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Health promoting properties and sensory characteristics of phytochemicals in berries and leaves of sea buckthorn (*Hippophaë rhamnoides*)

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Abstract

Sea buckthorn (*Hippophaë rhamnoides* L., SB), as a multi-functional plant, is widely grown in Asia, Europe and Canada. The berries and leaves of SB contain a diverse array of health-supporting phytochemicals, which are also related to the sensory qualities of berry and berry products. This review summarizes the biologically active key-compounds of the berries and leaves of SB, their health-promoting effects, as well as the contributions to the sensory quality of the berries. The target compounds consist of sugars, sugar derivatives, organic acids, phenolic compounds and lipophilic compounds (mainly carotenoids and tocopherols), which play an important role in anti-inflammatory and antioxidant functions, as well as in metabolic health. In addition, these compounds contribute to the orosensory qualities of SB berries, which are closely related to consumer acceptance and preference of the products. Studies regarding the bioavailability of the compounds and influence of the processing conditions are also part of this review. Finally, the role of the sensory properties is emphasized in the development of SB products to increase utilization of the berry as a common meal component and to obtain value-added products to support human health.

Keywords: Bioactive compounds, bioavailability, health effects, processing conditions, sea buckhorn, sensory quality

Introduction

Consumption of fruits and vegetables has been recommended in dietary guidelines to reduce the risk of various diseases and disorders (Martin et al. 2013). Sea buckthorn (*Hippophaë* *rhamnoides* L., SB), as a multi-functional plant, has attracted much attention due to the diverse array of nutrients and phytochemicals in its berries and leaves, such as polyphenols, carotenoids, and vitamin E (Bal et al. 2011; Ciesarová et al. 2020). These compounds have been claimed to have many health-promoting properties, related especially to anti-inflammatory activities (Ganju et al. 2005; Yang and Kortesniemi 2015), cellular antioxidant activities and anti-proliferative properties *in vitro* (Guo et al. 2017; Kim et al. 2010), as well as positive effects on the cardiovascular system (Olas 2016; Suomela et al. 2006; Xu et al. 2011). The nutritional attributes, medicinal and therapeutic potential, as well as health-related application of SB have been well reviewed (Olas 2018; Stobdan et al. 2013; Suryakumar and Gupta 2011).

Despite the indicated health-promoting properties, sea buckthorn berries are less commonly consumed as food or food ingredients due to their sensory properties (Laaksonen et al. 2016; Ma et al. 2017a). Their sensory characteristics are typically described as strongly sour, astringent and bitter, with a very low level of sweetness (Tang, Kälviäinen, and Tuorila 2001; Tiitinen, Hakala, and Kallio 2005). From the view of consumers, orosensory properties are the most important factors affecting the preferences, choices and acceptance of foods (Geertsen et al. 2016; Laaksonen et al. 2016). In order to obtain palatable products, malolactic fermentation (MLF) is used to reduce the high acidity of SB juice, and some other fruits are added to balance bitterness and astringency of sea buckthorn (Markkinen et al. 2019; Selvamuthukumaran, Khanum, and Bawa 2007; Tiitinen et al. 2006a; Tiitinen et al. 2007). Improving the sensory qualities of SB berries and related products will add their value, increase consumption, and create new markets for these commodities.

Generally, the content of sugars and acids, especially, the sugar/acid ratio plays an important role in determining the flavor and consumer acceptance of berries and berry-based products (Laaksonen et al. 2013; Laaksonen et al. 2016). Along with glucose and fructose, SB berries contain some less common sugar derivatives, e.g. ethyl β-D-glucopyranoside (β-EG) and sugar alcohols such as L-quebrachitol (1 L-2-O-methyl-chiro-inositol) and other derivatives of inositol in varying quantities, which may contribute to the sensory properties (Ma et al. 2017a; Yang 2009; Zheng et al. 2012). Flavonol glycosides (FGs) and proanthocyanidins (PAs) are the main phenolic compounds present in SB berries, which can cause astringency and bitterness of the plant-based foods and beverages (Ma et al. 2016; Teleszko et al. 2015; Yang et al. 2017). Comparing to PAs, FGs have lower threshold to induce diverse drying or puckering astringent mouthfeels in sensory evaluations (Bajec and Pickering 2008; Hufnagel and Hofmann 2008; Scharbert et al. 2004).

In addition to SB berries, the composition and content of bioactive compounds in the leaves have been well investigated, among which ellagitannins are the most abundant polyphenols (Ciesarová et al. 2020; Ma et al. 2019). The extracts of SB leaves have shown various pharmacological activities, such as anti-inflammatory activity and hepatoprotective effect (Geetha et al. 2005; Geetha et al. 2008; Marnila et al. 2013). The animal and human studies have indicated potential of these extracts in reducing the incidence of CVD, certain cancers, and age-related degenerative diseases (Guliyev et al. 2004). Recently, due to the increasing interest and consumption of herbal infusions from edible plants, there has been an increasing interest in utilization of SB leaves and converting them into tea-type beverage products (Ma et al. 2019). Despite these aforementioned health benefits and utilization, the majority of the SB leaves still remains under-utilized as agricultural waste after berry harvesting.

This current review aims to provide an overview of the bioactive compounds characteristic in SB berries and leaves, as well as their health-promoting properties and contributions to sensory properties of SB. Special emphasis is placed on the importance of SB as part of a healthy diet for reduction of risk of various chronic diseases. The first part presents the bioactive components, their bioavailability and health effects. The second part reviews research on contributions of these compounds to the sensory properties of the berries and berry products. The third part draws attention to the effects of processing conditions on the bioactive compounds. Moreover, the challenges of the development and processing of SB products are discussed.

Bioactive compounds in berries and leaves of sea buckthorn

Several epidemiological studies have linked diet, especially substantial consumption of plant-based foods, with decreased risk of chronic diseases. Sea buckthorn berries and leaves are characterized by high content of bioactive compounds (Table 1), which have been suggested to have various health-beneficial effects (Figure 1).

