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Understanding the role of specialized metabolites in Brassicaceae and Leguminosae seeds: implications for seed health, nutritional quality and sustainable agriculture

Comprendre le rôle des métabolites spécialisés dans les graines de Brassicacées et de Légumineuses : implications pour leur protection, leur qualité nutritionnelle et une agriculture durable

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Abstract

Specialized metabolites (SMs) influence seed physiology, defence, and nutritional quality. In crop species such as Brassicaceae and Leguminosae. SMs like tannins, glucosinolates, and some alkaloids contribute to seed protection against biotic and abiotic stresses. This review focuses on these two botanical families as case studies to illustrate the diversity and functional roles of SMs in seeds. Beyond their protective role, SMs shape the organoleptic properties of many foods and have significant health benefits, including antioxidant, antimicrobial, and potential protective effects against chronic diseases. However, some SMs can negatively affect seed nutritional quality due to their antinutritional or toxic properties. Managing this dual nature is a key challenge for crop improvement. It requires a striking balance between the beneficial and adverse effects of SMs on seed quality. Understanding SM biosynthesis and functions offers opportunities to optimize their composition via breeding, biostimulation, or biocontrol strategies, enhancing crop resilience and sustainability while minimizing reliance on synthetic inputs.

Résumé

Les métabolites spécialisés (MS) influencent la physiologie, la défense et la qualité nutritionnelle des graines. Chez les espèces cultivées telles que les Brassicacées et les Légumineuses, des MS comme les tanins, les glucosinolates et certains alcaloïdes contribuent à la protection des graines contre les stress biotiques et abiotiques. Cette revue se concentre sur ces deux familles botaniques comme cas d'étude, afin d'illustrer la diversité et les fonctions des MS dans les graines. Au-delà de leur rôle protecteur, les MS modulent les propriétés organoleptiques de nombreux aliments et possèdent des propriétés intéressantes pour la santé, notamment comme antioxydants, antimicrobiens et contre le développement de différentes maladies chroniques. Toutefois certains MS peuvent altérer la qualité nutritionnelle des graines en raison de leurs propriétés anti-nutritionnelles ou toxiques. Gérer cette dualité est essentielle pour l'amélioration des cultures, nécessitant un équilibre subtil entre les effets bénéfiques et délétères des MS sur la qualité des semences. Elucider la biosynthèse et les fonctions des MS offre des opportunités d'optimisation de leur composition grâce à des stratégies de sélection, de biostimulation ou de biocontrôle, améliorant ainsi la résilience et la durabilité des cultures tout en réduisant la dépendance aux intrants synthétiques.

Keywords

abiotic stress, biocontrol, biostimulation, biotic stress, metabolome plasticity, metabolomics, seed immunity, seeds specialized metabolites

Mots-clés

stress abiotique, biocontrôle, biostimulation, stress biotique, plasticité du métabolome, métabolomique, immunité des graines, métabolites spécialisés des graines

Seed physiology, nutritional value and stress tolerance: a focus on Brassicaceae and Leguminosae

Seeds are key players in crop production and breeding. Their physiological, metabolic and sanitary qualities determine agronomic performance and yield. During their development, dispersal and germination, seeds are exposed to biotic (e.g. bacteria, fungi, viruses, insects) and abiotic factors (e.g. heat, drought, toxic trace metals, etc.), which can negatively affect their quality and longevity. The transmission of “bioagressors” to and through seeds presents a significant global agronomic challenge, further intensified by the international trade. Recent advances in understanding molecular plant interactions with biotic and abiotic stresses increasingly highlight the role of both constitutive and inducible specialized metabolism (Lacchini and Goossens, 2020 ; Du *et al.*, 2024). These processes play a key role in shaping important aspects of seed and plant ecological interactions, as well as broader adaptation to environmental challenges.

Several studies have focused on characterization in plant vegetative tissues of biosynthetic pathways and regulations of various specialized metabolites (SMs) in response to biotic and abiotic stresses (Anzano *et al.*, 2022). However, much less is known about these processes in seeds, which are particularly important in many crop species, as they often serve as the primary product for industrial or nutritional purposes.

Effective management of seed health and resistance to pests and pathogens is thus essential for agriculture. Traditional use of synthetic treatments is declining, particularly within the European Union (EU), due to regulatory bans and growing concerns over environmental impact. Consequently, various biocontrol and biostimulation strategies are being developed and implemented to enhance seed performance and stress resistance.

Given the importance of SMs in seed ecology and nutrition, we focus on two major crop families, Brassicaceae (previously referred as Cruciferae) and Leguminosae (also known as Fabaceae), to illustrate these dynamics in agricultural contexts. These were chosen as case studies for three main reasons: (1) their global agronomic relevance, including the presence of major crops such as rapeseed, soybean, and pea, which reflects the growing interest in developing new strategies for biocontrol, biostimulation, and improving food and feed quality for these species; (2) their partially characterized and distinct metabolic composition, such as the presence of glucosinolates (GSLs) in Brassicaceae and saponins or isoflavonoids in Leguminosae; (3) their primary relevance in terms of oil (Brassicaceae) and protein (Leguminosae) content.

