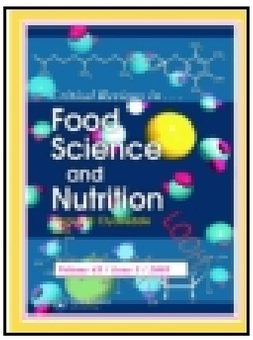

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REVIEW

Phenolic compounds in germinated cereal and pulse seeds: Classification, transformation, and metabolic process

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ABSTRACT

Natural phenolic compounds are rich in cereal and pulse seeds and their dietary functions tend to improve dramatically during germination. This article reviews recent research on the transformation of phenolic compounds during seed germination. In particular, it highlights the classification of crude phenolic compounds that can be divided into extractable and non-extractable phenolic compounds based on the biosynthesis process and extraction method. It also recommends grouping resorcinol lipids in the category of extractable phenolic compounds as non-polar solvent extractable phenolic compounds. Moreover, it discusses the variation of the different form of phenolic compounds and proposes a possible metabolic model of these phenolic compounds for seeds germination. This article is crucial for phenolic compounds research, cereal and pulse seeds germination, and food ingredients industry.

KEYWORDS

Extractable phenolic compounds; non-extractable phenolic compounds; antioxidants; ROS; phenolipids; germination; lipid oxidation

Introduction

Under the new rule from the U.S. Food and Drug Administration (FDA), manufacturers cannot add partially hydrogenated oils (PHOs) to foods after 18 June 2018, with the compliance date extension for certain uses of PHOs. Additionally, the Dietary Guidelines for Americans (2015–2020) and the World Health Organization (WHO)'s Guidelines on Saturated Fatty Acid and Trans-Fatty Acid Intake for Adults and Children both recommend to consume less than 10% of calorie from saturated fats per day by replacing saturated fats with unsaturated fats to decrease risk for noncommunicable diseases (NCDs) (U.S. Department of Health and Human Services 2015). The food manufacturers who used to use PHOs or high saturated fats indubitably need to reformulate their products by replacing PHOs or saturated fats with unsaturated fats to comply with the new regulation and respect nutritional recommendations. However, increased unsaturation in fatty acids profile will inevitably accelerate lipid oxidation, resulting in quality deterioration and food waste. To solve this dilemma, efforts to prevent lipid oxidation in foods containing high unsaturated fats have greatly increased. The addition of antioxidants has long been considered as the most effective strategy to prevent lipid oxidation. Synthetic antioxidants, which are deemed to be superior to other strategies, had been primarily used in foods to prevent lipid oxidation. In addition to a restrict regulation over the usage amount (200 ppm maximum in most cases), consumers' concerns on the safety of synthetic antioxidants with the preference for natural products have discouraged manufacturers on the continuation of utilizing synthetic antioxidants in the reformulated food products. Ultimately, this has elicited great enthusiasm both in the academia and food industry in search of alternative natural substances with antioxidant properties for food applications.

Natural phenolic compounds, the ubiquitous secondary metabolites in plant foods, usually act as antioxidants to protect them from oxidation by combating oxidative stress derived from free radicals, reactive oxygen species (ROS), and prooxidants (Brewer 2011; Naczk and Shahidi 2006). The antioxidant properties of natural phenolic compounds in our diet have been connected with their multifaceted functions in promoting human health (Rice-Evans 2001; Robbins 2003). Likewise, a well-reasoned hope to replace synthetic ones and effectively prevent food lipid oxidation has been placed on natural phenolic compounds that extracted from plant foods. Cereal and pulse crops are the top two plant foods providing the major calories and protein source to the human diet. Recent intervention researches performed on animals and humans indicate that cereal and pulse crops contain biologically active, yet relatively low amounts of phenolic compounds that are related to the reduced risk of chronic diseases (Jayathilake et al. 2018). A number of methods have been employed with the aim of improving the quantity and antioxidant activity of phenolic compounds in cereal and pulses. Germination, the process that has been used to soften seed kernels for centuries, has recently regained much interest through the success of improving the nutritional value, and reducing anti-nutritional factors specifically in pulses (Mäkinen and Arendt 2015; Sharma and Gujral 2010; Yeo and Shahidi 2015; Zhang et al. 2015). Germination has been regarded as a

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cheap and effective technique to boost the antioxidant activity of phenolic compounds in germinated cereal and pulse seeds so that they cannot only be incorporated into the human diet for improved health but also be utilized as food antioxidants to effectively prevent lipid oxidation.

Although a myriad of research has shown that germination is a promising means to increase the number of phenolic compounds in cereal and pulse, the dynamic changes of phenolic compounds is still a controversial procedure since it is currently a bottleneck to decipher the dynamic metabolism of phenolic compounds during cereal and pulse seed germination. For instance, a decreased content of extractable phenolic compounds during lentil germination was described by López-Amorós et al. (2006), and Xu et al. (2018a), while an opposite trend was reported by other researchers with extractable phenolic compounds increased consistently during lentil germination (Yeo and Shahidi 2015). Explanation of such paradoxical observations can be accomplished as long as the transformation of phenolic compounds during cereal and pulse germination is fully discovered. In general, there are three events in regard to the metabolism of phenolic compounds during seed germination. First, the synthesis of natural phenolic compounds starts from glucose or aromatic amino acids as can occur during seed germination. With the oxidative pentose phosphate, glycolytic and shikimate pathways, aromatic amino acid like phenylalanine, can be produced and transformed into phenolic acids in the cytosol (Herrmann and Weaver 1999). Phenolic acids then convert into flavonoids, stilbene, and coumarin in the endoplasmic reticulum. These phenolic compounds can be further polymerized or bounded with macromolecular nutrients, such as polysaccharides, proteins, and lipids, thereafter, stored in cell walls or vacuoles (Shahidi and Yeo 2016). Second, macromolecular nutrients are decomposed by enzymes (Paucar-Menacho et al. 2017) that results in the release of phenolic compounds from their bound form. Third, phenolic compounds are consumed to scavenge free radicals or work as intermediates of signal compounds. Seed species and germination environment are two important factors determining the transformation of phenolic compounds in that three events during germination. It is thus not surprising that the total content and antioxidant activity of phenolic compounds might either decrease or increase after a complex germination procedure.

Together with the complicated metabolism events of phenolic compounds during germination, the versatile solvent systems used for extracting and purifying phenolic compounds from germinated cereal and pulse have even aggravated the difficulties to truly understand the impact of germination on the quantity and antioxidant activity of phenolic compounds. For instance, Abdel-Aal et al. (2012) extracted phenolic compounds from barley with 80% methanol and named it as free phenolic compounds; Gan et al. (2016a) referred to 80% methanol extracted phenolic compounds from edible dry beans as soluble phenolic compounds; while Wang et al. (2016) used 40% ethanol to extract both free and soluble bound phenolic compounds from dry beans.

The overall purpose of this review is therefore to provide an up-to-date and comprehensive overview of quantity and antioxidant activity variations of phenolic compounds during cereal and pulse seeds germination. An attempt to correctly classify phenolic compounds extracted from cereal and pulse seeds on the basis of extraction methods and solvent polarity is first presented. Biosynthesis, transformation, and consumption of phenolic compounds during seed germination are discussed afterward. The metabolic model of phenolic compounds in seed germination is proposed in the end. With these results, researchers can have better ways to discover the phenolic compounds with greater antioxidant activity from germinated cereal and pulse seeds as natural food antioxidants.

The classification and antioxidant activity of phenolic compounds in cereal and pulse seeds

Over the past two decades, studies on various aspects of phenolic compounds have appeared which generate thousands of publications on the extraction and analysis of this category of compounds. However, the classification for crude phenolic compounds extracted from cereal and pulse seeds are still ununiformed. In general, crude phenolic compounds have been annotated on the basis of extraction methods, particularly their solubility in solvent or their partition ratio in the binary solvent system, yet these classification systems do not fully overlap. As shown in Table 1, one way to classify phenolic compounds is based on the solubility of phenolic compounds in solvents. For instance, phenolic compounds that dissolve in solvent (water/acetone/methanol) are named as free (Abdel-Aal et al. 2012; Xiang et al. 2017) or soluble phenolic compounds (Yeo and Shahidi 2015), while residues which cannot be dissolved into such solvents are named as bound (Xiang et al. 2017; Yeo and Shahidi 2015) or insoluble bound phenolic compounds (Krygier et al. 1982). Another way of classification relies on the partition ratio of phenolic compounds in solvents with different polarity, with water/acetone/methanol and diethyl ether/ethyl acetate (DE/EA) being the common combination. Phenolic compounds extracted by DE/EA from water are named as free phenolic compounds (Chen et al. 2015; Das and Singh 2016; Krygier et al. 1982), while the residues in the water phase are named as esterified (Krygier et al. 1982), conjugated (Chen et al. 2015), or bound phenolic compounds (Das and Singh 2016; Xiang et al. 2017; Yeo and Shahidi 2015).

Those two classification methods have ignored a portion of phenolic compounds in cereal and pulse seeds that cannot be extracted by polar solvent systems. For instance, a whole group of natural phenolic lipids in cereal and pulse seeds have been excluded in the current crude phenolic compounds classifications which attribute to the defatting pretreatment among those most prevalent extraction methods (Hung et al. 2011; Krygier et al. 1982; Masisi et al. 2016). This endows Total Phenolic Compounds (TPC), a parameter frequently used to quantify the whole category, with two different meanings. The parameter of TPC either

Table 1. Classification of crude phenolic compounds based on extraction methods in different cereal and pulse seeds.

	Water/organic solvent (DC 20–60)			
Seeds	Organic solvents (DC 4–6)	Water phase	Residues	References
Corn	Free		Bound	(Xiang et al. 2017)
Barley	Free		Bound	(Abdel-Aal et al. 2012)
Maize	Free		Bound	(Das and Singh 2016)
Rice	Free		Bound	(Alves et al. 2016)
Whole grain rice	Free		Bound	(Min et al. 2012)
Black soybean	Free		Bound	(Kim et al. 2016)
High amylose wheat grain	Free		Bound	(Van Hung et al. 2015)
Lentils	Soluble		Bound	(Yeo and Shahidi 2015)
Edible seeds	Soluble		Bound	(Gan et al. 2017)
Mung bean	Soluble		Bound	(Gan et al. 2016b)
Edible beans	Solvent-soluble		Solvent-insoluble	(Gan et al. 2016a)
Cranberry bean	Free	Conjugated	N.A.*	(Chen et al. 2015)
Barley	Free	Soluble phenolic acid esters	N.A.	(Yu et al. 2001)
Brown rice	Soluble	Soluble bound	N.A.	(Pal et al. 2016)
Beans	Free	Soluble conjugated	Insoluble bound	(Wang et al. 2016)
Barley	Free	Esterified	Insoluble bound	(Dvořáková et al. 2008)
Oilseeds	Free	Esterified	Insoluble bound	(Krygier et al. 1982)
Dry beans	Total phenolic acid		N.A.	(Ross et al. 2009)
Dark beans	Phenolic compound		N.A.	(López et al. 2013)
Pinto and black beans	Total phenolic composition		N.A.	(Xu and Chang 2009)
Edible seeds	Total soluble phenolics		N.A.	(Cevallos-Casals and Cisneros-Zevallos 2010)

*N.A., not available.

exclusively represents the total extractable phenolic compounds by polar solvents used (López et al. 2013; Ross et al. 2009; Xu and Chang 2009), or includes both the extractable and non-extractable phenolic compounds (Abdel-Aal et al. 2012; Xiang et al. 2017; Yeo and Shahidi 2015). Because of such differences on classification rather than others, contradictions are often observed in different studies. For example, Hübner and Arendt (2013) reviewed that free phenolic acids are mainly located in the pericarp of cereals. However, Das and Singh (2016) reported that free phenolic compounds of maize were mainly in the germ, while bound phenolic compounds were mainly located in the pericarp.

