nutraceuticals

Review

Plant Seed Mucilage—Great Potential for Sticky Matter

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Abstract: Some seeds of flowering plants can differentiate their seed coat epidermis into the specialized cell layer producing a hydrophilic mucilage with several ecological functions, such as seed hydration, protection, spatial fixation, stimulation of metabolic activity and development of seed. Due to the species- and genotype-dependent variabilities in the chemical composition of mucilage, mucilage does not display the same functional properties and its role depends on the respective species and environment. Mucilaginous substances, depending on their composition, exhibit many preventive and curative effects for human and animal health, which has significant potential in the agricultural, food, cosmetic and pharmaceutical industries. This paper summarizes the ecological, biological, and functional properties of mucilaginous plant substances and highlights their significant nutritional potential in terms of the development of functional foods, and nutraceuticals and dietary supplements. A paragraph describing the gene regulation of seed mucilage synthesis is included, and some recommendations for the direction of further research on mucilaginous substances are outlined.

Keywords: mucilages; ecological functions; human and animal health-promoting properties; application in agriculture; genes; nutritional components

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1. Introduction

Some plants are characterized by producing a large quantity of various above- and below-ground secretions called mucilages or exudates. These can be secreted by roots, leaves, stems, or seeds, and perform different functions depending on the plant species [1]. Myxodiaspores are plants with the ability to initiate the differentiation of seed coat epidermis into the specialized cell layer upon fertilization, which synthesizes hydrophilic mucilage in the Golgi apparatus. Subsequently, the mucilage is secreted into the apoplastic compartment via secretory vesicles [2,3]. The mucilage forms a shell around the seed in the form of a gel-like transparent capsule, which represents a kind of modified cell wall with all typical polysaccharides, i.e., celluloses, pectins and hemicelluloses. Examples of plants with seeds that produce mucilage include *Arabidopsis thaliana* L., *Ocimum basilicum* L., *Lepidium sativum* L., *Salvia sclarea* L., *Artemisia annua* L., *Linum usitatissimum* L. and *Artemisia leucodes* Schrenk [4,5].

2. Methodology

We used the keywords (seed mucilage) to query the PubMed® database https://pubmed.ncbi.nlm.nih.gov/ (accessed on 24 May 2022), and the query returned a total of 528 search results. Since 1999, we have been observing a linear increase in the number of articles on this topic, with a few exceptions. The first article on seed mucilage was written in 1932, and the highest number of articles on seed mucilage was published in 2021 (70), which only confirms the current trend of increasing interest in this functional food ingredient. In our research, we tried to link the already established knowledge on plant seed mucilage with new information. In total, 92 articles related to plant seed mucilage were used, with 41 of these being less than 5 years old. Three articles were written in 2022, thirteen in 2021, five in 2020, nine in 2019 and eleven in 2018.

3. Ecological Functions of Mucilage

Mucilaginous substances have several ecological functions for plants (Figure 1), including seed hydration and protection from desiccation and spatial fixation in the soil, which affects their topochory, epizoochory, endozoochory and hydrochory. In addition, they maintain the metabolic activity of the seed and encourage its development. Mucilage contains substances that serve as a source of energy for the seeds and microorganisms in the soil. The exact role of mucilage seems to depend on the species and environmental context [3,6]. *Eragostris pilosa* (L.) BEAUV. seeds produce mucilage that allows them to survive in dry habitats. Their mucilage consists of pectins that form uniform layers on the inner surface of the cell walls, which are bounded by a thin layer of cellulose preventing them from being released into the cell lumen. In the presence of water, these pectins are hydrated and cause the mucilage cells to swell up. Subsequently, they start to detach. The aforementioned ability of Eragostris creates suitable conditions for germination [7]. Similarly, even the seeds of *Henophyton deserti* COSS. & DUR. are drought resistant. Mucilage represents 30% of the seed mass in this species. It can increase the weight of seeds by up to 550%. It has been shown that the mucilage of *H. deserti* works as a physical barrier in the regulation of the diffusion of water and oxygen into the inner seed coat. With this mechanism, it can prevent germination from occurring in unsuitable conditions. It was proved experimentally that higher concentrations of PEG inhibit mucilage hydration, but salt concentration has no effect on it. Mucilage reduces both the percentage and rate of seed germination, especially at 10 °C, and at high concentrations of NaCl and PEG [8]. The ability of mucilage to reduce germination under mild osmotic stress and subsequently to assist germination once this stress is relieved has also been confirmed in *Nepeta micrantha* BUNGE [9]. In addition to drought, plant survival on the desert dunes also depends on the burial depth in the sand. In the experiments conducted with the *Artemisia sphaerocephala* KRASCH. seeds, it was found that mucilage significantly increased seed emergence at a 0.5 and 10 mm burial depth under low irrigation, at a 0 and 5 mm burial depth under medium irrigation, and at a 0 and 10 mm burial depth under high irrigation. Seed mucilage also reduced seed mortality at shallow sand burial depths [10]. In addition, seed mucilage increased the surface dislocation force, allowing the seeds to anchor in highly erosive soils. When mucilage seeds from 52 plant species varying in their characteristics were tested, it was found that the largest effect on the resistance to water flow during erosion is due to the mucilage mass. Moreover, resistance to flow was largely dependent on the water flow speed and the rate of seed germination [11]. When mucilage is released from the seed, various particles of sand and dirt adhere to the seeds and remain on the seed surface after drying. This leads to the formation of a physical barrier that protects the seeds from predators (e.g., ants) [12]. Mucilaginous substances also affect seed germination. In optimal laboratory conditions, the difference between mucilaginous seeds (s1) and seeds with the mucilage removed (s2) was only in the germination rate (s1: 97% germination after 26 h; s2: 63% germination after 26 h). When exposed to salt stress, the s1 seeds germinated up to 48% more than the s2 seeds [13]. This may also be due to the presence of some enzymes in the mucilage that may assist in breaking the radicle envelope of the seeds, whereas demucilaged seeds do not contain such apoplast enzymes. Examples of such enzymes include pectinases, β-D-xylosidases and α-L-arabinofuranosidases, which are found in the mucilage of flaxseed [5,14].

