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How postharvest variables in the pulse value chain affect nutrient digestibility and bioaccessibility

Dorine Duijsens | **Shannon Gwala** | **Andrea Pallares Pallares** | **Katharina Pälchen** | **Marc Hendrickx** | **Tara Grauwet**

Laboratory of Food Technology, Leuven Food Science and Nutrition Research Centre (LFoRCe), Department of Microbial and Molecular Systems (M2S), KU Leuven, Leuven, Belgium

Correspondence
Dorine Duijsens, Laboratory of Food Technology, Leuven Food Science and Nutrition Research Centre (LFoRCe), Department of Microbial and Molecular Systems (M2S), KU Leuven, Kasteelpark Arenberg 22 box 2457, 3001 Leuven, Belgium.
Email: dorine.duijsens@kuleuven.be

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Abstract

Pulses are increasingly being put forward as part of healthy diets because they are rich in protein, (slowly digestible) starch, dietary fiber, minerals, and vitamins. In pulses, nutrients are bioencapsulated by a cell wall, which mostly survives cooking followed by mechanical disintegration (e.g., mastication). In this review, we describe how different steps in the postharvest pulse value chain affect starch and protein digestion and the mineral bioaccessibility of pulses by influencing both their nutritional composition and structural integrity. Processing conditions that influence structural characteristics, and thus potentially the starch and protein digestive properties of (fresh and hard-to-cook [HTC]) pulses, have been reported in literature and are summarized in this review. The effect of thermal treatment on the pulse microstructure seems highly dependent on pulse type-specific cell wall properties and postharvest storage, which requires further investigation. In contrast to starch and protein digestion, the bioaccessibility of minerals is not dependent on the integrity of the pulse (cellular) tissue, but is affected by the presence of mineral antinutrients (chelators). Although pulses have a high overall mineral content, the presence of mineral antinutrients makes them rather poorly accessible for absorption. The negative effect of HTC on mineral bioaccessibility cannot be counteracted by thermal processing. This review also summarizes lessons learned on the use of pulses for the preparation of foods, from the traditional use of raw-milled pulse flours, to purified pulse ingredients (e.g., protein), to more innovative pulse ingredients in which cellular arrangement and bioencapsulation of macronutrients are (partially) preserved.

KEYWORDS
bioaccessibility, digestibility, macronutrients, minerals, pulses

1 | INTRODUCTION

Solutions need to be found to feed the expanding human population in a healthy and environmentally sustainable way. In this context, in 2019, the EAT–Lancet Commission defined a "planetary healthy diet" as a flexitarian diet mostly containing plant-based foods (Willett & Rockström, 2019). Pulses, the dry and edible grains of the *Fabaceae* family excluding oil extraction seeds (FAO, 1994), are increasingly being put forward as part of the abovementioned healthy and sustainable diets (WHO, 2019; Willett & Rockström, 2019) as they provide a wide array of nutrients

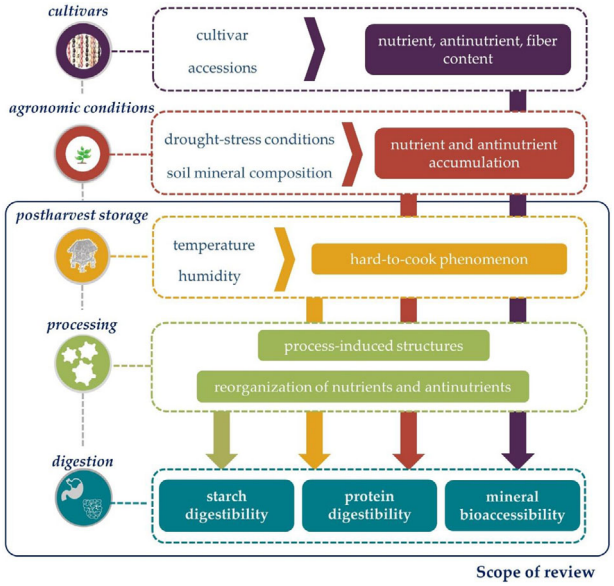

FIGURE 1 The complete pulse process chain: Factors affecting nutrient digestibility and bioaccessibility
Note: The blue box indicates the scope of this review.

including complex carbohydrates (slowly digestible starch and fiber), proteins, minerals, vitamins, and bioactive compounds. Pulses are an essential part in the diet of many populations, especially in developing countries, and are being reintroduced in developed countries at a fast pace after being out of fashion in the last decades. Pulses are grown under sustainable and environmentally friendly conditions and might be important crops for providing food security for future generations (FAO, 2019). Driven by the widely reported benefits of incorporating pulses in diets, government policy agendas, and more advanced seed technologies, the global pulse production has been rising steadily, reaching 92 billion kg in 2018 up from 70 billion kg in 2010 (FAO, 2021).

Before pulses are consumed, they pass along several agro-food chain stages (Figure 1). Each stage of the agro-food chain includes a broad set of variables, which can highly influence both the structure of foods (micro and macro) as well as the concentrations of nutrients and antinutrients. The pulse chain starts at the farm with the seeds that are planted. The cultivar or accession of the planted pulse seed is probably the first chain variable that can eventually affect nutrient bioaccessibility. Subsequently, the agronomic conditions under which pulses are cultivated (e.g., climate and soil conditions) influence the nutrient and antinutrient content accumulated in the seed. After harvesting, pulses are dried and stored for varying periods of time before processing. The stability of pulses upon long-term storage opens many possibilities for both subsistence farmers and the processing industry, in terms of stable seed reserves and production planning without seasonality constraints. However, prolonged storage at high temperature and relative humidity (e.g., over 25°C and 65%, respectively) can lead to the development of the undesirable hard-to-cook (HTC) phenomenon. HTC pulses require extended cooking times to become palatable, causing a decrease in their usability and nutritional and economic value (Aguilera & Stanley, 1985; Mattson, 1946; Walters, 1998). Pulses require a certain degree of processing before consumption, to increase their digestibility and make them more palatable. Preprocessing techniques such as soaking and dehulling are commonly followed by a thermal treatment such as cooking. Traditionally, pulses are consumed as whole seeds obtained after cooking at the household level, often incorporated into traditional dishes (such as dahl, different soups and stews) (Asif et al., 2013; Yadav et al., 2007). Chickpeas, dry beans, peas, and lentils are globally marketed whole, split, milled into flour, or in convenient, ready to (h)eat precooked forms (e.g., cans, pouches). More recently, pulses are being incorporated into several convenience foods as ingredients such as pulse flours or purified ingredients (Asif et al., 2013).

The EAT–Lancet Commission recommends a daily intake of 75 g of dry pulses (Willett et al., 2019). This daily consumption corresponds to a caloric intake of about 284 kcal, calculated using Atwater factors. However, the total amount of a particular macro- or micronutrient present in a pulse (or other plant-based food) does not reflect what is absorbed into the bloodstream because a not insignificant amount of the nutrients escapes gastrointestinal digestion (Capuano et al., 2018). In pulses, for instance, structural features (such as an intact cell wall and intracellular protein matrix) can act as a barrier hindering enzyme diffusion to the substrate (such as starch), affecting the rate and extent at which macronutrients are digested. As a consequence, the nutritional quality of foods such as pulses is attributed to both the concentration of nutrients present (e.g., high protein content) and their respective bioaccessibility, digestibility, and bioavailability (Seal & Brandt, 2007). Bioaccessibility refers to the amount of nutrient released from the food matrix and thus potentially available for absorption after digestion (Parada & Aguilera, 2007). Digestibility is a term used in the context of macronutrient digestion and refers to the enzymatic breakdown to smaller absorbable units (Rovalino-Córdova et al., 2018). Bioavailability refers to the amount of a nutrient that is absorbed into the bloodstream and is available at the active site (Etcheverry et al., 2012). *In vitro* digestion studies are of particular importance to unravel the patterns in which nutrients are hydrolyzed (digestibility) and released from the matrix (bioaccessibility) in a standardized, high-throughput, and inexpensive way (Mackie, 2020). Insights

acquired in these studies should lead to improved and more accurate predictions of the actual amount of nutrients and energy supplied by a food or meal upon ingestion. In turn, these improved predictions should lead to more accurate food labels and information, helping consumers to make informed and healthy choices.

To obtain insight into the digestibility and bioaccessibility of a particular nutrient, this review considers all factors across the pulse value chain, from the harvest of the seeds until digestion. The aim of this review is to give a complete overview of the current knowledge on how the different variables in the pulse value chain influence the nutritional quality of starch, protein, and minerals in different pulse types. Though important, other parameters, such as variables at the level of crop production, are outside of the scope of this review (see Figure 1). First, the most important features of pulses in terms of composition and structural hierarchy are given. Second, the effects of postharvest storage and processing on starch and protein digestibility, as well as mineral bioaccessibility, are extensively reviewed. Though postharvest storage chronologically precedes processing in the pulse value chain, the effect of processing is discussed first, because knowledge of traditional thermal processing is necessary to understand the effects of long-term storage and the HTC phenomenon on nutrient digestibility and bioaccessibility. The insights acquired in this review can be used by industry as well as households to design processing variables to steer the digestive functionality of pulses toward the nutritional needs of specific population groups. In a third part, an overview is given on how pulses are processed into several traditional as well as innovative foods. In addition to the use of raw-milled pulse flours and isolated (protein, starch, and fiber) fractions, innovative applications include the development of structurally complex pulse ingredients in which the inherent bioencapsulation of nutrients is retained. However, in this context, it is important to note that different pulse types can exhibit distinct characteristics (e.g., cell wall properties) and consequently show different types of behavior along the value chain.

2 | STRUCTURAL HIERARCHY OF PULSES

Pulses, like other plant-based foods, possess highly complex and organized natural structures that are self-assembled from different molecules (Do et al., 2018). Pulse seeds are dicotyledonous, consisting of principal structures such as the germ (embryo) with two cotyledons enveloped by a seed coat (testa) (Reyes-Moreno & Paredes-López, 1993).

The cotyledons form the most substantial part of the pulse seed, contributing to about 90% of the total seed weight and containing most macronutrients. The parenchyma cells are filled with starch granules surrounded by a protein matrix (protein bodies) and, for specific pulses, some oil bodies are present as shown in Figure 2 (Avanza et al., 2012; Berrios et al., 2006; Diedericks et al., 2020; Hughes & Swanson, 1986; Marconi et al., 2000). The size of starch granules can differ between pulse types and ranges from 10 to 50 μm (Pérez & Bertoft, 2010; Yousif et al., 2007), whereas protein bodies range from 5 to 10 μm. Cytoplasmic nutrients are encapsulated by a thick primary cell wall, composed of a polysaccharide matrix rich in pectic substances (41%), cellulose (31%), and hemicellulose (24%) in common beans (Reyes-Moreno & Paredes-López, 1993). However, the exact cell wall thickness and composition of different pulse types and cultivars can vary considerably (Shiga & Lajolo, 2006; Wang et al., 2010; Wood et al., 2018). Observations of pulse cross- sections using various microscopy techniques reveal that cotyledons consist of an organized arrangement of parenchyma cells, which are joined together by the pectin-rich middle lamella (Avanza et al., 2012; Diedericks et al., 2020). The complex native structural characteristics and morphology of the grain play an important role during food processing and digestion. Research has shown that the nutrient digestibility of pulses is highly influenced by its complex native structure, which is in turn affected by processing variables at the level of particle size, texture (hardness), and cell wall intactness and/or permeability, influencing the entrapment degree of nutrients inside cotyledon cells (Verkempinck et al., 2020).

The seed coat generally consists of several layers of distinct cells, which include the surface cuticle, palisade, subepidermal, and parenchyma cell layers (Umaid et al., 1984; Wood et al., 2011). The exact cell wall composition of the seed coat is pulse type dependent, with, for example, 56%–61% cellulose, 17%–26% hemicellulose, and 11%–15% pectic substances in common beans (Reyes-Moreno & Parades-López, 1993) and 18%–29% cellulose, 30% hemicellulose, and 10% pectic substances in chickpeas (Zhong et al., 2018). Seed coat properties, such as thickness and the extent of amorphousness of the palisade layer, influence the seed hydration properties during soaking and cooking (Yousif et al., 2007).