Flavonol glycosides

Flavonol glycosides (FGs) constitute the most abundant group of phenolic compounds in sea buckthorn berries. The total content of FGs varied from 23 ~ 400 mg/100 g FW (Ma et al. 2016; Teleszko et al. 2015; Yang et al. 2009; Zheng et al. 2016), which is up to 150 times higher than the levels reported in tomato fruit (2 mg/100 g FW), and 10 times higher than those in chokeberry (*Aronia melanocarpa*, 27 mg/100 g FW) and American cranberry (*Vaccinium macrocarpon*, 21 mg/100 g FW) (Mikulic-Petkovsek et al. 2012; Stewart et al. 2000). Among the flavonols, isorhamnetin is the typically most abundant aglycone (mean ~60 % of total flavonol aglycones), as isorhamnetin-3-*O*-rutinoside (I-3-R, mean ~30 % of total FGs) and isorhamnetin-3-*O*-glucoside-7-*O*-rhamnoside (I-3-G-7-Rh, mean ~10 % of total FGs) are two major FGs (Ma et al. 2016; Pop et al. 2013). The content of flavonols in the berries varies considerably due to origin, weather conditions, growth location, latitude, and harvest date (Kortesniemi et al. 2017; Kortesniemi et al. 2014; Ma et al. 2016; Yang et al. 2017; Zheng et al. 2012). In other fruits, isorhamnetin is less common than quercetin and kaempferol, except the copao fruit (*Eulychnia acida* Phil.), which is rich in I-3-R with content up to 54 g/100 g in phenolic extracts of epicarp (Belitz et al. 2004; Jiménez-Aspee et al. 2014).

On a dry weight basis, the content of flavonol glycosides in sea buckthorn leaves was reported to be close to the levels found in the berries (Pop et al. 2013). Leaves of SB contain flavonols up to 1400 mg/100 g DW comprising glycosides of isorhamnetin, quercetin and kaempferol, among which glycosides of isorhamnetin (~ 50 % of total FGs) represent the highest percentage. I-3-G-7-Rh and I-3-R are the two major FGs in leaves, which were also the major flavonols reported in the berries (Ma et al. 2019). Other FGs, such as isorhamnetin-3-*O*-glucoside (I-3-G) and rutin, were also found in both the leaves and the berries (Ma et al. 2016; Ma et al. 2019).

Flavonol glycosides in diet have gained increasing interest due to their particularly high antioxidant capacities and concomitantly strong health-promoting effects, such as anticancer activity, immunomodulatory activity and antimicrobial activity (Jacques et al. 2013; Xiao et al. 2016; Xue et al. 2015; Yang et al. 2018). It has been reported that increasing dietary intake of FGs of SB berry may play an important role in reducing the cardiovascular mortality (Cheng et al. 2003; Clair et al. 2002).

Various experiments showed that isorhamnetin and its derivatives have anti-inflammatory effects *in vivo* and *in vitro* (Yang et al. 2013) as well as anti-proliferative (Guo et al. 2017; Li et al. 2014; Teng et al. 2006), anti-viral (Apers et al. 2002), and anti-oxidative stress activities *in vitro* (Yang et al. 2014). Among the flavonoid aglycones of SB berries, isorhamnetin showed the highest anti-proliferative activity towards human liver cancer cell HepG2. Weaker anti-proliferative activity was observed by isorhamnetin-3-*O*-sophoroside-7-*O*-rhamnoside (I-3-S-7-Rh) and I-3-G-7-Rh, which, however, exhibited large amount in SB berries (Guo et al. 2017). The earlier results demonstrated that isorhamnetin extracted from the SB berries may reduce the lipid peroxidation and protein carbonylation in human plasma and oxidative stress induced by H_2O_2/Fe (Skalski et al. 2019). Isorhamnetin and isorhamnetin-3-*O*-glucuronide are reported to have a significant cytotoxic effects on human breast cancer MCF-7 cells *via* a ROS-dependent apoptosis pathway (Wu et al. 2018). Further, isorhamnetin is reported to inhibit atherosclerotic plaque development in apolipoprotein E knockout mouse (apoE −/−) (Luo et al. 2015). It is also demonstrated that this compound is a potent immunosuppressive agent and may be used to prevent and treat inflammatory and autoimmune diseases, as well as transplantation rejections (Shi et al. 2018). Moreover, a C-glucoside of isorhamnetin is one of the best radical scavengers among polyphenols of SB leaves (Radenkovs et al. 2018).

In human nutrition, quercetin represents the main flavonol (Ahn et al. 2008). There is growing evidence showing that quercetin is a potent natural antioxidant. There are also indications that quercetin may have a potential in management of chronic diseases, such as cardiovascular diseases and cancer (Lesjak et al. 2018; Nabavi et al. 2012; Russo et al. 2012). Besides quercetin, kaempferol glycosides display anti-obesity and anti-diabetic potential by reducing fat accumulation in adipose tissues, improving hyperlipidemic and diabetic conditions in obese mice (Zang et al. 2015).

The sugar moieties of the flavonol glycosides strongly influence the absorption efficiency of flavonols (Manach et al. 2005; Petersen et al. 2016). Flavonol aglycones and only some glucosides are absorbed in the small intestine. E.g. quercetin-3-*O*-glucoside is transported into the enterocytes by the sodium-dependent SGLUT1 transporter (Wolffram et al. 2002). Flavonols linked e.g. to a rhamnose may not be absorbed in the small intestine but they are fermented and degraded by the colonic microflora (Hollman and Katan 1997; Kahle et al. 2006). The bioavailability of quercetin glucoside is about 5-fold compared with that of rutinoside in humans (Graefe et al. 2001; Walle et al. 2000). An *in vitro* study suggested that the metabolites of I-3-G yielded by human intestinal flora, such as isorhamnetin, kaempferol, and quercetin, may improve the absorption of I-3-G by colonic mucosa (Du et al. 2014). This was supported by the findings of another study conducted by *in vivo* pharmacokinetics model, where quercetin and kaempferol increased the intestinal absorption of isorhamnetin extracted from the SB berries by regulating the activity and expression of the multidrug resistance-associated protein 2 (Xiao et al. 2019). Moreover, the addition of a small amount of SB oil was showed to enhance the absorption and bioavailability of the SB flavonols in humans (Suomela et al. 2006).

Tannins

Proanthocyanidins

Tannins consist of condensed and hydrolyzable tannins. Condensed tannins, known as proanthocyanidins (PAs), are oligomers and polymers of flavan-3-ol units produced through the biosynthetic flavonoid pathway widely distributed in the plant kingdom. The agricultural benefits as well as chemistry and biochemistry of PAs have been well summarized in literature (Aerts et al. 1999; Ferreira and Slade 2002; Marles et al. 2003).

The difference in subunits and bond positions/configurations results in the wide structural diversity in PAs, and the number of isomers increases markedly with an increase in the degree of polymerization (DP). Procyanidins (PCs) and prodelphinidins (PDs) consist only of (epi)catechin or (epi)gallocatechin, respectively. The most common in foods are B-type PAs, in which the monomeric units of flavan-3-ols are linked by C–C bonds (*via* C4–C8 and/or C4–C6). Again, the A-type PAs are less common and present in a few specific foods only, such as cranberries, lingonberries and avocados (Deng et al. 2013).