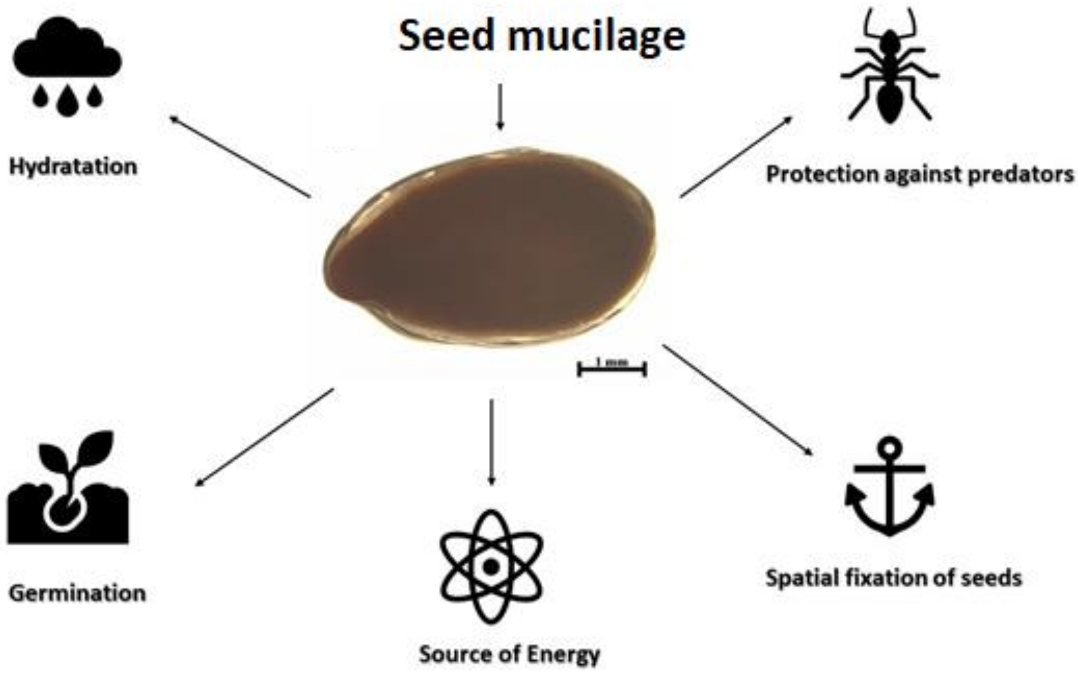

Figure 1. Ecological functions of mucilage (Kučka, elaborated based on [3–14].

4. Effects of Mucilage on Human and Animal Health

Depending on the composition, mucilaginous substances can exhibit antihypercholesterolemic, laxative and anticarcinogenic effects, and also have an effect on glucose metabolism. These effects help to prevent, or at least reduce, the risk of various major diseases such as diabetes, lupus nephritis, arteriosclerosis and hormone-dependent cancers [15–18]. *Cordia dichotoma* G. FORST. seed mucilage has been investigated for its antihypercholesterolemic effects. The study used rats, which were on a high-lipid diet, resulting in a significant increase in total cholesterol and low-density lipoprotein cholesterol, as well as in a significant decrease in antioxidant enzymes in the liver (glutathione reductase, glutathione peroxidase, glutathione-S-transferase, catalase and superoxide dismutase). Treatment with the *C. dichotoma* mucilage at a 0.5 and 1g per kg not only improved the lipid profile, but it also improved the liver and kidney function, even in the rats on a normal diet. Additionally, the antioxidant system in the liver was also improved [15]. The mucilage from *Abelmoschus esculentus* (L.) MOENCH, in addition to its antihypercholesterolemic effects, also had an effect on glucose levels when abnormal changes in body weight, water consumption, feed consumption and blood glucose levels occurred after 3 weeks of mucilage administration to alloxan-induced diabetic mice. At baseline, all mice had fasting blood glucose levels of approximately 4.1 mmol$\cdot$L^{-1}. After the induction of alloxan, the blood glucose concentration increased to 12.3 $\pm$ 0.8 mmol$\cdot$L^{-1} in one group and to 13.1 $\pm$ 0.8 mmol$\cdot$L^{-1} in the other group. After the administration of 150 mg per kg of mucilage to the first group, the blood glucose level decreased to 7.1 $\pm$ 0.4 mmol$\cdot$L^{-1} after three weeks, and in the second group the level decreased to 6.7 $\pm$ 0.4 mmol$\cdot$L^{-1} [18] after the administration of 200 mg per kg of mucilage. The laxative activities of flaxseed mucilage and oil have also been investigated. Flaxseed mucilage had laxative effects at doses of 1 and 2.5 g$\cdot$kg^{-1} with the resulting percentage increase of 65.06 $\pm$ 6.5% and 89.33 $\pm$ 4.04% in wet feces. The spasmogenic effect of flaxseed mucilage was completely blocked in the presence of atropine and partially blocked (63.9%) in the presence of pyrilamine. The laxative effect of both flaxseed mucilage and oil is probably mediated by the stimulation of cholinergic and histaminergic receptors, with a more pronounced cholinergic component in flaxseed mucilage [19]. Mucilage also exhibits anti-inflammatory and antioxidant effects, and the mucilage from fenugreek seeds showed a beneficial effect against rat arthritis when induced by intradermal injection of complete Freund's adjuvant. The maximum rate of edema inhibition was observed at a mucilage dose of 75 mg·kg^{-1} on the 21st day of adjuvant arthritis. After the treatment with mucilage from fenugreek seeds, the activity of inflammatory enzymes (cyclooxygenase-2 and myeloperoxidase) as well as the concentrations of thiobarbituric acid reactive substance decreased. On the other hand, there was an increase in the activity of antioxidant enzymes (catalase, superoxide dismutase, glutathione peroxidase), the levels of glutathione and vitamin C and lipid peroxidation. Additionally, the erythrocyte sedimentation rate and total white blood cell count increased significantly [20]. In addition, the prebiotic effect of chia mucilage, which is mainly due to the neutral mucilage polysaccharides, has been demonstrated. Compared to the low molecular weight prebiotics, the growth of some groups of intestinal bacteria, such as *Enterococcus* and *Lactobacillus*, is more delayed on mucilage but it lasts longer. The effects of chia mucilage at three different concentrations (0.3, 0.5 and 0.8%) on the growth and metabolic activity of human gut microbiota using the Simgi® dynamic gastrointestinal model have also been investigated. The researchers found that all mucilage concentrations significantly affected all bacterial groups of the gut microbiota, but the 0.3% concentration of chia mucilage had the most significant effect on the increase in total aerobes in the transverse colon and descending colon. Increases were also observed for lactic acid bacteria, *Enterococcus* spp. and *Staphylococcus* spp., and in contrast, no significant changes were observed for *Enterobacteriaceae*, *Clostridium* spp. and *Bifidobacterium* spp. By providing a substrate for the microorganisms, the chia mucilage also affects the resulting fermentation products, such as short-chain fatty acids (SCFAs). In the experiment, different values of SCFAs (acetic, propionic and butyric acid) were observed at different concentrations of chia mucilage, and the dependence of SCFA production on different parts of the gut was also observed. In the ascending colon, the greatest increase was observed on day 5 at a 0.5% concentration of chia mucilage, while in the transverse and descending colon, the increase was observed mainly on day 3 after the administration of chia mucilage. However, an increase was also observed in the transverse and descending colon on day 5 and day 8 at a 0.8% and 0.5% chia mucilage [21,22]. Recent studies suggest that flaxseed mucilage also exhibits antibacterial activity against several Gram-positive and Gram-negative bacteria using the agar well diffusion method and disk diffusion method. Mucilage showed strong antibacterial properties against all strains tested except *Listeria monocytogenes* [23]. There was also a potential to improve the course of chronic obstructive pulmonary diseases when the Pharmacopeial Unani formulation: linctus of flax mucilage [24] was used as the test drug. In Iranian traditional medicine, mucilage from quince seeds is used to treat skin wounds and burns. In a study on mucilage in rabbits, it was concluded that mucilage from quince seeds increases the level of growth factors in the wound fluids are involved in tissue repair, and therefore has good potential to promote wound healing at a 10–20% concentration [25]. The healing effects against the T-2 toxin-induced dermal toxicity in rabbits has also been demonstrated for mucilage obtained from quince seeds. This mucilage probably preserves the wound surface proteins whose synthesis is inhibited by the T-2 toxin. In addition, it is thought to act as a barrier against microorganisms and may also activate the growth factors and thereby facilitate skin healing [26]. In medicine, there is potential to use mucilage as a polymer capable of retaining water, for example, for wound dressings. An antibacterial wound dressing was prepared by the lyophilization of basil mucilage and with the addition of the antibacterial agent zinc oxide nanoparticles (ZnO-NPs). Hydrogen bonding and electrostatic interaction were confirmed between the slime and ZnO-NPs molecules. The resulting product was non-adhesive and non-toxic, with reasonable mechanical and thermal properties, which were further enhanced by the addition of ZnO to promote antibacterial capabilities. It was confirmed that the porosity, swelling and water retention of the product were suitable for use as a wound dressing. Due to its good porosity, basil mucilage gel is able to absorb a high volume of exudate from the wound surface. Water retention capacity is one of the most important properties of wound dressing because it allows the holding of water molecules within its structure.