3 | BIOCHEMICAL COMPOSITION OF PULSES

Pulses are a nutrient-dense food group providing large amounts of protein (slowly digestible) starch and fiber as well as minor components (e.g., vitamins and minerals). Typical ranges in the nutritional composition of four pulse

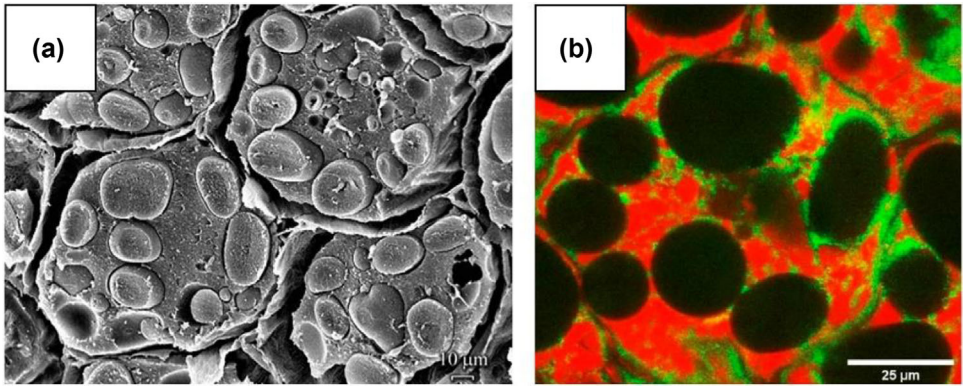

FIGURE 2 Microscopic images of cross sections of pulse cotyledon parenchyma cells. Panel (a) shows a scanning electron micrograph illustrating a cross-sectional view of cowpea cotyledon (scale bar = 10 µm); adapted from Avanza et al. (2012). Panel (b) displays a confocal laser scanning micrograph illustrating the cross-sectional view of a Bambara groundnut cotyledon: protein and oil bodies are shown in (fluorescent) red and green, respectively, and the black colored circular objects are starch granules (scale bar = 25 µm); adapted from Diedericks et al. (2020)

TABLE 1 Average starch, protein, lipid, and crude fiber content (% of dry weight) of different pulses

Pulse type	Starch	Protein	Lipids	Crude fiber
Bambara groundnuts	50.2–53.0[a,b]	16.6–22.1[j,b]	4.4–7.9[b]	4.9–22.9[a,h,j]
Common beans	36.1–52.3[c,d]	14.2–27.1[e,f]	0.8–2.5[c,e]	8.6–27.2[c,g]
Chickpeas	38.2–45.1[c,f]	18.5–22.9[c,f]	4.6–6.7[c,f]	9.9–24.6[c,f]
Lentils	46.0–50.0[c,g]	20.6–29.2[c,g]	0.8–2.2[c,g]	6.8–14.7[c,i]

Note: Data obtained from the following studies: [a]Yao et al. (2015); [b]Nti (2009); [c]De Almeida Costa et al. (2006); [d]Pujolà et al. (2007); [e]Campos-Vega et al. (2009); [f]Wang et al. (2010); [g]Dueñas et al. (2016); [h]Olaleye et al. (2013); [i]Wang et al. (2009); [j]Enweren and Hung (1996).

types, common bean (*Phaseolus vulgaris*), chickpea (*Cicer arietinum*), lentil (*Lens culinaris*), and Bambara groundnut (*Vigna subterranea*), are shown in Table 1. Only these pulses were considered as they are relevant examples for (the scientific literature documented in) this review, as well as in terms of consumption in different parts of the world (Calles et al., 2019). As can be seen from Table 1, pulse composition can vary both within a pulse type (depending on cultivar as well as growing and harvesting conditions) and between pulse types (e.g., Bambara groundnuts and chickpeas have a higher lipid content compared to common beans and lentils). For an extensive overview of the composition of multiple pulse types, the reader is referred to Hall et al. (2017).

3.1 | Carbohydrates

Carbohydrates broadly make up between 42% and 76% of pulse dry weight (De Almeida Costa et al., 2006; Hall et al., 2017). This group consists of starch, nonstarch polysaccharides as well as mono- and oligosaccharides with starch the major component (Hall et al., 2017; Hoover et al., 2010). The starch obtained from pulses consists of about 15%–30% of linear amylose and 75%–90% highly branched amylopectin (Pfister & Zeeman, 2016). Pulse starch granules are mostly oval and smooth-surfaced and have been shown to form C-type crystallites (Hoover et al., 2010). Structural and functional characteristics of pulse starches were extensively reviewed by Hoover et al. (2010) and Ren et al. (2021).

Although starch is a direct source of energy for the human body, overconsumption of highly digestible forms of this macronutrient is associated with several chronic metabolic disorders such as insulin resistance, obesity, and the development of type 2 diabetes (Aller et al., 2011; Eckel et al., 2005). After a meal, as a result of digestion, glucose from starch is absorbed into the bloodstream causing a rise in circulating glucose concentrations (Jenkins et al., 1981). The glycemic index (GI) and glycemic load (GL) are measures for the postprandial blood glucose response after the ingestion of a starch-containing meal and are mainly affected by the carbohydrate digestion and absorption rates (Jenkins et al., 1981; Singh et al., 2021). The reader is referred to Singh et al. (2021) for an extensive review of the GI of several pulses and pulse-based foods. Pulses are considered to have a low GI, caused by a slow and incomplete digestion of starch (high

slowly digestible and resistant starch content) and a high amount of dietary fiber (Chung et al., 2008; Tharanathan & Mahadevamma, 2003). Several studies report a correlation between *in vitro* starch digestibility and *in vivo* GI (Edwards et al., 2019; Englyst et al., 1992; Goñi et al., 1997), signifying that differences in *in vitro* starch digestion might predict differences in *in vivo* GI. Other studies even claim that the consumption of foods with a low GI could decrease the risk of developing diseases such as obesity, metabolic syndrome, and diabetes mellitus (Juanola-Falgarona et al., 2015; Tharanathan & Mahadevamma, 2003). Although the area under glucose curve has widely been used to document the glycemic effect of different carbohydrate foods, it is a fairly crude and arbitrary approach. *In vitro* digestibility analysis combined with data modeling provides more accurate time-dependent insight into the patterns of starch hydrolysis and consequent glucose release (Martinez, 2021). Starch digestibility can be affected by several intrinsic and extrinsic factors. Intrinsic factors include the amylose:amylopectin ratio, molecular order, and granule size (Chi et al., 2021; Du et al., 2014; Edwards et al., 2018), whereas extrinsic factors include macro- (such as viscosity) and microstructural matrix characteristics induced by processing, which determines the confinement of starch as will be discussed in Section 4. In this context, the composition of the food matrix is another noteworthy factor, because components such as polyphenols and cellulose can inhibit enzymatic starch hydrolysis (Dhital et al., 2015; Hanhineva et al., 2010).

Pulses are a rich source of dietary fiber, a large family of various carbohydrate polymers that are resistant to mammalian digestion but that can be (partially or completely) fermented by microbes in the gut, resulting in the formation of health-beneficial short-chain fatty acids (SCFAs, mainly acetic, propionic, and butyric acid) (Ercolini & Fogliano, 2018; Liu et al., 2020; Mortensen & Clausen, 1996; Tabernero & Gómez de Cedrón, 2017). As a result of this fermentation, gasses are formed, which might cause flatulence and thus digestive discomfort (McCrory e al., 2010). Carbohydrate fermentation and the resulting metabolite formation has been related to positive changes in gut microbiota and reduced risks of several diseases (both colon-related and metabolic syndromes), as reviewed recently by Wang et al. (2019). Additionally, the beneficial effects of fibers are increasingly being related to their three-dimensional structure. Intact cell walls have an added advantage compared to fiber isolates, because the former limits the bioaccessibility of macronutrients in the small intestine (Augustin et al., 2020). Moreover, the type of fiber and intrinsic cell wall properties play an important role determining cell wall permeability and starch digestibility, which is lower for chickpea compared to wheat flours (Edwards et al., 2021). In addition, the benefits of dietary fiber are related to their physicochemical properties such as water holding capacity. Foods with a high fiber content mostly have a lower caloric density and rate of starch digestion (McCrory et al., 2010; Tharanathan & Mahadevamma, 2003) and have a positive impact on gastrointestinal hormone signaling and nutrient digestion (Grundy et al., 2016). In this context, high fiber contents have been related to satiety and weight control (McCrory et al., 2010). An example of dietary fiber typical for pulses is resistant starch type I (starch encapsulated in cotyledon cells). Other examples include plant cell wall polysaccharides such as soluble oligosaccharides and pectin, and insoluble cellulose and hemicellulose as well as resistant starch (Grundy et al., 2016; Kutoš et al., 2003). Pectin typically consists of smooth homogalacturonan (HG), without side chains, and hairy rhamnogalacturonan (RG) I and II regions. Both HG and RG I are built up of an α-1,4-linked galacturonic acid (GalA) backbone that can be methylesterified (Voragen et al., 2009). Ionized nonmethylesterified GalA residues (COO–) can interact with several cations, possibly resulting in the formation of a pectin–mineral network known as the "egg-box" model (Caffall & Mohnen, 2009; Morris et al., 1982). Soluble fiber is well known for regulating blood glucose levels and reducing cholesterol. The exact mechanisms causing this effect are not yet fully understood. However, it is suggested that soluble fiber increases the viscosity of the food being digested and hence reduces nutrient absorption (Li et al., 2020).

Oligosaccharides (e.g., raffinose, stachyose, and verbascose) typically make up below 8%–9% (Bosi et al., 2019; Brummer et al., 2015; Fan et al., 2015) but can go up to 14% of the pulse seed weight (Hall et al., 2017), whereas only 1% of the seed weight comprises monosaccharides (Brummer et al., 2015; Hall et al., 2017), the latter mostly present in the cotyledon fraction (Sreerama et al., 2010). Oligosaccharides are not digestible by human digestive enzymes because of β-glycosidic bonds linking monosaccharides. Upon reaching the colon, these components can be fermented, causing flatulence in humans who do not regularly consume pulses (Hall et al., 2017). Although oligosaccharides are usually regarded as negative flatulence inducing components, they can also be seen as prebiotics (McCrory et al., 2010).

3.2 | Proteins

The protein content of pulses generally lies between 15% and 30% dry matter (see Table 1) (Boye et al., 2010; Hall et al., 2017). Pulse proteins are predominantly composed of water-soluble albumins (usually up to 20%) and salt-soluble globulins (generally over 50%), with ratios depending on variety and cultivar (Hall et al., 2017). Globulins are storage proteins made up of 33%–57% legumins (11S)

and 8%–45% vicilins (7S) varying between pulse types and cultivars (Boye et al., 2010; Hall et al., 2017). Albumins are mostly enzymes necessary for cell metabolism (Derbyshire et al., 1976; Osborne & Campbell, 1898). Glutelins and prolamins, as well as compounds such as trypsin inhibitors and lectins, make up a smaller fraction of the protein content (Duranti & Gius, 1997; Hall et al., 2017). Pulse proteins and their functionalities have been extensively reviewed by Boye et al. (2010) and Shevkani et al. (2019).