B-type PAs with DP from 2 to 11 have been detected by HILIC-ESI-MS in SB berries (Kallio et al. 2014). More than 60 combinations of (epi)catechins and (epi)gallocatechins of PA dimers and trimers were found in SB berries, in which (epi)gallocatechins were the main monomeric units (Kallio et al. 2014). The PA oligomers (DP 2−4, 4−26 mg/100 g DW) formed only a small part of the total PA pool (390−1940 mg/100 g DW) in the berries studied (Yang et al. 2017). PA oligomers (DP 6−9) of the SB pomace are composed mainly of PDs and smaller amounts of PCs (Rösch et al. 2004a). The PAs of SB seeds consist of catechin, epicatechin, gallocatechin and epigallocatechin (Fan et al. 2007). The majority of PAs, especially PAs with DP > 4 in SB berries, are reported to be present mainly in the seeds (Ma et al. 2017b). Genetic background and environmental factors have a significant influence on the content of PAs in SB berries. The content of total PAs is 2−3 fold in the berries of *H. rhamnoides* ssp. *rhamnoides* in northern Finland compared with the berries from southern Finland, but for oligomeric PAs (DP 2−4) the situation is *vice versa* (Yang et al. 2016). The environmental conditions, including the length and radiation sum of the growth season, as well as the temperature sum, are positively correlated with PA oligomers (DP 2−4), but negatively with the content of total PAs (Yang et al. 2016; Yang et al. 2017). According to Arimboor and Arumughan (2011), SB leaves contain a smaller amount of PAs compared to berries, and the average DP is 10.6.

Diet rich in PAs is associated with reduced risks of cardiovascular disease, neurodegenerative conditions, and metabolic syndrome (Aron and Kennedy 2008; Langhans 2017). PAs of SB pomace possessed higher or comparable antioxidant capacities to that of ascorbic acid or Trolox (Rösch et al. 2004b). No significant difference was detected in the antioxidant capacity measured by scavenging Fremy's salt between monomeric flavan-3-ols and dimeric PAs in SB (Rösch et al. 2004b). The PAs of SB seeds are reported to have the protective effect against light-induced retinal degeneration *in vivo via* antioxidant, anti-inflammatory and anti-apoptotic mechanisms (Wang et al. 2016). Moreover, anti-proliferative effects of PAs extracted from SB has been shown in human colon and liver cancer cell lines (Grey et al. 2010).

The biological activities of PAs *in vivo* depend on the DP value, which affects greatly the absorption of PAs. Data on absorption of flavan-3-ols has been conflicting. Absorption of flavan-3-ol dimers have been detected in humans and rats *in vivo* (Baba et al. 2002; McKay et al. 2015), whereas some studies failed to show absorption of PA dimers (Donovan et al. 2002;

Gonthier et al. 2003). Despite the high content PAs in some foods, flavan-3-ols are poorly absorbed. The polymers with a DP > 4 are not absorbable because of their large molecular size and the gut barrier (Manach et al. 2005). It has been shown that PAs of SB berries and leaves have the ability to precipitate proteins and to inhibit digestive enzymes, which might alter the digestion and bioavailability of proteins and phenolics (Arimboor and Arumughan 2011). Phenylvalerolactones and phenolic acids are the main microbial metabolites of PAs resulted from the action of the colon microbiota, which may contribute to the health-promoting properties of PAs *in vivo* (Ou and Gu 2014).

Ellagitannins

Ellagitannins (ETs) form a complex class of polyphenols, which are water-soluble and able to precipitate proteins and alkaloids. ETs are characterized by one or more hexahydroxydiphenoyl (HHDP) moieties esterified to a sugar. They are less frequently encountered, but berries such as strawberries and raspberries are major sources of intake of ETs in western diets.

The leaves of Finnish sea buckthorn (*Hippophaë rhamnoides* ssp. *rhamnoides*) are rich in ellagitannins (mean 76 mg/g DW), of which ten major compounds are identified and quantified (Moilanen et al. 2015; Suvanto et al. 2018). Among these compounds, hippophaenin C, stachyurin, and casuarinin were on average the most abundant, with their total concentrations adding up to 63 % of the total ETs in SB leaves (Suvanto et al. 2018). After dry-processing, the SB leaf products (tea-type beverages) are still rich in ETs with the concentrations ranging from 10 to 20 mg/100 mL infusions (Ma et al. 2019).

Literature concerning the absorption and metabolism of ETs in humans is limited. ETs are hydrolyzed to ellagic acid (EA) by the action of gastric acid and the intestinal enzymes (Mertens-Talcott et al. 2006). Part of EA is absorbed in the small intestine, while the remaining

EA and ETs are further metabolized to urolithins and hydroxy-6*H*-dibenzopyran-6-one derivatives by the colon microbiota (Cerdá et al. 2005). The gut microbiota may play an important role in the biological effects of ETs (Puupponen-Pimiä et al. 2013). EA is also proposed to be considered as a biomarker for human studies related to consumption of dietary ETs (Andreux et al. 2019; Ludwig et al. 2015; Seeram et al. 2004).

Despite the poor absorption, ETs may have important beneficial effects on gut health and physiological impacts on the whole body due to the metabolites produced through fermentation of ETs by gut microbiota. ETs, EA and their metabolites have a wide range of biological activities and health-promoting properties, such as antioxidative, anti-inflammatory and prebiotic effects (Heinonen 2007; Landete 2011). The isomers of galloyl-bis-HHDP-glucoses and HHDP-galloylglucoside which belong to ETs, had been found to be the most effective natural antioxidants among phenolics extracted from SB leaves (Radenkovs et al. 2018). Majority of the plant extracts ETs showed good metal ion chelating ability (Moilanen et al. 2016). Moreover, the antioxidative activities of ETs in SB leaves and leaf products are more likely due to the capacity of chelating metal ions than the radical scavenging activities by 2-deoxyribose assay (Ma et al. 2019). Strictinin, isostrictinin, and casuarictin purified from SB leaves, have antiviral and interferon-inducing activities, and these compounds have been used to develop therapeutic agents (Korekar et al. 2011).