Herein, we propose a rational classification to completely discover the phenolic compounds in cereal and pulse seeds by categorizing crude phenolic compounds into non-extractable (NEPs) and extractable phenolic compounds (EPs) groups. The EPs group can then be further classified as non-polar solvent extractable (NPSEPs) and polar solvent extractable (PSEPs) phenolic compounds, with the latter being further divided to soluble free (SFPs) and polar soluble bound phenolic compounds (PSBPs). As NPSEPs can be considered as non-polar soluble bound phenolic compounds, NPSEPs and PSBPs together make up soluble bound phenolic compounds (SBPs). In principle, this annotation could answer central questions of the efficacy of natural antioxidants for each category.

Non-extractable phenolic compounds

Non-extractable phenolic compounds (NEPs), due to its insoluble nature in water or organic solvents, are also known as insoluble bound phenolic compounds. The insoluble moieties that the phenolic compounds bound with, such as cellulose, arabinoxylan, chitin, hemicellulose, and polysaccharide-protein complex, make phenolic compounds non-extractable (Quirós-Sauceda et al. 2014; Saura-Calixto 2011). NEPs exist in the cell wall of most cereal and pulse seeds (Agati et al. 2012; Naczk and Shahidi 2004). NEPs play critical roles in the mechanical strength of cell wall, plant growth regulation, stress protection, and pathogen resistant (Naczk and Shahidi 2004).

The formation mechanism of NEPs has yet to be established. Speculated overview of the procedure is reported by Agati et al. (2012). SFPs and SBPs are synthesized in plant cells and secreted out, which are then escorted by vesicles to the cell wall to link with hemicellulose, cellulose, arabinoxylan, and other insoluble moieties, by hydrogen bonds, hydrophobic interactions, and covalent bonds (Saura-Calixto 2011). Alves et al. (2016) use α-amylase to hydrolyze NEPs of rice, which denoted that some insoluble bound moieties may contain 1–4 linkage glucoside.

Phenolic compounds can also be entrapped by polysaccharides to form steric hindrance that prevents them from being extracted. As a result, phenolic compounds on NEPs have a lower accessibility and availability (Quirós-Sauceda et al. 2014). Obviously, the antioxidant capability is limited by steric hindrance as well, which results in the increased endurance of antioxidant capability *in vivo*. The protective effect of non-starch polysaccharides on the attached phenolic compounds against enzymes in mouth, stomach, and small intestine has recently been reported (Lovegrove et al. 2017). When NEPs come to the large intestine, non-starch polysaccharides can be digested by colonic microflora that releases phenolic compounds (Maurer et al. 2013) to protect against colon cancer.

In order to quantify the total phenolic compounds and characterize the properties, the attached phenolic compounds should be liberated initially. Alkaline hydrolysis followed by acidic hydrolysis is widely applied to liberate phenolic compounds from NEPs. Then, DE/EA are employed to extract phenolic compounds from the hydrolyzed solution (Çelik et al. 2013). Additionally, enzymatic hydrolysis and microwave assisted hydrolysis have been utilized for the effective release of phenolic compounds on NEPs (Shahidi and Yeo 2016).

Extractable phenolic compounds (EPs)

Solvent extraction

A number of EPs, especially PSEBs have been extensively reviewed (Alves et al. 2016; Cheynier et al. 2013; Robbins 2003; Van Hung 2014). Basically, extractable phenolic compounds must be extracted prior to any applications. Most of the extraction procedures are based on the solubility of phenolic compounds that are governed by their structure and polarity (Naczk and Shahidi 2006). Dielectric constant (DC) is positively related to a solvent's polarity. Base on the principle that the more similarity of DC, the higher intermiscibility between two substances, NPSEPs, PSBPs, and SFPs can be separated, purified, and further investigated (Cheynier et al. 2013; Zhou and Elias 2012)

A classical extraction procedure for phenolic compounds has been detailed in numerous publications (Figure 1) (Alves et al. 2016; Wang et al. 2014). Generally, NPSEPs are extracted by non-polar solvents with the term of defatting. Then, PSEPs are extracted from defatted seeds meal using water or water/polar solvents, such as methanol (Casazza et al. 2010), ethanol (Casazza et al. 2010; Xu and Chang 2007), acetone (Bhat and Riar 2017), methanol/water (7/3, v/v) (Xu and Chang 2007), ethanol/water (63.5/100, v/v) (Bodoira et al. 2017), acetone/water (8/2, v/v) (Xu and Chang 2007), or water/acetone/methanol (6/7/7, v/v/v). After that, SFPs are extracted from PSEPs using medium-polar solvent, mainly DE (Khoddami et al. 2013) or DE/EA (1/1, v/v) (Bodoira et al. 2017) for at least 3 times. In order to know the properties of phenolic compounds attached on

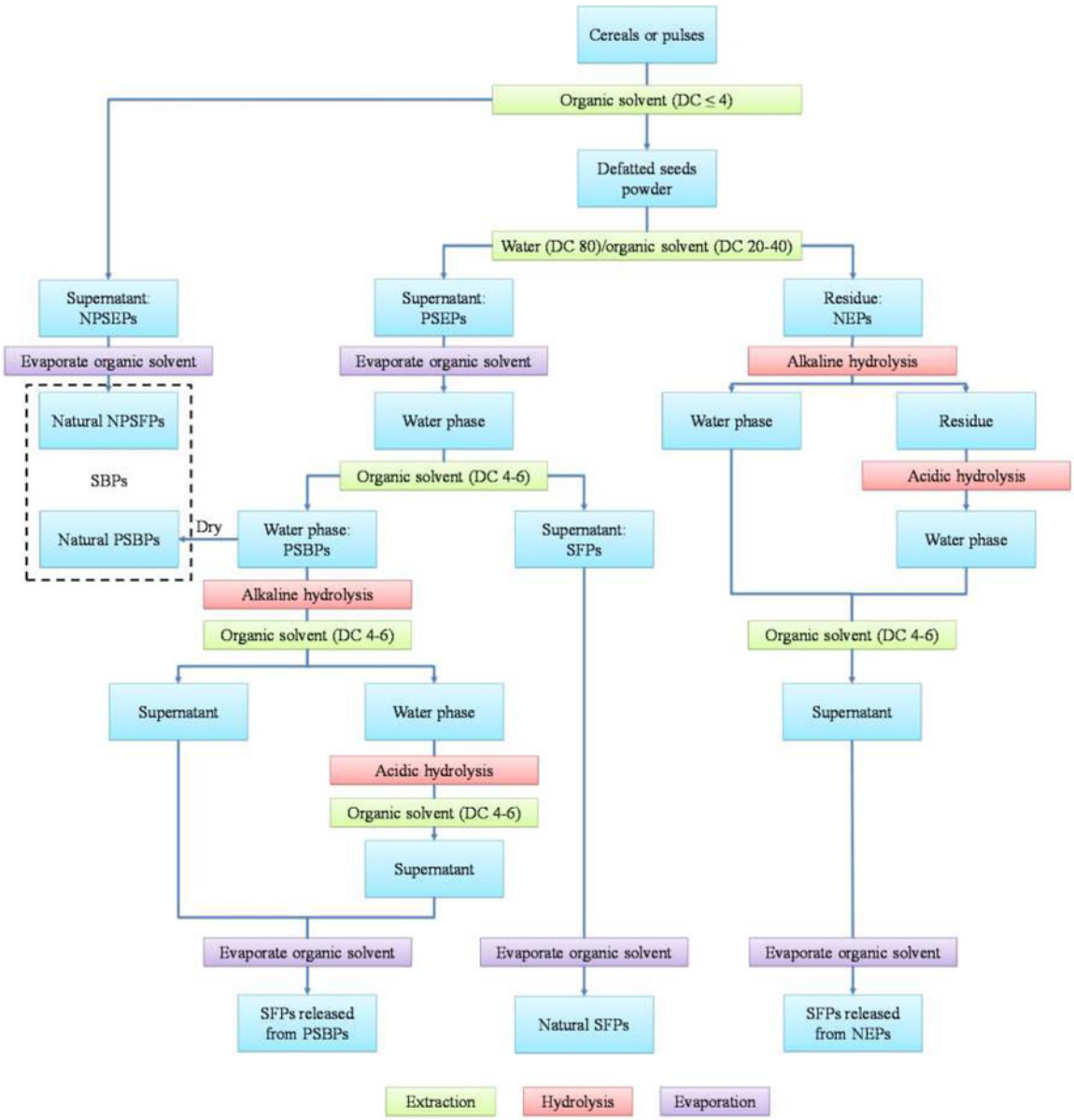

Figure 1. General extraction procedure of phenolic compounds. The DC value of organic solvents (20 °C): methanol (DC 33), ethanol (DC 24.5), acetone (DC 20.7), ethyl acetate (DC 6.02), diethyl ether (DC 4.34), cyclohexane (DC 2.02), hexane (DC 1.88). DC, dielectric constant; NEPs, nonextractable phenolic compounds; NPSEPs non-polar solvent extractable phenolic compounds; PSEPs, polar solvent extractable phenolic compounds; SFPs, soluble free phenolic compounds; PSBPs, polar soluble bound phenolic compounds; SBPs, soluble bound phenolic compounds.

the soluble moieties, PSBPs remaining in the water phase need to be hydrolyzed using NaOH and HCl so that attached phenolic compounds can be liberated. Using medium-polar solvent (DE/DA), phenolic compounds from PSBPs can be extracted and can then be considered as soluble free. Following such procedure, tannins, flavonoids, phenolic compounds, and lignans are extracted from cereals and pulse seeds (Bhat and Riar 2017; Bodoira et al. 2017; Xu and Chang 2007).

Nevertheless, it is difficult to extract the entire SFPs from PSEPs as medium polarity solvents for SFPs extraction can disperse into high polarity solvents at a certain ratio. In addition, small amounts of PSBPs and SFPs may disperse into medium-polar phase and polar phase, respectively (Chen et al. 2015). Therefore, extraction with multiple times (at least 3) is encouraged to receive relatively pure SFPs from crude PSEPs.