Although other families, such as Poaceae, produce agronomically valuable seeds and are also rich in important metabolites like benzoxazinoids, they are not discussed here.

Environmental factors, including soil composition, temperature, and microbiota, are known to modulate metabolite profiles (Fiehn, 2002; Nakabayashi and Saito, 2015). However, the metabolic and enzymatic pathways discussed here are widely conserved within each family and serve as robust starting points for comparative approaches.

Finally, this review aims to support efforts toward integrative seed improvement strategies, combining breeding, biocontrol, and biostimulation, to enhance seed vigour and stress resistance without compromising quality. This is particularly important for European agriculture, where policy shifts are driving the development of low-input, sustainable production systems offered contrasting and complementary examples of seed metabolism, with well-studied compounds such as GSLs in Brassicaceae and tannins, saponins or isoflavonoids in Leguminosae. Their agronomic importance, metabolic diversity, and documented health effects make them relevant models to explore how SMs can support more sustainable agricultural systems.

In this context, some plant-breeding programs aim to develop ideotypes that produce seeds with high vigour and resistance to both biotic and abiotic stresses. The main objective is to create new varieties better suited to diverse production systems by integrating biocontrol and biostimulation solutions to enhance resilience and performance, without compromising the quality of plant products for feed and food. This significant challenge for European agriculture directly impacts the seed industry, which must develop effective and sustainable methods to protect seeds and enhance their quality. These efforts are further guided by government policies promoting the development of alternative solutions to reduce chemical inputs in agriculture (Brunelle et al., 2024).

Seed metabolite landscapes in Brassicaceae and Leguminosae

Plants produce a vast array of organic compounds, referred as primary (PMs) and

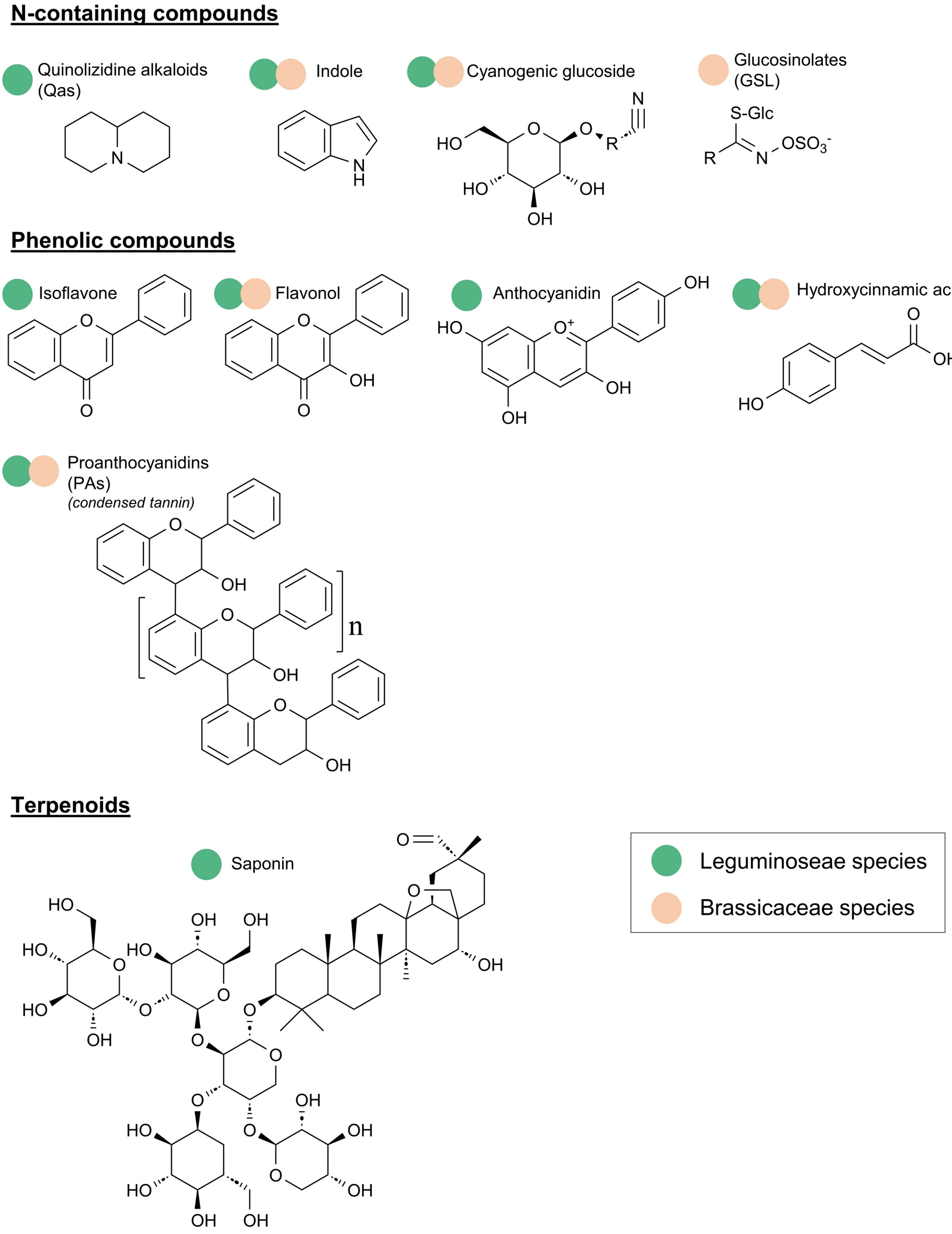


*Figure 1. Seed specialized metabolites of Brassicaceae and Leguminosae species. Chemical and core structures of nitrogen-containing compound, phenolic compound and terpenoid metabolic classes are showed for Leguminosae (*green circle*) and in Brassicaceae (*pink circle*).*

specialized metabolites (SMs). PMs include amino acids, nucleotides, sugars, lipids, and metabolic intermediates such as pyruvate.