Further, dietary ETs and EA have displayed antioxidative and anti-carcinogenic effects in the gastrointestinal tract. The colonic microbiota further metabolizes EA to urolithins (urolithin A, B, C, and D), which have been shown to have high bioavailability compared to their precursors, ETs and EA (Landete 2011; Puupponen-Pimiä et al. 2013). Urolithins, urolithin A in particular, were the most active compounds to reduce lipopolysaccaride-induced NF-κB activity (Rønning et al. 2020). Moreover, urolithin A stimulated mitophagy and improved muscle health in elderly individuals and in preclinical ageing people (Andreux et al. 2019). Although the microbial metabolite urolithin B showed lower antioxidant activity than ETs, urolithins may still display health benefits, such as estrogenic and/or anti-estrogenic activities (Cerdá et al. 2005). It is, however, worth to note that ETs may inhibit protease activities and affect the protein digestion (Mcdougall and Stewart 2005).

Phenolic acids

Both sea buckthorn berries and leaves are rich in phenolic acids, such as gallic, salicylic and caffeic acids. Gallic acid is dominant in both free and bound forms, contributing 66 % and 85 % of the total phenolic acids in SB pulp (soft parts of berry, ~1000 mg/kg DW) and leaves (~5000 mg/kg DW), respectively (Arimboor et al., 2008). Zadernowski et al (2005) reported that the salicylic acid (21−47 mg/kg DW) was the principal phenolic acid (55−74 % of the total phenolic acids) in SB berries of the six cultivars studied. The major fraction (approximately 70 %) of the phenolic acids in SB berries is found to be concentrated in seeds. Furthermore, the total phenolic acid content in the seed kernel (~5700 mg/kg DW) is higher than in the berry pulp and the seed coat (Arimboor et al. 2008). Genetic background has a great effect on the content of total phenolic acid, which has been reported to be highest in *H. rhamnoides* ssp. *yunnanensis*, followed by ssp. *mongolica,* ssp. *turkestanica* and ssp. *sinensis* (Guo et al. 2017).

Dietary phenolic acids can be rapidly absorbed and metabolized in humans (Lafay and Gil-Izquierdo 2008; Nardini et al. 2009). The influence of phenolic acids on both the expression and activity of enzymes has been studied with cell and animal models, involved in production of inflammatory mediators and in response to mediators of growth factors, cytokines and endotoxins (Russell, Wendy and Duthie 2011; Russell et al. 2008). Phenolic acids extracted from SB berries have been reported to be stronger free radical scavengers than flavonols (Tkacz et al., 2020). Among the phenolic acids of SB berries, gallic acid was observed to have stronger anti-proliferative activity towards human liver cancer cell HepG2 compared to protocatechuic acid and ferulic acid (Guo et al. 2017). Obesity leads in multiple inner organs to DNA damage which can be prevented by low amounts of gallic acid (Setayesh et al. 2019). Salicylic acid has an anti-inflammatory activity, which has been reported to reduce the risk of colorectal cancer (Paterson and Lawrence 2001). Caffeic acid displays the major effective anti-proliferative action when T47D human breast cancer cells were tested, even at low concentrations (Kampa et al. 2004).

Non-phenolic bioactive compounds

Lipophilic compounds

Sea buckthorn pulp oil is abundant in unsaturated fatty acids, such as palmitoleic, oleic, linoleic and linolenic acids. The high content of palmitoleic acid (16:1n-7) is typical for SB pulp/peel oil, but the content varies widely (20−45 %) depending on the origin of the plant (Yang and Kallio 2001). SB pulp/peel oil has been used for development of cosmetic products and for healing purposes due to palmitoleic acid forms a significant part of the epidermal lipids of human skin. Besides, palmitoleic acid has beneficial effects on epithelial tissues including the digestive, respiratory and urological organs, the vagina among postmenopausal women and the inner eyelid (dry eye syndrome) (Larmo et al. 2019; Larmo et al. 2014; Olas 2018). However, palmitoleic acid is absent in the seed oil, but linoleic (18:2n-6) and α-linolenic acids (18:3n-3) (close to 1∶1) comprises about 70 % of seed oil fatty acids (Yang and Kallio, 2001). Linolenic acid is important for the water permeability barrier of skin as a structural component of ceramides (Larmo et al. 2014). The composition of polyunsaturated fatty acids (PUFA) differs from those of most vegetable oils, e.g. the PUFAs of canola oil contain linoleic and α-linolenic acids at a ratio of close to 2:1 (Ursin 2003).

The color of sea buckthorn berries is mainly affected by the content and composition of carotenoids, the total content of which varies from 1 to 120 mg/100 g FW of berries (Yang 2001). Forty-one different carotenoids have been reported in various cultivars of SB berries (Bekker and Glushenkova 2001), the major compound being *β*-carotene (15–55 % of the total) (Yang 2001). The content of *β*-carotene varies from 0.2 to 17 mg/100 g FW in SB berries, and the concentrations of *α*-, *γ*-, and dihydroxy-*β*-carotene, zeaxanthin, and canthaxanthin exist at lower levels (Yang 2001; Yang and Kallio 2002). Lycopene is an important antioxidant present at high levels (8 mg/100 g FW) in SB berries, typically even higher in tomatoes (0.9–11 mg) (Malinowska and Olas 2016). Compared to the content in the berries, the level of total carotenoids is lower in sea buckthorn leaves (~4 mg/100 g DW) (Pop et al. 2014).

Tocopherols and tocotrienols (also referred to as vitamin E) are important bioactive components in SB berries. They are in human plasma the major lipid-soluble antioxidants, which play an important role in protection against oxidative stress (Ranard et al. 2019). Their total concentrations ranged from 8 to 32 mg/100 g FW in seeds and from 6 to14 mg/100 g FW in the whole berries, respectively (Kallio, Yang, and Peippo 2002). The large variation in amounts and composition of tocopherols and tocotrienols were found to be due to the genetic background, harvest year and date. The berries of ssp. *sinensis* contain more total tocopherols and tocotrienols than ssp. *mongolica*, among which *α*-tocopherol is the major compound (~80 % of total), the content varying from 43 to 116 mg/kg FW in berries (Kallio, Yang, Peippo, Tahvonen, et al. 2002). SB berries have higher levels of *α*-tocopherol in the early ripening period, while at later dates, *δ*-tocopherol levels increase (Andersson et al. 2008). Concentration of *γ*-tocopherol is higher in green berries, but the content rapidly declines to traces when berries turned from green to olive-yellow (Zadernowski et al. 2003). Compared to berries, SB leaves contain higher level of tocopherols (72–154 g/kg DW) (Sytařová et al., 2020).