Polar solvent extractable phenolic compounds (PSEPs)

Soluble free phenolic compounds (SFPs). Pure phenolic compounds in their free form are synthesized in plant cells via two main pathways. The shikimate pathway directly provides phenylpropanoids such as the hydroxycinnamic acids (C6–C3) and coumarins (C6-C3), and the polyketide (acetate) pathway produces simple other phenolic compounds (Kozubek and Tyman 1999). Most of the SFPs are derived from a combination of these two pathways. Chemically, SFPs have been classified into several groups such as phenolic acids (C6-C1 or C6-C3), coumarins (C6-C3), stilbenes (C6-C2-C6), flavonoids (C6-C3-C6), and polymers. Phenolic acids can be divided into hydroxybenzoic acids (C6–C1) (e.g. gallic, *p*-hydroxybenzoic, vanillic, syringic, and ellagic acids), and hydroxycinnamic acids (C6-C3) (e.g. *p*-coumaric, caffeic, ferulic, and sinapic acids) (Amarowicz and Pegg 2008). Coumarins (C6-C3) are present in different seeds (Shahidi and Yeo 2016). Stilbenes (C6-C2-C6) exist mainly in the form of resveratrol (Song et al. 2010). Flavonoids (C6-C3-C6) can be further classified as flavones, flavanones, flavonols, flavanonols, isoflavones, flavanols, and anthocyanidins based on the substitution patterns on the C3 structures (Shahidi and Ambigaipalan 2015). Owing to the polyhydroxy group (polar) and benzene ring (non-polar) structures, most of the pure phenolic compounds in free form are soluble in polar and medium-polar solvents, such as water/acetone/methanol and DE/EA and can be categorized as soluble free phenolic compounds (SFPs). They are also the major constituents of both SBPs and NEPs.

SFPs possess powerful antioxidant activity. Firstly, phenolic compounds have radical scavenging ability. Hydroxyl groups on SFPs have the ability to donate hydrogen atom or electron to neutralize free radicals, which are the primary oxidation factors (Cui and Decker 2016). Afterward, SFPs themselves become special radicals, which do not propagate as free radicals. Stable property of phenolic radicals is attributed to the delocalization function of the benzene ring (Kfoury et al. 2016). Secondly, SFPs have metal ion chelating capability (Shahidi and Ambigaipalan 2015). Metal ions are believed to be strong prooxidants of lipid oxidation. Hydroxyl groups and carboxyl groups on phenolic compounds can chelate metal ions, thus preventing metal ions initiated lipid oxidation.

Polar soluble bound phenolic compounds (PSBPs). Polar soluble bound phenolic compounds (SBPs) consist of a phenolic compound with a polar soluble moiety that renders phenolic compound a higher solubility in polar solvents. As a result, PSBPs can be extracted by polar solvents such as water, methanol, as well as acetone, and purified by removing SFPs with DE/EA (Gan et al. 2016a). Herein, we mainly discuss carbohydrates, the dominant soluble moieties that have been found in PSBPs from cereal and pulse seeds.

Phenolic compounds have been found to conjugate with variable soluble carbohydrates, including monosaccharides, disaccharides, oligosaccharides, and polysaccharides. Phenolic compounds bound to monosaccharides have been widely reported, such as quercetin-*O*-glucoside, apigenin-6-*C*-glucoside, ferulic acid hexoside, and etc. (Gan et al. 2016a; Paucar-Menacho et al. 2017). Phenolic compounds can also bound to disaccharides, such as quercetin-3-*O*-rutinoside and kaempferol-3-*O*-rutinoside (Zhang et al. 2015). Phenolic compounds bound to oligosaccharides have higher prebiotic activity, such as 3-*O*-(5-*O trans* feruloyl-α-*L*-arabinofuranosyl)-*D*-xylose and *O*-[5-*O*-(*trans*-feruloyl)-α-*L*-arabinofuranosyl]-(1→3)-*O*-β-*D*-xylopyranosyl-(1→4)-*D*-xylopyranose (Bento-Silva et al. 2018). Polysaccharides can be attached to phenolic compounds by hydrogen bonds, hydrophobic interactions, and covalent bonds, such as ester bonds and ether bonds (Dueñas et al. 2016; Quirós-Sauceda et al. 2014). Rao and Muralikrishna (2004) reported that ferulic acids and coumaric acids connected to the soluble polysaccharides in rice, maize, wheat, and finger millet.

The bioavailability, chemical stability, and antioxidant activity of phenolic compounds can be impacted upon the conjugation with soluble carbohydrates. Soluble carbohydrates are polyhydroxy compounds which can give rise to the hydrophilic property of the phenolic compounds attached, especially flavonoids (Tommasini et al. 2004; Xie et al. 2016). The majority of flavonoids, except for the subclass of catechin, are in the form of flavonoids-glycosides that result in higher bioavailability in the human body (Kumar and Pandey 2013). Soluble carbohydrates, particularly polysaccharides, can improve the chemical stability of phenolic compounds because of the steric hindrance that can protect phenolic compounds away from other oxidants (Fan et al. 2018; Qiu et al. 2017). Soluble dietary fibers would be the good examples which trap and protect phenolic compounds via ester bonds, hydrogen bonds, or electrostatic bonds (Quirós-Sauceda et al. 2014). Meanwhile, polysaccharides can also keep the phenolic compounds away from part of the light. This is evidenced by a study which indicated a significant improvement in the photostability of phenolic compounds by encapsulating phenolic compounds with cyclodextrin (Kfoury et al. 2016). Soluble carbohydrates can also improve the antioxidant activity of phenolic compounds by a synergistic effect. Numerous studies have found that crude polysaccharides have excellent free radical

scavenging capability (Fan et al. 2014; Sun et al. 2010, 2005; Wu et al. 2014; Zhao et al. 2012). It is possible that phenolic compounds conjugated on the polysaccharides are the main groups responsible for the free radical scavenging (Wang et al. 2016). Thus, soluble polysaccharides synergistically donate hydrogen from their activated reducing ends to these oxidized phenolic compounds. An adamant evidence is that PSBPs have been shown to exhibit higher antioxidant activity than hydrolyzed counterparts (Gan et al. 2016a; Wang et al. 2015; Wang et al. 2016). Our recent study also has shown that a substantial amount of higher molecular weight compounds (>5000 kDa) exists in acetone/water extracts of chickpea (Xu et al. 2018a). With the comparison between antioxidant activity of PSBPs and SFPs in both in vitro and in oil-in-water emulsion system, moieties of PSBPs has a synergistic effect with phenolic compounds (Xu et al. 2018b).

Non-polar solvent extractable phenolic compounds (NPSEPs)

Resorcinol lipids (Figure 2), also known as phenolic lipids, are the group of NPSEPs that have previously been precluded from phenolic compounds family of cereal and pulse seeds. The majority of this group in cereal and pulse seeds is removed during the initial defatting process before extracting and quantifying phenolic compounds. Thus, there is a lack of information in the literature on this group of antioxidants in regard to their antioxidant activity. Resorcinol lipids are most abundant in outer layers of cereal and pulse seeds where makes up the dietary fiber. In general, the highest amount of resorcinol lipids is in the testa layer of cereal bran such as rye and wheat (~1100 mg/kg d.w.) and relatively low in pulse seeds (~0.3 mg/kg d.w.) (Kulawinek et al. 2008; Landberg et al. 2007; Zarnowski and Kozubek 1999).

Resorcinol lipids comprise a resorcinol (1,3-dihydroxybenzene) base group alkylated at the position 5 (-R) with an odd-numbered non-isoprenoid aliphatic chain of various length (C5 to C29) either saturated (alkylresorcinols) or unsaturated (alkenylresorcinols) with 1 to 6 double bonds. The aliphatic chain length of resorcinol lipids in cereal and pulse seeds ranges from C13 to C27. They are amphiphilic in nature when short aliphatic chains (<C9) are attached to

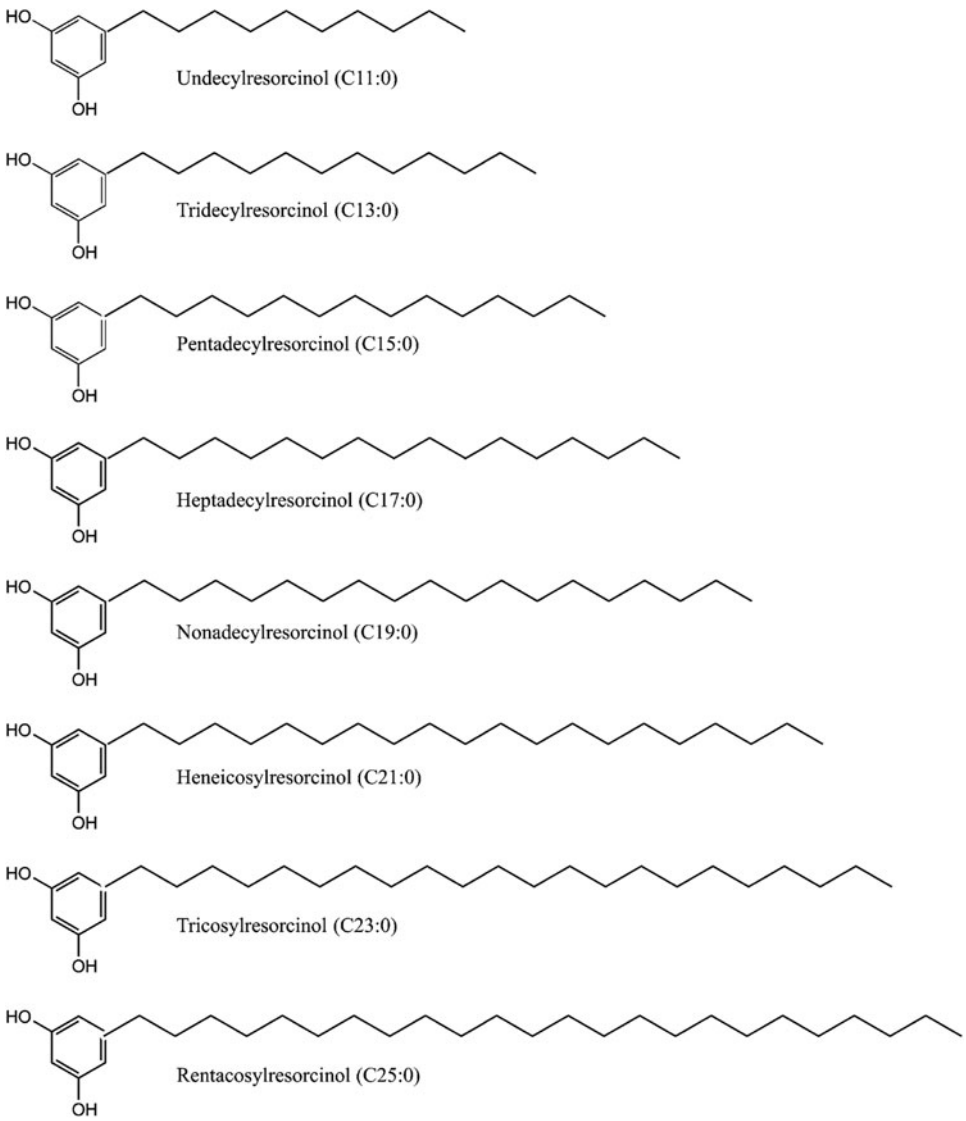

Figure 2. Chemical structures of common phenolic lipids (resorcinolic lipids) in cereal and pulse Seeds.

