



REVIEW ARTICLE

Seed coat matters: Exploring physical and biochemical composition influences on seed quality-A comprehensive review

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Abstract

Seeds are fundamental units of agricultural production and their quality is strongly influenced by the structural and functional properties of the seed coat. The seed coat, a maternally derived tissue originating from ovular integuments, plays a pivotal role in protecting the embryo, regulating water uptake, controlling gas exchange and mediating interactions with the external environment. This review comprehensively examines the development, structure, genetic regulation, physical and chemical composition, factors affecting development and functional significance of the seed coat. It particularly emphasises on its physical and biochemical composition and its influence on seed quality characters. Physical compositions such as seed coat colour and thickness significantly contribute to germination, vigour, dormancy, longevity and resistance to pests and diseases. Biochemical compositions, including polyphenols (phenolic acids, tannins, flavonoids, lignin), structural polysaccharides, alkaloids, lipids, waxes and specialised proteins are primarily contributed to protection mechanisms like mechanical strength, impermeability, antioxidant capacity and defence against pathogens and insects. The review also highlights the genetic mechanisms underlying seed coat development, including key regulatory genes and transcription factors. The environmental, hormonal, nutritional and genetic factors affecting seed coat formation are also critically reviewed. Therefore, understanding the complex interplay between seed coat composition and seed performance provides valuable insights for crop improvement, seed technological aspects and sustainable agriculture. The future research needs on functional genomics and innovative seed coating technologies may further enhance seed quality and crop productivity in agriculture sector.

Keywords: dormancy; germination; seed coat; seed coat colour; seed coat thickness; seed quality

Introduction

Seeds are the fundamental input for food production in agriculture system. They serve as the starting point for the cultivation of crops, representing the genetic potential that determines plant characteristics such as yield, disease resistance and nutritional content. Most of the seeds consist of 3 parts viz., embryo, endosperm and seed coat. The embryo is a tiny plant that has a root, a stem and one or more leaves. The endosperm is the nutritive tissue of the seed, often a combination of starch, oil and protein. The seed coat is a protective covering that helps to maintain seed viability for a long period of time (1).

The seed coat is the major component of the seeds to maintain integrity and quality. It is the outer layer of all developed seeds. The seed coat forms from the two integuments or outer layers of cells of the ovule, which derive from tissue from the mother plant, the inner integument forms the tegmen and the outer forms the testa. It plays a vital role in several processes, including maintaining the integrity of the seed components, shielding the embryo from harm and from pests and diseases, controlling gaseous exchanges between the embryo and the outside world,

helping in the dispersal of seeds and controlling imbibition and germination in several plant groups. The seed coat functions as a transient impermeable barrier to regulate water absorption and consequently germination in a number of plant groups. Therefore, seed coat as a primary modulator of interactions between the internal components of the seed and the external environment (2).

Seed coat composition like physical (colour and thickness) and biochemical composition (polyphenolic compounds, structural polysaccharides, alkaloids, lipids and waxes, specialised proteins) play a major role in seed quality. In physical composition seed coat colour and thickness are critical determinants of seed quality. It influences seed germination, vigour, dormancy and storage longevity. Light coloured and thinner seed coats generally offer faster germination and higher vigour, while darker, thicker coats provide better environmental protection, durability and pest resistance (3). Seed coat biochemical composition directly impacts seed quality, with phenolic compounds, lignins, flavonoids and other compounds are providing essential defence against pathogens and mechanical stress. Higher concentrations of these compounds, like increased lignin to promote enhance seed longevity, permeability control and storability (4).

Quality seeds are fundamental to agricultural productivity, serving as the primary input that influences crop yield and food security. High-quality seeds must possess physical, genetic, sanitary and physiological attributes, including freedom from pests and pathogens. It also ensures uniform seedling emergence and optimal plant density (5). Seed coat is a major part of the seed it mainly contributes the above quality seed functions. The physical and biochemical composition are the main factors that influence seed coat function and integrity. However, understanding and managing seed coat characteristics are essential for maximising seed quality and ensuring successful crop establishment. So, this review discusses seed coat and its composition's role on seed quality.

Development of seed and seed coat

Seed

The success of flowering plants in evolution can be largely attributed to their development of seed and sexual reproduction. The growth of a seed covered in maternal tissue, known as the seed coat (or testa), after double fertilisation is the most recognisable feature of angiosperms. Plant species from other clades have not been able to accomplish the property of enclosure, which protects the growing embryo and increases its chances of maturing and producing the next generation. An endosperm, an embryo and a seed coat make up the final shape of an angiosperm seed, which has the ovary as its progenitor structure on the female side. A union between an egg cell and an embryo is produced. The fusing of an egg cell and a sperm nucleus produce the embryo, whereas the fusion of two central cell nuclei and a second sperm nucleus produces the endosperm, which develops into a triploid structure in diploid species. The seed coat comes exclusively from mothers. The structure rapidly degenerates upon failure of fertilisation, guaranteeing that the assimilate invested in an unsuccessful seed is recycled (6). According to a previous study the ovule in seed plants is made up of the embryo sac encircled by the nucellus and the surrounding (7). Following fertilisation, the ovule becomes a seed, which houses an embryo embedded in nutritive tissues such the endosperm (angiosperms) or the mega gametophyte (plants with many layers). The testa encircles the developing embryo and the nutritional tissues. The endosperm or perisperm can make up the

nutritive tissue of ripe seeds in angiosperm species. Due to multiple fertilisation, the endosperm and embryo are of both father and maternal descent. Maternal tissues called testa and perisperm are produced when the integuments and nucellus differentiate, respectively. The integuments and the chalazal tissues are part of the testa. The testa is made up of multiple layers of distinct cell types that are the result of fertilisation induced ovular integument differentiation. The majority of dicotyledons (like *Arabidopsis* and beans) and monocotyledons (like wheat) have 2 integuments (bitegmic ovules). The families Rosaideae, Ericales, Asteridae and Solanaceae, which include tobacco, tomato and petunia, are the principal hosts of a single integument or unitegmic ovules (8). The integuments create a pore called a micropyle, which serves as the pollen tubes entrance. Another crucial area of the testa is the chalazal region, which is where the vascular tissues of the maternal funiculus connect to the seed. The hilum is the scar that remains after seed detachment, where the funiculus was linked. Testa tissue differentiation entails significant cellular alterations that ultimately result in programmed cell death (PCD) (9). Programmed cell death is essential for seed coat (testa) formation, endosperm elimination and leading to maturation. After PCD, seeds undergo desiccation, reducing metabolic activity and preparing for dormancy state. Mature seeds enter a quiescent stage, remaining dormant until favourable conditions to trigger germination (10). These are important processes involved in seed developmental stage. Seed development process of angiosperms and gymnosperms given below (Fig. 1).