The addition of ZnO-NPs slightly decreases porosity and swelling, but slightly increases water retention [27]. Mucilage has the potential to be used as a superdisintegrant in the production of pharmaceutical tablets by direct compression with other excipients and in wet granulation technology where the mucilage from basil seeds *(Ocimum basilicum* L.) was successfully used to produce the drug metoprolol tartarate [28]. Similarly, mucilage from plantain (*Plantago psyllium* L.) at a 3% (*w*/*w*) concentration can also be used as a drug binder. Studies indicate that paracetamol with this formulation is released more slowly than the traditional drug [29]. The *Ocimum basilicum* L. seed mucilage can also be used as a nasal gel containing paracetamol [30]. The mucilage from the seeds of *Lallemantia royleana* (Benth.) itself exhibits analgesic effects, and was used to create a mixture of commercial 2% lidocaine gel and a mucilage-containing gel (0.01 g·ml^{-1}), which increased the efficacy of this local anesthetic [31].

5. Potential Uses of Mucilage in Agriculture and Industry

Mucilaginous substances have potential in agriculture, food, cosmetics and pharmaceutical industries (Table 1) [32]. In the food industry, chia mucilage can be used as a low-fat source of fiber. The addition of 7.5% chia seed mucilage to a yogurt recipe reduced the degree of syneresis during storage compared to full-fat yogurt and improved the nutritional value of the yogurt by increasing the fiber content. In addition, the resulting yogurt had a higher consistency, firmness, viscosity and better resistance to stress. The sensory acceptability of the resulting yogurts in terms of acidity, creaminess and viscosity was similar to full-fat yogurts [33]. Similarly, the addition of flaxseed mucilage increased the viscosity and decreased yogurt syneresis. In addition, it decreased the cohesiveness and increased the stickiness of the blended yogurt, while its addition in combination with carboxymethylcellulose resulted in decreased stickiness, increased cohesiveness and elasticity. The mucilage of flax with the addition of carboxymethylcellulose resulted in an increase in *Lactobacillus bulgaricus* in the blended yogurt, although the addition of mucilage alone had little effect on the growth of this lactic bacterium. On the other hand, the addition of mucilage itself had a considerable effect on the growth of *Streptococcus thermophilus* [34]. The mucilage from chia seeds can serve as a substitution for some oil in mayonnaise, thus increasing its stability, textural parameters and reducing the amount of fats [35]. Similarly, the addition of chia mucilage to pie dough reduces the fat content and increases fiber and protein contents [36], and some studies have shown that chia mucilage can replace emulsifiers and stabilizers in the preparation of ice cream [37]. Mucilage can also be used to encapsulate important substances, such as probiotics, which can improve the functional properties of food. It has been shown that quince seed mucilage is able to increase the survival rate of *Lactobacillus rhamnosus* up to 72 °C by encapsulation, and is also suitable as a transport matrix in the gastrointestinal environment when the bacteria are released at an appropriate time after reaching the intestinal tract [38]. The mucilage and soluble proteins from chia and flax seeds can be used as encapsulating material for two probiotic bacteria: *Bifidobacterium infantis* and *Lactobacillus plantarum* [39]. Using the electrospinning method, it was possible to incorporate the flavonoid hesperetin into basil mucilage nanofibers in conjunction with polyvinyl alcohol. After a successful encapsulation, there was an increase in resistance to high temperatures (from 182 °C to 314 °C) and a decrease in their release rate in acidic environments (pH 1.2) [40]. Vitamin A was also encapsulated by a similar principle using watercress seed mucilage and polyvinyl alcohol. Again, its stability in acidic environments and against high temperatures was enhanced [41]. Last but not least, mucilage can be used to produce biodegradable and antimicrobial edible films that increase the shelf life of food. Films made out of the psyllium seed mucilage, oregano extract and glycerol as a plasticizer had effective antimicrobial activities against *Staphylococcus aureus* and *Escherichia coli* and extended the postharvest shelf life of strawberries to 16 days [42].

Table 1. Application of mucilage in industry and agriculture.