the hydroxybenzene ring; however becoming very hydrophobic as the aliphatic chain exceeding 11 carbon (Kozubek and Tyman 1999). The extraction of resorcinol lipids in cereal and pulse seeds can be achieved using Soxhlet extraction. An earlier study examined the impact of solvents including acetone, chloroform, cyclohexane, diethyl ether, ethyl acetate, and hexane, on Soxhlet extraction performance of resorcinol lipids from wheat (Zarnowski and Suzuki 2004). The results showed that each solvent yielded extracts that differed from each other in terms of resorcinol lipids contents and homolog compositions. Among the solvents, cyclohexane was recommended to separate resorcinol lipids since it was shown to be faster and more versatile than the rest. Recently, supercritical carbon dioxide extraction, because of its nontoxic, non-flammable, and environmentally friendly properties, has been applied to extract resorcinol lipids in cereal and pulse seeds. No difference in total resorcinol lipids content, relative homolog composition or total extract yield from wheat and rye was previously found between supercritical carbon dioxide extraction and ethyl acetate extraction (Landberg et al. 2007). However, a recent study indicated that resorcinol lipids content extracted from wheat bran was significantly lower in supercritical carbon dioxide extracts as compared to acetone extracts (Gunenc et al. 2015).

The antioxidant activity of resorcinol lipids extracted from cereal is a scarcely investigated subject. An earlier study suggested that five different type of synthetic alkylresorcinols (chain lengths C15:0, C17:0, C19:0, C21:0, and C23:0) did not exert potent antioxidant activity in the FRAP (ferric reduction ability of plasma) and DPPH (2,2-diphenyl-1-picrylhydrazyl) radical assays (Parikka et al. 2006). Recently, Elder and coworkers discovered, for the first time, the antioxidant activity of natural resorcinol lipids extracted from rye bran against stripped algae oil-in-water emulsions oxidation. The ability to scavenge oxygen radicals and stabilize radicals via resonance within their phenolic ring as well was proposed to be the antioxidant mechanism of resorcinol lipids (Elder et al. 2019).

In fact, the antioxidant activity of synthetic phenolic lipids, also named as phenolipids, has gained considerable popularity and importance in the past years. Most free phenolic compounds are high in polarity which result in the low solubility in oil. The polarity of phenolic compounds can be modulated after combining with a lipid via esterification, amidation, or etherification (Ramadan 2014). The lipid moieties of phenolipids can drive phenolic compounds into the hydrophobic environment and hinder the mobility of phenolipids (Kahveci et al. 2015). Although physical advantages of phenolipids have been mentioned, the length of the lipid chain appears to be a double-edged sword, especially in an emulsion system. In terms of antioxidant activity, phenolipids with too long or too short lipid chain has poor antioxidant activity than the ones with medium chain length. Six to twelve carbon atoms were reported to be optimal chain length for saturated lipids moieties in phenolipids. The relationship between lipid chain length and antioxidant activity can be drawn as a parabolic figure, which also named as a cutoff effect (Kahveci et al. 2015). With the in-depth study and enlarged application of synthetic phenolipids in food systems, the antioxidant activity of resorcinol lipids from cereal and pulse seeds alone or in combination with other natural antioxidants may become a new hot area in the field of natural antioxidants.

Impact of germination on the transformation of phenolic compounds

Germination of cereal and pulse seeds

Germination of cereals and pulse seeds has been used for centuries to improve their nutritional characteristics. Nutrient content improvement, nutritional availability enhancement, nutrition species increment, and antinutrients reduction have been reported by numerous studies (Hübner and Arendt 2013; Kaukovirta-Norja et al. 2004; Wang et al. 2015; Wu et al. 2012).

Basically, germination starts from seed hydration (Figure 3). Water is absorbed by dry seeds with concentration gradient and diffusion. In turn, the respiratory activity increased, *de novo* gibberellic acids are synthesized in the germ. With the increased mobility, which is attributed to water, gibberellic acids move from embryo to aleurone layer as a molecular signal. Enzymes such as carbohydrase, protease, and lipase are synthesized with the signal and secreted into the endosperm. Starch, proteins, and lipids are degraded and used for respiration and synthesis of new cell constituents, such as phenolic compounds. Phenolic compounds bound to these macromolecular nutrients are changed during germination. Meanwhile, cell wall, which contains a number of NEPs, breaks down during seed germination. In the meantime, new varieties of bound phenolic compounds are synthesized from SFPs to generate signal and defense compounds. Finally, the shoot and rootlets developed (Nelson et al. 2013; Sangsukiam and Duangmal 2017).

In addition, many studies have shown that reactive oxygen species (ROS) play a pivotal role in seeds germination as signaling molecules. Gomes and Garcia (2013) use ROS theory to explain the germination procedure. ROS derivate from the reduction of oxygen, which gives rise to superoxide radical, hydrogen peroxide radical, hydroxyl radical, and singlet oxygen (Carocho and Ferreira 2013). After quiescent seeds imbibing water, ROS intentionally generate from electron transport chain in mitochondria, electron transfer of photosynthesis in the chloroplast, lipid catabolism in glyoxysome, and among others (Bailly 2004).

However, excess ROS cause damage to DNA (Buetler et al. 2004), carbohydrate, protein, and lipids (Carocho and Ferreira 2013). The damage of ROS to DNA gives birth to a signal that seeds need produce more enzyme to protect themselves against ROS. Three different kinds of enzymes are then synthesized (Gill and Tuteja 2010) which include (i) enzymes for directly scavenging radicals, such as catalase, superoxide dismutase, and glutathione peroxidase; (ii) enzymes for synthesizing phenolic compounds, such as 3-dehydroquinate synthase, 3-dehydroquinate dehydratase, shikimate dehydrogenase, chalcone synthase, and chalcone isomerase; and (iii) enzymes for transformation of phenolic

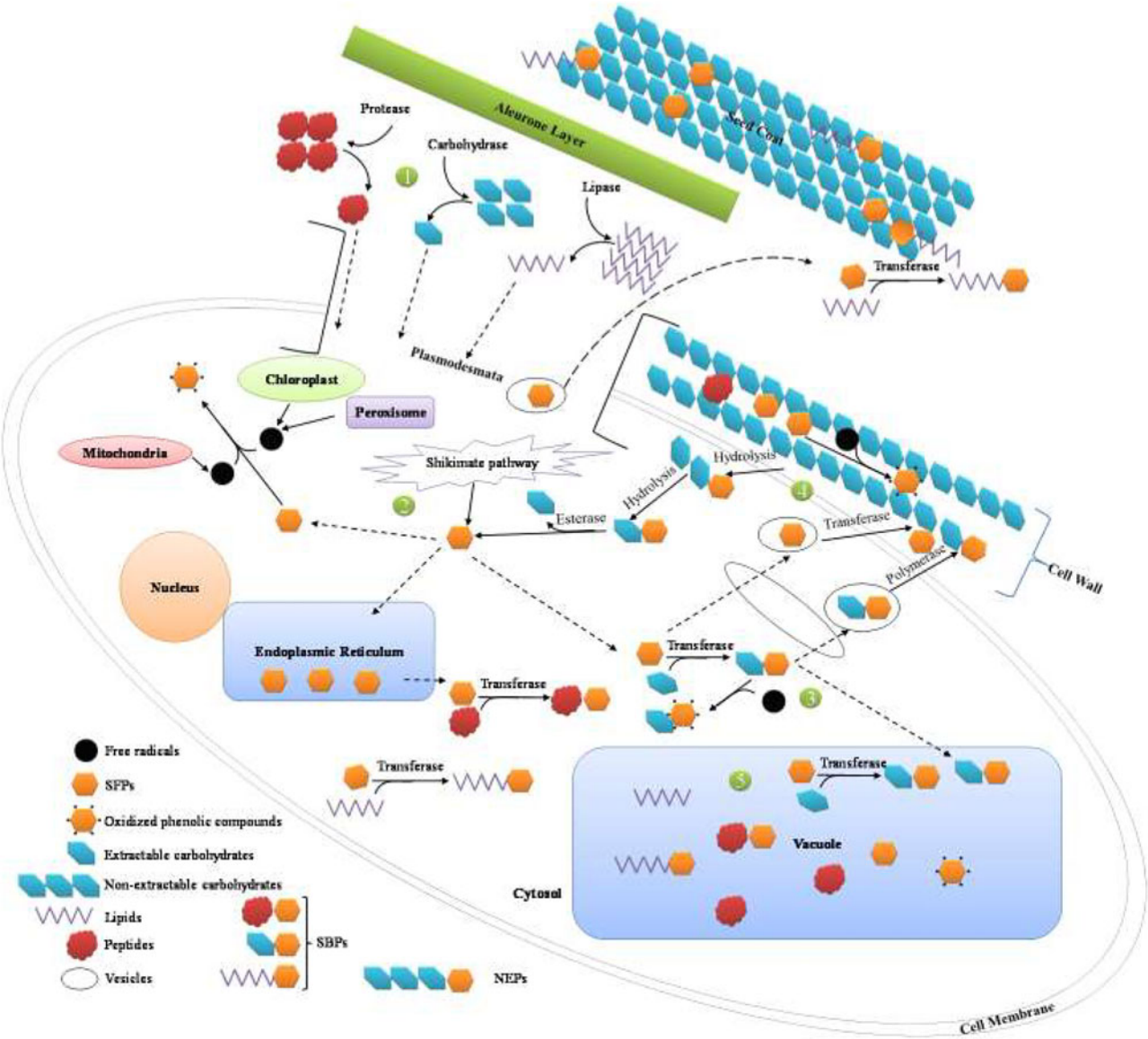

Figure 3. Proposed variation of phenolic compounds during seeds germination. (1) Gibberellic acids move from embryo to aleurone layer as molecular signals. Enzymes such as carbohydrase, proteinase, and lipase are synthesized and secreted. Starch, proteins, and lipids are degraded and transported into other cells for respiration and synthesis of new cell constituents; (2) Shikimate pathway synthesize *de novo* phenolic compounds and SFPs can also be released from their bound form with esterase; SFPs can be used for scavenging free radicals, synthesize superior phenolic compounds, and bound to moieties with transferases, such as glucosyltransferase, acyltransferase, and galactosyltransferase; (3) SBPs can be synthesized from SFPs or released from NEPs by hydrolase. SBPs can be consumed by scavenging free radicals, decomposing into SFPs, and transport to the cell wall to form NEPs; (4) NEPs are mainly synthesized from SFPs and SBPs. With enzymes, such as α-xylosidase, β-galactosidase, and β-glucosidase, NEPs can be converted into SBPs. In addition, NEPs can also be oxidized by free radicals; (5) Most of the SBPs storage in the vacuole. Moreover, phenolic compounds and nutrients can be combined with transferase in the vacuole.

compounds, such as acyltransferase, methyltransferase, and glycosyltransferase.