Oils from SB seeds and pulp are rich in phytosterols at concentration varying from 1.2 to 1.8 mg/g in the seed oil, and from 12 to 23 mg/g in the pulp oil of berries (Li et al. 2007; Sajfrtová et al. 2010). The total quantity of phytosterols in SB oil exceeds that of soybean oil by 4-20 times (Stobdan et al. 2013). Twenty-two different phytosterols have been reported in SB seed oil, among which *β*-sitosterol is the most important constituting 57−76 % of the seed sterols and 61−83 % of the pulp/peel sterols, respectively (Li et al. 2007; Yang et al. 2001). The concentration shows only little variation between subspecies and collection sites of SB, but depends on the method of extraction (Li et al. 2007; Yang et al. 2001). Phytosterols of SB have been reported to lower serum cholesterol concentrations and decrease the risk of hypercholesterolemia-induced cardiovascular disorders (Olas 2018).

SB oil displays anti-atherogenic, cardio-protective, anti-platelet aggregation, antiulcer and anti-depressive properties, which have been attributed to carotenoids, tocopherols, tocotrienols and sitosterol, and demonstrated using cell cultures, animal models, and clinical trials in humans (Basu et al. 2007; Johansson et al. 2000; Olas 2018; Xing et al. 2002). An eyelid spray emulsion-enriched SB oil has a significant beneficial effect on eye dryness, burning and other symptoms of human (Larmo et al. 2019).

Sugars, sugar derivatives and sugar alcohols

The major monosaccharides in sea buckthorn berries are glucose and fructose, and trace amounts of sucrose has also been determined (Tiitinen, Hakala, and Kallio 2005; Yang 2009; Zheng et al. 2012). *β*-EG is a compound characteristic for SB and rarely found in other edible berries or fruits. The presence of *β*-EG was reported in SB for the first time in 2006 (Tiitinen et al. 2006b). Also, presence of the corresponding methyl derivative in SB was reported later (Lindstedt et al. 2014). In some berries of *H. rhamnoides* ssp. *rhamnoides*, *β*-EG is the most abundant compound (1.9 g/100 ml juice) in the sugar fraction (Yang 2009). The content of *β*-

EG varies significantly with genetic background, harvesting time, and origin (Yang 2009; Zheng et al. 2011; Zheng et al. 2012). During ripening and over-ripening, the content of *β*-EG in the berries of ssp. *rhamnoides* increased, whereas the content of glucose decreased (Yang 2009).

Ethyl and methyl glucosides have been reported to have some relevance to physiological effects (Higgins et al. 1996; Storlien et al. 1986). However, literature is hardly available on their absorption and metabolism in humans or animals. Based on a NMR metabolomics study, both ethyl and methyl glucosides have been detected in human plasma and urine after a single meal of SB berries (Lindstedt et al. 2014) Moreover, *β*-EG was shown to decrease blood pressure in SHR rats and stroke-prone spontaneously hypertensive rats after intravenous injection of the compound (Matsubara et al. 1989; Sawabe and Matsubara 1999). *β*-EG was rapidly absorbed in the blood stream and easily excreted in urine after oral administration, but traces of *β*-EG were recognized in the rat even 24 h after oral administration (Mishima et al. 2008).

The presence of inositols, methyl inositols and L-quebrachitol in SB was reported for the first time in 2009 (Kallio et al. 2009). In the berries of ssp. *sinensis*, L-quebrachitol was the most abundant sugar alcohol (0.2–1.1 g/100 mL juice), followed by methyl-*myo*-inositol, and *myo*-inositol (Zheng et al. 2011). The genetic background of SB berries affects the content of methyl inositols, which is higher in ssp. *sinensis* (means 0.8 g/100 mL juice) than in ssp. *rhamnoides* (means 0.3 g/100 mL juice) and ssp. *mongolica* (means 0.2 g/100 mL juice*)* (Yang 2009). Based on the NMR fingerprints, L-quebrachitol is important for the identification of ssp. *sinensis* as the most distinctive marker in SB berries (Su et al. 2014). L-quebrachitol, inositols and methyl inositols are significant regulators of physiological processes of plants and humans. L-quebrachitol may increase the fasting insulin level in plasma in db/db mice (Xue et al. 2015). The earlier studies found that orally administered inositols can decrease hyperglycemia and hyperlipidemia, and have an influence on insulin secretion and generation of mediators in diabetic rats (Fonteles et al. 2000; Nascimento et al. 2006). Further, insulin resistance-related diseases, such as polycystic ovary syndrome and gestational diabetes are related to derangements in inositol metabolism (Muscogiuri et al. 2016).

Organic acids

Malic acid is the most abundant organic acid in SB berries, followed by quinic and ascorbic acids (vitamin C) (Tiitinen, Hakala, and Kallio 2005; Yang 2009; Zheng et al. 2012). Ascorbic acid and even citric acid have antioxidant properties (Hraš et al. 2000). Ascorbic acid is among the major antioxidants in SB berries, and its content correlates positively with the free-radical scavenging capacity of the corresponding fraction (Gao et al. 2000). Besides this, ascorbic acid cures the variety of clinical symptoms known as scurvy, repairs the mucosa injuries, as well as acts as a co-substrate of many important dioxygenases, and has an indirect effect on mRNA transcription (Arrigoni and De Tullio 2002; Gupta et al. 2006; Levavasseur et al. 2015). In some studies, ascorbic acid content varied from 50 to 4 000 mg/100 g in fresh berries, and the mean value was around 1 000 mg/100 g FW, which is higher than the levels found in many other berries, such as strawberries (65 mg/100 g FW), raspberries (29 mg/100 g FW), and blackberry (21 mg/100 g FW) (Korekar et al. 2014; Lee and Kader 2000; Tang 2002). Genotype, time of harvest, processing techniques, and storage conditions all affect the content of ascorbic acid in SB berries and berry products (Gutzeit et al. 2008; Kallio, Yang, and Peippo 2002; Xu et al. 2015). Moreover, ascorbic acid content has shown a positive correlation with the total phenolics and carotenoids in SB berries (Korekar et al. 2014). The SB leaves were reported to contain ascorbic acid on average 2100 mg/kg DW (Jaroszewska and Biel 2017).