The nutritional quality of proteins in food is determined by the total quantity of protein, its digestibility and the amino acid composition, and more specifically the ratio between essential amino acids (Vaz Patto et al., 2015). In terms of amino acid composition, pulses are rich in lysine, leucine, aspartic acid, glutamic acid, and arginine, but have very low quantities of sulfur-containing methionine, cysteine, and tryptophan (Boye et al., 2010). Although meat, milk, and eggs are seen as high-quality protein sources due to their complete amino acid composition and high amount of (largely bioavailable) vitamins and minerals, high meat consumption is often associated with a large impact on the environment and a high caloric and saturated fat intake (Boye et al., 2010). Besides, protein provision based solely on animal sources is not sustainable in the context of the continuously expanding world population (Iqbal et al., 2006). Therefore, there is an increasing demand for high-quality and sustainable plant-based protein sources. Pulses have been proposed as plant-based protein sources, as their amino acid profile is complementary to that of lysine-deficient cereals (e.g., wheat, maize, rice) (Azman Halimi et al., 2019; Boye et al., 2010; Iqbal et al., 2006; Mubaiwa et al., 2017). This fact is essential, considering that cereal crops are the staple food of many developing countries with a high prevalence of malnutrition. Hence, encouraging diversification of the diet by increasing the intake of (locally available) pulses can be a food-based strategy of reducing the prevalence of malnutrition in these regions (Boye et al., 2010; Semba, 2016). Additionally, it should be noted that the digestibility of pulse proteins is lower than that of animal proteins, due to structural features (Carbonaro et al., 2015) and the presence of antinutritional factors (e.g., protease inhibitors and tannins) (Boye et al., 2010) as discussed in Section 4.2. Regardless, pulses have an important potential in the sustainable provision of sufficient protein (and various amino acids) in (plant-based) diets, both in the Western and developing world.

3.3 | Lipids

Most pulses contain no more than 1% lipids, except for a few pulse types such as the Bambara groundnut (1%–8%), chickpea (3%–10%) (Jukanti et al., 2012), and Bengal and black gram (0%–5%) (Krishna et al., 1997). The lipophilic fraction is often rich in tocopherol, which possesses a high antioxidant capacity (Gopala Krishna et al., 1997; Yao et al., 2015). The lipids in pulses are mostly free and unsaturated (Campos-Vega et al., 2010), with linoleic and linolenic acid as the major fatty acids (about 20%–22% of fatty acids) (Hall et al., 2017). Fatty acid composition can, however, vary with pulse species, cultivar, environment, and so forth (Hall et al., 2017).

3.4 | Minerals and vitamins

Pulses contain appreciable amounts of minerals such as Mg, Ca, Fe, and Zn in comparable ranges as reported for several cereals and vegetables (Marles, 2017; Srikumar, 1993), with exact quantities largely varying and depending on genetic and environmental factors (Ribeiro et al., 2012). The mineral composition of four pulse types is given in Table 2. The contribution of pulses to human mineral supply becomes increasingly important, as pulses become an important part of sustainable and healthy human diets (e.g., as a plant-based protein source). Though pulses contain significant amounts of minerals, several components present in pulses limit their bioaccessibility, meaning that not all ingested minerals are available for absorption into the blood stream, as will be discussed in Sections 4.4 and 5.4. However, minerals such as copper, chromium, iron, and zinc are essential micronutrients for human health because they have to be taken up from food (Campos-Vega et al., 2010). Minerals are important cofactors for many physiological and metabolic enzymes.

Pulses are also rich in particular vitamins, such as B vitamins: folate (B9), thiamine (B1), riboflavin (B2), niacin (B3), and pyridoxine (B6) (Campos-Vega et al., 2010; Hall et al., 2017). Additionally, pulses possess moderate amounts of tocopherol (a form of vitamin E) (Campos-Vega et al., 2010). Vitamins are essential micronutrients, necessary for the normal growth, maintenance, and function of the human body (Hall et al., 2017).

3.5 | Antinutrients

Pulses contain several components that can affect their nutritional quality and lead to reduced digestion and absorption of nutrients as well as a lowered (sensorial) acceptability (Campos-Vega et al., 2010). These components are therefore often inactivated by cooking (Campos-Vega et al., 2010; Reyes-Moreno & Parades-López, 1993; Vaz Patto et al., 2015). However, some of these components can exert protective effects on the human body as well,

TABLE 2 Average mineral content of different pulses (mg/100 g dry matter)

Pulse type	Ca	Mg	Fe	K	Zn	P
Bambara groundnuts	78.0[a,f]	20.9[a]	3.0–5.9[a,e,f]	370.0–1240.0[e,f]	25.6[a]	296.0–460.0[e,f]
Common beans	75.6–197[b,d]	160–250[b,d]	5.41–7.0[b,d]	1505.0[b]	3.0[b,d]	495.8[d]
Chickpeas	81.7–165.0[b,d]	147.0–169.0[b,d]	4.59–7.0[b,d]	994.5–1060[b]	3.4–4.1[b,d]	394.0–451.5[b]
Lentils	57.5–71.0[c,d]	99.3–129[c,d]	6.4–9.7[c,d]	844.0–943.0[c]	2.6–3.8[b,d]	308.0–407.0[c]

Note: Data obtained from the following studies: [a]Olaleye et al. (2013); [b]Wang et al. (2010); [c]Wang et al. (2009); [d]Sandberg (2002); [e]Fasoyiro et al. (2006); [f]Amarteifio et al. (2006); [g]Hummel et al. (2020).

because they can have antioxidant properties, stimulate the immune system, modulate detoxifying enzymes, regulate lipid and hormone metabolism, protect against DNA damage, and so forth (Campos-Vega et al., 2010).

Examples of antinutrient compounds are pectin, phytates, phenolic compounds, enzyme inhibitors, and lectins. Pectin is a complex heteropolysaccharide, primarily located in the middle lamella of pulse cell walls (De Almeida Costa et al., 2006; Díaz et al., 2010; Hall et al., 2017; Sreerama et al., 2010), which can interact with minerals when ionized, rendering them unavailable for absorption (Section 4.3). Phytic acid (myo-inositol hexakisphosphate or IP_6) is mainly present in protein bodies in the pulse cotyledon and has the ability to bind starch and proteins strongly and chelate divalent mineral cations, decreasing mineral bioaccessibility (Oomah et al., 2008; Rousseau, Pallares Pallares, et al., 2020). Phenolic compounds (such as tannins) are most importantly located in the seed coat and have been found to inhibit protein and starch digestion and diminish mineral bioavailability (Kardum & Glibetic, 2018; Sandberg, 2002; Sreerama et al., 2010). Enzyme inhibitors (α-amylase and protease inhibitors) decrease the digestibility of complex carbohydrates and proteins through inhibition of the respective digestive enzymes (Díaz-Batalla et al., 2006; Vaz Patto et al., 2015) and are mostly present in the cotyledons of pulses (Sreerama et al., 2010). To conclude, lectins are erythrocyte-agglutinating glycoproteins that can be found in most plant-based foods, especially in pulses (Obiro et al., 2008). Both enzyme inhibitors and lectins are, however, largely inactivated through thermal treatment such a cooking (Campos-Vega et al., 2010).

4 | THE EFFECT OF TRADITIONAL THERMAL PROCESSING ON NUTRIENT DIGESTION OF PULSES

As mentioned in the introduction, there is an important discrepancy between the starch, protein, and mineral content of food and the degree to which these nutrients can be absorbed into the bloodstream. Consequently, the digestibility and bioaccessibility of foods can be determined in order to know the amount of nutrients enzymatically broken down into smaller absorbable, and/or potentially available, units after digestion (Etcheverry et al., 2012; Parada & Aguilera, 2007; Rovalino-Córdova et al., 2018). These characteristics are highly dependent on both compositional and structural features of the food, and both are affected by processing (as shown in Figure 1). Pulses require processing before consumption in order to increase their nutritional value, palatability, and sensorial quality such as taste, aroma, and texture (Chigwedere, Njoroge, et al., 2019; Kinyanjui et al., 2015; Ma et al., 2011). In the following sections, the effect of traditional thermal processing on the digestibility of starch and protein, and the bioaccessibility of minerals, will be discussed in detail.

The most traditional process steps are soaking and cooking. The main goal of soaking is to hydrate seeds, thereby shortening the required cooking time (Kinyanjui et al., 2015). During thermal processing (e.g., 60 min at 95°C in excess water for common beans [Pallares Pallares et al., 2018]), proteins denature and starch gelatinizes, causing an increase in the digestibility of these macronutrients (Chigwedere et al., 2018; Dueñas et al., 2016). Moreover, antinutritional and toxic components are partially or completely eliminated (Dueñas et al., 2016). Softening of pulses during thermal treatment can be attributed to both starch gelatinization and progressive solubilization of middle lamella pectin, the latter being the rate-limiting step (Bernal-Lugo et al., 1997; Chigwedere et al., 2018; Njoroge et al., 2016). The gradual solubilization of middle lamella pectin during thermal treatment causes the main mechanism for tissue failure upon mechanical disintegration of pulses (as occurs during mastication) to shift from cell breakage to cell separation (Chigwedere et al., 2018; Njoroge et al., 2016). In contrast, upon mechanical disruption (e.g., milling) of non-thermally treated pulse tissue (e.g., raw), cell breakage is the main mode of tissue failure, causing the cellular organization to be lost and nutrients to be released and become more accessible to digestive enzymes. Methods applied by several researchers to isolate pulse cotyledon cells have been reviewed very recently by Pallares Pallares et al. (2021). The intact cell wall bioencapsulates cell contents and acts as a physical barrier hindering macronutrient digestion (Bhattarai et al., 2017; Dhital et al., 2016;

Edwards et al., 2015; Pallares Pallares et al., 2018; Rovalino-Córdova et al., 2019). Moreover, the cell wall and dense cytoplasmic matrix (with protein matrix and starch granules) can affect the degree of starch gelatinization and protein denaturation during thermal treatment, which in turn affects macronutrient digestibility as well (Bhattarai et al., 2017; Rovalino-Córdova et al., 2019).

Through the use of microscopic imaging techniques, it has been demonstrated that starch and protein digestion in pulse cells are the result of digestive enzyme diffusion inside the cells and diffusion of hydrolysis products outside the cell (Pallares Pallares et al., 2018; Rovalino-Córdova et al., 2018, 2019; Zahir et al., 2020). Intact pulse cells (partially) retain their structural integrity upon *in vitro* digestion, with starch and protein gradually leaving the cells as a function of digestion time (Bhattarai et al., 2017; Pallares Pallares et al., 2018; Rovalino-Córdova et al., 2018). More detail on starch and protein digestion in thermally treated pulses will be given in Sections 4.1 and 4.2, respectively. Thereafter, the effect of thermal treatment on mineral bioaccessibility in pulses will be discussed in Section 4.4.

4.1 | Starch digestibility of thermally treated pulses

The intactness of the cell, a densely packed matrix encapsulated by a cell wall, is a major factor hindering, and thus slowing down, amylolysis during *in vitro* digestion of different pulses (Berg et al., 2012; Bhattarai et al., 2017; Dhital et al., 2016; Edwards, Veerabahu, et al., 2020; Mishra et al., 2012; Rovalino-Córdova et al., 2018). In this regard, pulse cell wall structure is very different from other plant-based foods, such as cereals. Edwards et al. (2021) found that amylolysis in cooked chickpea flours (with residual cellular intactness) is restricted due to a low permeability of the cell wall to α-amylase, contrary to more permeable wheat endosperm cell walls. Damage (due to mechanical, enzymatical, or thermal processes) or modulations (due to germination or fermentation) to the cell wall can therefore affect the rate and extent of starch digestion (Berg et al., 2012; Dhital et al., 2016; Mishra et al., 2012; Rovalino-Córdova et al., 2018). Apart from providing a barrier function, the presence of an intact cell wall can restrict starch gelatinization during thermal processing due to cytoplasmic confinement (Bhattarai et al., 2017). Moreover, cell wall material can delay starch digestion through significant binding of α-amylase (Bhattarai et al., 2017). In more detail, Dhital et al. (2015) reported that reversible, nonspecific (mixed type) adsorption of α-amylase to cellulose (and other insoluble fibers) depletes the enzyme from the solution and thus decreases the rate of starch hydrolysis in a concentration-dependent manner. Water-soluble fibers cause direct inhibition of α-amylase following another mechanism, possibly with a degree of specificity (Slaughter et al., 2002).