Seed coat

The seed coat is a maternally derived structure originating from the ovular integuments (12). The development of the seed coat begins after fertilisation. It originates from the ovules protective layers called integuments, which surround the female gametophyte before fertilisation. Typically, an ovule has 2 integuments outer and an inner integument although some species may have only one. Following fertilisation, these integuments undergo a series of coordinated cellular, morphological and biochemical changes, including cell division, expansion, lignification and deposition of various substances. These changes lead to following process:

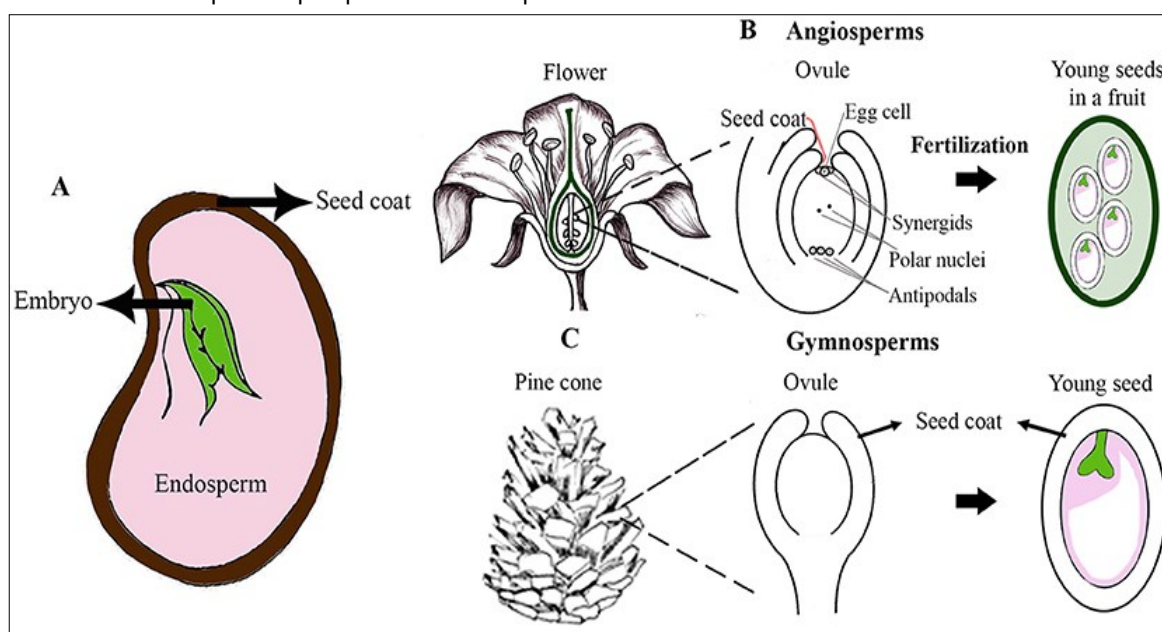


Fig. 1. Seed development in angiosperms and gymnosperms.

(A) The three main parts of a seed; (B) Seed development in angiosperms; (C) Seed development in gymnosperms (11).

i. Initiation after fertilisation: Seed coat development is initiated immediately after fertilisation of the egg cell. As the zygote begins to develop into an embryo, the surrounding maternal tissues the integuments simultaneously start to differentiate and grow. Although these maternal tissues do not contribute genetically to the embryo, they play a crucial role in its protection and development (13).

ii. Cell division and expansion: During the early stages, the integument cells undergo rapid cell division, expanding the volume of the ovule and enveloping the developing embryo and endosperm. Cell proliferation is tightly regulated to ensure the correct size and shape of the seed coat, which must accommodate the growing embryo (14).

iii. Cell differentiation and layer formation: As development progresses, the integument cells start to differentiate into distinct layers with specialised functions. The outer integument typically differentiates into the outermost layers of the seed coat. These cells often become elongated and thick-walled, forming the palisade layer (macrosclereids) that contributes to mechanical strength and impermeability (15).

a) Outer integument: Often thickens and becomes lignified or suberised, contributing to the permeability. The outer integument, to the formation of multiple distinct layers in the mature seed coat, each serving specific protective and functional roles. One of the 2 protective layers surrounding the ovule that develops into part of the seed coat after fertilisation, forms the mechanically strong and durable outer protective layer through cell differentiation and thickening (often lignified or suberised), acts as a barrier against physical damage, pathogens and environmental stress, contributes to seed coat coloration by accumulating phenolic compounds and pigments and regulates seed dormancy by controlling water permeability forming, especially in legumes, the hard, impermeable testa responsible for physical dormancy (hardseededness). Beneath this layer, cells may form the osteosclereid (hourglass) layer, which adds rigidity and structural support.

b) Inner integument: The second protective layer surrounding the ovule that contributes to seed coat formation after fertilisation, typically develops into the inner layers of the seed coat, providing structural support, often remaining thinner and less lignified than the outer integument and playing roles in nutrient transfer, cushioning the embryo and sometimes influencing seed coat permeability and dormancy characteristics. The number and arrangement of layers can vary significantly between species and are influenced by genetic and environmental factors.

iv. Secondary cell wall thickening: One of the prominent processes in seed coat development is the secondary thickening of cell walls. Cells in the outer layers deposit materials such as lignin, suberin and cutin into their walls, which increases hardness and reduces permeability. This biochemical reinforcement is essential for creating a physical barrier to water and pathogens (16). Lignin provides rigidity and resistance to microbial attack. Suberin and cutin are lipid-based polymers, create hydrophobic barriers that control water and gas movement.

v. Accumulation of chemical compounds: The developing seed coat accumulates various phenolic compounds, tannins, flavonoids and waxes. These substances serve multiple functions like phenolics and tannins contribute to colour and defence against pests and pathogens. Waxes and cuticular materials impart waterproofing properties. Some metabolites influence seed coat permeability, thereby regulating dormancy and germination (17).

vi. Maturation and desiccation: As the seed matures, the seed coat completes its development by finalising the structural modifications, dehydrating to prevent premature germination, forming a tough outer barrier capable of protecting the embryo during dispersal and storage. During this phase, the seed coat becomes physically hardened in some species, particularly legumes, resulting in hardseededness, where the seed coat is impermeable to. This development is tightly regulated and species-specific water (18). Seed coat development process of angiosperms and gymnosperms was given below (Fig. 2).