Bioactive compounds eliciting taste of sea buckthorn

Consumers preferred a red color of SB berry, however, color and intensity of aroma effect only less on the pleasantness of berry (Tang, Kälviäinen, and Tuorila 2001). A balanced sweet taste may be the major characteristics contributing to the sensory appeal of berries and berry products, and it also affects the preferences and choices of consumers (Geertsen et al. 2016; Laaksonen et al. 2016). The sugar/acid ratio, a crucial factor for sweetness, is much lower in SB than in most of the common berries. Astringency and bitterness of SB are typically perceived as negative factors limiting its consumption (Ma et al. 2017a). These sensory properties also present challenges for exploitation of SB berries and berry-based products as ingredients in food industry. Hence, it is crucial to study the role of various metabolites in the sensory profile of SB. More knowledge is needed for improving the sensory quality and consumer acceptance of SB products. Figure 2 illustrates sensory profile and how bioactive compounds contribute to the taste properties of sea buckthorn berries.

Sweetness and sourness

Sweetness is a key factor influencing the overall liking of a berry, thus affecting also the pleasantness of sea buckthorn berries and berry products (Laaksonen et al. 2016; Tang, Kälviäinen, and Tuorila 2001). SB is perceived with low intensity of sweetness. The two major sugars, glucose and fructose, as well as the sugar/acid ratio, are responsible for the sweetness (Tiitinen, Hakala, and Kallio 2005). The sugar derivatives or alcohols, e.g. L-quebrachitol showed only little correlation with the sensory attributes (Ma et al. 2017b).

Sea buckthorn berries are characterized with intense sourness due to the high content of malic acid (Tiitinen, Hakala, and Kallio 2005; Tiitinen et al. 2006b). Ascorbic and quinic acids also contribute to sourness. Moreover, quinic acids has a close association with astringency in SB juices (Ma et al. 2017a). The intensity of sourness is negatively related to sweetness but positively with astringency of the juices (Tiitinen, Hakala, and Kallio 2005; Tiitinen et al.

2006b). Citric acid is related to the liking of SB juices, but it has less effect on the sourness (Ma et al. 2017a)

Astringency

Astringency is an important sensory characteristic of SB berries, of which mouth-drying and puckering astringency are the main sub-qualities (Ma et al. 2017b; Tiitinen, Hakala, and Kallio 2005). Phenolic compounds are considered as the major contributors to astringency of foods and beverages (Ma et al. 2014; Soares et al. 2017). Notable abundance of FGs and PAs have been reported in SB berries (Ma et al. 2016; Yang et al. 2017). Compared to the PAs, FGs played a more important role in astringency of SB purees (Ma et al. 2017b). FGs have been found to induce a multi-astringent sensation even at low concentration. Among them, rutin has been reported to elicit astringent perceptions already at very low concentrations (0.61 mg/L) in bottled water (Scharbert, Holzmann, and Hofmann 2004; Schwarz and Hofmann 2007). SB is rich in rutin, the average level being 10 mg/100 g FW in the berries of ssp. *sinensis* (Ma et al. 2016). However, quercetin glycosides are reported to have little impact on the astringency in SB purees of six cultivars studied (Ma et al. 2017b). Isorhamnetin glycosides dominate in the FGs of SB berries, of which isorhamnetin-3-*O*-sophoroside-7-*O*-rhamnoside (Is-3-S-7-Rh) has close association with the astringency of SB purees, although the sensory thresholds of individual isorhamnetin glycosides for astringency have not been established (Ma et al. 2016; Ma et al. 2017b).

Proanthocyanidins are key compounds for astringency of wine, the composition of the monomeric units playing a more important role than other PA variables such as the total concentration and degree of polymerization (Quijada-Morín et al. 2012). Moreover, the type of specific linkage between the monomeric units also affects the astringent intensity, e.g. catechin-(4→8)-catechin, being less astringent than either catechin-(4→6)-catechin or catechin-(4→8)-epicatechin (Peleg et al. 1999). Composition and contents of the PA oligomers, such as dimers and trimers, have been investigated in the SB berries (Kallio et al. 2014). Monomers are significantly less astringent than the dimers or trimers, whereas the latter two do not differ significantly from each other. Monomers and dimers are crucial astringent compounds in red wine (Hufnagel and Hofmann 2008). However, these well-known astringent components have been reported to show less astringent impact than FGs in the SB purees studied (Ma et al. 2017b). The content of PAs and the PC/PD ratio affect the astringent properties of black currant juices. Furthermore, higher PC/PD ratio and lower content of PAs associate with decreased astringency (Laaksonen et al. 2015).

The astringent sensory thresholds of the monomer (-)-epicatechin (270 mg/L) and the trimeric procyanidin C1 (260 mg/L) were about 2.5 times higher than all the dimeric procyanidins B1, B2, and B3 (110-120 mg/L), and the monomer (+)-catechin had similar threshold as the dimers (Table 2). Procyanidins are more astringent than ETs, but the latter have lower thresholds for astringent detection, ranging from 0.2 to 6.3 µmol/L as shown by studies carried out with tannins extracted from oak wood chips (*Quercus alba* L. and *Quercus robur* L.) (Glabasnia and Hofmann 2006). The astringent response is a combined function of the ability of a given tannin to bind soluble proteins and its tendency to interact with proteins *via* hydrophobic binding. The ability of PCs to saturate soluble proteins and then to bind membrane-bound proteins was more efficient than that of the ETs (Hofmann et al. 2006). SB leaves are rich in ETs. However, their contributions to the sensory quality of products derived from SB leaves has not been investigated, although the sensory thresholds of two individual ETs for astringency and bitterness have been reported (Table 2).

In addition to the phenolic compounds described above, it is well documented that various phenolic acid derivatives and organic acids contribute to the astringent oral sensations of food products (Challacombe et al. 2012; Hufnagel and Hofmann 2008; Lawless et al. 1996). Puckering astringency has been reported to relate positively to sourness elicited by various organic acids (malic, quinic and ascorbic acids) and the total acid content in SB juices (Ma et al. 2017b). An increase in astringency of phenolic compounds is often associated with a decrease in pH (Peleg and Noble 1999). Although it has been stated that astringency of bread and crackers was linked with *p*-hydroxybenzoic and vanillic acids (Challacombe et al. 2012), their roles in the sensory quality of SB berries or berry product have not been investigated. Due to the effects of food matrices on the astringency perceived, some astringent substances, tannic acid and alum will taste more astringent in water solution than in more complex matrices, such as wine or orange juice (Valentová et al. 2002).