These molecules are essential for core cellular processes, growth, development, and reproduction. By contrast, SMs (formerly referred to as secondary metabolites) are not directly required for basic survival, but play crucial roles in plant–environment interactions, including defence and adaptation to stress. Their production is often species-specific tissue-specific, or environment-specific, and they exhibit a wide structural and functional diversity (Corso *et al.*, 2020; Barreda *et al.*, 2024).

Based on their chemical and core structure, SMs are usually classified into three main groups: terpenoids, nitrogen-containing compounds (*i.e.* alkaloids and GSLs) and phenylpropanoids (*a.k.a.* phenolic compounds). This classification follows widely accepted biochemical taxonomies found in textbooks and reviews rather than recent experimental studies (Wink, 2010).

Many of these SMs are highly accumulated in seeds of several key plant families, including Brassicaceae and Leguminosae, which are the focus of this review due to their agricultural, nutritional, and metabolic significance (Derbyshire and Delange, 2020; Corso e*t al.*, 2021; Bulut *et al.*, 2023).

These two families were selected as case studies because they exhibit contrasting yet complementary seed metabolic profiles, harbouring unique SMs such as GSLs in Brassicaceae and isoflavones or alkaloids in Leguminosae (Figure 1). Furthermore, both families include model species and crops of agronomic importance, making them relevant for translational research into sustainable agriculture.

Notably, variation in SM composition across species or genotypes is shaped by both genetic and environmental factors, although the relative contribution of each remains underexplored in seeds.

Specialized metabolites in Brassicaceae seeds

Brassicaceae seeds accumulate significant amounts of phenolic compounds and GSLs (Figure 1). In particular, high levels of cinnamic acids and flavonoids are accumulated in the model species *Arabidopsis thaliana*, as well as in the crop species *Brassica* and *Camelina sativa* (Corso *et al.*, 2020; 2021). *A. thaliana* seeds mostly accumulate two types of flavonoids, notably flavonols and proanthocyanidins (PAs, or condensed tannins).

PAs are biosynthesized and accumulated in the inner integument of the seed coat, while flavonols are found in both the seed coat and seed embryo tissues (Debeaujon *et al.*, 2003; Lepiniec *et al.*, 2006). Although glycosylated quercetin and kaempferol rhamnosides are the most abundant flavonoids in developing and mature *A. thaliana* seeds, other forms, such as aglycones (e.g. isorhamnetin) or glycosides (combinations of one or two rhamnoside and/or other glucoside residues) have also been detected (Routaboul *et al.*, 2006; Matsuda *et al.,* 2010; Routaboul *et al.*, 2012; Corso *et al.*, 2020). In *Brassica napus* (rapeseed) seeds, the major synthesized phenolic compounds are sinapine (sinapoylcholine) and sinapic acid, belonging to the cinnamic acid category, that accumulate together with the flavonoids epicatechin, quercetin, and kaempferol derivatives (Jiang *et al.*, 2013; Tan *et al.,* 2015).

Similarly, *Camelina sativa* seeds accumulate a wide range of flavonols and cinnamic acids (Barreda *et al.*, 2025). A recent study reported that a wide variety of decorated flavonols (i.e. flavonol core structures harbouring glycosyl and/or malonyl groups) can be identified in camelina seeds (Boutet *et al.*, 2022). Unlike other species, including several Leguminosae, anthocyanin accumulation is typically absent or very low in the seeds of rapeseed and camelina under standard conditions (Barreda *et al.,* 2024). However, other studies have reported the presence of genes involved in anthocyanin biosynthesis in seed coats of some Brassicaceae genotypes, notably black-seeded *Brassica napus* (Qu *et al.*, 2013). Nevertheless, the presence of this metabolic class has never been unequivocally confirmed by metabolomic analyses in seeds of Brassicaceae species.

Furthermore, GSLs are sulphur-containing nitrogen compounds produced by Brassicaceae and a few other plant families, including Capparaceae or Cleomaceae (Fahey *et al.*, 2001; Bhatla and Lal, 2018; Nguyen and Dang, 2021). Brassicaceae species present a variable qualitative and quantitative GSL compositions in seeds. For instance, *C. sativa* accumulates long carbon chain methionine-derived GSLs (from 8C to 11C), whereas *A. thaliana* and *B. napus* accumulate short/mid chain methionine-derived GSLs, with up to 8C and 6C, respectively (Czerniawski *et al.*, 2021; Missinou *et al.*, 2022; Barreda *et al.*, 2025).