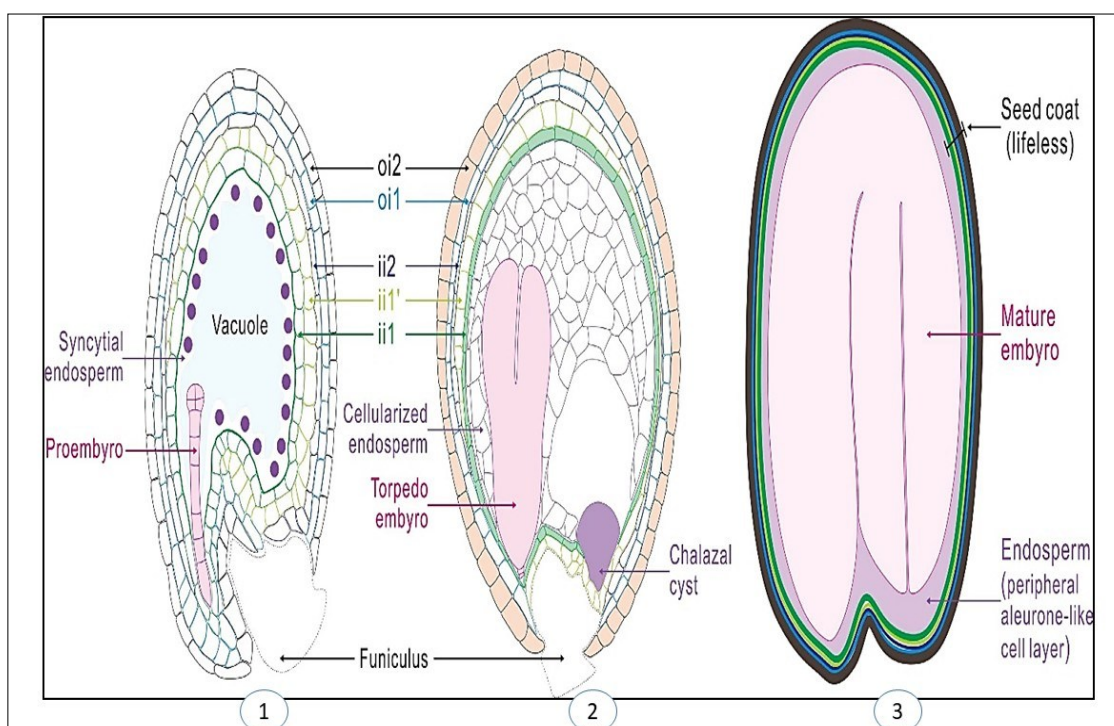


Fig. 2. Seed coat development process in *Arabidopsis thaliana*.

(1) Initiation after fertilisation, cell division and expansion; (2) Cell differentiation and layer formation; (3) Maturation and desiccation (19).

Layers of seed coat

Seed coat has different distinct layers during seed coat development and formation. These layers play a major role in seed coat ultra-structural properties (20, 21). Some important layers are:

i. Mucilaginous epidermal cells: Mucilaginous epidermal cells in the seed coat are specialised cells that synthesise, store and release hydrophilic polysaccharides (mainly pectins and cellulose) upon hydration. They form a volcano-shaped secondary cell wall called a columella, which ruptures on wetting to create a gel-like capsule essential for seed hydration, protection and dispersal. E.g., *Arabidopsis*.

ii. Palisade cells (acrosclereids): These are elongated, tightly packed cells forming the outermost protective barrier. Their thick, lignified walls and presence of cutin/waxes contribute to water impermeability. E.g., soybean.

iii. Osteosclereids (Hourglass cells): Located beneath the palisade layer, these cells provide mechanical strength and rigidity to the seed coat. E.g., soybean.

iv. Parenchymatous layer: Composed of loosely arranged living cells; this layer may store metabolites or degenerate during seed maturation. E.g., soybean.

v. Endothelium layer: It is a specialised, often single-layered, cellular layer, also known as the “integumentary tapetum”, that develops from the inner epidermis of the inner integument in many angiosperm seeds. It acts as a nutrient transferring tissue for the developing embryo sac and is often rich in cytoplasm and tannins.

vi. Aleurone layer: The aleurone layer is the outermost, protein-rich layer of the endosperm in cereal grains (like wheat, maize and barley) and some dicots (soybean). As a living, often single-celled layer, it stores proteins, lipids and minerals and plays a crucial role in germination by secreting enzymes, such as amylase, to digest the starchy endosperm, supporting seed development and acting as a defence barrier.

vii. Crushed endosperm layer: A crushed endosperm layer refers to remnants of endosperm cells located between the outer aleurone layer and the inner embryo (cotyledon) in maturing seeds. These cells die via PCD during the final stages of seed maturation, leaving behind a thin and compressed layer. The schematic diagram of seed coat layers are shown in (Fig. 3).

Hard and soft seed coat development

i. Hard seed coat: Hard seed coat is thick cuticle and the radial as well as tangential walls of the macrosclereids are thickened. The

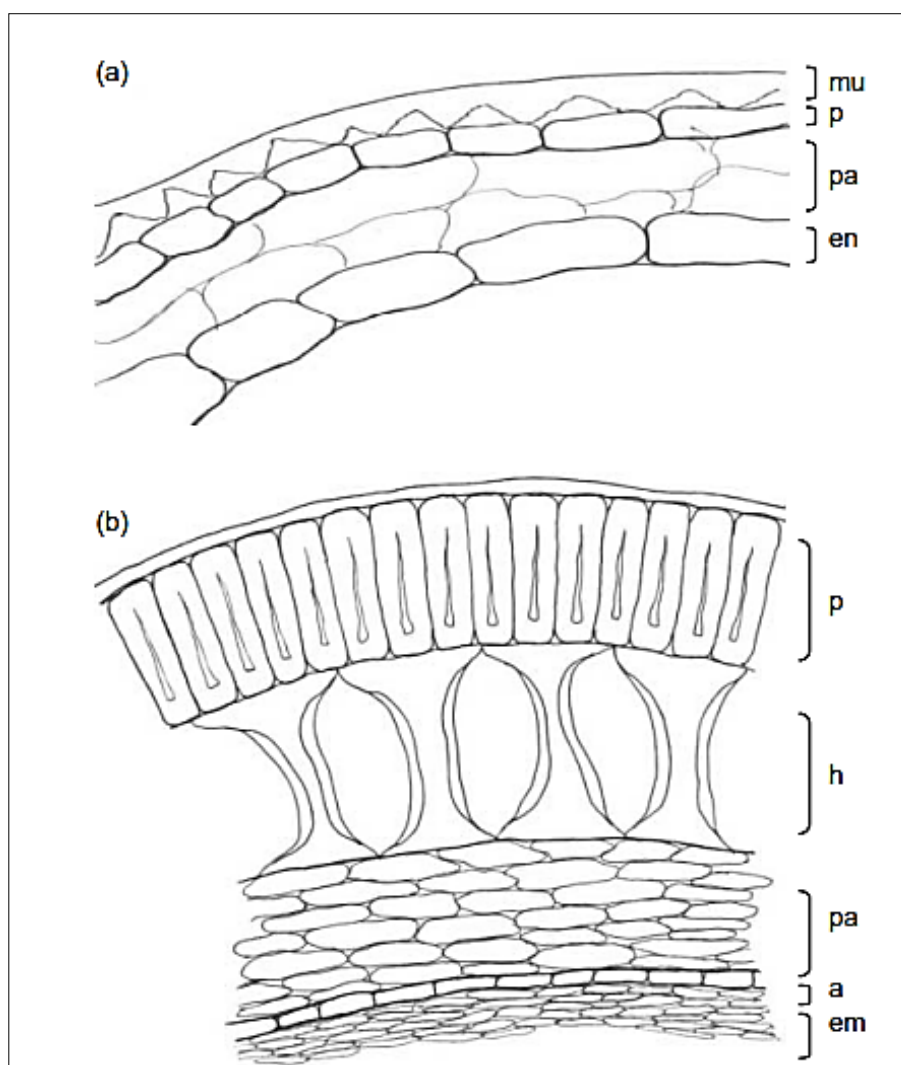


Fig. 3. Schematic diagrams of different seed coat layers in *Arabidopsis thaliana* and soybean (20, 21).

(a) *Arabidopsis thaliana*: The seed coat at the torpedo stage. mu: mucilaginous epidermal cells; p: palisade; pa: parenchymatous cells; en: endothelium layer.