As a result, biopolymer moieties and phenolic parts in both extractable phenolic compounds and non-extractable phenolic compounds would be dramatically changed during cereal and pulse seeds germination.

Impact of germination on non-extractable phenolic compounds (NEPs)

Basically, cell walls are made up of insoluble polysaccharides and can be divided into cell wall on the endosperm and pericarp. They can combine phenolic compounds to protect nutrients from being decomposed by bacteria or insects (Fardet 2015).

During germination, cell wall on the surface of seeds would be loosened, divided, and become extensibility. Polysaccharides are major components of the cell wall. Taken pectin as an example, pectin would be demethylesterificated by methylesterases during germination, which makes cell wall of seeds extensible (Muller et al. 2013). In addition, new varieties of polysaccharides can be synthesized to extend the spatial of the seeds. For instance, xyloglucan can be synthesized by biosynthetic enzymes, including α-fucosyltransferase, β-galactosyltransferase, α-xylosyltransferase, and β-(1,4)-glucan synthase (Buckeridge 2010).

However, the endosperm cell wall would be degraded which exposes nutrients to enzymes (Andriotis et al. 2016). Galactomannans and mannans family are the constituents of the endosperm cell wall. They can be decomposed by enzymes, such as α-galactosidase, *endo*-β-mannanase, and *exo*-β-mannosidase, after being activated during germination. In addition, xyloglucan would disappear due to activation of enzymes, such as α-xylosidase, β-galactosidase, β-glucosidase, and xyloglucan-endo-β-glucanase (Buckeridge 2010). As a result, germination can change the composition of polysaccharides which are connected to phenolic compounds

Formation of non-extractable phenolic compounds (NEPs) during germination

Phenolic compounds bound to the insoluble polysaccharides may increase upon germination due to activated enzymes. Dueñas et al. (2016) reported that *p*-coumaric acid, ferulic acid, and sinapic acid bound to the insoluble fiber in dark beans were potentiated dramatically during germination, from 0.22, n.d, and 0.37 μg/g to 8.18, 25.90, and 2.60 μg/g, respectively (Table 2). Y. Wang et al. (2016) reported that *p*-coumaric acid, ferulic acid, and sinapic acid bound to the insoluble moieties in black rice increased 11.8, 5.3, and 1.4 times, respectively, after 96 h germination (Table 2). The activation of both enzymes in the phenylpropanoid biosynthetic pathway and endogenous esterases is postulated to be one of the core reasons for such increase (Wang et al. 2016).

The formation of NEPs can also be attributed to cell division. The extension of the cell wall is accompanied with cell growth, which induces phenolic compounds to be transferred onto the cell wall. Wang et al. (2015) reported that the content of caffeic acid, *p*-coumaric acid, and ferulic acid hydrolyzed from insoluble part of flaxseed was 0.26, 0.63, and 1.60 mg/100g (d.w.), which increased to 8.49, 7.13 and 9.85 mg/100g (d.w.), respectively, after germination.

Consumption of non-extractable phenolic compounds (NEPs) during germination

Non-extractable phenolic compounds (NEPs) are consumed when phenolic compounds scavenge radicals generated during germination resulting in the formation of polymers. Dueñas et al. (2016) reported that insoluble flavonoids and tannins, including (+)-catechin, procyanidin, luteolin, kaempferol, and quercetin, were consumed after germination in dark beans and lentils (Table 2). The decrease of some insoluble anthocyanidins, phenolic acids, and flavonols was also observed in corn after germination (Paucar-Menacho et al. 2017).

In addition, NEPs can be converted into extractable ones with the hydrolysis of insoluble moieties by enzymes, such as amylases, proteases, α-glucanase, and other hydrolytic enzymes. These enzymes can degrade the biopolymer moieties of NEPs. For instance, the phenolic acids associated with arabinoxylan and β-glucan in quinoa seeds were released after germination (Carciochi et al. 2016). In fact, NEPs in barley attenuated significantly after malting, while the PSBPs potentiated was observed in the barley malting (Dvořáková et al. 2008). The authors inferred that the increase of PSBPs might be from the hydrolysis of NEPs.

Impact of germination on extractable phenolic compounds (EPs)

During seed germination, microbial and environmental stresses can produce free radicals to damage seeds. It is necessary to develop a defense mechanism through the synthesis of secondary metabolites (Sangsukiam and Duangmal 2017). Therefore, EPs, including NPSEPs and PSEPs are believed to be the intermediates of the defensive compounds or the direct radical scavengers. As NPSEPs and PSBPs are both soluble bound phenolic compounds (SBPs), they are assumed to have a similar metabolic mechanism. Therefore, this section would be discussed based on SFPs and SBPs.

Formation of soluble free phenolic compounds (SFPs) during germination

In general, there are three potential routes accounting for the formation of SFPs during seed germination. First, the increase of SFPs can be attributed to inversion from bound phenolic compounds. As the protease, carbohydrase, and lipase would be released from aleurone layer of seeds to endosperm or activated directly in the endosperm. These enzymes result in the hydrolysis of proteins, carbohydrates, and lipids. The phenolic compounds bound to these moieties might be released as SFPs. Kim et al. (2016) reported that free functional components, such as phenolic acids and flavonoids (Table 3), significantly increased during germination, while bound functional components substantially attenuated over the course of 6 days of germination. The author proposed that some NEPs had been converted into SFPs during germination. Carciochi et al. (2016) explained that endogenous esterases synthesized during germination may be responsible for the release of phenolic compounds originally bound in the seed matrix.

Second, during seed germination, protein, starch, and lipids can be decomposed into amino acids, glucose, and acetyl CoA that are the direct or indirect substrates for *de novo* synthesis of phenolic compounds. Consequently, the rise of the enzyme responsible for the conversion of these substrates into phenolic compounds is important as well (Carciochi et al. 2016). El-Soud et al. (2013) treated chickpea seeds with 50 ppm of ellagic acid to assess the variation in the sensitivity of chickpea seedlings to osmotic stress. Briefly, a remarkable increase of phenylalanine ammonia lyase and chalcone synthase were observed along with the potentiated tolerance of chickpea seedlings to osmotic stress (El-Soud et al. 2013). This mechanism can also be used to explain the increase of free phenolic compounds during flaxseed (*Linum usitatissimum* L.) germination as reported by Wang et al. (2015). For 10 days of germination, free caffeic acid and *p*-coumaric acid in flaxseed kept increasing, from 0.26 and 0.26 mg/100g (d.w.) to 16.54 and 4.33 mg/100g (d.w.), respectively (Table 3).

Third, the regulation of excessive ROS is also a potential pathway to potentiate the yield of SFPs. During photosynthesis

Table 2. Non-extractable phenolic compounds (NEPs) changed during seed germination.

Seeds and germination time	Classes	Phenolic compounds	Ungerminated (μg/g)*	Germinated (μg/g)	Moieties	References
Adlay seed (*Coix lachryma-jobi* L.)	Hydroxycinnamic acids	*p*-Coumaric acid	13.84	17.45	N.A.	(Xu et al. 2017)
Germinated 4.5 days		Ferulic acid	34.21	26.69	N.A.	
		Isoferulic acid	22.9	21.67	N.A.	
Black mung bean Germinated 5 days	Hydroxycinnamic acids	Caffeic acid	2.51 mg/100 g d.w.	6.72 mg/100 g d.w.	N.A.	(Gan et al. 2016b)
		Ferulic acid	2.10 mg/100 g d.w.	5.57 mg/100 g d.w.	N.A.	
		p-Coumaric acid	1.50 mg/100 g d.w.	22.0 mg/100 g d.w.	N.A.	
	Flavone	Apigenin flavone glucoside	41.5 mg/100 g d.w.	1.92 mg/100 g d.w.	N.A.	
		Apigenin-6-C-glucoside	14.4 mg/100 g d.w.	n.d.	N.A.	
Black soybean (*Glycine max* L.)	Hydroxycinnamic acids	Chlorogenic acid	2.35	5.55	N.A.	(Kim et al. 2016)
Germinated 4 days		Caffeic acid	0.38	15.6	N.A.	
		p-Coumaric acid	3.23	4.38	N.A.	
	Flavonol	Quercetin	2.46	2.55	N.A.	
		(+)-Catechin	7.2	15.09	N.A.	
	Flavanone	Naringin	37.85	42.06	N.A.	
		Hesperidin	n.d.	3.45	N.A.	
	Hydroxybenzoic acids	Salicylic acid	3.48	2.25	N.A.	
		Protocatechuic acid	0.81	0.27	N.A.	
		Veratric acid	1.13	0.61	N.A.	
	Isoflavone	Biochanin	0.88	n.d.	N.A.	
Black rice (BP602)	Hydroxycinnamic acids	Sinapic acid	39	54.6	N.A.	(Wang et al. 2016)
Germinated 4 days		Ferulic acid	207.3	1098.6	N.A.	
		p-Coumaric acid	42.5	501	N.A.	
Dark beans (*Phaseolus vulgaris* L.)	Hydroxybenzoic acids	Protocatechuic acid	7.1	n.d.	Insoluble fiber	(Gan et al. 2016a;
Germinated 7 days		Protocatechuic aldehyde	7.23	n.d.	Insoluble fiber	Gan et al. 2016a)
		p-Hydroxybenzoic acid	2.86	n.d.	Insoluble fiber	
		p-Hydroxybenzoic aldehyde	3.25	n.d.	Insoluble fiber	
	Hydroxycinnamic acids	Sinapoyl aldaric acid	0.34	n.d.	Insoluble fiber	
		trans-*p*-Coumaric acid	0.22	8.18	Insoluble fiber	
		trans-Ferulic acid	n.d.	25.9	Insoluble fiber	
		Sinapic acid	0.37	2.6	Insoluble fiber	
	Flavonol	Kaempferol dihexo-side-rhamnoside	1.06	n.d.	Insoluble fiber	
		Quercetin derivative	n.d.	0.36	Insoluble fiber	
		Kaempferol-*O*-acylhexoside	n.d.	0.12	Insoluble fiber	
Flaxseed (*Linum usitatissimum* L.)	Hydroxycinnamic acids	Caffeic acid	0.23 mg/100g d.w.	7.40 mg/100g d.w.	N.A.	(Wang et al. 2015)
Germinated 10 days		*p*-Coumaric acid	0.63 mg/100g d.w.	6.57 mg/100g d.w.	N.A.	
		Ferulic acid	1.60 mg/100g d.w.	7.52 mg/100g d.w.	N.A.	
Green mung bean (*Vigna radiata*)	Hydroxycinnamic acids	Caffeic acid	3.16 mg/100 g d.w.	46.6 mg/100 g d.w.	N.A.	(Gan et al. 2016a)
Germinated 5 days		Ferulic acid	2.03 mg/100 g d.w.	8.26 mg/100 g d.w.	N.A.	
		p-Coumaric acid	1.50 mg/100 g d.w.	39.7 mg/100 g d.w.	N.A.	
	Flavone	Apigenin flavone glucoside	38.6 mg/100 g d.w.	1.39 mg/100 g d.w.	N.A.	
		Apigenin-6-C-glucoside	11.8 mg/100 g d.w.	n.d.	N.A.	
Lentils (*Lens culinaris* L.)	Hydroxybenzoic acids	Gallic acid	2.54	1.75	Insoluble fiber	(Dueñas et al. 2016)
Germinated 7 days		Gallic aldehyde	2.23	0.62	Insoluble fiber	
		Protocatechuic acid	4.27	2.1	Insoluble fiber	
		Protocatechuic aldehyde	8.84	5.69	Insoluble fiber	
		p-Hydroxybenzoic acid	2.48	n.d.	Insoluble fiber	
		p-Hydroxybenzoic aldehyde	1.45	1.11	Insoluble fiber	
		p-vanillin	51.36	n.d.	Insoluble fiber	
		Vanillic acid	n.d.	2.25	Insoluble fiber	
	Flavanol	(+)-Catechin-3-*O*-hexoside	0.84	n.d.	Insoluble fiber	
		(+)-Catechin	0.53	n.d.	Insoluble fiber	
	Flavone	Luteolin rhamnoside-hexoside	0.36	n.d.	Insoluble fiber	