Next to the cell wall, the protein matrix embedding starch and limiting α-amylase diffusion forms a second barrier delaying amylolysis (Rovalino-Córdova et al., 2019). As a consequence, starch digestibility is dependent on the gradual enzymatic degradation of the protein matrix upon digestion (Gwala, Pallares Pallares, et al., 2020; Rovalino-Córdova et al., 2019). Rovalino-Córdova et al. (2019) showed that pepsin activity during the gastric phase, although only responsible for 5% of protein digestion in isolated common bean cotyledon cells, causes a 20% increase in the amount of starch digested during the small intestinal phase. In contrast, no evidence could be found for the influence of starch digestion on protein digestion, indicating that the presence of starch does not limit access of proteases to protein bodies (Rovalino-Córdova et al., 2019).

4.1.1 | Effect of thermal treatment intensity on starch digestion kinetics

The effect of thermal treatment intensity on *in vitro* starch digestion kinetics has been studied in detail for cells isolated from common bean cotyledons. Pallares Pallares et al. (2018) showed that the barrier effect of common bean cotyledon cell walls can be modified through variation of the thermal treatment time. The presence of the cell wall barrier causes the occurrence of a lag phase (delay) in *in vitro* small intestinal starch digestion, during which the starch hydrolysis is very slow as the cell wall limits encounters between α-amylase and its substrate (Pallares Pallares et al., 2018). In common beans, increasing process intensity leads to increasing cell wall porosity, which has been related to the solubilization of cell wall pectin (Zahir et al., 2020). Cells with a higher degree of process-induced cell wall porosity could be more permeable to digestive enzymes and therefore showed shorter lag phases and higher reaction rate constants of *in vitro* starch hydrolysis (Pallares Pallares et al., 2018).

These findings imply that varying the cooking time applied to pulses in the home or industry could affect starch hydrolysis rates during *in vitro* digestion. Although it could be hypothesized that this insight can be applied to other pulse types, it should be noted that this behavior is largely dependent on the cell wall (polymer) composition and properties, and how these are affected by (thermal) processing. Gwala, Pallares Pallares, et al. (2020) confirmed that the *in vitro* starch digestion rate and extent in cells isolated from Bambara groundnut increase with thermal treatment time. However, these authors reported

that the lag phase for *in vitro* starch digestion in Bambara groundnut cells is reduced in comparison to common bean cells. It has been hypothesized that these differences may be attributed to a higher treatment time dependency of cell wall pectin solubilization in common beans compared to Bambara groundnuts. To conclude, differences in cell wall properties between different pulse types may significantly influence the extent and the way in which cell walls are affected by processing, thereby altering macronutrient digestion (Gwala, Pallares Pallares, et al., 2020).

The effect of thermal treatment time on *in vitro* starch digestion kinetics has also been established for whole Bambara groundnuts. Seeds with a higher thermal treatment time (120 min) were characterized by a lower starch digestion rate constant as compared to seeds with a shorter treatment time (60 min) (Gwala et al., 2019). This can be explained by greater pectin solubilization with a longer treatment, leading to a higher extent of cell separation and relatively more intact cells bioencapsulating starch and hindering digestion (Gwala et al., 2019). In contrast, shorter treatment times lead to relatively more seed breakage and release of cell content (nutrients), which are in turn more readily accessible to digestive enzymes. From these studies, it may be concluded that, for whole pulse seeds, thermal processing intensity can affect cell wall integrity and consequently the starch digestion rate through (i) the porosity of the cell wall (Pallares Pallares et al., 2018) and (ii) the degree of cell separation upon mechanical disintegration leading to intact cells (Gwala et al., 2019). The relationship between cell wall properties and the (starch) digestive properties of different pulse types is yet to be fully explained.

Additionally, physical entrapment of starch granules by the protein and cytoplasmic matrix is a major structural factor delaying amylolysis. As a consequence, *in vitro* starch digestion of isolated common bean cells could be facilitated by increasing thermal treatment intensity, leading to increased protein degradation (Gwala, Pallares Pallares, et al., 2020; Rovalino-Córdova et al., 2019). In contrast, an even more intense thermal treatment may lead to extensive protein aggregation, thus forming a stronger barrier for starch digestion (Drulyte & Orlien, 2019) (see Section 4.2).

4.1.2 | Storage after thermal treatment and starch retrogradation

Storage of pulses postcooking or after repeated freeze–thaw cycles can result in the retrogradation of starch (Wang et al., 2008). During retrogradation, short and long amylose and amylopectin chains reassociate into a semicrystalline structure (Morris, 1990). This process is rapid for amylose, which has a smaller molecular size and lower hindrance compared to amylopectin, for which retrogradation may take several days to occur (Miles et al., 1985; Wang et al., 2015). The ratio of ordered to disordered α-glucan chains (determined by FTIR) at the starch granule surface is low for gelatinized starch and increases upon retrogradation (Patel et al., 2017). Mechanistically, the higher ordering of retrograded starch granules inhibits pancreatic amylase, hindering its catalytic efficiency during digestion (Patel et al., 2017).

The effect of retrogradation on starch amylolysis has not been widely studied in whole cooked pulses. In one study, (postcooking) storage of Ayocote beans (*Phaseolus coccineus*) resulted in a lower starch digestibility as a result of starch retrogradation. The resistant starch content increased with storage time. As can be seen in Table 3, the amount of resistant starch that is formed during retrogradation is dependent on the storage time and temperature conditions, as well as the botanical source of the starch. For many pulses, refrigeration temperatures (4°C) will create more RS type III than storage at room temperature (Yadav et al., 2010). In another study by Edwards, Veerabahu, et al. (2020), the effect of thermal treatment and refrigeration on *in vitro* digestibility of starch in chickpea flour was determined. Refrigeration of a gelatinized sample decreased *in vitro* starch digestibility, but when these samples were gelatinized again (after refrigeration) they showed an even higher starch digestibility compared to the gelatinized sample (Edwards, Veerabahu, et al., 2020).

It can be concluded that, in addition to cell-wall entrapment of starch (see Section 4.1), postcooking retrogradation can be a strategy to increase the slowly digestible and resistant starch content in cooked pulses. Both entrapped and retrograded starch occur, for example, in ready-to-eat refrigerated meals (such as salads) containing cooked pulses. The design of food products with more resistant starch is nutritionally important as it ensures (s)lower starch hydrolysis (Wang & Copeland, 2013) and the delivery of undigested starch to the colon where it can serve as a substrate for fermentation (Cummings & Branch, 1986; Topping & Clifton, 2001).

4.2 | Protein digestibility of thermally treated pulses

Rovalino-Córdova et al. (2019) showed that small intestinal proteolysis affects bean proteins to a greater extent than gastric proteolysis. Only 5%–10% of all protein becoming bioaccessible upon digestion has been attributed to pepsin during the gastric phase for Bambara groundnuts, common beans, and soy beans (Gwala, Pallares Pallares, et al., 2020; Rovalino-Córdova et al., 2019; Zahir et al., 2020). This

TABLE 3 Resistant starch (RS) (% dry matter) content of cooked pulses as affected by storage conditions (mean ± SD; $n = 3$)

Pulse type	After cooking	4°C/12 h	4°C/24 h	25°C/12 h	25°C/24 h
Chickpeas	4.92 ± 0.17^{a}	6.09 ± 0.09^{c}(23.7)	6.03 ± 0.10^{c}(22.5)	$5.21 \pm 0.09^{a,b}$(5.8)	5.34 ± 0.06^{b}(8.5)
Peas	3.95 ± 0.40^{a}	5.15 ± 0.08^{b}(30.3)	5.52 ± 0.13^{c}(39.7)	3.99 ± 0.08^{a}(1.01)	4.23 ± 0.10^{a}(7.1)
Lentils	5.09 ± 0.06^{a}	$5.62 \pm 0.11^{b,c}$(10.4)	5.88 ± 0.16^{c}(15.5)	$5.32 \pm 0.11^{a,b}$(4.5)	5.50 ± 0.14^{b}(8.0)
Kidney beans	$4.54 \pm 0.09^{a,b}$	$4.87 \pm 0.09^{c,d}$(7.3)	5.12 ± 0.04^{d}(12.8)	4.31 ± 0.09^{a}(5.1)	$4.62 \pm 0.03^{b,c}$(1.8)

Note: Adapted from Yadav et al. (2010): The values in parentheses show the percentage increase or decrease over the control value (resistant starch after cooking). Mean values with different superscript letters in the same row differ significantly ($P < 0.05$).

difference in enzyme action can be attributed to the specificities of the proteolytic enzymes under consideration. On the one hand, pepsin has a broad specificity but preferably cleaves peptide bonds between aromatic amino acids such as phenylalanine, tryptophan, and tyrosine (Sitrin, 2014), whereas pulses are typically poor in sulfur-containing amino acids and tryptophan (Boye et al., 2010). On the other hand, trypsin and chymotrypsin preferably cleave polypeptide chains at C-terminal basic amino acids such as arginine and lysine, and/or at large hydrophobic residues (phenylalanine, tryptophan, and tyrosine) (Feher, 2012; Sitrin, 2014). The amino acids most abundantly present in beans, such as lysine, aspartic acid, leucine, arginine, phenylalanine, and methionine, are thus an ideal substrate for trypsin and chymotrypsin, which might explain the more efficient action of small intestinal proteases in protein hydrolysis during *in vitro* digestion (Boye et al., 2010; Rovalino-Córdova et al., 2019). The limited extent of gastric compared to small intestinal proteolysis has been confirmed microscopically as well (Gwala, Pallares Pallares, et al., 2020; Rovalino-Córdova et al., 2019). Although the extent of protein digestibility in the gastric phase is limited, it significantly affects small intestinal starch digestibility (Rovalino-Córdova et al., 2019), as shown in Section 4.1.

4.2.1 | Effect of thermal treatment intensity on protein digestion kinetics

For cells isolated from Bambara groundnuts with a higher cooking time, the rate constant and extent of protein hydrolysis after the small intestinal phase are significantly higher (Gwala, Pallares Pallares, et al., 2020). Although autoclaving generally increased protein digestibility for several tropical pulse types, this was not the case for most of these pulse types upon boiling (Torres et al., 2016). Moreover, no increase in protein digestion could be observed with increasing thermal treatment time for *Canavalia* (jack bean) (Torres et al., 2016). From these results, it could be concluded that the effect of thermal treatment on protein digestion kinetics is dependent on pulse type and processing method/intensity.

Protein digestion kinetics could be influenced by several mechanisms occurring during pulse thermal treatment. First, longer treatment times are expected to increase cell wall permeability (see Section 4.1), facilitating protease diffusion toward the protein in the cell. Second, thermal treatment may reduce the content of antinutrient factors, for example, trypsin inhibitors, ultimately improving protein digestibility (Bora, 2014; Gilani et al., 2012). Third, the secondary structure of the protein (after processing) has been reported to highly affect digestibility (Carbonaro et al., 2012). Longer treatment times and increasing protein denaturation can render proteins either more susceptible or more resistant to human digestive enzymes (Salazar-Villanea et al., 2016). Protein denaturation can cause the formation of random coils, exposing groups that are inaccessible in the native form of the protein and increasing susceptibility to digestive proteases (Carbonaro et al., 2012; Montoya et al., 2006; Rovalino-Córdova et al., 2019; Salazar-Villanea et al., 2016). This is of particular importance for phaseolins, the main storage proteins in pulses such as beans, which are highly indigestible in the raw state (Montoya et al., 2006). Phaseolins are rich in β-sheet conformations, which require denaturation to become prone to enzymatic hydrolysis (Carbonaro et al., 2012; Rovalino-Córdova et al., 2019). However, physical constraints provided by the cell wall and packed cytoplasmic matrix can limit and delay protein denaturation and unfolding during thermal treatment (Rovalino-Córdova et al., 2019). In contrast, it should be noted that, through the formation of intra- and intermolecular interactions, protein aggregation can occur upon increasing thermal treatment intensity, rendering the protein less accessible and less susceptible to enzymatic hydrolysis (Drulyte & Orlien, 2019; Salazar-Villanea et al., 2016). However, the formation of disulfide (S–S) bridges is unlikely to be the case in pulses, because pulse proteins are deficient in S-containing amino acids (Boye et al., 2010). Other proposed mechanisms for protein aggregation (in pulses)

are Maillard-type reactions, protein oxidation reactions, and interactions between amino acids (Gerrard et al., 2012; Meade et al., 2005; Salazar-Villanea et al., 2016; Schwarzenbolz & Henle, 2010; Torres et al., 2016).