Application Area	Plant Source	Applied Form	Achieved Properties	Reference
Food industry	*Salvia hispanica* L., *Linum usitatissimum* L.	Additive in yogurts	Improved nutritional properties, syneresis and viscosity	Refs. [33,34]
	Salvia hispanica L.	Additive in mayonnaise	Increased stability, reducing fat	Ref. [35]
	Salvia hispanica L.	Additive in cakes	Improved nutritional qualities	Ref. [36]
	Salvia hispanica L.	Additive in ice cream	Replacement for stabilizers and emulsifiers	Ref. [37]
	Salvia hispanica L. *Linum usitatissimum* L. *Cydonia oblonga* MILLER	Encapsulation of probiotics	Better resistance in the digestive tract	Refs. [38,39]
	Ocimum basilicum L. *Lepidium sativum* L.	Encapsulation of vitamins and flavonoids	Better resistance in the digestive tract	Refs. [40,41]
	Plantago psyllium L.	Production of edible films	Increased food shelf life	Ref. [42]
Pharmaceutical industry	*Lallemantia royleana* (BENTH.)	Formation of gels	Healing effects against dermal toxicity and burns	Ref. [31]
	Ocimum basilicum L.	Wound dressing formation	Antimicrobial effects	Ref. [27]
	Ocimum basilicum L. *Plantago psyllium* L.	Formation of medicinal tablets	Slower release, replacement of chemical preparations	Refs. [28,29]
	Ocimum basilicum L.	Formation of nasal gel	Analgesic effects	Ref. [30]
Cosmetics	*Salvia hispanica* L.	Gel formation	UV-protective effects	Ref. [43]
Agriculture	*Salvia hispanica* L.	Hydrogels in arid areas	Retention of water	Refs. [44,45]
Engineering industry	*Linum usitatissimum* L.	Biocomposite binder	Inexpensive and biocompound	Ref. [46]

In cosmetics, chia seed mucilage has promising potential due to its high photostability under UV light and muco-adhesion, which promotes the adhesion of the formulation to the mucosa [43]. In agriculture, mucilage can be used as a hydrogel that retains water in the rhizosphere, which, in addition, reduces surface tension and increases soil viscosity and the hysteresis index [44]. Therefore, it is potentially possible to use mucilage for plant growth in arid deserts [45]. In the industry, mucilage is used as a binder for biocomposite materials in which plant fibers serve as a reinforcing component [46].

6. Physical and Chemical Properties of Mucilage

As a natural product, the composition of mucilage can vary in space and time depending on a variety of external and internal conditions [47]. In addition, there are also significant variations in the chemical composition and functional properties of mucilage among different plant species and varieties (Table 2) [48]. In general, the seed mucilage of different plants is mainly composed of polysaccharides. Mucilaginous polysaccharides are a source of energy for microorganisms, absorb water, exchange cations and allow the plant to adhere to solid surfaces in the rhizosphere [49]. The composition of polysaccharides is mainly influenced by the enzymes secreted by the plant during water imbibition along with mucilage [5]. The mucilage coat of myxodiaspores seeds represents a modified cell wall. Chemically, it is mainly composed of the polysaccharide groups typical for the cell wall, mainly hemicelluloses (cellulose type of mucilage—e.g., *Neopallasia pectinata* (PALL.) POLJAKOV), but very often pectins are the main component (pectin type of mucilage—e.g., *Linum usitatissimum* L.) [50]. The flax mucilage of the Eden cultivar mainly consists of rhamnogalacturonan-I (52–62%), which is influenced by the enzymes rhamnogalacturonase and β-d-galactosidase, and arabinoxylan (27–36%), which is related to the activity of the enzymes α-l-arabinofuranosidase, β-d-xylosidase and β-xylanase. The highest value of xylanase activity was observed after 4 h of seed hydration, resulting in the low viscosity of the polysaccharides, which mainly contained pectic sugars. Maximum glycosidase activities were observed 24 to 48 hours after the application of water hydration, and mucilaginous substances, which were tightly bound to the cell walls, were released. The presence of β-d xylosidase and α-l-arabinofuranosidase activities was also confirmed [5]. By their high molecular weight, the polysaccharides of linseed mucilage represent about 3 to 9% of the total weight of the seed and are divided into two components: neutral and acidic. The neutral component is composed of D-xylose, L-arabinose and D-galactose in a ratio of 6.2:3.5:1, while the acidic component contains L-rhamnose, L-fucose, L-galactose and D-galacturonic acid in a ratio of 2.6:1:1.4:1.7 [48,51]. On average, flax varieties with yellow seeds were found to have a higher content of neutral polysaccharides (arabinoxylans) due to the presence of the s1 gene, while brown seeds had a higher content of acidic polysaccharides (pectins) [52]. In addition to polysaccharides, they also contain glycoproteins and various bioactive components, such as tannins, alkaloids and steroids to a lesser extent [32,49,53]. The main constituent of the mucilage of *Lepidium perfoliatum* L. species is the highly methyl esterified homogalacturonan (HG). In addition, a significant amount of callose and hemicellulose and a small amount of weakly methyl esterified HG were present in the seed coat mucilage of *L. perfoliatum* L. [2]. *Lallemantia royleana* (BENTH.) seed mucilage, similar to other mucilage, is mainly composed of carbohydrates (76.74%), of which the most abundant monosaccharides are galactose (36.28%) and arabinose (35.96%). The less abundant monosaccharides are rhamnose (15.18%), xylose (7.38%) and glucose (5.20%). In addition to carbohydrates, the mucilage of *L. royleana* (BENTH.) seeds is also composed of protein (3,86%), ash (9,92%) and moisture (9,48%). Overall, it contains 82.56 ± 1.6 µg GAE/mg of phenolic compounds [54]. A similar polysaccharide content of *Lallemantia royleana* (BENTH.) mucilage (Figure 2) was also determined by [55]. The researchers observed that *Lallemantia royleana* (BENTH.) mucilage consisted of arabinose (37.88%), galactose (33.54%), rhamnose (18.44%), xylose (6.02%) and glucose (4.11%) [55]. The mucilage from basil is mainly composed of high-molecular-weight polysaccharides (2320 kDa), which consist of glucose, galactose, mannose, arabinose, xylose and rhamnose. The polysaccharides of basil mucilage are slightly acidic due to the presence of uronic acid (6.51%) [56]. Chia seed mucilage contains 93.8% carbohydrates, which form the following monosaccharide units: xylose, glucose, arabinose, galactose, glucuronic acid and galacturonic acid [57]. These subsequently form D-xylosyl and D-glucosyl residues in a 2:1 ratio. Additionally, it contains 22 to 25% 4-0-methyl-D-glucuronopyranosyl residues. The acetates of xylitol, glucitol and 4-O-methylglucitol are present in a ratio of 8:4:3. Another component of the polymer is 4-O-methyl-D-glucuronic acid [58]. The mucilage from the seeds of *Hyptis suaveolens* L. contains acidic and neutral heteropolysaccharides in a ratio of approximately 1:1. The neutral polysaccharides are composed of galactose, glucose and mannose, which form the polysaccharides galactoglucan (30%) and galactoglucomannan (70%), while the acidic polysaccharides contain residues of fucose, xylose and 4-O-methylglucuronic acid [21,59]. The total carbohydrate content of watercress mucilage is 87.4%, of which the most abundant carbohydrates are mannose (38.9%), arabinose (19.4%), galacturonic acid (8.0%), fructose (6.8%), glucuronic acid (6.7%), galactose (4.7%), rhamnose (1.9%) and glucose (1.0%) [60].