(b) Soybean: A mature seed coat. p: palisade layer; h: hourglass cells; pa: partially crushed parenchyma; a: aleurone; em: crushed endosperm.

walls of the macrosclereid cells have suberised caps that are embedded in a pectic cuticular matrix that makes up the subcuticular layer. The epidermis is continuous with macrosclereid cells across the hilar region, which has similarly thickened cells. The macrosclereids are densely cytoplasmic and contain small and large vacuoles filled with tannin. The osteosclereid layer is composed of large, vacuolated cells and develops thicker walls adjacent to the intercellular spaces that were formed distally in this cell layer in the hard-seeded line. These cells are separated by large intercellular spaces and contain fewer organelles than the underlying cotyledon parenchyma cells (22). Hard seed coats are typically present in legume crops (e.g., black gram). The hard seed coat development pictures are depicted in Fig. 4.

ii. Soft seed coat: Soft seed coat contains thin cuticle and outer tangential wall is thinner and more electron translucent than that of the hardseeded line. The cytoplasm contains a centrally located nucleus and several organelles and a major part of the cytoplasm is vacuolated. These vacuoles are completely or incompletely filled

with tannin. The osteosclereid layer develops thicker walls adjacent to the intercellular spaces, which have formed distally in this cell layer. The ultrastructural features of the cells are essentially the same as those of the hard-seeded line. Thin-walled cotyledon parenchyma cells are filled with amyloplasts that contain large starch grains and electron dense cytoplasm. Small intercellular spaces were observed between the cells of the parenchyma layer (22). Soft seed coat was observed in certain legume crops (e.g., Bengal gram). The image of the soft seed coat development is shown in Fig. 5.

Gene expression during seed and seed coat development

Genes involved in seed development

Gene expression during seed development is a tightly orchestrated temporal process, generally categorised into three distinct physiological phases like morphogenesis, maturation and desiccation (25). The different types of genes involved in seed development are listed in Table 1.

Table 1. Different types of gene involved in seed development

Phases	Process and genes	Reference
Morphogenesis (Pattern formation)	Patterning genes: Genes like <i>WUSCHEL-RELATED HOMEODOMAIN (WOX)</i> are critical factor for establishing apical-basal polarity in the zygote.	(25)
	Hormonal regulators: Auxin (AUX), cytokinin (CTK) and brassinosteroids (BR) drive early cell expansion and division. Specifically, <i>auxin response factors</i> (e.g., <i>FtARF2</i>) play a role in promoting fruit and embryo enlargement by extending the cell division cycle.	(26)
	Master regulators (AFL Subfamily): The leafy cotyledon genes (<i>LEC1</i> , <i>LEC2</i>) and <i>FUSCA3</i> (<i>FUS3</i>) are essential for initiating the maturation program. For example, <i>LEC1</i> has been found to prevent premature embryo greening in rice plant.	(27)
Maturation (Storage accumulation)	Storage proteins: Large scale up regulation of genes encoding seed storage proteins (SSPs) occurs, providing the necessary nitrogen (N) and energy for future germination of seed.	(25)
	Abscisic acid (ABA) signalling: The transcription factor <i>ABI3</i> acts as a central hub, integrating ABA signals to promote maturation while repressing germination related genes.	(28)
	Protective genes: There is a massive upregulation of late embryogenesis abundant (LEA) proteins and heat shock proteins (HSPs) , which act as molecular chaperones to protect cellular structures as water is lost.	(29)
Desiccation (Metabolism and dormancy)	Metabolic shutdown: Transcriptional switches lead to the repression of genes involved in photosynthesis, respiration and the cell cycle to enter a quiescent state.	
	Dormancy regulation: The balance between ABA (promoting dormancy) and gibberellins (GA) (promoting germination) is critical. Genes like <i>DOG1</i> and <i>WRKY41</i> (which upregulates <i>ABI3</i>) are key players in maintaining this state.	(30)

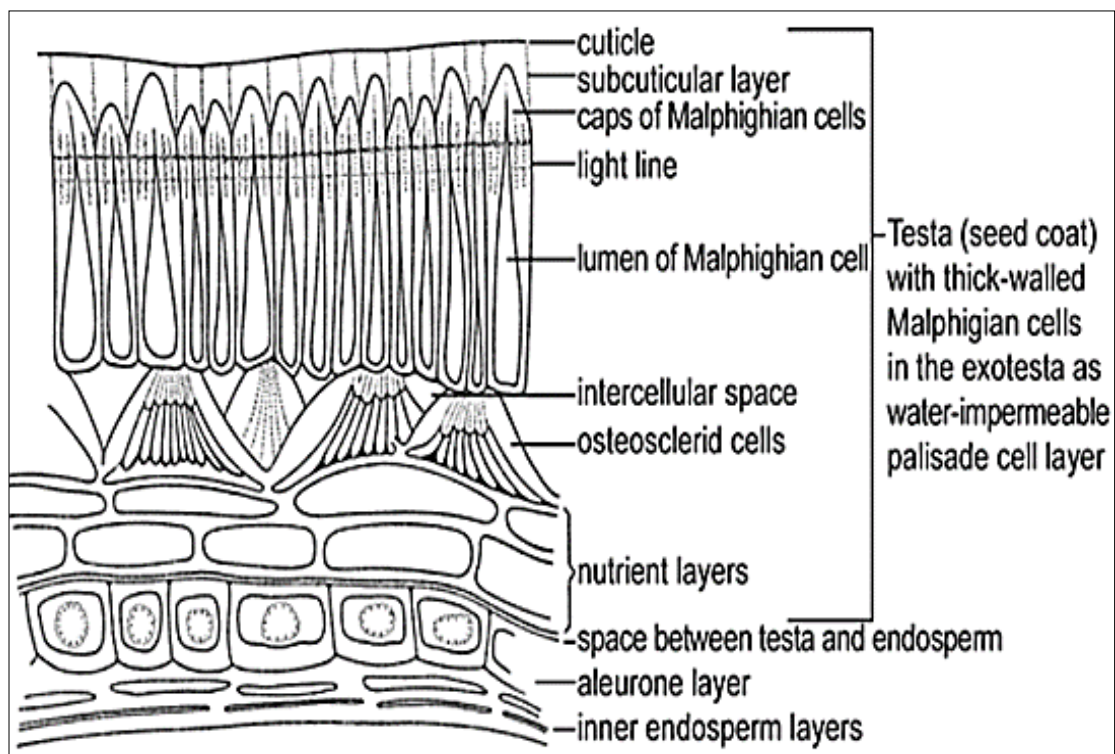


Fig. 4. Hard seed coat development in crops (23).