Interestingly, recent results have shown that the side-chain length of GSLs correlates with their spatial distribution in seeds. In particular, the 3C-7C short/mid chain methionine-derived GSLs, which is present in both *A. thaliana* and *B. napus,* but not in *C. sativa*, were accumulated in the seed embryo (SE). In contrast, the long chain methionine-derived GSLs (8C-11C), characteristic of *C. sativa* species (except for the 8C methionine-derived GSLs that can also be synthesized by *A. thaliana)*, accumulate in the seed coat and endosperm (SCE) tissues (Amyot *et al.*, 2019 ; Czerniawski *et al.*, 2021 ; Barreda *et al.*, 2025). Furthermore, *A. thaliana* produces benzyl GSLs that are not detected in *C. sativa* species (Czerniawski *et al.*, 2021).

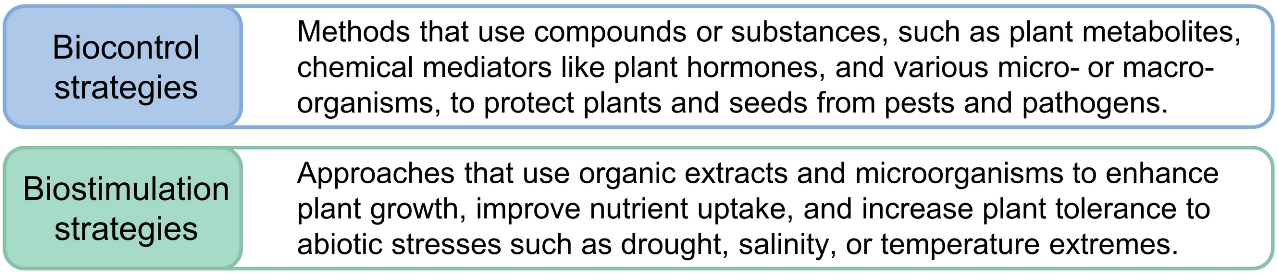
The accumulation patterns and chemical diversity of GSLs suggest not only a developmental regulation but also a specific localization within seed tissues, likely contributing to differential stress resilience and nutritional profiles (Barreda *et al.*, 2025).

Specialized metabolites in Leguminosae seeds

Legume seeds also accumulate diverse SMs, particularly flavonoids, PAs, isoflavonoids (Wink, 2013) (Figure 1). For instance, common bean *Phaseolus vulgaris* and cowpea *Vigna unguiculata* accumulate flavonoid metabolites such as anthocyanins, while isoflavones (flavonoids) are found in high concentrations in soybean (*Glycine max*) (Wink and Mohamed, 2003; Wink, 2013; Corso *et al.*, 2020). Although isoflavone compounds are not directly responsible for seed colour, their higher abundance in black-seeded soybean varieties compared to yellow-seeded ones could be linked to genetic and environmental regulations influencing isoflavone composition (Azam *et al.*, 2024). This observation highlights the need to further investigate how environmental factors influence seed metabolite biosynthesis.

In contrast to soybean and other legume species, Australian Papilionoideae taxa lack isoflavone biosynthesis, suggesting an independent evolutionary trajectory for this metabolic pathway in these species (Wink and Mohamed, 2003; Wink, 2013). Besides isoflavonoids, Leguminosae species also produce alkaloids such as quinolizidine alkaloids (QAs). These compounds, structurally characterized by a bicyclic nitrogen-containing heterocycle, accumulate in the seeds of Genisteae species, including lupin (*Lupinus spp.*) (Wink and Mohamed, 2003; Mancinotti *et al.,* 2022). QAs are synthesized in leaf chloroplasts and subsequently transported into other organs and tissues, including seeds, *via* the phloem (Wink and Mohamed, 2003).

In addition, legume seeds, particularly in *Glycine* and *Medicago* genera, also accumulate saponins (triterpenoid glycosides) with both protective and potentially



Biocontrol strategies	Methods that use compounds or substances, such as plant metabolites, chemical mediators like plant hormones, and various micro- or macro-organisms, to protect plants and seeds from pests and pathogens.
Biostimulation strategies	Approaches that use organic extracts and microorganisms to enhance plant growth, improve nutrient uptake, and increase plant tolerance to abiotic stresses such as drought, salinity, or temperature extremes.

Figure 2. Definitions of biocontrol and biostimulation strategies. Information was retrieved from (Fravel, 2005; Stenberg et al.*, 2021; Code rural et de la pêche maritime, 2021; Du Jardin, 2015; European Union, 2019).*

antinutritional properties (Wink, 2013; Mancinotti *et al.*, 2022). These compounds, while widely studied in leaves or roots, are increasingly recognized for their roles in seed protection and food quality.

Together, the Brassicaceae and Leguminosae families provide two complementary models to understand how specialized seed metabolism shapes adaptation, protection, and value in agricultural systems. Their diverse metabolic profiles, including species-specific SMs and tissue-localized accumulation patterns, offer rich perspectives for improving seed quality and crop sustainability.

Seed specialized metabolites in Brassicaceae and Leguminosae: dual roles in seed defence and nutrition

Specialized metabolites exhibit biological activities that can positively impact plant and seed health, serving as potential biocontrol agents against biotic stresses or as biostimulants to cope with abiotic stresses (Figure 2).