Table 2. Carbohydrate composition of some seed mucilages.

Plant Source of Seed Mucilage	Carbohydrates	Reference
Linum usitatissimum L.	Rhamnogalacturonan and arabinoxylan	Ref. [5]
Linum usitatissimum L.	D-xylose, L-arabinose, D-galactose, L-ramnose, L-fucose, L-galactose, D-galacturonic acid	Ref. [51]
Lepidium perfoliatum L.	Methylesterified homogalacturonan, callose, hemicellulose	Ref. [2]
Lallemantia royleana BENTH.	Galactose, arabinose, rhamnose, xylose, glucose	Refs. [54,55]
Ocimum basilicum L.	Glucose, galactose, mannose, arabinose, xylose, rhamnose	Ref. [56]

Table 2. *Cont.*

Plant Source of Seed Mucilage	Carbohydrates	Reference
Salvia hispanica L.	Xylose, glucose, arabinose, galactose, glucuronic acid, galacturonic acid	Ref. [57]
Salvia hispanica L.	Residues of D-xylosyl, D-glucosyl, 4-0-methyl-D-glucuronopyranosyl	Ref. [58]
Hyptis suaveolens L.	Galactose, glucose, mannose, galactoglucan, galactoglucomannan, fucose, xylose, 4-O-methylglucuronic acid	Refs. [21,59]
Lepidium sativum L.	Mannose, arabinose, galacturonic acid, fructose, glucuronic acid, galactose, rhamnose, glucose	Ref. [60]

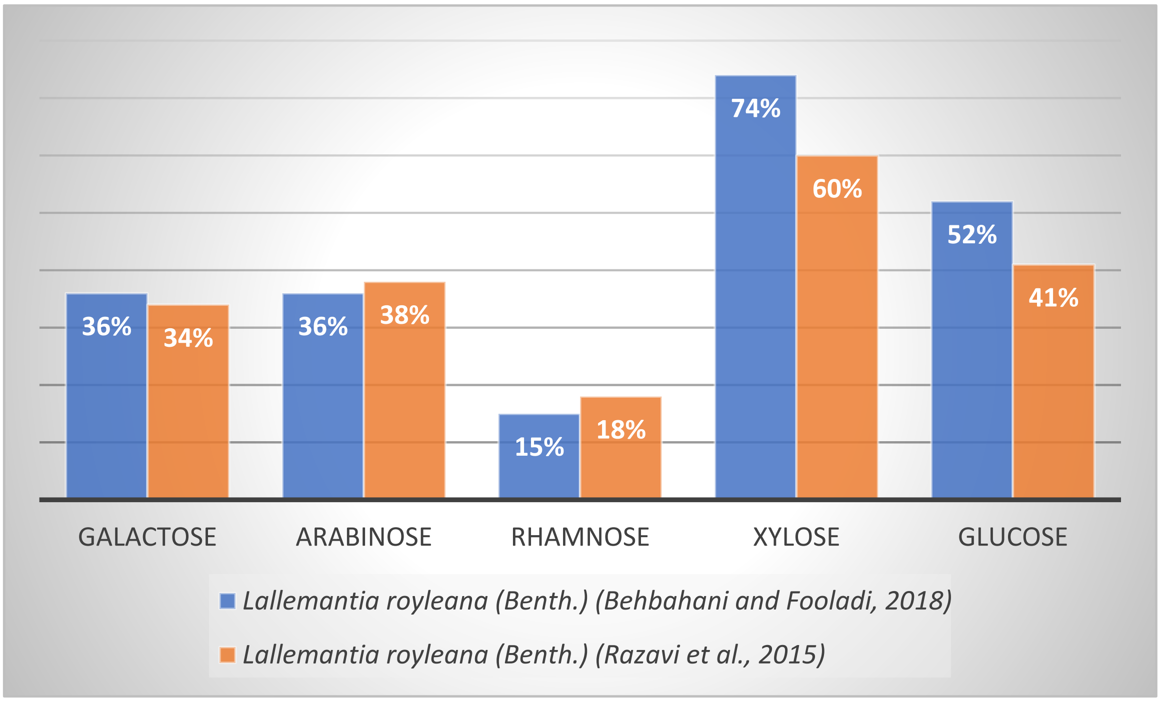

Figure 2. Difference in carbohydrate composition of *Lallemantia royleana* (BENTH.) seed mucilage between two studies [54,55].

When comparing the mucilage from several plants, it was observed that the lipid content of mucilage generally tended to be low. For example, the lipid content in the mucilage of yellow mustard was only 0.2%, 0.5 to 0.7% in flax, 4.76% in tamarind and 1.85% in watercress seeds. However, mucilage lipids provide important functions for the plant, improving their water uptake and desorbing the adsorbed phosphorus on the soil particles in the rhizosphere. The amount of protein varies considerably from plant to plant, with Indian plantain seed mucilage containing 0,94% protein, *Artemisia sphaerocephala* (KRASCH.) mucilage up to 24,1%, tamarind seed mucilage 14,78% and linseed mucilage having a protein content of between 4,4 and 15,1%. Mucilage proteins break down mucilage polysaccharides into the forms available to microorganisms, they respond to biotic and abiotic stresses, and mobilize nutrients in the rhizosphere [49,53,61]. An average mineral content of plant mucilage is 5.6% and they are also important in the exchange of cations between the plant and the rhizosphere and improve the coupling of the liquid phase of the soil with the water content [49]. Altogether, six chemical elements—copper, zinc, cobalt, lead, chromium, chromium and cadmium—have been detected in the mucilage of flaxseed [48]. The most abundant chemical element in cress mucilage is calcium (0.17%), but it also contains sodium, potassium and magnesium [60].

Although the chemical composition of mucilage is well known, its structural organization is unclear. The fibrillar character of the individual mucilage components is demonstrated by both the pectic and cellulosic types of mucilage. However, due to the presence of cellulose microfibrils, cellulose mucilage is much more organized [50]. Using critical point drying (CPD) and scanning electron microscopy (SEM), the structural details of mucilage were resolved down to the nanoscale. The mucilaginous fibrillar components generally form a network of cellulose fibers that serve as a scaffold for other polysaccharide fibers, which often branch out and are found between or on the surface of the cellulose fibers. The cellulose fibrils are long, thick, unbranched and, by being attached to the surface of the seeds, prevent the loss of the mucilage cover by mechanical impact. Interestingly, the structural organization of mucilage varies among plant species, which is important for water binding and storage [4]. Pectic mucilage, on the other hand, has a fibrous, convoluted and more homogeneous structure than the cellulosic type [50].