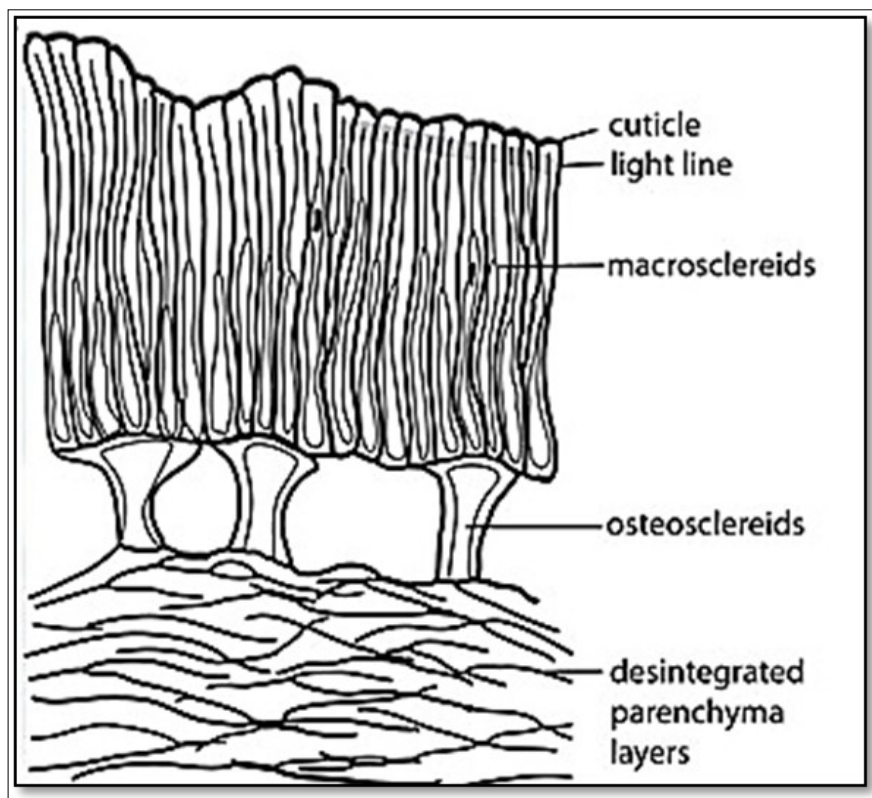


Fig. 5. Soft seed coat development in crops (24).

Genes involved in seed coat development

Genes involved in seed coat formation are largely associated with the flavonoid biosynthesis pathway, lignin biosynthesis and transcriptional regulation. Key genes include those encoding basic helix-loop-helix (bHLH), WD-repeat proteins and E3 ubiquitin ligases, which regulate flavonoid pathway enzymes affecting seed coat colour and pattern in cowpea and brassica species. In transcription factors such as TT8, TTG1, MYB family members, NAC, bHLH, AP2 or EREBP and WRKY play crucial roles in modulating seed coat development by controlling proanthocyanidins accumulation and lignification processes (31). Genetic studies in *Arabidopsis* highlight the involvement of MADS-domain proteins SEEDSTICK (STK), GORDITA (GOA) and AUXIN RESPONSE FACTOR 2 (ARF2) in coordinating cell expansion, proliferation and pigment production in the seed coat (32). Lignin biosynthesis genes like CCR-LIKE (CCRL) influence seed coat content and hardness by regulating carbon allocation between phenylpropanoid compounds and oil during seed development process (33). Some of the genes involved in seed coat characteristic development are depicted in Table 2.

Table 2. The different types of genes involved in seed coat characteristic development

Crops	Key genes for seed coat characters	Function	References
Arabidopsis	TT family, AP2, AGL44	Master regulators of colour and size	(34)
Rice	SDR4, Rc/Rd	Dormancy and pericarp colour	
Canola	MUC121, MYB52	Seed coat content and mucilage	(35)
Cotton	GhMYB25, GhCPC	Fibre initiation and length	(36)

Composition of seed coat

There are two main composition influencing seed coat functions like., physical composition and biochemical composition. The different functions of these compositions were described in (Fig. 6).

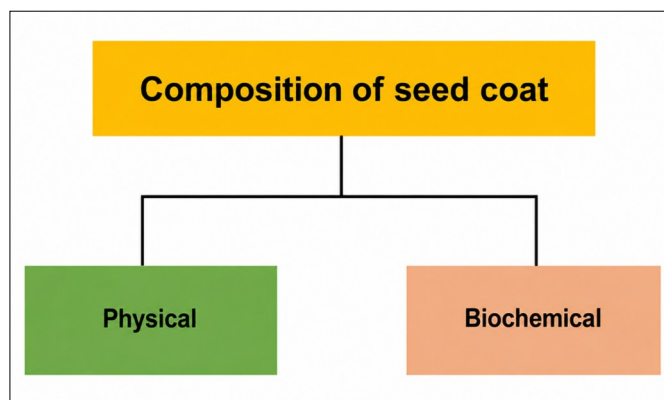


Fig. 6. Seed coat compositions.

Physical composition influence on seed coat functions

Physical composition is mainly comprising seed coat colour and seed coat thickness. These two characters are mainly playing role on seed quality parameters like germination, vigour, dormancy, seed longevity and seed health (Fig. 7).

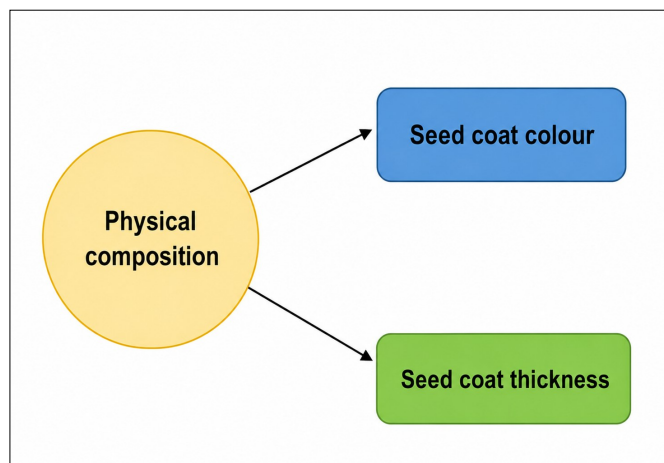


Fig. 7. Physical composition of seed coat.

i. Seed coat colour: The seed coat, which varies in structure among species, protects the integrity of the seeds by allowing gasses and water to enter the tissues. As a seed coat reaches maturity, its own colour develops. Within-species variations in seed colour are linked to the collection of seeds from various fruit developmental stages and some genetic variations with the developmental variations (37). Thus, in this regard, the colour of the seed coat influences germination, dormancy, vigour and other quality parameters of the seed. Therefore, the below picture showed the variations in seed coat colour in sunflower (Fig. 8).

Based on this seed coat colour variation and its impact on germination, vigour, dormancy and nutritional quality are reviewed below.

a. Germination and vigour: Germination and vigour are a major physiological event in the seeds. Seed coat colour showed the difference in the germination and vigour. So, the effect seed coat colour on germination here reviewed under. According to a previous study (38) it is identified that four cowpea accessions with lighter colours (GH7175 and GH8800) showed greater vigour, germination and higher seed quality than those with darker colours (GH3677 and GH2323) at 6, 12, 18, 24 and 30 months after storage. Two black seed coat colour genotypes of soybean consistently showed higher vigour and longevity under natural and both the years of accelerated ageing and serve as a source of alleles for higher seed longevity (39). According to a previous experiment (40) the genotypes of flax seed that are darker brown in colour and have the maximum vigour, germination, seed yield, oil content and protein content are dominant in South America. Similar results are explained in Table 3.