A faster hydrolysis of the protein matrix bioencapsulating starch can in turn facilitate starch hydrolysis (Gwala, Pallares Pallares, et al., 2020), see Section 4.1. In Bambara groundnuts, where differences in treatment time did not seem to greatly affect cell wall permeability, a positive effect of thermal treatment time on protein digestibility could be observed, leading to an increase in the starch digestion rate (Gwala, Pallares Pallares, et al., 2020).

4.3 | Process-induced hardness as a material property to predict macronutrient digestion in Bambara groundnuts

For Bambara grountnuts, hardness can be a useful food design parameter predicting *in vitro* starch and protein digestion kinetics (Gwala, Pallares Pallares, et al., 2020). In general, the average hardness of Bambara groudnuts decreased with increasing thermal treatment time. Moreover, lower hardness levels were accompanied by higher rate constants for starch and protein hydrolysis. However, considerable variability in the hardness levels of Bambara groundnuts with a certain cooking time could be observed (Gwala, Pallares Pallares, et al., 2020). Therefore, seeds with the same thermal treatment time were sorted into hardness levels and starch and protein digestion kinetics were evaluated for cells isolated from these seeds.

Interestingly, it could be observed that starch and protein digestion kinetics of cells isolated from Bambara groundnuts with different thermal treatment times but similar hardness values were comparable in terms of rate and extent. As expected, a lower hardness value coincided with a higher macronutrient hydrolysis rate and extent. However, cells isolated from Bambara groundnut seeds with different hardness levels, but identical cooking times, did not show differences in lag phases for *in vitro* starch digestion. It was therefore concluded that the cell wall barrier hindering nutrient digestion is not affected by hardness category. For protein, however, samples with a lower hardness value (due to a longer thermal treatment) were characterized by a higher degree of protein denaturation and unfolding, facilitating enzymatic attack and increasing protein digestion rate and extent. As a consequence, the facilitated hydrolysis of the protein matrix encapsulating starch increased the rate of starch hydrolysis in cells isolated from Bambara groundnut seeds with a low hardness (Gwala, Pallares Pallares, et al., 2020).

It can be concluded that for the case of Bambara groundnuts, hardness can be a useful tool to tailor and predict *in vitro* starch and protein digestibility. However, additional research is necessary before this observation could be generalized to other pulse types.

TABLE 4 Average total and bioaccessible mineral concentration (mg/100 g of cooked sample) in one serving of fresh whole common beans (Canadian wonder) after being soaked and cooked for 60 min at 95°C

	Mg	Ca	Fe	Zn
Total concentration in raw whole beans[a]	193.8	129.8	6.1	2.0
Contribution to ADR (%)[b]	55.4	18.5	101.5	20.3
Total concentration in cooked whole beans[a]	53.2	74.3	2.3	1.4
Bioaccessible mineral concentration[a]	29.4	24.7	1.0	0.6
Contribution to ADR (%)[b]	8.4	3.5	16.5	6.3

[a]Values are based on Rousseau, Celus, et al. (2020).
[b]Contribution of the mineral concentration to the average daily requirement (ADR) of Mg, Ca, Fe, and Zn was calculated based on average daily requirement values of 350, 700, 6, and 10 mg/day, respectively (EFSA, 2017).

4.4 | Mineral bioaccessibility of thermally treated pulses

Despite their high mineral concentrations (e.g., Mg, Ca, Fe, and Zn), pulses contain several antinutrients such as phytic acid and cell wall polymers (pectin). These antinutrients chelate minerals, rendering them inaccessible for absorption into the blood stream. As a result, as can be seen in Table 4, the mineral quality of pulses such as common beans is not high (Rousseau, Celus, et al., 2020). The negative influence of phytate and fiber on Zn and Fe bioaccessibility was reported for other pulse types as well, such as chickpea, French bean, cowpea, and red, green, and black gram (Hemalatha et al., 2007b). In this context, it should be noted that the presence of an intact cell wall does not hinder mineral bioaccessibility (Rousseau, Pallares Pallares, et al., 2020). One successful way of improving mineral bioaccessibility is dehulling (as shown in Table 5). For common beans, chickpeas and green gram, mineral bioaccessibility is lower in cooked whole seeds compared to dehulled cotyledons because seed coats contain higher amounts of different mineral chelators (Hemalatha et al., 2007a; Rousseau, Celus, et al., 2020). Moreover, enzymatic degradation of mineral chelators (e.g., due to pectinase or

TABLE 5 Average bioaccessible mineral concentration (mg/100 g of cooked sample) in one serving of fresh whole common beans (Canadian wonder) or cotyledons that were soaked and cooked (95°C) for 30, 60, and 120 min

		Bioaccessible mineral concentration			
	Cooking time	Mg	Ca	Fe	Zn
Whole bean	30 min	33.3	32.5	1.2	0.7
	60 min	29.4	24.7	1.0	0.6
	120 min	23.3	16.2	0.9	0.2
Cotyledon	30 min	28.0	13.2	1.2	0.8
	60 min	21.8	11.5	1.2	0.8
	120 min	18.4	10.8	1.0	0.7

Note: Values are based on Rousseau, Celus, et al. (2020).

phytase action as occurs during fermentation) could be a strategy to improve mineral bioaccessibility (Rousseau, Pallares Pallares, et al., 2020). However, the low bioaccessibility of most minerals in pulses indicates that populations mostly relying on pulses for the supply of minerals might be at risk for deficiencies.

4.4.1 | Effect of thermal treatment intensity on mineral bioaccessibility

During thermal treatment of common beans, mineral bioaccessibility is affected by both changes in mineral–antinutrient interactions and leaching of minerals. It has been hypothesized that mineral chelators become more accessible with increasing cooking time, for example, due to pectin solubilization, increasing the chelation of minerals rendering them less bioaccessible (Rousseau, Celus, et al., 2020). Moreover, in both common beans and Bambara groundnuts, significant leaching of minerals occurs upon cooking, with Mg more susceptible to leaching than Fe, Zn, and Ca (Gwala, Kyomugasho, et al., 2020; Rousseau, Celus, et al., 2020). The higher extent of Mg leaching may be attributed to its low interaction with antinutrients. Several explanations can be found in literature for the poor chelation properties of Mg. First, it could be hypothesized that minerals bind to chelators with a strength proportional to their electronegativity and atomic mass. Because Mg has a lower atomic mass compared to Ca, Fe, and Zn, the latter are expected to be more easily chelated (Kyomugasho et al., 2017). Second, the binding mechanism between Mg and pectin, through polycondensation, is found to be weaker than and different from the binding mechanism between Ca, Fe, and Zn-ions, following the "egg-box" model (Celus et al., 2018).

The effect of cooking time on the mineral bioaccessibility of both whole and dehulled common beans is shown in Table 5. Since Ca, Mg, Fe, and Zn bioaccessibility of common beans decreases with thermal treatment time (Rousseau, Celus, et al., 2020), it is recommended to keep the cooking time of common beans as short as possible to keep the bioaccessible mineral content as high as possible. Consequently, when choosing a cooking time, it is important to find the optimum between an acceptable hardness and digestibility of macronutrients, together with as high as possible a bioaccessible mineral amount. The same recommendations could be drafted for Bambara groundnuts, because Ca, Mg, and Zn bioaccessibility decreased upon thermal treatment in Bambara groundnuts, whereas Fe bioaccessibility seemed unaffected (Gwala, Kyomugasho, et al., 2020). Although the relation between thermal treatment time and mineral bioaccessibility seems similar for common beans and Bambara groundnuts, this is not necessarily the case for all pulses. In another study on multiple pulse types, Zn bioaccessibility decreased, whereas Fe bioaccessibility increased in most of the studied varieties (Hemalatha et al., 2007a). Therefore, additional research on the exact effect of thermal treatment on the bioaccessibility of specific minerals in different pulse types is necessary before generalizing any of the conclusions stated in this section.

5 | THE EFFECT OF THE HTC PHENOMENON IN PULSES ON NUTRIENT DIGESTION

As previously mentioned, pulses possess the beneficial property that they can be stored for extended periods of time. Because processing of pulses occurs regardless of postharvest storage, this step in the value chain was discussed first in this review, even though storage of raw, dried pulses chronologically occurs before processing (see Figure 1). However, postharvest storage can have major consequences for nutrient digestibility and bioaccessibility and should therefore be taken into account. Upon prolonged storage at temperatures above 25°C and a relative humidity above 65%, pulses can develop the HTC phenomenon (Njoroge et al., 2015; Reyes-Moreno et al., 2000; Yi et al., 2016). Very recently, it has been shown that the HTC phenomenon is developed upon storage of common beans at temperatures above their glass transition temperature (T_g), with the rate of HTC development increasing with the difference between storage temperature and T_g (Kyomugasho et al., 2021). For example, for some common bean varieties, at a moisture content of 10% (a relevant lower limit for dry pulse seeds) T_g would be around 20°C indicating that stability cannot be guaranteed during storage at temperatures exceeding T_g, possibly resulting in the development of the HTC phenomenon (Kyomugasho

TABLE 6 A summary of hard-to-cook theories and their nutritional implications

Hypothesis	Mechanism (summary)	Nutritional quality implication
Pectin–cation–phytate theory	Redistribution of cations driving them into the cell walls and middle lamella.	Increased mineral chelation and a decrease in mineral bioaccessibility.
Lignification theory	Crosslinking of polyphenols with proteins or with other cell wall polymers.	Decreased protein digestibility.
Protein–starch hypothesis	A more robust protein network formation around starch granules.Reduced starch swelling.	A decrease in both protein and starch digestibility.
Lipid oxidation theory	A decrease in plasmalemma integrity.	Increased mineral loss during soaking and cooking. Synergistic effect with pectin–cation–phytate theory—decreased mineral bioaccessibility.

Note: Based on the following studies: Hentges et al. (1991); Hincks and Stanley (1986); Jones and Boulter (1983); Liu et al. (1992); Mattson (1946); Paredes-López et al. (1991); Reddy et al. (1982); Reyes-Moreno et al. (1994); Richardson and Stanley (1991).

et al., 2021). Storage in these conditions is quite common in developing countries with tropical climates, where pulses are crucial staple foods (Galiotou-Panayotou et al., 2008; Shiga et al., 2004). HTC pulses require a longer cooking time to achieve sufficient softening to render them palatable (Njoroge et al., 2015; Reyes-Moreno & Parades-López, 1993). In addition to the increased energy requirements for pulse preparation (fuel or burning wood), HTC pulses also show decreased textural and nutritional quality, resulting in a decrease in consumer acceptance and substantial economic losses (Ferreira et al., 2018; Kinyanjui et al., 2015; Yi et al., 2016). Upon developing the HTC phenomenon, different pulse types show changes in mineral distribution, color (darkening), and solubility of pectin fractions, as well as a decreased phytic acid content and an increase in total phenolic and lignin content (Chigwedere, Njoroge, et al., 2019; Parmar et al., 2017; Pirhayati et al., 2011). Cooking time is therefore an often-used criterion for the evaluation of the quality of pulses (Kinyanjui et al., 2015). During prolonged cooking of HTC pulses, an increased amount of solids can leach out and heat-labile vitamins can be destroyed (Kinyanjui et al., 2015). Section 5.1 gives an overview of existing hypotheses concerning this HTC phenomenon. Nutritional changes in terms of protein and starch digestibility and the bioaccessibility of minerals are discussed in Sections 5.2, 5.3, and 5.4 respectively.

5.1 | HTC: Hypotheses and state-of-the-art

Several hypotheses have been drafted to explain the mechanisms causing the HTC phenomenon, of which an overview can be found in Table 6. Broadly, these hypotheses can be subdivided into enzymatic and nonenzymatic theories. A detailed description of the biochemical changes occurring in pulses upon the development of the HTC phenomenon has been published by Chigwedere, Njoroge, et al. (2019).