7. Functional Properties of Plant Seed Mucilage

The mucilaginous substances of the plants are odorless, colorless and tasteless. In addition, they are non-toxic and biodegradable [32]. Mucilage can also exhibit good photostability; for example, mucilage obtained from the seeds of *Salvia hispanica* L. showed a degradation percentage of 6.6% after 120 min under UV light [43]. Three parameters in the extraction of mucilage have a great influence on the functional properties of mucilage—temperature, pH and water/seed ratio. It has been observed that the maximum values of extraction, viscosity, emulsion stability, foam stability, solubility and water absorption capacity (9.3 g/g) of the *Eruca sativa* MILL. seed mucilage could be achieved at an extraction temperature of 65.5 °C, pH 4 and a water-to-seed ratio of 60:1 [62].

A very important indicator of the quality of mucilage is its molecular weight because the polymer chains interact when the mucilage dissolves, and mucilage with a high molecular weight can improve its viscosity. This property can be used to improve the texture of foods and it also affects the mouthfeel of the consumer [63]. The molecular weight of mucilage also affects the emulsifying and foaming properties [64]. The mucilage of different plants has different molecular weights, for example, the mucilage from the seeds of *Hyptis suaveolens* L. contains an anionic fraction responsible for swelling and viscous behavior with an average molar mass of 0.35×10^6 g·mol^{-1}, while the neutral polysaccharide fraction (in a 1:1 ratio) exhibits an average molar mass of 0.047×10^6 g.mol^{-1} [59]. The neutral component of flaxseed mucilage has a lower molecular weight (1.47×10^6 g·mol^{-1}) than the acidic part (1851×10^6 g·mol^{-1}) [65]. The molecular weight of the *Lallemantia royleana* BENTH. in WALL. seed mucilage is 1.19×10^6 g·mol^{-1}, *Salvia hispanica* L. 2.3×10^6 g·mol^{-1}, and the molecular weight of the *Ocimum basilicum* L. seed is 2.32×10^6 g·mol^{-1} [54,66]. Another study of *Lallemantia royleana* BENTH. in WALL. seed mucilage showed that the molecular weight was 1.294×10^6 g·mol^{-1} [55].

The solubility of mucilage improves with increasing temperatures, where the lowest solubility values for flax mucilage were observed at 20 °C (24.52% to 30.95%) and the highest at 80 °C (64.5% to 69.15%) [48]. It was observed that the mucilage from both white and black chia seeds showed similar solubility values between 30 and 60 °C. Black chia seed mucilage showed the greatest solubility at 70 °C (80.65%), while the solubility of white chia seed mucilage remained constant [67]. The solubility of *Eruca sativa* MILL. at 65.5 °C was 28.5% [61] and the solubility of *Lepidium perfoliatum* L. seed mucilage was approximately 20% at 60 °C [68].

Furthermore, mucilage exhibits thermostable properties with high degradation temperatures, for example, tamarind seed mucilage starts to lose weight at 175 °C and chia seed mucilage at 244 °C [49,53]. Black chia seed mucilage has a higher thermal decomposition temperature (286.8 °C) than white chia seed mucilage (269.4 °C) [67].

Another property of mucilage is its ability to retain water, which is dependent on pore size, capillary action and the amount of protein components present in the mucilage. Flax mucilage has a higher water retention capacity compared to microbial xanthan mucilage and lower water retention capacity compared to plant guar mucilage [69]. The mucilage from the seeds of *Lepidium perfoliatum* L. showed a similar trend; the water absorption capacity (around 20 $g.g^{-1}$) was lower than guar but almost identical to xanthan. It is suggested that the lower water absorption rate by *L. perfoliatum* L. seed mucilage compared to guar is due to the strong degree of interaction between the polysaccharide chains and hence the lower interaction with water [68]. In tamarind seed mucilage, the water holding and oil retention capacities have been shown to increase with temperature [61]. The water absorption capacity of basil seed mucilage is higher (35.16–38.96 $g \cdot g^{-1}$) than its oil absorption capacity (5.40–17.38%) [70]. The water absorption capacity of chia seed mucilage is 54.24 ± 0.47 $g \cdot g^{-1}$ and the water holding capacity is greater (35.49 ± 0.24 $g \cdot g^{-1}$) than its oil holding capacity (7.72 ± 0.36 $g \cdot g^{-1}$) [67]. The water absorption capacity of *Eruca sativa* Mill. was 9.3 $g \cdot g^{-1}$ [62].

Mucilage proteins are characterized by their good foaming properties; foam stability increases with increasing the mucilage concentration. Chia seed mucilage has $96.5 \pm 1.6\%$ foam stability at a 0.1% concentration and $97.8 \pm 1.2\%$ at a 0.3% concentration [67]. Foam stabilization is also affected by the water/seed ratio (negatively) and temperature (positively) during mucilage extraction. Quince seed mucilage had a 94.89% emulsion stability and a 21.36% foam stability [71] and *Eruca sativa* Mill. mucilage had an emulsion stability of 87% and foam stability of 87.5% [62]. The foam stability of *Lepidium perfoliatum* L. seed gum also increased with increasing concentrations, but was lower compared to xanthan and guar gums at similar concentrations. This trend was probably due to the differences in viscosity of the continuation phase [68].

Mucilage can also form a cold-solidifying thermo-reversible gel. The strength of this gel is influenced by the dissolution temperature, pH and addition of minerals. With higher dissolution temperatures, the strength of the gel increases, and the addition of NaCl and complex phosphate salt decreases the strength. If we want to increase the strength, we can add $CaCl_2$ at a low concentration (<0.3 wt.%), and its strength decreases at higher concentrations [72]. The strength of *Hyptis suaveolens* (L.) Poit. seed mucilage gel also increased by the addition of sucrose (1, 3, 5, 10 and 20% *w/v*) to a 0.5% mucilage dispersion. This caused the gel to exhibit its shear-thinning behavior to a lesser extent, which had a stabilizing effect [73].