b. Seed dormancy: Seed dormancy is a state in which seeds do not germinate under favourable conditions. Seed coat colour has been reported to be associated with dormancy in several crops. In soybean, light-coloured F3 hybrid seeds (yellow and green) were comparatively non-dormant, whereas dark-coloured seeds (brown and black) were comparatively dormant (45). In carob, four distinct

seed coat colours, namely chocolate brown, clear brown, greenish brown, and yellowish brown, were identified. Clear-coloured (yellowish brown) seeds showed strong coat dormancy, with a low germination percentage, whereas chocolate-brown seeds showed no signs of dormancy. Without any pre-treatment, the maximum germination percentage of chocolate-brown seeds ranged from 80 to 88 % (46). In subabul, light-brown-coloured seeds recorded higher germination (88 %) with lower dormancy, whereas dark-brown seeds showed lower germination (31 %) and higher dormancy (47). Soybeans with darker seed coats contain higher concentrations of anthocyanins and proanthocyanidins than those with lighter seed coats, and increased tannin contents in the cell walls are associated with increased dormancy in many species (48).

c. Nutritional quality of seeds: Nutritional quality of seeds varied for based on the seed coat colour. According to a previous study (49) it was stated that the biochemical makeup of flax seeds, the seed coat colour is one of the important factors. The findings suggested that brown-seeded flax is a reliable source of protein, fibre and antioxidant compounds, especially lignins, tocopherols and phenolics, which can be utilised in the pharmaceutical and food additive industries to improve human health and nutrition. The oil derived from yellow seed flax has a remarkable nutritional and therapeutic value due to its high content of polyunsaturated fatty acids and mucilage (50). It was stated that genotypes belonging to black group exhibited highest mean neutral detergent fibre, acid detergent fibre, lignin, free amino acids and tannins and lowest saponins and contents varied significantly from brown, green and yellow group in soybean seeds.

d. Effect of seed coat colour on seed longevity: The colour of the seed coat is more than just an aesthetic trait; it is a primary physiological indicator of a seed's longevity (its ability to remain viable during storage). This relationship is driven by the presence of specific chemical compounds, primarily phenolics and flavonoids, which provide both physical and chemical protection (51). Similar results are explained in Table 4.



Fig. 8. Seed coat colour variations in sunflower seeds.

Table 3. Effect of seed coat colour on germination and vigour of some crop species

S. No.	Crop	Colour of seed coat	Role in germination and vigour	References
1.	Cowpea	Pigmented (black, brown, dark brown, grey, dark grey seed colour)	Cowpea genotype with pigmented seed had higher vigour as compared to cowpea genotypes with unpigmented seed	(41)
2.	Yard long bean	Bicolour (Brown and Black)	Highest germination percentage and vigour index	(42)
3.	Sunflower	Black colour	Increase the percentage of field emergence and index of germination rate	(43)
4.	Bambara groundnut	Black-speckled colour	Greater seed vigour and viability	(44)

Table 4. Effect of seed coat colour on seed longevity of some crop species

S. No.	Crop	Colour of seed coat	Role in seed longevity	References
1.	Soybean	Black (Small-seeded)	Higher longevity under natural and accelerated ageing; strong	(39)
2.	Cowpea	Pigmented > unpigmented	Pigmented seed coats deteriorate more slowly under hot, humid storage and retains germination longer	(41)
3.	Bambara groundnut	Light > dark	Light landrace had higher germination and better longevity after ageing than dark land race	(44)

e. Effect of seed coat colour on seed health

Insect: Seed coat colour significantly influences the insect behaviour, particularly ovipositional preferences and larval development in various beetle species. For bean beetle *Callosobruchus maculatus*, females prefer to lay eggs on brown seed coat areas over white ones in cowpea (52). Similarly, in red gram the pulse beetles show a preference for light yellow seed coats over darker brown varieties for orientation and oviposition but seed coat colour does not affect their survival (53). In cowpea weevils, non-host seed coats like *Phaseolus vulgaris* reduce oviposition and larval survival by impairing digestion rather than embryonic development, indicating biochemical effects of seed coat components (54). Seed coat colour combined with hardness also affects resistance to safflower fly infestation in darker and harder seeds exhibit greater resistance compared to white seeded cultivars (55). Overall, darker or pigmented seed coats tend to deter insect ovipositional and improve resistance through physical and biochemical mechanisms.

Pathogens: Seed coat colour is linked to pathogen resistance in several crops, often due to the presence of phenolic compounds such as anthocyanins and proanthocyanidins that have antimicrobial properties. In black soybean seed coats contain higher total phenolic content and show stronger antimicrobial effects against foodborne pathogens like *Salmonella* and *Escherichia coli* compared to yellow seed coats (56). Similarly, red grained rice varieties with proanthocyanidins in their seed coats exhibit enhanced resistance to fungal infections and reduced mycotoxin accumulation compared to white grained rice varieties (57). In peas, pigmented seed coats (coloured by anthocyanins) are associated with resistance to *Fusarium avenaceum* (root rot), while non-pigmented seeds tend to be more susceptible (58). These findings collectively indicate that seed coat pigmentation often correlates with increased resistance to various pathogens through biochemical defences inherent in the pigments or other associated compounds.

ii. Seed coat thickness: Seed coat thickness plays an important role in seed quality parameters like germination, vigour, dormancy, longevity and seed health. Since the Palaeozoic era, seeds have been carrying a seed coat that aids in the dissemination of the fertilisation products while also protecting and nourishing it. By altering its thickness, the seed coat evolved to accommodate various environmental conditions and reproductive tactics (59). The evaluation of seed coat thickness under natural diversity and seed coat thickness on seed quality aspects discussed here.

Evaluation of seed coat thickness at natural diversity

i. Integument numbers: The integument anatomy of these pre-ovules varied according on the species, it was usually lobed, vascular bundled and separated from the nucellus. The ovule has been found to be partially encased by leaf-like structures called cupules, which paleo botanists generally consider to be the

predecessor of a second integument. The integument of modern gymnosperm ovules is most likely similar to that of primitive seed plants and these ovules are also unitegmic. Angiosperms, on the other hand, evolved two bitegmic integuments, known as outer integument (oi) and inner integument (ii). Although unitegmic appeared multiple times during the evolution of angiosperms, phylogenetic analyses indicate that bitegmic is the ancestral condition in angiosperms (60).

ii. Integument cell thickness: The chalazal dermal tissue is the source of two layered dermal integuments, while three layered sub-dermal integuments have two dermal and one sub-dermal cell layer. Moreover, integuments are multiplicative because they can create additional cell layers through periclinal cell division of subdermal or dermal cell layers (61).

iii. Integument thickness along the ovule polarity axes: Along the ovule polarity axes, there can be a considerable variation in both integument number and cell thickness. A micropyle form on the distal side of the ovule as a result of integument expansion. Because oi or ii contribute to the production of micropyles, the majority of bitegmic ovules are amphistomic. Rarely, if just the oi or ii integuments, produce the micropyle, angiosperm ovules can be endospermic or exostomic (60). According to a previous study (62), endostomic ovules exhibit distal thickening of the ii at the micropyle where the ii is not covered by the oi, indicating that oi restricts ii growth.

iv. Molecular regulations: At stage two of ovule development in Arabidopsis, the proximal funiculus differentiates a vascular strand, the central chalaza starts integument primordia and the distal nucellus develops a megaspore mother cell. These morphological changes indicate the presence of the ovule proximal distal polarity axis (63). Ovule proximal distal patterning appears to happen sequentially, beginning from the distal nucellus and moving toward the funiculus, according to genetic and molecular findings (64).