Very briefly, the pectin–cation–phytate theory states that enzymatic dephosphorylation of phytate (IP_6) under the influence of phytase into forms with a lower phosphorylation degree (inositol phosphates IP_5, IP_4, and others) and a lower chelating capacity may result in the release of some divalent mineral cations (Gwala, Kyomugasho, et al., 2020; Hurrell et al., 2003). These minerals could subsequently diffuse into the middle lamella and crosslink pectin-carrying negative charges due to enzymatic demethoxylation (Chigwedere et al., 2018; Galiotou-Panayotou et al., 2008; Kinyanjui et al., 2015; Paredes-López et al., 1991). The formation of insoluble pectates in the cell wall middle lamella upon storage impedes the process of pectin solubilization during cooking, slowing down tissue softening and cell separation (Chigwedere et al., 2018; Van Buggenhout et al., 2009).

Cations such as Ca^{2+}, Mg^{2+}, Zn^{2+}, and, Fe^{2+}, which are present in pulses, may exist either in a free state, or chelated to other molecules. Phytate is the principal store of phosphorus in pulse seeds and, because of its ionic nature, it naturally chelates some minerals (Reddy et al., 1982). The phytase activity is hypothesized to increase during postharvest storage at elevated temperatures and relative humidity, releasing cations (Galiotou-Panayotou et al., 2008; Mattson, 1946). The released cations finally migrate to the cell wall and the middle lamella where they might crosslink with the demethylesterified pectin to form insoluble pectates (Reyes-Moreno & Parades-López, 1993). In contrast to what is expected according to the traditional pectin–cation–phytate theory, Chigwedere, Nkonkola, et al. (2019) found that the degree of methoxylation (DM) of common bean pectin does not change during long term storage, suggesting that enzymatic demethoxylation

upon prolonged storage does not play a major role in the development of HTC. An adapted version of this theory has therefore been proposed, stating that divalent mineral cations released due to phytate hydrolysis in the cotyledons crosslink pectin due to its inherent DM (Chigwedere, Nkonkola, et al., 2019).

A second enzymatic mechanism proposed for the development of HTC is the lignification theory (del Valle & Stanley, 1995; Garcia et al., 1998). Lignification is suggested as a stress-response reaction initiated by high-temperature and high-humidity storage conditions (Hincks & Stanley, 1987). In this theory, it is proposed that polyphenols, soluble tannins, and free aromatic amino acids are released from the seed coat upon enzymatic degradation of proteins, and consequently migrate to the cotyledons (Hincks & Stanley, 1986; Reyes-Moreno et al., 2000). Mobilized phenolic compounds can bind to water-soluble cell wall components such as pectates, depositing a lignin-like material that reinforces cotyledon cell walls and middle lamella (Chigwedere et al., 2018; del Valle & Stanley, 1995; Garcia et al., 1998; Kinyanjui et al., 2015). In this context, it is important to mention the more recent findings by Chigwedere et al. (2018), which showed that the cooking behaviors of stored whole common beans and cotyledons (without seed coat) are not significantly different. From this, it could be concluded that the migration of tannins from the seed coat contributes insignificantly to the development of HTC in common beans, as compared to the reactions taking place in the cotyledons.

Some other, though less studied, nonenzymatic mechanisms for the occurrence of the HTC phenomenon have been hypothesized. They include, among others, structural changes in starch, changes in storage proteins due to protein insolubilization, and denaturation due to tissue acidification, membrane damage, as well as multiple mechanisms including oxygenation and polymerization of lipids (Chigwedere et al., 2018; Galiotou-Panayotou et al., 2008; Garcia-Vela & Stanley, 2006; Liu et al., 1993; Njoroge et al., 2015; Reyes-Moreno & Parades-López, 1993; Richardson & Stanley, 1991). However, the exact mechanism(s) responsible for the development of the HTC phenomenon still have to be elucidated. Though the adapted version of the pectin–cation–phytate theory seems plausible and well supported by research, contributions of other mechanisms (such as interactions with membrane bound protein [Chigwedere et al., 2019]) cannot be excluded and should be researched further.

5.2 | Effect of HTC on starch digestibility

Gwala et al. (2019) determined the *in vitro* starch digestion kinetics of Bambara groundnuts with distinct HTC levels, all generated from the same fresh batch (unaffected by storage above T_g). Tissue softening is slowed in HTC pulses due to changes in cell wall properties occurring during long-term storage (as listed in Section 5.1). After a fixed cooking time (e.g., 60 min), as expected, HTC Bambara groundnuts had a higher residual hardness as compared to their fresh counterparts. Consequently, HTC Bambara groundnuts showed a higher level of cell rupture and release of cell contents, which were readily available for digestive amylases. As a result, HTC Bambara groundnuts showed a higher rate of starch digestion as compared to fresh seeds after a fixed cooking time (Gwala et al., 2019).

In the same study, Gwala et al. (2019) obtained Bambara groundnuts of similar hardness levels from seeds of different HTC levels by adapting the cooking time. These seeds, with similar hardness (but distinct HTC) level, showed comparable *in vitro* starch digestion kinetics. Rather than attributing the differences in starch digestion kinetics to the HTC level, they should be attributed to the hardness of the seed after thermal treatment and the consequent prevalent mechanism of tissue failure (microstructure) upon mechanical disintegration (Gwala et al., 2019). This confirms that hardness, as affected by processing, can be used as a material property to steer and predict starch digestion kinetics in Bambara groundnuts, as mentioned in Section 4.3, both fresh and after development of HTC phenomenon.

5.3 | Effect of HTC on protein digestibility

Significant decreases in vitro protein digestibility can be found upon the development of the HTC phenomenon in cooked common beans, chickpeas, cowpeas, and black beans (Nyakuni et al., 2008; Reyes-Moreno et al., 2000; Tuan & Phillips, 1991). This decrease in protein digestibility has been confirmed in vivo in rats for HTC cowpeas (Tuan & Phillips, 1991). Medina-Godoy et al. (2012), Ruiz-Ruiz et al. (2012), and Segura-Campos et al. (2014) extracted proteins from both fresh and HTC chickpeas and common beans and studied their digestibility. First, a lower yield for protein extraction was noticed for both HTC chickpeas and common beans as compared to their fresh counterparts, which may be caused by chemical changes occurring during storage, rendering the proteins less soluble (Medina-Godoy et al., 2012). Second, a lower in vitro protein digestibility was observed for protein extracts from HTC common bean and chickpeas compared to their fresh counterparts (Ruiz-Ruiz et al., 2012; Segura-Campos et al., 2014).

Several hypotheses have been drafted to explain the effect of long-term storage on the protein digestibility of

different pulses. One of them states that the same factors responsible for increased cooking times upon inducing the HTC defect also cause the decrease of protein digestibility (Ruiz-Ruiz et al., 2012; Segura-Campos et al., 2014). During storage, proteins may form complexes with several components, such as other proteins, starch, hemicelluloses, and minerals, and undergo structural changes (Nyakuni et al., 2008; Ruiz-Ruiz et al., 2012; Segura-Campos et al., 2014; Tuan & Phillips, 1991). Another possible explanation for the decrease in protein solubility and digestibility could be interactions between proteins and phytic acid, which may cause substrate blocking at the active sites of proteolytic enzymes (Medina-Godoy et al., 2012; Nyakuni et al., 2008; Ruiz-Ruiz et al., 2012). Moreover, Liu and Phillips (1993) observed that HTC cowpeas showed a coarse coagulated/aggregated protein matrix with tightly embedded starch granules upon soaking and cooking. These authors hypothesized that storage of cowpeas at high temperature and relative humidity decreases the coagulation temperature of proteins. According to this hypothesis, next to pectin solubilization, the hardness of beans upon thermal treatment is dependent on the competition for water between starch (for swelling) and proteins (for coagulation). When protein coagulation prevails, a water-restricting barrier is formed, preventing starch from swelling. Moreover, protein coagulation and aggregation could cause a decrease in their solubility and thermal stability (Liu & Phillips, 1993), potentially decreasing protein digestibility.

In addition to the abovementioned hypotheses, an increase in high-molecular-weight tannins, as well as lignin and lignified protein, was observed upon storage of common beans at high temperature and high relative humidity (Martín-Cabrejas et al., 1997). For chickpeas, a decrease in seed coat tannins was observed upon inducing the HTC defect, whereas the tannin concentration in the cotyledon increased (Reyes-Moreno et al., 2000). These findings indicate the possible role of seed coat tannins in the development of HTC (Reyes-Moreno et al., 2000). It has been hypothesized that, as a result of storage, tannins may migrate from the seed coat to the cotyledon, where they can react and polymerize with proteins and carbohydrates (Reyes-Moreno et al., 2000). In addition, the increased cotyledon tannin concentration might also have another effect. Tuan and Phillips (1991) stated that the activity of endogenous proteases during long-term storage at high temperatures and relative humidity can lead to the formation of bean protein hydrolysates. Instead of increasing the overall protein digestibility, these protein hydrolysates might undergo interactions with polyphenols such as tannins, ultimately diminishing their digestibility (Martín-Cabrejas et al., 1997; Segura-Campos et al., 2014). The mechanisms proposed in this paragraph include the migration of seed coat tannins and polyphenols to the cotyledon as a result of HTC development. However, the findings of Chigwedere et al. (2018) demonstrate that the HTC phenomenon can develop during storage, regardless of the presence of the seed coat (Section 5.1), and thus possible tannin migration.

TABLE 7 Average bioaccessible mineral concentration (mg/100 g of cooked sample) in one serving of soaked and cooked (60 min, 95°C) whole common beans (Canadian wonder) that were fresh or stored for 8 or 20 weeks at 35°C and 80% relative humidity

	Storage time	Bioaccessible mineral concentration			
		Mg	Ca	Fe	Zn
Whole bean	0 weeks	29.4	24.8	1.0	0.6
	8 weeks	31.7	19.1	0.6	0.5
	20 weeks	29.8	10.4	0.5	0.2
Cotyledon	0 weeks	21.8	11.5	1.2	0.8
	8 weeks	22.0	10.2	0.8	0.5
	20 weeks	20.6	5.2	0.6	0.5

Note: Values are based on Rousseau, Celus, et al. (2020).

In this context, it is important to note that the effect of adapting the cooking time to align hardness levels in seeds with different HTC levels on protein digestibility of pulses has not yet been studied. It might be that, as for protein and starch digestion kinetics in fresh Bambara groundnuts with distinct hardness levels (Section 4.3), and for starch digestion kinetics in stored Bambara groundnuts (Section 5.2), hardness can be used as a material property affected by processing to steer and predict protein digestion kinetics in stored pulses. Additional research is needed in this area.

5.4 | Effect of HTC on mineral bioaccessibility

The effect of the development of the HTC phenomenon on pulse mineral bioaccessibility has been studied by several authors. As a result of postharvest storage, minerals can be displaced by being released from one binding agent, possibly followed by chelation by another (Rousseau, Celus, et al., 2020). For common beans, as shown in Table 7, the solubility and bioaccessibility of Ca, Zn, and Fe decrease with the development of the HTC phenomenon, whereas Mg bioaccessibility is not significantly affected (Rousseau, Celus, et al., 2020). This may be explained by the lower affinity of mineral antinutrients to Mg (as explained in Section 4.4). Moreover, the effect of postharvest storage on mineral bioaccessibility showed the same trend for whole common beans and dehulled cotyledons, implying a

nonsignificant effect of the seed coat (Rousseau, Celus, et al., 2020).

The effect of the development of the HTC phenomenon in Bambara groundnuts on the bioaccessibility of Ca, Mg, Zn, and Fe was studied by Gwala, Kyomugasho, et al. (2020). These authors found that Ca bioaccessibility and solubility decreased upon HTC development. This effect could be attributed to an observed increase in Ca–pectin crosslinking upon storage (Gwala, Kyomugasho, et al., 2020). As could be expected, Mg was found to be the most bioaccessible mineral among the four studied minerals, possibly due to the lower affinity of antinutrients (Section 4.4). In Bambara groundnuts, in contrast to common beans, ageing did not seem to influence the bioaccessibility of trace elements Zn and Fe (Gwala, Kyomugasho, et al., 2020). Upon storage, little migration of minerals could be observed between seed coat and cotyledons. Due to the prolonged cooking times, necessary to render HTC Bambara groundnuts palatable, Mg showed the most striking decrease in concentration due to leaching (72%), followed by Fe (57%) and Zn (48%) (Gwala, Kyomugasho, et al., 2020).