As the concentration of mucilage increases, its viscosity increases as well. The viscosity and elasticity are also influenced by chemical composition, with both variables increasing at a higher concentration of xylose and lower concentration of uronic acid. The viscosity of linseed mucilage ranges from 0.02 to 0.28 Pa·s, while the viscosity of basil seed mucilage ranges from 0.19 to 0.714 Pa·s. Depending on the variety and concentration, mucilage can behave as a viscous liquid, viscoelastic liquid or almost an elastic body [70,74]. The water/seed ratio during extraction had the highest effect on the viscosity of the quince seed mucilage, and increasing the extraction time at temperatures of up to 45 °C decreased the viscosity. Under optimum extraction conditions, the viscosity of the mucilage was 1.47396 Pa·s [71]. The viscosity of *Eruca sativa* Mill. in optimal conditions was 0.357 Pa·s [62]. The viscosity of the *Lepidium perfoliatum* L. seed gum decreased with the increasing shear rate. The highest viscosity (approximately 3 Pa·s) was noted at a shear rate of approximately 15 ($1 \cdot s^{-1}$). The comparison of the viscosity of *Lepidium perfoliatum* L. seed gum with other commercial gums with the same shear rate showed that the viscosity of this gum was higher than in locust beans, lower than in guar and almost identical to the viscosity of xanthan. As with other types of mucilage, increasing the concentration of the solution leads to an increase in the viscosity of *L. perfoliatum* seed mucilage, and increasing the temperature up to 65 °C leads to a decrease in viscosity. Interestingly, the addition of NaCl, KCl, $CaCl_2$ and $MgCl_2$ salts also influenced the viscosity of the mucilage, showing a rapid decrease in viscosity after the addition of 0.2% of any of the salts [68]. Although the mucilage from *Lallemantia royleana* Benth. exhibited a similar molecular weight to most seed mucilage, the intrinsic viscosity (23.06 $dL \cdot g^{-1}$) was higher [55].

8. Gene Regulation of Seed Mucilage Synthesis

The epidermal cells of plants that secrete mucilage are influenced by several genes during the development phase, leading to changes in their extracellular matrices. Most research has focused on the epidermal cell genes of *Arabidopsis thaliana* L. Research on the *COBRA-LIKE 2* (*COBL2*) gene, a member of the COBRA-LIKE gene family, found that it has a specialized function in maintaining a proper cellulose deposition in the seed mucilage [75]. Additionally, the MUM 2 gene, a member of glycosyl hydrolase family 35, was identified. Its localization is in the cell wall of *A. thaliana*, with the MUM 2 protein entering the apoplast via the endoplasmic reticulum and the Golgi apparatus network. Overall, the MUM2 gene exhibits β-galactosidase activity and has a negligible effect on the amount of mucilage produced or the seed morphology; on the other hand, it is essential for the proper structure of the produced mucilage [76]. The β-galactosidase activity of the MUM2 gene may also be complemented by the TESTA-ABUNDANT2 (TBA2), PEROXIDASE36 (PER36) and MUCILAGE-MODIFIED4 (MUM4) genes, and thus may be involved in modifying the polysaccharide composition of seed mucilage [77]. It was possible to isolate a sequence of 308 base pairs of the MUM4 gene that controls the expression of the reporter gene in both *A. thaliana* L. and *Camelina sativa* (L.) Crantz seed coat cells and is regulated by the same cascade of transcription factors as endogenous MUM4 [78]. KNAT3 and KNAT7, members of the KNOX class II gene family, act as positive regulators of the biosynthetic gene RG-I MUCILAGE-MODIFIED 4 (MUM4, AT1G53500) and thus affect the production of mucilage in *A. thaliana* L. at early developmental stages [79]. The mucilage from *A. thaliana* L. is mainly composed of rhamnogalacturonan I, the size of which is influenced by the MUCILAGE-RELATED70 (MUCI70) gene with glycosyltransferase activity. Additionally, the CuAOα1 gene encoding a putative copper amine oxidase of clade 1a affects the production of pectin and influences the amount of rhamnogalacturonan I in the outer mucilage layer [80]. The MUM1 gene in *A. thaliana* L. encodes the transcription factor LEUNIG_HOMOLOG (LUH), which is localized in the nucleus. According to the research, the LUH/MUM1 transcriptional activator could be a positive regulator of the gene-encoding enzymes required for the extrusion of mucilage—MUM2, SUBSILIN PROTEASE1.7 and β-XYLOSIDASE1 [81]. The *A. thaliana* L. gene GALACTURONOSYLTRANSFERASE-LIKE5 (AtGATL5), which is localized in both the endoplasmic reticulum and Golgi system, could also be involved in the regulation of the final size of mucilage rhamnogalacturonan I [82]. The *A. thaliana* L. UUAT1 gene encodes a protein localized in the Golgi apparatus that transports the UDP-glucuronic acid and UDP-galacturonic acid in vitro. UDP-glucuronic acid is a precursor of many seed mucilage polysaccharides and, after synthesis in the cytosol, it is transported to the Golgi apparatus lumen where it is converted to UDP-galacturonic acid, UDP-arabinose and UDP-xylose. This suggests that the UUAT1 gene has a key role in the composition of seed mucilage [83]. CELLULOSE SYNTHASE 5 (CESA5)/MUCILAGE-MODIFIED 3 (MUM3), MUM5/MUCI21, SALT-OVERLY SENSITIVE 5 (SOS5) and FEI2 gene influences the adherence of A. thaliana mucilage. While MUM5 and CESA5 act as synergists by providing the adhesion of pectin to the seed through cellulose and xylan biosynthesis, SOS5 and FEI2 encode an arabinogalactan protein [84]. The PECTIN METHYLESTERASE INHIBITOR6 gene promotes mucilage release in *A. thaliana* L. by inhibiting the activities of endogenous pectin methylesterase that demethylate homogalacturonan [85]. The genes *A. thaliana* L. TRANSPARENT TESTA 8, SUBTILISIN-LIKE SERINE PROTEASE, GALACTUROSYL TRANSFERASE-LIKE 5, MUCILAGE-MODIFIED 4, AGAMOUS-LIKE MADS-BOX PROTEIN AGL62, GLYCOSYL HYDROLASE FAMILY 17 and UDP-GLUCOSE FLAVONOL 3-O-GLUCOSYLTRANSFERASE play a role in mucilage synthesis and release, seed coat development and anthocyanin biosynthesis, and are among the promising candidate genes of flaxseed [86]. The gene-encoding pectin methylesterases (PMEs), which control the level of pectin methylesterification, influence the structure and organization of *A. thaliana* mucilage. Of the PMEs observed, the PME58 gene showed the highest expression [87]. The direct activation of this gene is provided by two transcription factors in *A. thaliana* L., BLH2 and BLH4, which are significantly expressed in mucilage-secreting cells and thus positively regulate PMEs. In addition to PME58, they also affect the expression of the genes PECTIN METHYLESTERASE INHIBITOR6, SEEDSTICK, and MYB52 [88]. Conversely, the MUD1 gene, which encodes a nuclear RING domain protein and is highly expressed in the developing seed coat of *A. thaliana* L., negatively regulates the PME levels. MUD1 expression causes a reduction in the expression of PME-related genes, including MYB52, LUH, SBT1.7, PMEI6 and PMEI14 [89].

