, multi-omics offer profound insights into texture and palatability, revealing how genetic variations influence protein composition, cell-wall structure and carbohydrate profiles that define mouthfeel. This integrated knowledge empowers legume breeders and geneticists to move beyond traditional methods, enabling targeted breeding, precise gene editing and optimised processing strategies to develop new varieties with superior and consistent sensory attributes, ultimately driving greater consumer acceptance and reinforcing the vital role of legumes in global food security. Additionally, leveraging multi-omics technologies promotes sustainable agriculture by producing resilient legume crops with consistent quality under varying environmental conditions [276,277].

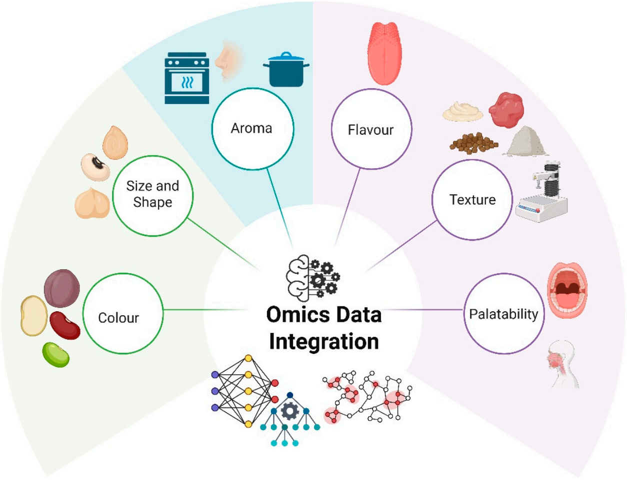

Figure 3. Integrating multi-omics datasets (genomics, transcriptomics, proteomics and metabolomics) is crucial for a comprehensive understanding of complex sensory traits in legumes.

In the future, integrated multi-omics datasets will facilitate precise crop breeding by identifying key genetic variations and biological elements contributing to desirable sensory traits. Omics approaches aid in identifying key biomarkers and pathways for targeted breeding or biotechnological interventions. Advanced bioinformatics tools are essential for managing and interpreting the vast datasets generated by these studies, facilitating the identification of gene-metabolite-protein interactions relevant to sensory characteristics. However, the sheer volume and heterogeneity of these datasets present significant challenges. This is where artificial intelligence (AI) and machine learning (ML) come into play, offering powerful tools for effective data integration. Additionally, single-cell analysis using techniques such as single-cell mass spectrometry offers insights into cell-specific metabolic profiles, revealing hidden phenotypes and rare cell types that contribute to the overall sensory quality. Metabolic engineering, driven by metabolomics insights, enables the modification of specific metabolic pathways to enhance the production of desirable compounds influencing flavour and aroma. The genetic determinants of aroma and volatile compounds in legumes and pulses have garnered increasing attention in recent years due to their significant role in improving sensory appeal and facilitating consumer acceptance of food product development. Continued investment in this area will contribute to the sustainable production and consumption of legumes, aligning with global efforts to promote plant-based diets and food security. Furthermore, studying stress responses under abiotic and biotic conditions helps uncover alterations in metabolite and protein profiles, informing breeding strategies to develop legume varieties that maintain favourable sensory traits despite environmental fluctuations.

Legume pangenomics [278], i.e., the study of the entire set of genes within a species, including both core (present in all individuals) and accessory (present in a subset) genes, offers a powerful approach to enhance sensory traits in legumes. Sensory traits, such as texture and palatability, are highly polygenic and influenced by structural variations (SVs), including presence-absence variations (PAVs) and copy number variations (CNVs). A single reference genome cannot fully capture this variation. Pangenomics overcomes this limitation by capturing the full genetic repertoire, providing a more comprehensive foundation for improving such complex traits. Pangenomes also allow for the identification of novel genes or alleles (particularly those in the accessory genome) and the development of highly accurate markers for sensory traits, thereby enabling more effective marker-assisted selection (MAS) or genomic selection (GS) in legume breeding programs. Additionally, pangenomes can reveal the full complement of genes involved in the biosynthesis of bitter compounds (e.g., alkaloids, saponins and certain polyphenols) or "beany" (e.g., lipoxygenases). Some germplasm may possess unique alleles or even gene deletions that lead to reduced levels of these undesirable compounds [279]. The development of pangenomes supports the characterisation of gene PAV within crop species, as well as comparison with wild and exotic relatives. This process can identify genes that have been lost during breeding and selection, which may confer beneficial agronomic attributes that can be reintroduced into elite germplasm for evaluation. This directly applies to sensory traits where specific genes might have been lost during domestication, leading to altered palatability [280]. Furthermore, it is anticipated that combining panomics approaches with advanced breeding technologies will accelerate genetic gains in food legumes, enhancing their sensory traits [281]. This foundational knowledge is essential for developing more palatable, consumer-friendly legume varieties through advanced breeding and gene-editing strategies, ultimately contributing to increased consumption and food security.

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