Bitterness

The sensation of bitterness is considered to be the most complex taste quality in humans, due to the wide variety of compounds that elicit bitterness and to the apparently large number of genes encoding receptors for this taste modality. Flavonol aglycones (FAs) may activate the taste receptors of bitterness and are perceived as bitter (Roland et al. 2013). Various monomeric flavonoids, such as (+)-catechin, (−)-epicatechin and (−)-epigallocatechin, have been reported to activate the receptors TAS2R14 and TAS2R39 of human bitter taste (Roland et al. 2013; Soares et al. 2013). Among the PAs, the maximum intensity of bitterness follows the order: monomers > dimers > trimers (Peleg et al. 1999). Moreover, the specific linkage between monomeric units has an influence on bitterness, e.g. the catechin-catechin dimer linked by a 4→6 bond is more bitter than the catechin-(4→8)-catechin dimer (Peleg et al. 1999).

In general, most of the phenolic compounds may be perceived as astringent at notably low concentrations, but as bitter only at high concentrations. For instance, the taste threshold of (+)-catechin for bitterness was 290 mg/L in water in a triangle test, which is much higher than the astringent threshold reported (119 mg/L, Table 2) (Hufnagel and Hofmann 2008). Castalagin and vescalagin were identified in SB leaves and their thresholds for bitterness were both around 1600 mg/L, which was 1500-fold higher than the astringency thresholds (Table 2) (Glabasnia and Hofmann 2006; Hofmann et al. 2006; Moilanen et al. 2015). Additionally, some non-bitter, astringent phenolic compounds such as rutin, may enhance intensity of the perceived bitterness of some bitter compounds, such as caffeine (Scharbert and Hofmann 2005).

Interestingly, the well-known bitter PA oligomers (dimers, trimers and tetramers) did not correlate closely to the bitter taste in SB purees (Ma et al. 2017b). However, the ratios between acids and phenolic compounds, such as acids/PA dimers and acids/FGs, correlated strongly and positively to bitterness (Ma et al. 2017b). Beta-D-glucopyranosides are perceived as bitter through the binding of TAS2R16 receptor, which is one of 25 TAS2R receptors involved in perception of bitterness (Bufe et al. 2002; Meyerhof et al. 2010; Sakurai et al. 2010). *β*-EG is positively related to the bitterness of SB juices, so are the ratios *β*-EG/acids and *β*-EG/sugars (Ma et al. 2017a).

Based on the relationship between chemical compounds and sensory quality in a previously established PLS model, a model was investigated to predict the sensory properties of SB berries (Ma et al. 2017b; Ma et al. 2020). In this model, the mouth-drying astringency of SB berries can be predicted the most reliably, having the highest regression coefficients with quinic acid (0.12), total PAs (0.12) and I-3-S-7-Rh (0.11). I-3-S-7-Rh is also a strong factor for predicted sweetness (-0.07) and sourness (0.08)(Ma et al. 2020).

Effect of processing on bioactive compounds

The processing methods and parameters, such as temperature, pressure, pH and time, can markedly affect the bio-accessibility and nutritional quality of berry products (Amarowicz et al. 2009; Bakkalbaşi, Menteş and Artik 2008; Rodríguez-Roque et al. 2015). Processing of SB juice is a complex operation, in which many factors affect the quality of the final products. Conventional thermal processing, such as high-temperature-short-time (HTST) treatment, is used for assuring safety and to extend the shelf life of foods. It often causes undesirable changes in quality and sensory characteristics of the products, resulting in loss of flavor and development of off-flavor. Good stability of ascorbic acid is recognized in the SB juice during short-time heating as well as high retention during juicing and consequent technological processing (Seglina et al. 2006). Content of the total ascorbic acid in SB juice reduced by 5−11 % during the HTST processing which is negligible in comparison to the production of juice concentrate.-During this process, the loss of ascorbic acid can reach the level of 50 % due to the multiple steps such as clarification, filtration and thermo-vacuum evaporation (Gutzeit et al. 2008). Non-thermal, high pressure (200−600 MPa) pasteurization process is also applied for commercial production of SB juices of superior quality, retaining high antioxidant activity to meet demands of the consumers (Alexandrakis et al. 2014). Additionally, high pressure homogenization can be used to alter the physical properties and thus to enhance the color by reducing the size of the particles in the puree, leading to lighter and more yellow SB products (Aaby et al. 2020).

Sea buckthorn oil is the most recognized product, which can be pressed or extracted from the berry pulp or seeds. Supercritical carbon dioxide (SC-CO_2) has been widely applied to extract oils from both seeds and pulp of SB berries (Yang 2001; Yang and Kallio 2002; Yang et al. 2011). The SC-CO_2 extraction increases the yield and reduces the thermal and oxidative damages of the bioactive components in the extract compared to solvent extraction. For example, a higher yield of phytosterols (*β*-sitosterol) from SB seeds is achieved compared to extraction with hexane (Sajfrtová et al. 2010; Yang et al. 2011).

Although the processing methods of SB have been widely investigated in many studies, limited information is available concerning behavior of the bioactive compounds in different processes. Heating (50–100 °C) affects significantly the contents of flavonoids in SB extracts, but less the contents of other polyphenols and carotenoids (Ursache et al. 2017). However, Aaby et al. (2020) reported that pre-heating treatment (80 °C, 10 min) of the SB berries prior to sieving increased the yield of the purees (80 % to 84 %) and concentration of the total carotenoids (27 % to 65 %), but had an effect neither on ascorbic acid nor the total phenolics. Zvaigzne (2018) showed that ultra-high temperature treatment decreased ~10 % the content of total carotenoids compared to its content in fresh SB juices, but had less effect on the highest acidity and the contents of ascorbic acid, total phenolics and vitamin E, as well as antioxidant capacities (DPPH, FRAP and ABTS). Polyphenols of SB berries, when added to sausages, have remarkable thermal stability (remain 70 % on average) (Püssa et al. 2015). Contents of various linoleic acid oxylipins and of isorhamnetin glycosides decreased during cooking of the enriched sausages, whereas the content of quercetin glycosides remained constant (yield 99 %) (Püssa et al. 2015). Along with changes in bioactive compounds, processing conditions have a crucial impact on antioxidant activity of SB products (Bakkalbaşi, Menteş and Artik 2008; Kyriakopoulou et al. 2013; Ma et al. 2019). The radical scavenging ability of phenolics of SB berries extracted by methanol after freeze-drying, was higher than that of the phenolics obtained with microwave extraction of fresh berries (Kyriakopoulou et al. 2013).