Seed coat thickness on seed quality aspects

Imbibition and germination

Seed coat thickness plays a critical role in seed germination by influencing water uptake (imbibition) and dormancy mechanisms. In *Leucadendron species*, thinner seed coats in winged seeds allow high permeability and germination without smoke or heat, while thicker seed coats in nutlets reduce water uptake and increase the need for smoke or heat to break dormancy, suggesting seed coat thickness regulates germination responses to environmental cues like fire (65). Similarly, in wild pea (*Pisum sativum subsp. elatius*) thicker seed coats correlate with stronger physical dormancy and lower germination rates, with environmental factors such as temperature range influencing dormancy patterns (66). Seed coat thickness also imposes mechanical restraint on radicle emergence in *Chenopodium hircinum*, where thicker coats reduce water absorption and germination, but dormancy breaking treatments that weaken the coat and it alleviate dormancy (67).

Dormancy

Seed coat thickness plays a significant role in seed dormancy by acting as a physical barrier that restricts water uptake and radicle emergence, thereby maintaining dormancy. In *Medicago falcata*, thicker palisade layers in the seed coat correlate with hard seeds exhibiting low germination rates and prolonged dormancy, alongside biochemical changes such as increased flavonoids and altered hormone levels that reinforce dormancy (68). Similarly in wild pea, seed coat thickness shows only a moderate correlation with permeability and dormancy, with genetic loci controlling traits independently (69). Additionally, research on chickpea and *Rubus* species highlights that phenolic compounds in the seed coat contribute to hardness and dormancy, indicating that chemical composition alongside thickness influences dormancy status (70).

Seed health

Insect

Seed coat thickness plays a critical role in protecting seeds from insect infestation, particularly by bruchid beetles such as *Callosobruchus maculatus* and *Acanthoscelides obtectus*. Thicker seed coats can act as a physical barrier that prevents first instar larvae from penetrating the seed. Its significantly reducing larval survival and adult emergence; for example, seed coats thicker than 0.1 mm strongly hinder larval entry in several leguminous species (71). Seed coat thickness positively correlates with resistance to infestation in broad bean and soybean varieties where thicker coats reduce egg laying, progeny production and seed damage by bruchids (69). The thicker seed coats in legumes like *Vigna unguiculata* reduce larval survival of the cowpea beetle, with seed coats three times thicker showing greater resistance (70). Overall, strengthening seed coat defences both physical thickness and chemical properties represent an effective strategy to reduce insect infestation and protect seeds during storage and in natural conditions.

Pathogen

Seed coat thickness is strongly associated with resistance to pathogens providing a physical barrier that limits infection. In peanuts, the seed coat acts as both a physical and biochemical

barrier against *Aspergillus flavus* infection, where multi-layered structures and phenolic compounds inhibit fungal growth and aflatoxin contamination (71). Within lentil species, thicker seed coats correlate with higher seed survival during soil burial and enhanced protection from pathogen pressure (72).

Biochemical composition influence on seed coat functions

Biochemical composition is comprised of polyphenolic compounds (tannins, lignin and phenolic acids), structural polysaccharides, alkaloids, lipids and waxes and specialised proteins. They are mainly involving protection mechanism of seeds from other biotic and abiotic factors. The functions of biochemical composition are reviewed (Fig. 9).

I. Polyphenolic compounds

Polyphenols are a large family of naturally occurring organic compounds found abundantly in plants. They are primarily known for their antioxidant properties and their role in protecting seeds and plants against ultraviolet (UV) radiation, pathogens and physical damage (73).

i. Phenolic acids: Phenolic acids are a low molecular weight in many seed coats. They contribute to colour, defence, seed longevity and strong antioxidant capacity that can be nutritionally useful. Legume and oilseed coats commonly contain hydroxy benzoic acids (gallic, protocatechuic, 4-hydroxybenzoic, vanillic, syringic and salicylic) and hydroxyl cinnamic acids (caffeic, p-coumaric, ferulic, sinapic). In coloured pea coats have much higher total phenolic acids than white coats; benzoic acids dominate in coloured, ferulic and p-coumaric acid in white. Wall bounded phenolics and condensed tannins correlated with antioxidant assays are better vigour and germination in pea (74). Peanut seed coat contains the hydroxycinnamic and benzoic acids are inhibiting *Aspergillus flavus* and aflatoxin (71).

ii. Tannins: Tannins in seed coats are condensed polyphenols concentrated in the outer integuments of many seeds. They strongly influence seed permeability, dormancy, colour, antioxidant capacity, resistance to pests and nutritional quality. In *Arabidopsis*, tannin impregnated “tannic cell walls” form a continuous apoplastic barrier fused to the cuticle. It limits water and

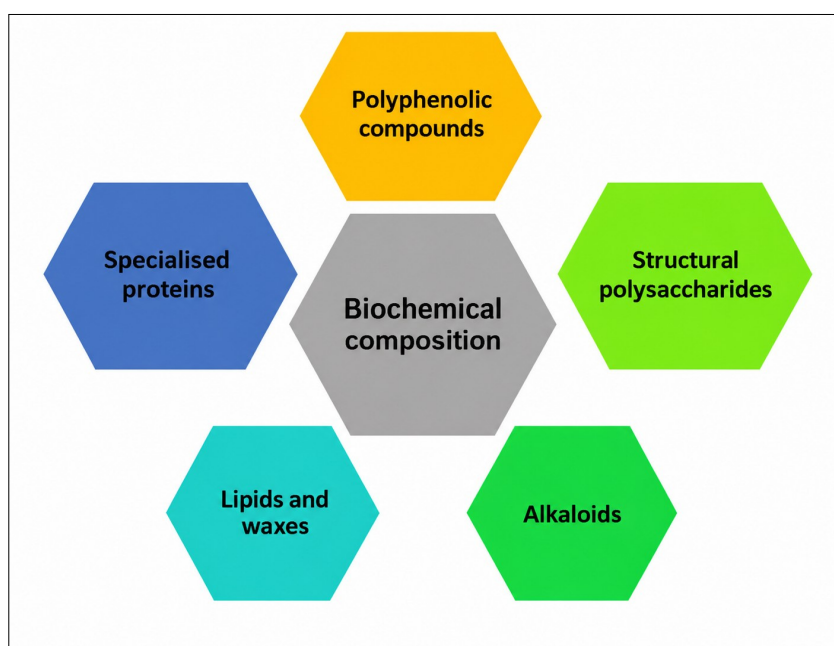


Fig. 9. Biochemical composition of seed coat.

oxygen entry and protecting against oxidative damage. Thus, supporting dormancy and viability of seeds. Transparent testa (Tannin deficient) mutants show higher permeability, earlier seed coat rupture, weaker coats and lower dormancy (75). In soybean, higher phenols and tannins in black, impermeable seed coats correlate with dormancy and fewer cracks, whereas low tannin white coats are permeable and prone to imbibition injury (76). In cowpea, bruchid larvae infestation revealed that undamaged seeds from a susceptible line with high tannin levels in the seed coat had more tannins than heavily infested seeds from another line low tannin levels (77).