While SMs contribute to plant health (e.g. as antioxidants or antimicrobials), they can also negatively affect human and animal health. Some act as dose-dependent toxins or alter the organoleptic properties of food and feed (Salim *et al.*, 2023) (Figure 3).

Tannins are involved in antioxidant and pathogen responses

Condensed tannins are flavonoids found in the seeds of most crop species, including Leguminosae and Brassicaceae (Jain *et al.*, 2009; Auger *et al.*, 2010). They can interact with other pigments, such as anthocyanins, thereby altering their hues and intensities. Additionally, tannin oxidation is responsible of seed browning or darkening (Pourcel *et al.*, 2007). Thus, dark-coloured seeds generally contain high concentrations of tannins, while light-coloured seeds have negligible levels (Deshpande *et al.*, 1982; Jain *et al.*, 2009; Auger *et al.*, 2010).

Like many other SMs, tannins exhibit a duality between negative properties for food and feed (e.g. antinutritional or toxic) and protective beneficial properties for both animals and plants.

Regarding their negative properties, tannins were historically considered as antinutritional factors due to their ability to interact and form complexes with proteins (Jain *et al.*, 2009; Bolade, 2016) (Figure 3A). These complexes reduced protein digestibility and the availability of amino acids in seeds of Leguminosae species, which are rich in protein content (Singh, 2017), as well as in Brassicaceae species (e.g. rapeseed and camelina) that could be used as alternative sources of proteins (Jain *et al.*, 2009; Avanza *et al.*, 2013; Agarwal, 2016). Hence, domestication and