The abovementioned findings were confirmed for cowpeas with distinct HTC levels but aligned hardness (by adapting the cooking time) by Kruger et al. (2015), who noticed a decrease in the Ca, Zn, and Fe bioaccessibility in cowpeas upon prolonged storage at high moisture levels and temperatures. However, in another study carried out by Martinez Meyer et al. (2013), the mineral bioaccessibility was determined in flours obtained from (thermally untreated) common beans with induced distinct HTC levels. In this case, Fe and Zn bioaccessibility was found to increase with the induction of the HTC phenomenon, whereas for some other studied cultivars, the Fe bioaccessibility seemed to decrease and/or the Zn bioaccessibility was not affected during storage. It should be taken into account that leaching due to (for HTC pulses prolonged) cooking was not taken into account in this study because raw flours were analyzed.

Several authors have tried to explain these findings using the pectin–cation–phytate theory. According to this hypothesis (Section 5.1), a redistribution of minerals would occur upon the development of HTC in pulses (Gwala, Kyomugasho, et al., 2020; Reyes-Moreno & Parades-López, 1993). It could be confirmed for both Bambara groundnuts and common beans that the degree of phosphorylation decreases during prolonged storage, inducing the release of phytate-chelated minerals (Gwala, Kyomugasho, et al., 2020; Rousseau, Celus, et al., 2020). However, the mineral bioaccessibility did not seem to increase with storage, indicating that a reorganization may occur between mineral chelators. Minerals that are released from phytate during storage might be chelated by other molecules (e.g., pectin) (Gwala, Kyomugasho, et al., 2020; Rousseau, Celus, et al., 2020). It should be noted that the chelating capacity of pectin is caused by its inherent DM, which does not increase due to enzymatic hydrolysis during postharvest storage of common beans and Bambara groundnuts, as shown by Rousseau, Celus, et al. (2020) and Gwala, Kyomugasho, et al. (2020), respectively.

Overall, it can be stated that although pulses contain high amounts of minerals, these are quite poorly accessible for absorption in the small intestine (Section 4.4). From the results in Table 7, it can be concluded that postharvest storage and the induction of the HTC phenomenon negatively affect mineral bioaccessibility and that this effect cannot be cancelled out by conventional cooking.

6 | INNOVATIVE APPLICATIONS OF PULSES AS INGREDIENTS IN FOODS

Over recent years, pulses are increasingly being incorporated as ingredients into several innovative foods, which can be convenient for consumers as they allow them to increase their pulse intake without drastically changing their dietary habits (Asif et al., 2013). In this context, pulse flours are being used for the partial (enrichment) or total replacement of traditional ingredients in many (often wheat-based) product formulations (Laleg, Barron, et al., 2016; Petitot et al., 2010; Rocha-Guzman et al., 2008; Sozer et al., 2017). Very recently, in addition to raw-milled pulse flours, innovative pulse powders containing whole intact cells are being produced and successfully incorporated into new food products with improved nutritional characteristics (Bajka et al., 2021; Delamare et al., 2020; Edwards, Ryden, et al., 2020). The physicochemical, technofunctional, and digestive properties of cells isolated from pulses (using several techniques) have been extensively reviewed by Pallares Pallares et al. (2021). In addition, purified pulse protein, starch, and fiber extracts can be incorporated into diverse processed foods as functional ingredients (Boye et al., 2010). Different agro-food chain steps applied in the development of these foods can ultimately affect digestibility characteristics of both macronutrients and minerals.

6.1 | Use of (whole) pulse flours

Pulse flours are traditionally manufactured by mechanically disrupting raw pulses. As a result of milling and depending on milling intensity (and the obtained particle sizes), cellular barriers are broken and cell contents released (Aguilera et al., 2009; Edwards et al., 2021; Ma et al., 2011; Verkempinck et al., 2020). An array of studies

has been carried out with the aim of (partially) substituting wheat flours with pulse-based flours, affecting the nutrient composition and proportions of the final food. This aspect has been extensively reviewed by Monnet et al. (2019). In general, pulse flours contain more fiber, protein, and minerals but less starch than wheat flour, with about the same lipid content (Monnet et al., 2019). Additionally, several nutrient characteristics such as the shape of starch granules, amylose to amylopectin ratio, cell wall and fiber properties, and the type of proteins are different for pulse versus wheat flours (Edwards et al., 2021; Hoover et al., 2010; Kumar et al., 2016; Monnet et al., 2019). Gluten is the most abundant protein in wheat. The gluten network structure, caused by a high degree of covalent linking by disulfide bonds between S-containing amino acids in different polypeptides, mainly contributes to the elastic, cohesive, and viscous characteristics of the dough and finished product (Campos et al., 1997; Miñarro et al., 2012; Monnet et al., 2019; Padalino et al., 2016). Pulse proteins, deficient in S-containing amino acids, do not have the capacity to form these strong and extensive network structures (Iqbal et al., 2006). Consequently, the (partial) substitution of wheat gluten by pulse proteins largely affects the processability and technological and textural properties of food products (Monnet et al., 2019). The gelatinization and denaturation temperatures of pulse starch and protein are higher than those for cereals, necessitating adaptations in food processing (Monnet et al., 2019). Moreover, the incorporation of (increasing ratios of) pulse flours can cause defects in attributes important to consumers such as structure, mouthfeel, texture, cooking quality, color, and flavor (Gómez et al., 2008; Laleg et al., 2017; Monnet et al., 2019; Padalino et al., 2016; Portman et al., 2020). Despite these challenges, pulse flours have been successfully incorporated into formulations for the manufacturing of cakes, bread, cookies, and pasta showing improved nutritional properties such as an increased protein, slowly digestible starch, fiber, and phenolic compound content (Asif et al., 2013; Gallegos-Infante et al., 2010; Gómez et al., 2008; Laleg, Barron, et al., 2016; Petitot & Micard, 2010; Portman et al., 2020; Turfani et al., 2017). The partial addition of faba bean flour to wheat-based pasta formulations results in a dilution of the protein network and a higher protein digestibility as compared to wheat-based pasta (Laleg, Barron, et al., 2016). In addition to partial substitution, the possibility of manufacturing completely pulse-based (and thus gluten-free) bread and pasta using mixtures of pulse flours has been investigated (Aguilar et al., 2015; Giuberti et al., 2015; Laleg, Cassan, et al., 2016; Miñarro et al., 2012). Some experiments have been carried out regarding chickpea bread and pasta made from pure faba bean, pea, lentil, and black-gram flours, with promising physicochemical characteristics and an increased protein, fiber, and ash content but decreased starch and fat content (Laleg et al., 2017; Laleg, Cassan, et al., 2016; Miñarro et al., 2012; Rosa-Sibakov et al., 2016; Trevisan et al., 2019; Turco et al., 2019). In the case of pulse pasta, the weak protein network leads to higher leaching of starch and soluble protein during pasta cooking and a lower sensorial and textural quality of the cooked product (Laleg, Cassan, et al., 2016; Petitot et al., 2010; Rosa-Sibakov et al., 2016; Sozer et al., 2017). Only a few studies have assessed the impact of complete replacement of wheat by pulse flours on protein digestibility, establishing an increase in *in vitro* protein hydrolysis for 100% faba bean pasta compared to regular wheat-based pasta (Laleg et al., 2017). In contrast, the *in vitro* starch digestibility (as a percentage of total starch) of pure wheat and faba bean pasta did not differ significantly (Rosa-Sibakov et al., 2016). However, the fraction of resistant starch in pulse pasta is significantly higher and the fraction of available carbohydrates lower, when compared to commercial cereal-based gluten-free pastas, which are often made of rice or maize mixtures (Laleg, Cassan, et al., 2016; Trevisan et al., 2019).

Pulse flours may also be used in liquid or semisolid foods as emulsifiers, thickeners, and protein supplements, as their composition is rich in starch, proteins, and fiber (Asif et al., 2013). The proteins in a pulse flour can stabilize emulsions by adhering to the water–oil interface, orienting hydrophobic groups to the oily phase and hydrophilic groups to the watery phase, for example, in salad dressings (Khazaei et al., 2019). Moreover, due to the thickening effect of starch in pulse flours, the viscosity of foods such as soups and sauces can be increased (Ma et al., 2016; Sozer et al., 2017). Pulse flours with suitable flow behavior (e.g., chickpea) can also be used for protein supplementation of liquid foods with low viscosity, such as drinks high in protein (e.g., imitation milk, infant formula) (Asif et al., 2013; Sozer et al., 2017; Zare et al., 2015). Alternatively, lentil and chickpea flours can be utilized to increase the protein content and improve technological functionality (such as cloud stability and turbidity) of low-viscous liquid foods such as orange and apple juice (Sozer et al., 2017; Zare et al., 2015). Furthermore, the fiber present in pulse hulls (e.g., lentil hulls) may act as a thickener or bulking agent, as it can interact with other emulsion components by physical entrapment and/or embedding in the network structure, causing increased water retention and enhanced textural properties (Ma et al., 2016).

A technique that can be used to create expanded snack products from, for example, chickpeas and beans is extrusion (Asif et al., 2013; Berrios, 2006; Thakur et al., 2019). Corn-based snacks fortified with common bean flour show a higher protein and polyphenol concentration but a denser, less expanded, and harder structure (Anton et al., 2009). In this regard, an array of expanded lentil and chickpea snacks are already available on the market. Extrusion can be used to increase starch solubility and decrease

protein solubility, improving textural and sensorial characteristics (Anton et al., 2009; Berrios, 2006; Kristiawan et al., 2018). Extrusion of whole pinto bean flour was reported to completely inactivate protease inhibitors, leading to an increased in vitro protein digestibility (Balandrán-Quintana et al., 1998). Additional insights are, however, required regarding the effect of different processing techniques (such as extrusion) on nutrient digestibility in pulse-based foods.

6.2 | Use of purified pulse ingredients

Next to using whole pulse flours, several other ingredients can be isolated from pulses. These ingredients are increasingly being applied in the food industry, as is discussed in the next paragraphs, to improve the nutritional composition of foods. However, research on the effects of protein, starch, and fiber extraction and the incorporation of these extracts in food formulations on nutrient digestibility is missing and further research is necessary.

6.2.1 | Use of extracted pulse proteins

Protein-enriched flours (dry matter consisting of <60% protein), protein concentrates (>60% protein), and isolates (>85% protein) can be incorporated into food formulations with the aim of improving the nutritional composition and/or providing specific desired functional attributes (Jarpa-Parra, 2018; Khazaei et al., 2019). Important functional properties of pulse proteins are the pH-dependent solubility, water binding, fat binding, emulsification, foaming, gelation, thickening, and flavor binding (Boye et al., 2010; Khazaei et al., 2019; Toews & Wang, 2013). Concentrated pulse proteins can be used in several food applications, such as protein shakes and industrial imitation milk (Boye et al., 2010; Shevkani et al., 2019), as an emulsifier in soups and sauces (Singhal et al., 2016), in formulations of meat alternatives (e.g., plant-based burgers and sausages) (Shevkani et al., 2019), and processed meat products (e.g., the use of adzuki bean flour as a meat extender and fat replacer in beef meat balls) (Aslinah et al., 2018). Moreover, isolated pulse proteins have a potential use in gluten-free and wheat-containing bakery products. Pea protein isolate was found to improve dough and bread quality and delay staling in gluten-free bread formulations (Mariotti et al., 2009), whereas modified cowpea protein improved textural properties and sensory acceptability in wheat bread and sponge cake (Campbell e al., 2016). Moreover, different pulse proteins (such as lentil and white bean) showed appropriate technological properties for use in cake and muffin formulations (Bildstein et al., 2008; Shevkani & Singh, 2014).