	Flavonol	Kaempferol dihexoside	1.37	Insoluble fiber	
		Kaempferol rutinoside	0.3	Insoluble fiber	
		Quercetin-3-*O*-glucoside	1	Insoluble fiber	
		Kaempferol rhamnoside dihexoside	n.d.	Insoluble fiber	
		Kaempferol-3-*O*-glucoside	0.61	Insoluble fiber	
		Kaempferol	1.64	Insoluble fiber	
Red rice (BP480)	Hydroxycinnamic acids	Sinapic acid	32.2	N.A.	(Wang et al. 2016)
Germinated 4 days		Ferulic acid	167.9	N.A.	
		p-Coumaric acid	79.5	N.A.	
White rice (BP015)	Hydroxycinnamic acids	Sinapic acid	32.2	N.A.	(Wang et al. 2016)
Germinated 4 days		Ferulic acid	227.5	N.A.	
		p-Coumaric acid	97.8	N.A.	

	Flavonol	Kaempferol dihexoside	n.d.	Insoluble fiber	
		Kaempferol rutinoside	n.d.	Insoluble fiber	
		Quercetin-3-*O*-glucoside	n.d.	Insoluble fiber	
		Kaempferol rhamnoside dihexoside	2.45	Insoluble fiber	
		Kaempferol-3-*O*-glucoside	n.d.	Insoluble fiber	
		Kaempferol	n.d.	Insoluble fiber	
Red rice (BP480)	Hydroxycinnamic acids	Sinapic acid	51.5	N.A.	(Wang et al. 2016)
Germinated 4 days		Ferulic acid	906.4	N.A.	
		p-Coumaric acid	445.2	N.A.	
White rice (BP015)	Hydroxycinnamic acids	Sinapic acid	41.8	N.A.	(Wang et al. 2016)
Germinated 4 days		Ferulic acid	705.3	N.A.	
		p-Coumaric acid	371.6	N.A.	

Note: *In general, the unit is μg/g, except the unit followed with numbers; n.d., not detected; d.w., dry weight; N.A., not available.

of chloroplast, some electron would be overcharged to generate free radicals. More free radicals would stimulate the gene to transcribe more enzyme to protect organelles from the attack of free radicals, such as enzymes work in the shikimate pathway. Liu et al. (2016) studied the effect of light-emitting diodes on pea (*Pisum sativum* L.) germination and found that germination with blue, red, yellow light can increase the concentration of phenolic acids and flavonoids compared to the dark condition.

Consumption of soluble free phenolic compounds (SFPs) during germination

One mechanism corresponding to the consumption of SFPs during germination is their capacity for the neutralization of ROS. As is well known, numerous free radicals generate during seed germination. SFPs can donate hydrogen or electron to scavenging free radicals which in return become relatively stable phenolic compounds radicals (Pisoschi and Pop 2015).

Phenoloxidase and peroxidase enzymes might lead to a decrease in amount of SFPs as well. During germination, the phenoloxidase and peroxidase enzymes increase in seeds (Canada 1985). These enzymes can oxidize a wide range of hydrogen donors, including phenolic acids, flavonoids, and polyphenols (Richard-Forget and Gauillard 1997). Xu et al. (2017) studied the changes of nutritional properties of adlay seeds during a 60 h of germination. They speculated that the decrease of free phenolic acids, such as syringic acid and ferulic acid, may be oxidized by these enzymes (Table 3).

The other mechanism responsible for the consumption of SFPs is that the original phenolic acids are metabolized either bound to the moieties like quinic acid, or converted into superior phenolic compounds like flavonoids and then bound to moieties or polymerized (Terpinc et al. 2016). In addition, SFPs can be transported to the cell wall with vesicles and form NEPs (Shahidi and Yeo 2016).

Impact of germination on soluble bound phenolic compounds (SBPs)

The impact of germination on SBPs is complicated and can be generally described in two-fold. On one hand, the transformation of soluble moieties on SBPs, such as soluble carbohydrates, proteins, and lipids determine the changes of SBPs after germination. On the other hand, the changes of phenolic compounds also contribute to the final quantity of SBPs after germination. During seed germination, SBPs can be synthesized through the connection of the *de novo* phenolic compounds and the soluble moieties. Meanwhile, original soluble moieties are decomposed, while *de novo* soluble moieties are synthesized during germination. In this regard, synthesis enzymes and hydrolytic enzymes dominate these reactions and lead to the modification of SBPs both in structure and amounts (Wang et al. 2014).

Soluble carbohydrates transformation during germination

The average carbohydrates content is around 50–70% in different seeds. Carbohydrates in seeds can be divided into

Table 3. Soluble free phenolic compounds (SFPs) changed during seed germination.

Seeds and germination time	Classes	Phenolic compounds	Ungerminated (μg/g)*	Germinated (μg/g)	References
Adlay seed (*Coix lachryma-jobi* L.)	Hydroxybenzoic acids	Protocatechuic acid	1.27	29.45	(Xu et al. 2017)
Germinated 4.5 days		*p*-Hydroxybenzoic acid	28.06	85.90	
		Vanillic acid	11.21	39.28	
		Syringic acid	17.20	4.68	
	Hydroxycinnamic acids	*p*-Coumaric acid	3.11	63.86	
		Ferulic acid	8.67	5.43	
		Isoferulic acid	7.07	6.25	
		Chlorogenic acid	66.17	14.80	
		Caffeic acid	5.26	120.43	
Black soybean (*Glycine max* L.)	Hydroxybenzoic acids	Gallic acid	1.11	n.d.	(Kim et al. 2016)
Germinated 4 days		Veratric acid	2.17	0.53	
		Protocatechuic acid	85.57	57.36	
		Salicylic acid	13.01	15.39	
	Hydroxycinnamic acids	Phloretic acid (Hydro-*p*-coumaric acid)	70	130.58	
		p-Coumaric acid	2.96	0.39	
		Ferulic acid	2.14	2.21	
	Flavanone	Naringin	107.10	135.77	
		Naringenin	31.44	161.58	
	Isoflavone	Biochanin	0.17	7.2	
Buckwheat (*Fagopyrum esculentum Moench*)	Hydroxybenzoic acids	Gallic acid	2.62	5.92	(Zhang et al. 2015)
Germinated 3 days		3,4-Dihydroybenzoic acid	n.d.	4.58	
		2,3,4-Trihydroxybenzoic acid	1.68	1.57	
		p-Hydroxybenzoic acid	19.59	84.75	
		Vanillic acid	1.20	8.81	
		Syringic acid	n.d.	7.20	
	Hydroxycinnamic acids	Chlorogenic acid	7.83	126.78	
		Caffeic acid	8.03	6.35	
		p-Coumaric acid	1.74	6.13	
		Ferulic acid	4.37	6.02	
		Sinapic acid	2.20	2.84	
		trans-3-Hydroxycinnamic acid	0.75	148.08	
	Flavone	Myricetin	n.d.	3.84	
		Luteolin	1.87	2.06	
	Flavonol	Quercetin	n.d.	1.61	
		Kaempferol	0.95	3.73	
Flaxseed (*Linum usitatissimum* L.)	Hydroxycinnamic acids	Caffeic acid	0.26 mg/100 g d.w.	16.54 mg/100 g d.w.	(Wang et al. 2015)
Germinated 10 days		*p*-Coumaric acid	0.26 mg/100 g d.w.	4.33 mg/100 g d.w.	
Purple corn (*Zea mays* L.) Germinated 6 days	Hydroxybenzoic acids	Vanillic acid	4.92	6.08	(Paucar-Menacho et al. 2017)
Quinoa seeds (*Chenopodium quinoa* Willd.) Germinated 3 days	Hydroxybenzoic acids	*p*-Hydroxybenzoic acid	0.22 mg/100 g d.w.	0.94 mg/100 g d.w.	(Carciochi et al. 2016)
		Vanillic acid	0.88 mg/100 g d.w.	8.54 mg/100 g d.w.	
	Hydroxycinnamic acids	*p*-Coumaric acid	0.09 mg/100 g d.w.	1.96 mg/100 g d.w.	
		Ferulic acid	0.57 mg/100 g d.w.	3.61 mg/100 g d.w.	
	Flavonol	Quercetin	0.23 mg/100 g d.w.	1.36 mg/100 g d.w.	
		Kaempferol	0.15 mg/100 g d.w.	0.27 mg/100 g d.w.	
Soybean (*Glycine max* L.)	Hydroxybenzoic acids	Benzoic acid	127.12 μmol/100 g d.w.	75.14 μmol/ 100 g d.w.	(Guzmán-Ortiz et al. 2017)
Germinated 6 days		Gallic acid	134.22 μmol/100 g d.w.	420.10 μmol/100 g d.w.	
		Syringic acid	44.18 μmol/100 g d.w.	323.46 μmol/100 g d.w.	
		Vanillic acid	4.32 μmol/100 g d.w.	n.d.	
	Hydroxycinnamic acids	Chlorogenic acid	7.80 μmol/100 g d.w.	142.27 μmol/100 g d.w.	
		Ferulic acid	48.48 μmol/100 g d.w.	48.60 μmol/100 g d.w.	
		p-Coumaric acid	20.95 μmol/100 g d.w.	52.79 μmol/100 g d.w.	
	Flavanol	Catechin	38.38 μmol/100 g d.w.	159.95 μmol/100 g d.w.	
		Protocatechuic acid	39.06 μmol/100 g d.w.	173.21 μmol/100 g d.w.	
	Flavonol	Quercetin	523.82 μmol/100 g d.w.	955.29 μmol/100 g d.w.	