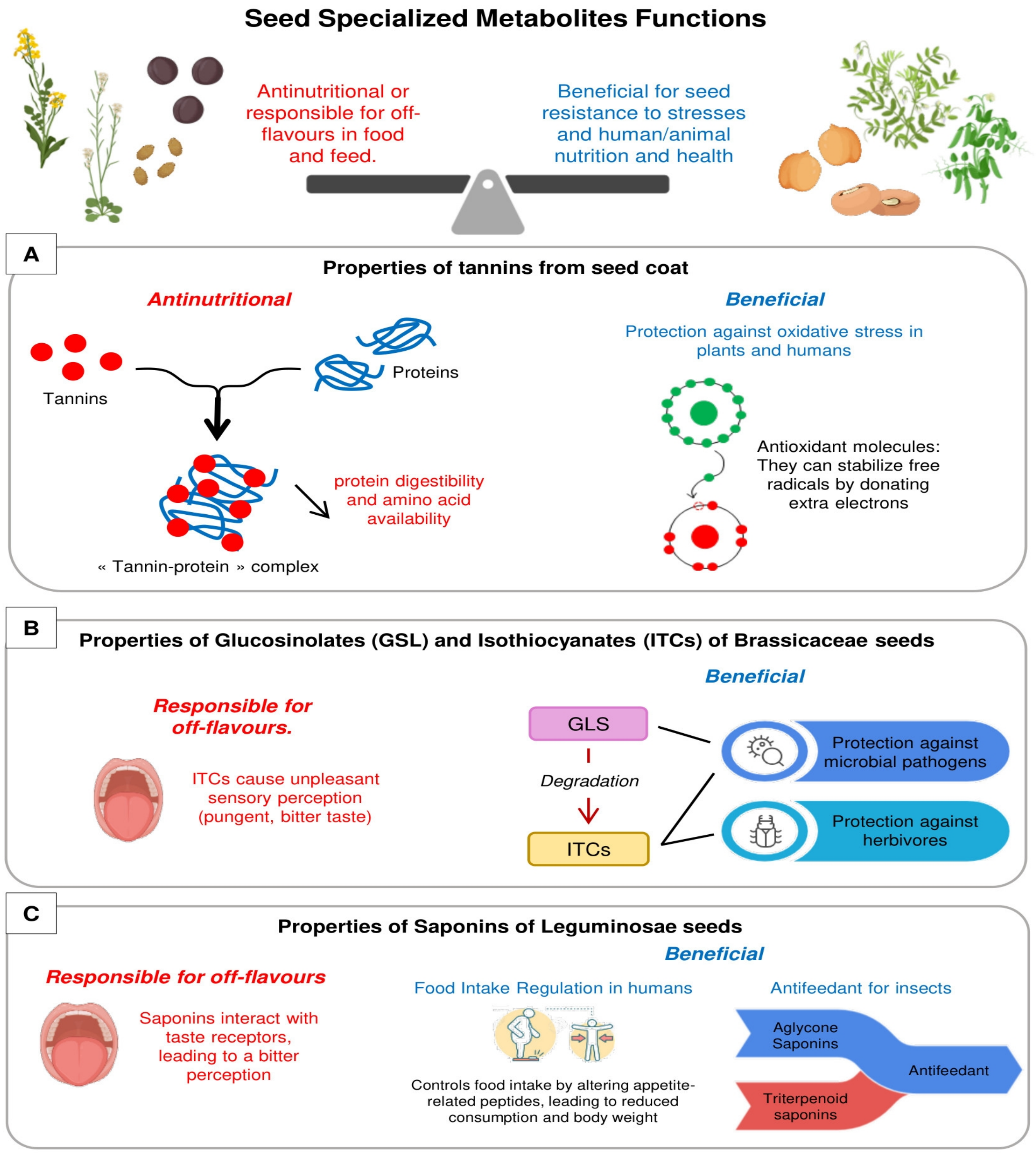


*Figure 3. Dual roles of seed specialized metabolites (SMs) in Brassicaceae and Leguminosae. SMs have both positive (*blue*) and negative (*red*) effects on plants, animals, and humans. This dual role influences seed defence, stress resistance, and nutritional quality. The figure illustrates the roles/functions of (A) tannins, (B) glucosinolates and (C) saponins (from Navarro del Hierro* et al.*, 2018; Di Gioia* et al.*, 2019; Chakraborty* et al.*, 2023; Barreda* et al.*, 2024).*

breeding processes have aimed to reduce tannin content in crop seeds. For example, rapeseed meal derived from black-seeded varieties contained significant levels of condensed tannins, which have antinutritional effects on monogastric animals. The development of yellow-seeded varieties with reduced tannin levels, achieved by modifying seed coat composition, has improved rapeseed meal quality (Lipsa *et al.*, 2012; Gołębiewska *et al.*, 2022). Ruminants have a more robust digestive system and are less affected by tannins, making rapeseed meal a more versatile feed component for these animals (Brenes *et al.*, 2004).

Despite their drawbacks, tannins can display several positive effects on animal and human health mainly as antioxidants (e.g. in cocoa, coffee, tea or legumes) preventing chronic diseases (e.g. cardiovascular, cancer, inflammation) or exhibiting more specific activities against bacterial or viral infections (Hassanpour *et al.*, 2011). Similarly, seed-coat tannins play important functions in protecting plants and seeds from oxidative damage caused by environmental factors (Troszyńska *et al.*, 2002) (Figure 3A).

Tannins have shown antipathogenic activities both *in vitro* and *in vivo* (e.g. by foliar application) by inhibiting a broad spectrum of microbial pathogens (Huang *et al.*, 2024). Additionally, a potential toxicity for herbivores has been suggested for these molecules. This activity is mainly linked to tannin oxidation, which can lead to the formation of semiquinone and quinone radicals, resulting in the production of reactive oxygen species (ROS) in the high-pH guts of insects (Barbehenn and Constabel, 2011).

In another work, Wang *et al.* (2012) showed an upregulation of the proteins involved in condensed tannins biosynthetic pathway in peanut (*Arachis hypogaea*) seeds infected by *Aspergillus flavus*. Peanut genotypes with darker, or more intensely coloured, seed coats also exhibited thicker seed coats, which were positively correlated with higher condensed tannin content and the inhibition of *A. flavus* development (Sanders and Mixon, 1979).

Glucosinolates in Brassicaceae seeds

Glucosinolates metabolites present both antinutritional (for humans) and beneficial/defensive (for humans/animals and plants) properties and their accumulation is known to be modulated by environmental stresses in the seeds of Brassicaceae species (Boutet *et al.*, 2022; Mácová *et al.*, 2022) (Figure 3B).

The unpleasant and antinutritional effects of GSLs are attributed to the bitter taste and toxicity of some of their degradation products, respectively (López-Moreno *et al.*, 2022; Salim *et al.*, 2023) (Figure 3B). Indeed, most GSLs are chemically and thermally stable but their hydrolysis products, such as thiocyanates, isothiocyanates (ITCs) and nitriles, are highly unstable and present strong biological activities (Salim *et al.*, 2023). Seeds of *B. napus* contain high levels of GSLs (100 µmol / g) (Di Gioia *et al.,* 2019).

Domestication and breeding efforts since the 1970s have aimed to reduce these levels (Di Gioia *et al.,* 2019). The Polish spring *B. napus* cultivar “Bronowski” was selected as a line with very low GSL levels in seeds and has been used as a genetic source to develop low-GSL rapeseed lines, including double-zero (low GSLs in seeds and zero erucic acid in the oil) rapeseed lines (Kondra and Stefansson, 1970). Toxic activities of GSLs are mostly attributed to thiocyanate ions, ITCs and oxazolidine-2-thiones. These GSL degradation products can interfere with thyroxine production by reducing the iodine supply to the thyroid (Di Gioia *et al.,* 2019).

In particular, the thiocyanate ion acts as a competitive inhibitor of the sodium/iodide transporter in thyroid cell membranes, potentially inducing hyperthyroidism (Dai *et al.*, 1996). Moreover, thiocyanate groups have been reported to contribute to bitter taste and interact with odour receptors (Wieczorek *et al.*, 2018) (Figure 3B). Progoitrin and its related degradation product, goitrin, are among the GSLs displaying the most severe health detrimental properties since they can induce goiter (Felker *et al.*, 2016; Di Gioia *et al.*, 2019). Some specific GSLs adversely affect taste and may also exhibit antinutritional or toxic properties. Nevertheless, generalisation across all GSL structures should be avoided, as some GSLs may offer beneficial properties for human and animal health.