6.2.2 | Use of extracted pulse starches

In recent years, several new botanical materials such as pulses are being used as unconventional starch sources. However, the isolation of pulse starches is not as straightforward as the isolation of starch from roots and tubers, because pulses are higher in protein and lipids and pulse starch granules are smaller than their tuber or root counterparts (Kringel et al., 2020). However, methods have been developed to successfully isolate (amylose rich) starch from beans, peas, lentils, and so forth, as extensively covered in a review by Kringel et al. (2020). It should be remarked that these pulse-based starches are inherently rich in resistant starch and have a high amylose to amylopectin ratio (Oyeyinka et al., 2017). Purified pulse starches have several applications in the food industry, for example, as thickening agents in soups or sauces.

6.2.3 | Use of extracted pulse fibers

In order to obtain health-related dietary fiber intake recommendations, fiber is commonly being added to formulations of several foods such as snacks and bakery products (Dalgetty & Baik, 2003; Sivam et al., 2010). In this regard, pea hull fiber enrichment of snacks was found to have the potential to increase fiber intake in the elderly (Alyousif et al., 2020). Fiber enrichment can alter functional properties of food products, such as texture, gel forming, thickening capacity, viscosity, and water and oil retention. For example, adding high fractions of fiber to bread dough mixtures dilutes wheat gluten, lowering gas retention and leaf volume (Dalgetty & Baik, 2003; Sivam et al., 2010). However, incorporation of soluble cotyledon fibers resulted in more attractive breads with regard to crumb structure and color, when compared to breads containing insoluble or hull fibers (Dalgetty & Baik, 2003). Gil Martens et al. (2017) extensively reviewed the positive functional properties of pea hull fiber (a mixture of soluble and insoluble fiber) as a sustainable source of dietary fiber for food enrichment. Pea hull fiber was found to be rich in dietary fiber and biologically active compounds (such a polyphenols), as well as to increase the viscosity and water and oil binding capacity of several food formulations (Gil Martens et al., 2017).

6.3 | Use of powders containing intact pulse cells

Very recently, researchers have been trying to exploit the structural organization of pulses for the design of functional foods. These novel foods could stimulate consumption of (potentially) low-GI starch, pulse protein, and dietary fiber (Delamare et al., 2020). In this regard, peas,

chickpeas, lentils, and beans were precooked to develop a pulse powder containing intact cells (PulseON) (Edwards, Ryden, et al., 2020). PulseON powders have a nutritional composition similar to their "traditional" pulse flour counterparts, but they contain an increased amount of type I resistant starch. These powders showed a lower *in vitro* starch digestibility (<40% starch digested after 90 mins of small intestinal digestion) compared to (dry-milled) pulse flours in which the cell contents are free (>80% starch digestion within 30 min of small intestinal digestion) and a low–medium GI in vivo (Edwards, Ryden, et al., 2020).

The potential of (partially) replacing wheat flour with cellular pulse powder as ingredients for biscuit and bread production has been evaluated (Bajka et al., 2021; Boukid et al., 2019; Delamare et al., 2020). PulseON has a higher water holding capacity as compared to dry-milled pulse flours (Edwards, Ryden, et al., 2020). Moreover, it was observed that the structural (cellular) integrity of the PulseON powder was maintained during biscuit and bread processing, as well as digestion (Bajka et al., 2021; Delamare et al., 2020). Importantly, breads and biscuits were obtained with acceptable quality attributes, such as texture, appearance, and palatability (Bajka et al., 2021; Delamare et al., 2020). It appeared that incorporating the cellular ingredient can enhance the nutritional value of biscuits and breads, by lowering the starch hydrolysis index and increasing both the fiber and resistant starch content. Importantly, for bread rolls containing cellular pulse powder, a lowered glycemic response (GI) could be confirmed *in vivo* (Bajka et al., 2021). Interestingly, for biscuits, the starch hydrolysis index decreased with increasing cellular powder to wheat flour ratio, even in very low concentrations (Delamare et al., 2020). This can be explained by the fact that the presence of PulseON limits water accessibility for the gelatinization of wheat starch during thermal treatment (Delamare et al., 2020).

From the above, it can be concluded that incorporation of a cellular pulse ingredient (PulseON) in several foods can be a strategy for increasing the consumption of type I resistant starch and possibly decrease the GI of staple foods (Bajka et al., 2021; Delamare et al., 2020; Edwards et al., 2015). It should, however, be taken into account that in order to manufacture these cellular powders, pulses have to be soaked, thermally treated, wet sieved, and air-dried in order to obtain a microbiologically stable powder. In the context of sustainability, it should be mentioned that all these manufacturing steps require energy and, depending on the maximal yield of cellular powder (45%–63%), waste streams are created. The creation of new waste streams should be avoided when developing innovative sustainable and healthy foods (and food ingredients). In this regard, both liquid and solid co-streams of pulse processing have useful functional and nutritional properties, which could be harnessed for synergistic and sustainable pulse-derived ingredient developments. For example, the cooking water (aquafaba) of pulses can be repurposed as vegan egg-white substitute high in protein, with both foaming and emulsifying properties (Buhl et al., 2019). Moreover, seed coats can be applied for fiber enrichment in foods such as bread (Dalgetty & Baik, 2006).

7 | CONCLUSION

Pulses play an important role in healthy and sustainable human nutrition as environmentally friendly sources of protein, (slowly digestible) starch, fiber, minerals, and vitamins. The health-beneficial properties of pulses can be attributed to both the composition and the complex structural hierarchy of the tissue, in which nutrients are bioencapsulated in cells. Both factors are highly affected by the different phases in the food processing chain. The aim of this review was to list all phases of the pulse value chain from harvest to consumption that might affect the composition and structure of pulses and hence influence their behavior upon digestion. It should, however, be noted that preharvest variables can significantly affect the composition of pulses as well but were not discussed in this review.

Before consumption, pulses must undergo at least some form of thermal processing. During cooking, cell wall properties of pulses are affected on two levels: (i) gradual pectin solubilization at the middle lamella causes cell separation upon mechanical disruption of tissue, and (ii) gradual increase of cell wall permeability. The overall effect of these processes determines the residual degree of nutrient bioencapsulation and consequently the accessibility to digestive enzymes and digestibility patterns of starch and protein. However, the effect that thermal processing exerts on the microstructure and digestive characteristics largely depends on cell wall properties and thus varies greatly between pulse types. More research is necessary to fully elucidate the link between cell wall properties, thermal processing, microstructure, and digestive properties quantitatively and mechanistically.

Postharvest storage of dry pulses at elevated temperature and relative humidity causes the development of the HTC phenomenon, giving rise to economic and nutritional losses. For Bambara groundnuts, adapting the cooking time of HTC and fresh seeds, resulting in equivalent seed hardness, aligns their starch digestion kinetics. The effect of aligning hardness levels in seeds with different HTC levels on protein digestibility has not been sufficiently studied. Moreover, the prolonged cooking times required to sufficiently soften HTC seeds will cause more leaching and a lower bioaccessibility of minerals. Importantly, the effect of the development of the HTC phenomenon on

the nutritional quality is dependent on pulse type. HTC development can be prevented by controlling storage conditions, which is unfortunately impossible for many subsidence farmers in developing countries. In this regard, it might be possible to select or improve existing varieties that are less prone to development of the HTC phenomenon. In addition to this, attempts have been made to valorize HTC pulses, for example, by producing protein concentrates from HTC common beans that possess good technofunctional properties (Segura-Campos et al., 2014).

The information provided in this review can be used to select processing conditions to optimize nutrient digestibility and bioaccessibility for certain population groups. By adapting processing variables, cell wall barriers can be altered, ultimately affecting both starch and protein digestibility. For instance, for population groups that require low-GI foods, starch digestion in pulses can be slowed down by adapting the processing conditions to maintain maximal (cellular) structural integrity, whereas other population groups (children, the elderly) may require more readily available starch and protein. Regarding minerals, it can be concluded that bioaccessibility is low. To exploit the inherent mineral content of pulses, different strategies can be applied such as dehulling, applying shorter cooking times, not discarding the cooking liquid containing leached minerals, and enzymatically degrading mineral antinutrients (as occurs during fermentation). It should be noted that in most research cited in this review, digestion is evaluated at the level of in vitro digestion. This is an inexpensive, reproducible, high-throughput method to study the influence of different processing variables on the digestion of a particular nutrient under controlled circumstances (Mackie, 2020). However, in vivo validation of these results is needed to make extrapolations and conclusions valid for humans.

A not insignificant part of ingested nutrients is not absorbed into the blood stream and reaches the colon where they are fermented. Pulses have been reported to exert beneficial effects on gut health due to the presence of several nutrients resistant to digestion (Clemente & Olias, 2017; Tabernero & Gómez de Cedrón, 2017). Until now, in vitro digestion studies have mostly focused on the oral, gastric, and small intestinal reactors. Fermentation studies, in contrast, have mostly focused on (mixtures of) purified fiber or pulse polysaccharide fractions instead of real (complex) food systems (De Preter et al., 2011; Parkar et al., 2019; Tabernero & Gómez de Cedrón, 2017). Hence, the effect of intrinsic (micro)structural complexity of real food systems on fermentation kinetics remains under explored. Very recently, research in this area has been emerging, with Rovalino-Córdova et al. (2020) studying the effect of cell wall encapsulation on the fermentation of common bean starch (resistant starch type I). However, additional research is necessary into the fermentation of processed complex (pulse) food systems, taking into account the effect of prior gastrointestinal digestion. A profound understanding of these processes could lead to the design of process parameters aiming to not only steer nutrient digestion (and absorption) but also substrate delivery to the colon for fermentation (Ercolini & Fogliano, 2018). While designing foods that delivers nutrients to the gut microbiota, it should be noted that although the fermentation of carbohydrates results in the formation of health-beneficial SCFAs, colonic fermentation of proteins is generally regarded as detrimental due to the formation of compounds such as branched-chain fatty acids and phenolic and indolic compounds (Ercolini & Fogliano, 2018; Tabernero & Gómez de Cedrón, 2017). However, Bowman–Birk protease inhibitors, which are extremely resistant to digestive conditions, have been reported to exert beneficial effects on gut health (Clemente & Olias, 2017). Moreover, indolic compounds, metabolites from the microbial tryptophan metabolism in the gut, are emerging as potentially beneficial bioactive compounds, mediating the regulation of intestinal immunity as ligands of, for example, the aryl hydrocarbon receptor (AhR) and pregnane X receptor (PXR) (Gao et al., 2018).

As well as providing an overview of the traditional pulse value chain, this review gives a summary of the new strategies being applied with the aim of increasing the consumption of health-beneficial pulses. Pulses are increasingly being incorporated into innovative foods, as whole or purified ingredients, to improve their nutritional profile. However, the use of purified pulse ingredients raises the question of sustainability, as different processing steps and waste streams are being introduced. Moreover, the specific digestive patterns characteristic of pulses can get lost during the production of dry-milled (whole) pulse flours or pulse-derived ingredients and their incorporation into food products. A notable development has been the incorporation of cellular pulse powders into an array of foods (Bajka et al., 2021; Delamare et al., 2020; Edwards, Ryden, et al., 2020). In addition to responding to the many technological challenges arising from the development of these pulse-enriched products, additional studies of the (especially protein) digestive behavior, as well as colonic fermentation of the nonabsorbed fraction, are necessary.

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AUTHOR CONTRIBUTIONS

Dorine Duijsens: Conceptualization; Funding acquisition; Visualization; Writing-original draft. Shannon Gwala: Conceptualization; Visualization; Writing-original draft. Andrea Pallares Pallares: Writing-review & editing. Katharina Pälchen: Writing-review & editing. Marc Hendrickx: Writing-review & editing. Tara Grouwet: Conceptualization; Funding acquisition; Writing-review & editing.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ORCID

Dorine Duijsens https://orcid.org/0000-0003-0152-4087
Andrea Pallares Pallares https://orcid.org/0000-0002-9052-9738
Katharina Pälchen https://orcid.org/0000-0001-6315-7660
Marc Hendrickx https://orcid.org/0000-0002-3823-0851
Tara Grauwet https://orcid.org/0000-0002-5156-4792

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