The production of mucilage at different developmental stages from the *Aechmea sphaerocephala* (GAUDICH.) Baker seeds is influenced by 21 key regulatory genes (AsNAM-1 to AsNAM-17, AsAP2-1, AsAP2-2, AsKNAT7 and AsTTG1) whose expressions were different at 10, 20, 30, 40, 50, 60 and 70 days after flowering. In the period of 10 to 30 days after flowering, both the AsNAM and AsAP2 genes stimulated the production of mucilage by their expression. In the period of 40 to 70 days after flowering, the expressions of AsNAM and AsAP2 were reduced, and conversely, the increase in AsKNAT7 expression inhibited the formation of mucilage [90]. The transcription factors MYB-bHLH-WD40 (MBW) and APETALA2 (AP2) had a key effect on the production of mucilage in the *A. sphaerocephala* (GAUDICH.) Baker seeds. The increased accumulation of UDP-glucose was mediated by an increased expression of phosphoglucomutase (pgm) and uridine glucose diphosphorylase (UGPase) and decreased expression of UDP-glucose 4-epimerase (GALE), UDP-glucose 6-dehydrogenase (UGDH) and UDP-glucose 4,6-dehydratase (RHM). The accumulation of UDP-xylose (UDP-Xyl) was influenced by an increased expression of UDP-apiose/xylose synthase (AXS) and decreased expression of UDP-arabinose 4-epimerase (UXE) [91]. The transparent testa glabra 1 (TTG1) gene encodes the transcription factor of *Lepidium perfoliatum* that plays a role in epidermal cell differentiation and the release of mucilage. This gene is 1032 bp long, it encodes 343 predicted amino acids and contains WD40 motifs [92]. An overview of the genes/transcription factors, their function in the mucilage process and spatial localization is shown in Tables 3 and 4.

Table 3. Function of genes/transcription factors in the mucilage process.

Function in the Process	Genes/Transcription Factors	Reference
Mucilage synthesis and release	*Transparent testa 8; subtilisin-like serine protease; galacturosyl transferase-like 5; mucilage-modified 4; agamous-like MADS-box protein AGL62; glycosyl hydrolase family 17; pectin methylesterase inhibitor 6*	Refs. [85,86]
Mucilage amount	*Mucilage-modified 2 (MUM2)*	Ref. [76]
Mucilage proper structure	*Mucilage-modified 2 (MUM2)*	Ref. [76]
Mucilage polysaccharide composition	*Mucilage-modified 2 (MUM2) + testa-abundant 2 (TBA2); peroxidase 36 (PER36); mucilage-modified 4 (MUM4)*	Ref. [77]
Mucilage production	*Knotted arabidopsis thaliana 3 (KNAT3) and knotted arabidopsis thaliana 7 (KNAT7)*	Ref. [79]
Mucilage cellulose deposition	*Cobra-like 2 (COBL2)*	Ref. [75]
Mucilage composition	*UDP-uronic acid transporter1 (UUAT 1)*	Ref. [83]
Mucilage extrusion	Leunig homolog (LUH)/*mucilage-modified 1 (MUM 1); enzymes MUM 2; subsilin protease 1.7; beta-xylosidase 1*	Ref. [81]
Mucilage adherence Mucilage structure and organization	*Cellulose synthase 5 (CESA5)/mucilage-modified 3 (MUM3)* *Pectin methylesterase 8 (PME 8)* + BLH 2 and BLH 4	Ref. [84] Refs. [87,88]
Mucilage rhamnogalacturonan I size	*Mucilage-related 70 (MUCI 70); galacturonosyltransferase-like 5 (GATL 5)*	Ref. [80]
Mucilage rhamnogalacturonan I amount	*Copper amine oxidase 1 (CuAOX 1)*	Ref. [80]

Notes: genes are shown in italics.

Table 4. Spatial localizations of some genes included in the mucilage process.

Spatial Localization	Genes/Transcription Factors	Reference
Epidermal cells	*Cobra-like 2 (COBL2)*	Ref. [75]
Cell wall	*Mucilage-modified 2 (MUM2)*	Ref. [76]
Seed coat cells	*Mucilage-modified 4 (MUM4)*	Ref. [77]
Mucilage-secreting cells	BLH 2 and BLH 4	Ref. [88]
Nucleus	Leunig homolog LUH	Ref. [81]
Endoplasmic reticulum; Golgi apparatus	*Galacturonosyltransferase-like 5 (GATL5)*	Ref. [82]
Golgi apparatus	*UDP-uronic acid transporter1 (UUAT 1)*	Ref. [83]
Developing seed coat	*Mucilage defect 1 (MUD1)*	Ref. [89]

Notes: genes are shown in italics.

9. Summary

Specific cells of some plants can produce hydrophilic mucilage in the Golgi apparatus and subsequently secrete it into the apoplastic space. This mucilage has several vital functions for the plant: it protects the seeds from desiccation, fixes the seeds in the soil, protects the seeds from predation, influences seed germination and serves as a source of energy for the seeds. In addition, it is priceless in agriculture and the food industry because it serves as an additive in various foods, and it is also used in the production of edible films and the encapsulation of probiotics. It is also used in human and veterinary medicines as it has antihypercholesterolemic, antibacterial, laxative, healing, anti-inflammatory and anticarcinogenic effects, and it influences glucose metabolism and acts as a prebiotic. It can be used in the manufacture of tablet medicines and for wound dressings.

Mucilage is mainly composed of polysaccharides, which vary between the species and varieties, but it also contains other components, such as proteins, lipids, ash, moisture, phenolics and minerals to a lesser extent. The mucilaginous substances of plants are odorless, colorless and tasteless; they have a high degradation temperature; good foaming properties and a high water retention capacity. In the future, mucilaginous substances have great potential to be used as potential nutraceuticals in disease prevention and treatment.

10. Future Perspectives

For the development of functional foods, food supplements or nutraceuticals, it is necessary to research more extensively the genotypic variability of the biochemical composition of mucilage and its biological and other properties (according to the purpose of use). The identification of the specific plant genotype reflecting the appropriate/required parameters of seed mucilage is crucial for advancing the usability of this potential nutraceutical. Therefore, detailed knowledge of the molecular mechanisms behind the regulation of mucilage biosynthesis mainly at the epigenetic level (microRNAs) should become the focus of future research.

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