For instance, several ITCs present anticancer, anti-inflammatory, and antipathogenic activities, and contribute to fight against many health disorders (Di Gioia *et al.*, 2019; Naveen and Rehna, 2019; Salim *et al.*, 2023). Sulforaphane and benzyl ITC, deriving from glucoraphanin GSL and glucotropaeolin GSL respectively, displayed strong anticancer activity (Clarke *et al.,* 2008; Xie *et al.*, 2017; Dinh *et al.*, 2021; Asif *et al.*, 2023).

Other ITCs showed chemopreventive activities, such as the 4-methylthiobutyl ITC, deriving from glucoerucin GSL, which can specifically induce cytotoxicity in tumor-initiating cells via the p53-independent pathway (Lamy *et al.*, 2013).

In recent decades, targeted breeding and molecular strategies have aimed to reduce toxic or unpalatable GSLs in Brassicaceae seeds, while preserving or enhancing the beneficial GSLs with health-promoting or defence-inducing properties. For instance, 5C aliphatic GSLs have been reduced in seeds of *B. napus* by crossing a cultivar with a Chinese cabbage line (*B. oleracea*) that presents a non-functional GSL-ELONG gene (Hirani *et al.*, 2013).

Reduction of the detrimental progoitrin levels while increasing the beneficial glucoraphanin levels has also been achieved in *B. napus* seeds by using RNA interference (RNAi) using GS-ALK (homologous of *A. thaliana AOP2* gene) from *B. oleracea* (Liu *et al.*, 2012). Moreover, the mutation of the glucosinolate transporter (*GTR*) genes, which are involved in the import of GSLs into seeds from maternal vegetative tissues, prevented the accumulation of GSLs in *A. thaliana*, *C. sativa*, *B. rapa* and *B. juncea* seeds (Nour-Eldin *et al.*, 2012; Nour-Eldin *et al.*, 2017; Hölzl *et al.*, 2023). Hence, this strategy allowed the maintenance of high levels of defensive GSLs in the vegetative parts, while reducing their content in seeds intended for industrial use.

A wide range of antipathogenic activities has been associated with GSLs and their degradation products (e.g. ITC), making these compounds good candidates as biocontrol solutions (Figure 3B). The methylated/methoxylated indole GSL 4-methoxyindole-3-ylmethyl GSL (4MOI3M) is involved in biotic stress response in Arabidopsis (Bednarek *et al.*, 2009; Tao *et al.*, 2022). Indeed, the myrosinase penetration2 (PEN2)-dependent breakdown products of 4MOI3M constitute antifungal defences in *A. thaliana* (Bednarek *et al.*, 2009). The enzymes responsible for 4MOI3M biosynthesis from 4-hydroxyindol-3-ylmethyl GSL (4OHI3M), namely indoleglucosinolate O-methyltransferase 1 (IGMT1) and indole-glucosinolate O-methyltransferase 2 (IGMT2), are induced in *A. thaliana* upon fungi infection. This is paralleled by the accumulation of the corresponding 4MOI3M metabolite and enhanced resistance to the pathogens (Tao *et al.*, 2022). Interestingly, Tao *et al.* (2022) suggested that due to the loss of camalexin biosynthesis in Brassica crops, the pathway producing 4MOI3M is crucial for *Alternaria brassicicola* resistance in Chinese kale (*Brassica oleracea* var. *alboglabra* Bailey).

Differently, *igmt5* mutants, impaired in 1-methoxyindol-3-ylmethyl GSL (1MOI3M) production from the O-methylation of 1-hydroxyindol-3-ylmethyl GSL (1OHI3M), displayed an enhanced resistance against the root-knot nematode *Meloidogyne javanica* (Pfalz *et al.,* 2016). The authors suggest that 1OHI3M and/or its derivatives have toxic and/or deterrent effects on nematodes and that its methylation could serve to avoid self-toxicity (Pfalz *et al.*, 2016).

Besides biotic factors, environmental conditions (Boutet *et al.*, 2022), agronomic practices and sulphur/nitrogen (S/N) nutrition (Rangkadilok *et al.*, 2004) strongly influence the accumulation of seed specialized metabolites, including GSLs.

Terpenoids, alkaloids and phytates in Leguminosae seeds

The presence of terpenoids, alkaloids, and phytates can limit the use of seeds due to their impact on taste or potential toxicity. Nevertheless, these compounds play a defensive role against bioagressors, thereby offering potential as biocontrol agents (Figure 3C).

Saponins are glycosylated terpenoid compounds with a core structure based on a steroid or triterpenoid aglycone (composed of 6 isoprene units and 30 carbon atoms) (Moses *et al.*, 2014) (Figure 1). Saponins affect the nutritional value of legume seeds by being poorly absorbed in the gut and by inhibiting key digestive enzymes (Navarro del Hierro *et al.*, 2018) (Figure 3C). In addition, the presence of saponins can alter seed organoleptic quality by increasing their bitterness (Heng *et al.*, 2006 ; Vernoud *et al.*, 2021) (Figure 3C). However, saponins may also offer health benefit, such as lowering cholesterol and potentially reducing the risk of cardiovascular disease (Marrelli *et al.*, 2016 ; Singh *et al.*, 2017 ; Singh, 2017). In plant species, saponins give a substantial contribution to resistance against herbivores making them good candidates as biocontrol agents. Indeed, similarly to what has been observed for humans, saponins are associated with digestibility issues in insects. Some studies indicated that aglycone saponins, but not their glycosylated forms, increased insect mortality by reducing food intake and disrupting intestinal transit (Adel *et al.,* 2000 ; Taylor *et al.*, 2004) (Figure 3C). In insects, these compounds can form complexes with cholesterol, thereby hindering digestion by blocking sterol absorption and disrupting moulting and ecdysis (replacement of the cuticle) (De Geyter *et al.,* 2007 ; Adel *et al.*, 2000 ; Taylor *et al.*, 2004).