Note: *In general, the unit is μg/g, except the unit followed with numbers; n.d., not detected; d.w., dry weight.

sugars (monosaccharides, disaccharides, and oligosaccharides), starch (polysaccharides), and dietary fibers (polysaccharides) with the ratio approximately of 15, 50, and 35%, respectively (Hall et al. 2017).

Total carbohydrates are supposed to be attenuated during germination as they are the energy and carbon source for seed germination. Enzymes, such as α-amylase, β-amylase, β-glucanase, and arabinofurosidase are reported to hydrolyze starch and dietary fibers into sugars (Hübner and Arendt 2013; Kaukovirta-Norja et al. 2004). These sugars, especially monosaccharides, participate in oxidation pentose phosphate pathway, glycolysis pathway, shikimate pathway, and Krebs cycle to produce energy and secondary metabolites during seed germination (Sattar, Ali, and Hasnain 2017). The degradation of total starch and dietary fiber contents has been detected in germinated pulse seeds (Sozer et al. 2017) and

cereal seeds (Hübner and Arendt 2013). Different seeds have different reductions of starch. For instance, germinations of mung bean, chickpea, and cowpea were reported to have 5–6% reductions (Uppal and Bains 2012), while kidney bean was observed to reduce 50% of starch (Mbithi et al. 2001). Germination of lupin and soybean did not affect the starch content, but decreased the oligosaccharide content, and increased the total sugar (Kaczmarska et al. 2017).

Excessive ROS is another vital factor responsible for the decrease of carbohydrates. During the initial stages of carbohydrates synthesis, shorter chain species of sugar are formed, such as glycoaldehyde, whose chain is too short to form a ring structure. These shorter chain sugars can be oxidized by ROS instead of forming C5 and C6 sugar (Carocho and Ferreira 2013).

In consequence, the transformation of carbohydrates connecting to phenolic compounds would result in the dramatic changes of SBPs during seed germination.

Soluble bound phenolic compounds (SBPs) increased during germination. The formation of SBPs can be initiated by the phenolic compounds esterifying to the newly formed soluble carbohydrates via glycoside. López et al. (2013) employed HPLC–ESI/MS to analyze phenolic compounds extracted from germinated and ungerminated pulses. Derivatives of ferulic and *p*-coumaric acid were identified with a fragment molecular ion $[M\text{-}H]^-$ at m/z 209.1 corresponding to the aldaric acid residue, which was a proof of phenolic compounds esterified with carbohydrates. Besides glycoside, malonyl glucosides and acetyl glucosides were also reported by researchers (Lin and Lai 2006).

With the accumulation of free phenolic compounds, enzymes such as glucosyltransferase, galactosyltransferase, and acyltransferase are activated to connect phenolic acids with soluble carbohydrates (Bontpart et al. 2015; Ono et al. 2010). Zhang et al. (2015) conveyed that C-glycosyl flavones in buckwheat dramatically produced for 3 days of germination, as the contents of luteolin 8-C-glucoside (orientin), luteolin 6-C-glucoside (isoorientin), apigenin 8-C-glucoside (vitexin), and apigenin-6-C-glucoside (isovitexin) increased from 1.72, 0.95, 1.29, and 1.36 μg/g to 478.31, 500.23, 477.20, and 515.47 μg/g, respectively.

In addition to the new synthesis, the degradation of NEPs to SBPs may also be important during germination (Terpinc et al. 2016). This was evidenced by the study of Koyama et al. (2013) who observed that rutin in buckwheat kernel increased during soaking step of germination, which was transferred from the NEPs in the hull.

Soluble bound phenolic compounds (SBPs) decreased during germination. Similar to the consumption of SFPs, SBPs can also be consumed by free radicals and phenoloxidase during germination. Additionally, the decrease of SBPs may be due to the induction of phenolic acid esterases (Rao and Muralikrishna 2004). Rao and Muralikrishna (2004) reported that during germination, coumaric acid and ferulic acid bound to soluble polysaccharides in rice (9.43 and 104 μg/g), maize (22.75 and 8.36 μg/g), wheat (0.28 and 98.0 μg/g), and ragi seeds (5.91 and 209 μg/g) decreased to 2.98 and 68.0 μg/g, 8.36 and 35.4 μg/g, 0.89 and 49.3 μg/g, 0.88 and 86.8 μg/g, respectively. They speculated the results may be attributed to the phenolic acid esterases. Tapin et al. (2006) used feruloyl esterase to release phenolic compounds from wheat and the enzyme effectively increased the liberation of phenolic compounds such as ferulic acid and coumaric acid on SBPs.

Move over, the decomposing of the seed coat may release some SBPs from the cell wall which can be further broken down by enzymes. Gan et al. (2016b) reported that apigenin flavone glucoside and apigenin-6-C-glucoside dropped sharply during germination of black and green mung bean (Table 4). They concluded that the apigenin flavone glucoside and apigenin-6-C-glucoside were from the seed coat. Thereafter, the SBPs bound with carbohydrates attenuated as the seed coat faded away with 5 days of germination.

Making this more complicated, Dueñas et al. (2016) reported that some SBPs in Dark beans (*Phaseolus vulgaris* L.) diminished after germination, such as protocatechuic aldehyde, *p*-hydroxybenzoic acid, *p*-hydroxybenzoic aldehyde, while others like sinapoyl aldaric acid and *trans*-ferulic acid increased sharply. Meanwhile, some phenolic acids in lentils (*Lens culinaris* L.) such as *p*-hydroxybenzoic acid had no significant change after germination (Table 4).

Protein and lipid transformation during germination

Both protein and lipid are the energy source for seed germination (Yan et al. 2014). In general, protein content increases during germination. Although many proteins can be hydrolyzed by protease into amino acids, dipeptides, and polypeptides, these substances can be synthesized into *de novo* proteins again, such as enzymes (Sattar, Ali, and Hasnain 2017). In this point, proteases change the configuration of protein rather than the content of protein. In addition, due to the respiration, the dry weight of seeds decreases, which results in the increase of the protein percentage.

Lipids are metabolized into energy and sugar during seed germination. Briefly, with the activation of lipase, free fatty acids can be hydrolyzed from triacylglycerides. Free fatty acids are transferred into peroxisome (also called glyoxysome in oilseeds) and generate reducing power and acetyl-CoA, which is called β-oxidation. Thereafter, acetyl-CoA converts into sucrose with the glyoxylate cycle and gluconeogenesis (Borek et al. 2015; Gibbons et al. 2000; Yan et al. 2014).

During germination, excessive ROS may be produced, which would covalently oxidize proteins (Gill and Tuteja 2010). ROS can form cross-linkage due to the propagation of free radicals. For instance, ROS can abstract two H atom from two different cysteine residues to form disulfide bridges (Hancock et al. 2006). In addition, free radical can cleave peptide bonds (Carocho and Ferreira 2013). Furthermore, amino acids can be carbonylated by ROS. For instance, cysteine residues of protein can be carbonylated into cysteic acid thus losing its bioactivity as protein (Gill and Tuteja 2010).

Additionally, an excessive amount of ROS generate during seed germination can damage lipid mainly with two procedures. ROS can oxidize polyunsaturated fatty acids to generate lipid radicals, which then react with oxygen

Table 4. Soluble bound phenolic compounds (SBPs) changed during seed germination.

Seeds and germination time	Classes	Phenolic compounds	Ungerminated (μg/g)*	Germinated (μg/g)	Moieties	References
Black mung bean (*Vigna radiata*)	Flavonol	Rutin	n.d.	84.9 mg/100 g d.w.	Disaccharide	(Gan et al. 2016b)
Germinated 5 days	Flavone	Apigenin flavone glucoside	78.7 mg/100 g d.w.	11.9 mg/100 g d.w.	Monosaccharide	
	Flavone	Apigenin-6-C-glucoside	99.0 mg/100 g d.w.	n.d.	Monosaccharide	
Buckwheat (*Fagopyrum esculentum Moench*)	Flavone	8-C Glucoside of luteolin	1.72	478.31	Monosaccharide	(Zhang et al. 2015)
		Luteolin-6-C-glucoside	0.95	500.23	Monosaccharide	
Germinated 3 days		Vitexin	1.29	477.2	Monosaccharide	
		Isovitexin (apigenin-6-C-glucoside)	1.36	515.47	Monosaccharide	
	Flavonol	Quercetin-3-*O*-rutinoside	131.18	551.89	Disaccharide	
		Kaempferol-3-*O*-rutinoside	0.29	1.57	Disaccharide	
		Quercitrin	0.12	0.95	Monosaccharide	
Dark beans (*Phaseolus vulgaris* L.)	Hydroxybenzoic acids	Gallic aldehyde	n.d.	0.23	Soluble fiber	(Dueñas et al. 2016)
Germinated 7 days		Protocatechuic acid	1.18	1.07	Soluble fiber	
		Protocatechuic aldehyde	2.38	n.d.	Soluble fiber	
		p-Hydroxybenzoic acid	2.2	0.53	Soluble fiber	
		p-Hydroxybenzoic aldehyde	1.54	0.34	Soluble fiber	
	Hydroxycinnamic compounds	Sinapoyl aldaric acid	n.d.	0.13	Soluble fiber	
		trans-Ferulic acid	n.d.	0.76	Soluble fiber	
Green mung bean (*Vigna radiata*)	Flavonol	Rutin	n.d.	84.9 mg/100 g d.w.	Disaccharide	(Gan et al. 2016b)
Germinated 5 days	Flavone	Apigenin flavone glucoside	83.0 mg/100 g d.w.	4.65 mg/100 g d.w.	Monosaccharide	
	Flavone	Apigenin-6-C-glucoside	118.0 mg/100 g d.w.	n.d.	Monosaccharide	
Lentils (*Lens culinaris* L.)	Hydroxybenzoic acids	*p*-Hydroxybenzoic acid	1.27	1.27	Soluble fiber	(Dueñas et al. 2016)
Germinated 7 days		*p*-Hydroxybenzoic aldehyde	0.77	0.62	Soluble fiber	
	Flavonol	Kaempferol-3-*O*-glucoside	0.56	n.d.	Soluble fiber	
		Kaempferol diglucoside	n.d.	0.51	Soluble fiber	
Purple corn (*Zea mays* L.)	Anthocyanidin	(Epi)catechin (4-8)-Cyanidin 3,5 diglucoside	183.87	53.94	Disaccharide	(Paucar-Menacho et al. 2017)
Germinated 6 days		(Epi)catechin (4-8)-Pelargonidin 3,5 diglucoside	25.44	14.17	Disaccharide	
		(Epi)catechin (4-8)-Cyanidin 3,5 diglucoside	29.35	18.41	Disaccharide	
		(Epi)catechin (4-8)-Peonidin 3,5 diglucoside	19.76	18.28	Disaccharide	
		(Epi)catechin (4-8)-Cyanidin 3-malonylglucoside-5 glucoside	60.88	23.07	Disaccharide	
		Cyanidin 3,5 diglucoside	25.01	16.25	Disaccharide	
		Cyanidin 3-*O*-glucoside	1406.96	926.06	Monosaccharide	
		(Epi)Catechin (4-8)-Pelargonidin 3,5 diglucoside	32.7	24.29	Disaccharide	
		Pelargonidin 3-*O*-glucoside	111.57	55.62	Monosaccharide	
		Cyanidin 3-*O*-malonylhexoside	61.05	37.09	Monosaccharide	
		Peonidin-3-*O*-glucoside	163.75	156.21	Monosaccharide	
		Cyanidin 3-*O*-malonylhexoside	98.66	100.49	Monosaccharide	
		Cyanidin 3-*O*-(6"-malonylglucoside)	820.7	553.24	Monosaccharide	
		Delphinidin 3-*O*-glucoside	47.36	n.d.	Monosaccharide	
		Peonidin 3-*O*-(6"-malonylgucoside)	20.06	26.58	Monosaccharide	
		Pelargonidin 3-*O*-(6"malonylgucoside)	117.6	88.86	Monosaccharide	
		Cyanidin 3-*O*-(3",6"-dimalonylglucoside)	37.6	28.15	Disaccharide	