iii. Flavonoids: Flavonoids in seed coats play crucial roles in pigmentation, antioxidant activity, seed coat development and resistance to pathogens. In peanut seed coats, flavonoids such as anthocyanins, aurones and chalcones enhance antioxidant activity and resistance to *Aspergillus flavus* (78). In *Arabidopsis* and other plants, flavonoids including proanthocyanidins (PAs), flavonols like kaempferol and quercetin derivatives accumulate predominantly in the seed coat influencing seed coat structure and longevity (79). Over accumulation of specific flavonols such as kaempferol-3-rhamnoside can disrupt seed coat differentiation and reduce seed longevity was seen in *Arabidopsis* tt7 mutants (80). Overall, flavonoids are integral to seed coat function across species by modulating physical barriers, defence mechanisms and seed longevity.

iv. Lignin: One of the primary phenolic substances found in the tissues of gymnosperms and angiosperms. Its term, derived from the Latin word "lignum," which means wood, is found in the vascular tissues of plants (81). Shading stress can increase lignin in soybean seed coats, thickening them and prolonged seed longevity under deterioration (82). In *Arabidopsis*, higher lignin deposition in the outer integument restricts water uptake and slows germination; reduced lignin seeds content in some seeds leads to higher permeability and faster germination (83).

II. Structural polysaccharides

Seed coat structural polysaccharides primarily include cellulose, hemicellulose (such as xylan and glucomannan) and pectin, which together form mucilage that covers the seed surface and aids in hydration and germination. The mucilage acts as a gel like capsule composed of a cellulose scaffold intertwined with other polysaccharides. It provides mechanical stability and crucial water retention function for seed (84). In *Arabidopsis*, genes involved in cellulose and hemicellulose biosynthesis have been identified, revealing that xylan side chains link pectin directly to cellulose and highlighting complex interactions among these polymers in the seed coat (85). Variations in polysaccharide composition and structure influence seed coat properties such as hardness and cooking behaviour, as seen in common beans where pectin interactions with divalent ions affect texture (86). The multi-layered seed coat structure often includes lignified and suberised layers alongside polysaccharides, contributing to physical protection and water permeability control during seed swelling (87).

III. Alkaloids

Alkaloids in seed coats play important roles in plant defence and seed quality. In *Argemone mexicana*, a significant portion of the alkaloid "sanguinarine" is tightly bound to the seed coat, it persists during germination and provides chemical protection against herbivores or pathogens (88). Similarly, in *Lupinus angustifolius*

seed coat colour correlates with alkaloid content, white seeds showing lower alkaloid levels this trait can be used to identify low alkaloid genotypes for breeding (89). In *Sophora alopecuroides*, "quinolizidine" alkaloids are unevenly distributed between seed coat and cotyledon play a major role on mobilisation during seed development and germination (90). Overall, alkaloids localised in the seed coat contribute to chemical defence mechanism and influence seed traits relevant for plant survival.

IV. Lipids and waxes

Lipids and waxes on seed coats play crucial roles in protecting the embryo from environmental damage, pathogens and water loss. In *Arabidopsis*, seed coats accumulate various lipid polyesters and waxes, including very long chain fatty acids (VLCFAs), wax esters and suberin. These are contributing to their protective barrier functions (91). Wax composition varies among plant species and organs in faba bean seed coats, primary alcohols are dominate the wax profile with lower compared to aerial organs. Its reflecting organ-specific biosynthesis linked to ecological functions (92). In sunflower seeds, wax esters accumulate mainly in the hull through the action of wax synthase enzymes that esterify Acyl-CoA with long-chain alcohols (93).

V. Specialised proteins

Specialised proteins in seed coats play diverse roles including structural support, defence and regulation of seed coat properties. In *Arabidopsis*, the seed coat mucilage contains abundant proteins such as Testa Abundant (TBA) family, which are secreted during seed coat differentiation and may serve as useful markers for targeting seed coat epidermis cells (94). Soybean seed coats express a class I chitinase with antifungal activity that contributes to defence against pests and pathogens, highlighting the protective role of seed coat proteins (95). In rice, an extension like protein OsPEX1 modulates water permeability of the seed coat by influencing cutin suberin deposition and affecting germination rates (96). These findings demonstrate that specialised proteins in seed coats contribute to physical protection, biochemical defence, regulation of water and solute permeability essential for seed viability and germination.

Factors affecting seed coat formation

The seed coat formation was mainly influenced by four factors viz., genetic, hormonal, environmental and nutritional.

Genetic factor

It determines the layer number (unitegmic or bitegmic) and specialised cell types like macrosclereids (18).

Hormonal factor

It determines the auxin from the endosperm triggers seed coat expansion; ABA and GA balance regulations in dormancy (97).

Environmental factor

The changes in environmental cues like heat and drought increase thickness and impermeability. Then the moisture swings can cause cracking of seeds (18).

Nutritional factor

It determines the nutrient levels in seed coat. E.g., nitrogen affects the storage capacity and structural integrity (32).

Functional role of the seed coat

The seed coat plays several vital functions in seeds. They are:

Mechanical protection

Shields the embryo from physical injury, UV light and desiccation process (98).

Water regulation

Controls water uptake through the micropyle or hilum. In hard seeds, it promotes impermeability due to a continuous palisade layer and waxy coating (12).

Gas exchange

Some seeds allow controlled oxygen diffusion through specific regions of the seed coat (99).

Dormancy regulation

Seed coats with suberin, lignin, or phenolic deposits often result in physical dormancy (hard seeds). This prevents premature germination under unfavourable conditions (100).

Defence mechanism

Phenolic compounds in the seed coat have antifungal and antimicrobial properties. Acts as a barrier against insect infestation, pathogen infection and microbial invasion (13).

Future role of seed coat in agriculture

Future studies regarding the seed coat are shifting from viewing it merely as a passive physical barrier to recognising it as a dynamic, maternal organ that regulates germination, protects against stress and acts as a channel respond to various environmental conditions. Key future roles for seed coat research include genetic modification to improve crop establishment, the development of sustainable, multifunctional seed coatings, identifying the niche area in seed germination and dormancy and enhancing seed storage longevity (Fig. 10).

Conclusion

The seed coat is a vital structural and functional component of seeds, playing a central role in determining seed quality and overall plant performance. Its physical characteristics, particularly colour and thickness, along with its complex biochemical composition, significantly influence key seed traits such as germination, vigour, dormancy, longevity and resistance to pests and pathogens. The presence of compounds like polyphenols, lignin, flavonoids, lipids and waxes and specialised proteins enhance mechanical strength, regulates permeability and provides effective defence mechanisms. Moreover, seed coat development is a highly regulated process controlled by genetic, hormonal, environmental and nutritional factors, highlighting its dynamic nature rather than being merely a passive protective layer. Understanding the interactions between these factors and seed coat properties offers valuable opportunities for improving seed quality through breeding and biotechnological approaches. In the context of modern agriculture, optimising seed coat traits can contribute significantly to better crop establishment, enhanced stress tolerance, improved storage potential and sustainable crop productivity. Future research focusing on molecular regulation, functional genomics and innovative seed technologies will further strengthen the role of the seed coat in advancing agricultural efficiency and food security in agriculture.

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Fig. 10. Future role of seed coat.

Authors' contributions

The review article conceptualized by RU and KA wrote under the supervision of RU. CV, TA, GP and MV reviewed the manuscript and edited by RU and KA. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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