In lupin species, QAs have been associated to the bitterness of seeds. These compounds account for approximately 1 % of the seed dry weight (Hama and Strobel, 2019). Low-QA varieties, known as “alkaloid-free lupin” or “sweet lupin”, have been developed to enhance their organoleptic qualities (Iqbal *et al.*, 2020). However, these varieties are more susceptible to generalist aphids (e.g., *Myzus persicae*), which preferentially feed on the phloem of “sweet lupins” rather than QAs-rich lupins, a pattern observed with other sap-sucking insects as well. Furthermore, other pests, such as rabbits and leaf miners, also avoid QAs-rich lupins (Hartmann, 1988; Zou *et al.*, 2020). These alkaloids are toxic to many pests, affecting their nervous system (Wink *et al.*, 1998). Consequently, the improvement in the taste of lupins has been accompanied by increased vulnerability to pests, highlighting the importance of balancing quality and stress resistance to ensure agricultural and food security.

In plant seeds, most phosphorus is stored as phytic acid (inositol hexaphosphate, IP6), a molecule that not only serves as a phosphorus reserve but also functions as a signalling compound involved in regulatory processes and stress responses during plant development (Sparvoli and Cominelli, 2015). Although not classified as a SM, phytic acid can exhibit properties and functions typically associated with these metabolites. In legumes such as common beans, over 95 % of phytic acid is concentrated in the cotyledons (Ariza-Nieto *et al.*, 2007). Phytates are considered as antinutritional compounds due to their ability to chelate essential mineral elements such as iron, zinc, and calcium, thereby reducing their bioavailability in the gastrointestinal tract

(Silva and Bracarense, 2016). Additionally, they inhibit key digestive enzymes, including pepsin and amylase, potentially impairing nutrient absorption (Kumar *et al.,* 2010). Phytates also provide significant benefits thanks to their antioxidant, anticancer and antipathogenic activities (Kumar *et al.*, 2010; Silva and Bracarense, 2016). Furthermore, the antioxidant properties of IP6 may protect seeds by chelating reactive metal ions and reducing oxidative stress, as demonstrated by its ability to inhibit hydroxyl radical formation (Graf and Eaton, 1990).

Conclusion and perspectives

As highlighted in this review, seed SMs play a crucial role in protecting plants and seeds against biotic and abiotic stresses, while also exhibiting biological activities that can have both positive or negative effects on human and animal nutrition and health. These compounds indeed also impact the organoleptic quality of food and feed, and affect nutrient bioavailability, for example, by reducing nutrient or protein intake, absorption, and utilization (Salim *et al.*, 2023). These dual roles of SMs are summarized in Figure 3, which illustrates their involvement in both seed defence and nutritional outcomes.

Tannins, GSLs and their degradation products, phytic acid, saponins, and alkaloids are among the main antinutritional (for human and animal nutrition) and defensive (for plants and seeds) compounds found in the seeds of Brassicaceae and/or Leguminosae species.

Numerous studies have highlighted that environmental conditions strongly influence the production and accumulation of SMs in seeds (Boutet *et al.*, 2022; Mácová *et al.,* 2022; Parker *et al.*, 2024). In the current context of climate change, it is crucial to elucidate the impact of environmental factors, such as high temperatures, water deprivation, or elevated atmospheric CO_2 levels, on the synthesis, modification, transport, and degradation of SMs, particularly those having some impacts on human and animal nutrition and health. In this light, it is essential to evaluate and study SM plasticity (i.e., environmental influence), their distribution at the tissue level and their biological activities to determine whether they act as antinutritional and/or beneficial compounds. This information, combined with various omic data, including transcriptomics, proteomics, and metabolomics, could help identify the genes and pathways involved in SM accumulation. While the use of gene editing in agriculture remains controversial, especially in Europe, biotechnological approaches to modulate SM content in seeds provide a proof of concept for future breeding programs. Once validated through genome engineering-based biotechnology, these traits can be introgressed into elite lines using conventional breeding methods, albeit over extended timeframes.

Finally, these insights open the door to innovative solutions, including the development of biocontrol and biostimulation strategies that enhance seed and plant performance, while preserving product quality for feed and food.

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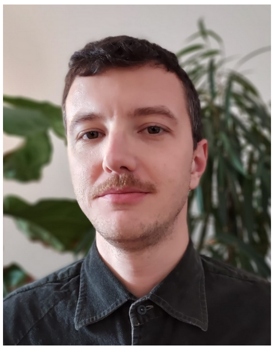

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