		Peonidin 3-*O*-(6''-malonylglucoside)	208.81	239.51	Monosaccharide	
		Pelargonidin 3-*O*-(3'',6''-dimalonylglucoside)	59.01	53.19	Disaccharide	
		Peonidin 3-*O*-(3'',6''-dimalonylglucoside	34.59	52.55	Disaccharide	
	Hydroxybenzoic acids	Vanillic acid hexoside	n.d.	1.69	Monosaccharide	
	Hydroxycinnamic acids	Ferulic acid hexoside	0.76	n.d.	Monosaccharide	
	Flavone	2''-*O*-pentoside-8-C-hexoside Luteolin	12.19	5.97	Disaccharide	
	Flavonol	Kaempferol rhamnoside hexoside	13.23	12.6	Disaccharide	
		Quercetin 3-*O*-hexoside	22.83	13.98	Monosaccharide	
		Quercetin-3-*O*-rutinoside	35.91	23.4	Monosaccharide	
		Kaempferol-*O*-hexoside	n.d.	25.42	Monosaccharide	
		Isorhamnetin-*O*-hexoside	12.56	n.d.	Monosaccharide	
		Quercetin-*O*-glucoside	28.09	19.9	Monosaccharide	
		Isorhamnetin-3-*O*-rutinoside	28.65	16.76	Monosaccharide	
		Kaempferol-3-*O*-glucoside	42.38	n.d.	Monosaccharide	
		Isorhamnetin-3-*O*-glucoside	41.75	32.86	Monosaccharide	
		Kaempferol acetylhexoside	25.68	21.27	Monosaccharide	
Soybean (*Glycine max* L.) Germinated 6 days	Isoflavone	Daidzin	293.33 μmol/100 g d.w.	514.16 μmol/100 g d.w.	Monosaccharide	(Guzmán-Ortiz et al. 2017)
		Genistin	159.04 μmol/100 g d.w.	340.49 μmol/100 g d.w.	Monosaccharide	

Note: *In general, the unit is μg/g, except the unit followed with numbers; n.d., not detected; d.w., dry weight.

forming peroxyl radicals, hydroxyl radicals, etc. (Chen et al. 2013). The hydroxyl radicals are reactive and can attack the hydrophobic chain of phospholipids, the constituents of the cell membrane. Oxidized phospholipids then have a repulsion effect with each other and make the cell membrane bump and even breakdown (Gill and Tuteja 2010).

Currently, no detailed study has been performed to investigate the dynamic changes of phenolic-protein type of SBPs and resorcinol lipids during germination. More studies are encouraged to further elucidate the changes of protein-phenolic compounds and lipid-phenolic compounds during germination.

The metabolic process of phenolic compounds in germinated seeds

Due to the intricate bioreaction occurring during germination, comprehensive factors should be considered to clarify the transformation rules of phenolic compounds. Proposed variation of phenolic compounds during seeds germination is shown in Figure 3.

The increase of SFPs can stem from the shikimate pathway or the release from both SBPs and NEPs. The decrease of SFPs may due to the transformation of SFPs into SBPs and/or NEPs. Moreover, SFPs can be consumed by free radicals or phenoloxidase. The variation of SFPs (Δ SFP) can be obtained as the following equation:

$$\Delta\ \mathrm{SFP} = \ n'_{SFP} - n_{SFP} = n_{syn} + n_{rel} + n'_{rel} - n_{trans} - n'_{trans} - n'_{rs} \quad (1)$$

(n_{SFP}: SFP in ungerminated seeds; n'_{SFP}: SFP in germinated seeds; n_{syn}: SFP synthesized from shikimate pathway; n_{rel}: SFP released from SBP; n'_{rel}: SFP released from NEP; n_{trans}: SFP transformed into SBP; n'_{trans}: SFP transformed into NEP; n'_{rs}: SFP consumed by free radicals or enzymes)

SBPs, which including PSBPs and NPSEPs, can be derived from the transformation of SFPs and decomposition of NEPs during germination, while SBPs can decompose into SFPs and transform into NEPs. SBPs can also be consumed to scavenge radicals. The variation of SBPs (Δ SBP) can be described as the following equation:

$$\Delta\ \mathrm{SBP} \ = \ n'_{SBP} - n_{SBP} = n_{trans} + n''_{rel} - n_{rel} - n''_{trans} - n''_{rs} \quad (2)$$

(n_{SBP}: SBPs in ungerminated seeds; n'_{SBP}: SBPs in germinated seeds; n_{trans}: SFPs transformed into SBPs; n_{rel}: SFPs released from SBPs; n''_{rel}: SBPs released from NEPs

n''_{trans}: SBPs transformed into NEPs; n''_{rs}: SBPs consumed by free radicals or enzymes)

NEPs can be originated from the transformation of SFPs and SBPs during germination, while NEPs would be hydrolyzed and released into SFPs and SBPs. NEPs also protect seeds from free radicals and other oxidative stress. The variation of NEPs (Δ NEP) can be expressed as the following equation:

$$\Delta\ \mathrm{NEP} \ = \ n'_{NEP} - n_{NEP} = n'_{trans} + n''_{trans} - n'_{rel} - n''_{rel} - n'''_{rs} \quad (3)$$

(n_{NEP}: NEPs in ungerminated seeds; n'_{NEP}: NEPs in germinated seeds; n'_{trans}: SFPs transformed into NEPs; n''_{trans}:

SBPs transformed into NEPs; n'_{rel}: SFPs released from NEPs; n''_{rel}: SBPs released from NEPs; n'''_{rs}: SBPs consumed by free radicals or enzymes)

We set the change of total phenolic content (Δ TPC) as:

$$\Delta\ \mathrm{TPC} = \Delta\ \mathrm{SFP} + \Delta\ \mathrm{SBP} + \Delta\ \mathrm{NEP} \quad (4)$$

The total phenolic compounds consumed to scavenge free radicals and other oxidative stress is:

$$n_{rs} = n'_{rs} + n''_{rs} + n'''_{rs} \quad (5)$$

By combining Equations (1)–(5), a simplified Equation (6) is achieved:

$$\Delta\ \mathrm{TPC} = n_{syn} - n_{rs} \quad (6)$$

As shown in Equation (6), if the Δ TPC of germinated seeds increased, it means the phenolic compounds synthesized from shikimate pathway can scavenge excessive free radicals generated during germination. If the Δ TPC of germinated seeds decreased, it means the phenolic compounds synthesized from shikimate pathway cannot scavenge excessive free radicals. In order to keep seeds germinating, free radicals as a signal would stimulate DNA (El-Maarouf-Bouteau and Bailly 2008) to transcribe more enzymes for the shikimate pathway, such as phenylalanine ammonia lyase and chalcone synthase, or for directly radical scavenging, such as catalase, superoxide dismutase, and glutathione peroxidase generated during germination.

In addition, phenolic compounds consumed by scavenging radicals can be calculated using this equation, as the variation of total phenolic content can be estimated with different assays, such as Folin-Ciocalteu methods (Zheng et al. 2009) and HPLC-QTOF-MS (Mekky et al. 2015). The substrate of the shikimate pathway, such as phenylalanine, can be intentionally added. As a result, ΔTPC and Δn_{syn} can be estimated. With Equation (6), phenolic compounds consumed for scavenging radicals can be calculated. Based on this principle, Yu et al. (2016), reported the variation of individual phenolic compounds with feeding phenylalanine during peanut germination.

Conclusion

It is well documented that variation of phenolic compounds during seed germination is extremely complicated. To better understand this variation, the key step is to unify the term of raw phenolic compounds in cereal and pulse seeds by classifying them into non-extractable and extractable groups, with the latter being further divided into SFPs, SBPs (including PSBPs and NPSEPs).

Although the terms of raw phenolic compounds have been unified, the evaluation of antioxidant activity of natural phenolic compounds still has contradictory results in comparison with some of literature, since different extraction and evaluation methods can influence the evaluated phenolic compounds. Besides, other potential antioxidants (e.g. peptides, polysaccharides, and ascorbic acids) that remain in the extracts should be taken into account. Moreover, most of the phenolic compounds are connected with carbohydrates, proteins, and lipids in plants with a covalent bond, hydrogen bond, or electrostatic bond. The interaction between phenolic compounds and their moieties should be considered for the proper application of germinated seeds extracts.

SFPs can be synthesized and transformed with enzymes generated during seed germination. Germination of seeds can also affect the macromolecules, such as carbohydrates, proteins, and lipids, which results in the dramatical change of SBPs and NEPs. ROS are critical factors in understanding the effect of seeds germination on phenolic compounds as well.

In the future, more studies should be conducted and concentrated on the special extraction for each category of raw phenolic compounds and the evaluation methods of phenolic compounds. As such, the detected antioxidant activity can be correlated with the structural properties of the characterized categories, which helps identify natural antioxidants with superior efficacy. Additionally, the kinetic model should be set up and verified for the transformation of phenolic compounds with different categories during germination. With the kinetic model, one can better understand how phenolic compounds transform during cereal and pulse germination and target the formation of phenolic compounds with a particular interest.

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