Numerous tea-type beverages and powdered products can be manufactured of SB leaves through drying, which cause changes in the phytochemicals, texture, shape, and color of the leaves (Kyriakopoulou et al. 2013; Ma et al. 2019). After drying of the leaves at four different temperatures (50, 60, 80 and 100 °C), contents of the total phenolics, carotenoids and chlorophyll reduced by 28–40 %, 42–62 % and 45–71 %, respectively (Guan, Cenkowski, and Hydamaka 2005). The SB leaves processed by steam at high temperature (80–90 °C) resulted in the highest content of total ETs and phenolics in the tea-type infusions of the leaves. The non-thermal drying methods (freeze-drying and air-drying) led to higher antioxidant activities in the infusions than the thermal drying (Ma et al. 2019). The change in phytochemicals depends on the drying method, time, temperature, and type of compounds (Aaby et al. 2020;

Chan et al. 2009; Guan, Cenkowski, and Hydamaka 2005); Ma et al. 2019). The highly astringent ETs, such as vescalagin and castalagin, may be converted into less astringent degradation products during thermal process (Glabasnia and Hofmann 2007). Thus, the unit processes should be designed and optimized to improve sensory quality and maximize the protection of targeted bioactive components in SB products.

Development and challenge of sea buckthorn products in the future

Sea buckthorn berries are rich in health-supporting phytochemicals. Therefore, it is worthwhile to develop more food and health-care products of different parts of the plant and to promote its large-scale exploitation. Selection of the raw materials and technologies influence the quality of the products. Furthermore, special challenges in development are due to the sensory qualities of SB berries, especially astringency and bitterness elicited by the wide set of the phenolic compounds. Astringency and bitterness are generally considered as negative factors reducing the consumer acceptance and liking of berry products (Lesschaeve and Noble 2005; Verbeke 2006). However, astringency and bitterness can provide complex and balanced tastes in some specific types of beverages, such as coffee, tea, beer and wine (Geertsen et al. 2016). Certain degree of complexity in taste may enhance consumer acceptance of fruit juices as well.

The oral sensations of pure SB juice (average pH 3.1) characterized by high acidity need to be balanced to obtain palatable products (Beveridge et al. 1999; Laaksonen et al. 2016; Tiitinen, Hakala, and Kallio 2005). Thus, to reduce the sourness and astringency, some fruits, such as papaya and grapes, are often added to SB juice at varying proportions to produce mixed beverages (Selvamuthukumaran, Khanum, and Bawa 2007). Malolactic fermentation (MLF) may also be used to reduce the content of malic acid and thus the sourness of SB juice, maintaining simultaneously the health-promoting phenolic compounds (Markkinen et al. 2019;

Tiitinen et al. 2006a; Tiitinen et al. 2007). Additionally, the perception of bitterness can be reduced by blocking the bitter taste receptor hTAS2R39. E.g. three 6-methoxyflavanones were shown to reduce hTAS2R39 activation by epicatechin gallate (Roland et al. 2014). SB berries have been used as a novel probiotic cell immobilization carrier, which improved the physicochemical characteristics and the aroma of frozen yogurts (Terpou et al. 2019). Although the sensory properties limit the consumption of SB berries as fresh fruit and as raw material for food processing to some extent, SB products from berries and leaves have a great potential as healthy food as well as raw materials and ingredients for health care products and animal nutrition.

Recently, tea-type beverages processed from sea buckthorn leaves have been developed, which are sensory acceptable to consumers and contain high content of antioxidants (Ma et al. 2019). Besides the SB leaves, the current side-streams such as branches and bark, as well as residues from juice and oil extraction can be processed into value-added products, since they still retain abundant valuable nutrients and non-nutritive bioactive compounds (Puganen et al. 2018; Sharma et al. 2008).

Conclusions

Sea buckthorn is rich in nutritive and non-nutritive bioactive components, which are associated with various health-promoting effects. Extensive research efforts and results have shown the potential health effects of different fractions and products of sea buckthorn berries and leaves in management of chronic health problems, such as metabolic disorder and inflammation. However, the majority of the research has been carried out *in vitro* and in animal models. More human intervention studies are needed to validate the health benefits of sea buckthorn berries and products. Further, there is an insufficient understanding of the contribution of individual bioactive compounds or groups of bioactive compounds to physiological effects observed of sea buckthorn berries, leaves, as well as fractions and products derived from the berries and leaves.

Consumption of sea buckthorn is often limited by the unique sensory properties characterized by high intensities of acidity, astringency and bitterness. Only a very limited number of studies have been performed to determine the components contributing to sensory attributes of sea buckthorn berries and products. Bioactive constituents, such as phenolic compounds, vitamin C, organic acids, and sugar derivatives, likely have a strong influence on the sensory properties, especially astringency and bitterness of the sea buckthorn berries and berry-based products. More research is needed to understand the contribution of different compounds and their interaction with food matrix on the perception of the sensory qualities. It is also important to explore the role of lipophilic components as well as interactions between different components of different groups of compounds (lipophilic vs. hydrophilic; volatile vs. non-volatile) in the determining the taste and flavor profile of sea buckthorn. Further studies are also needed to improve the understanding on the impact of processing on bioactive and flavor compounds in sea buckthorn and to develop innovative processing technologies for targeted modification of the composition and sensory properties of sea buckthorn products. Such knowledge is needed to guide plant breeding and product development to improve orosensory qualities of sea buckthorn berries and products, which is essential for promoting the consumer acceptance and consumption of sea buckthorn.

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Figure captions

Figure 1. The classification, example structures and potential health benefits of bioactive compounds in the sea buckthorn berries and leaves.

Figure 2. Sensory profile and compounds contributing to taste properties of sea buckthorn berries. The data of sensory profile is based on the mean of 4 European cultivars (Tytti, Terhi, Hergo and Leikora)(Ma et al. 2017b).

Table 1. Concentrations of main bioactive components in sea buckthorn berries and leaves.

Components^1	**Berries^2**	**References**	**Leaves^2**	**References**
Flavonol glycosides				
Q-3-*O*-rutinoside	3.8–10 mg/100 g FW	(Ma et al. 2016)	0.5–0.8 mg/g DW	(Ma et al. 2019)
	1.3-7.4 mg/100 g FW	(Yang et al. 2009)	0–76.1 mg/100 g DW	(Pop et al. 2013)
Q-3-*O*-glucoside	3.2–8.8 mg/100 g FW	(Ma et al. 2016)		
Q-3-*O*-sophoroside-7-O-rhamnoside	1-120 mg/100 g DW	(Chen et al. 2007)	~20 mg/100 g DW	(Pop et al. 2013)
I-3-*O*-glucoside	5.3–11 mg/100 g FW	(Ma et al. 2016)	0.3–0.4 mg/g DW	(Ma et al. 2019)
	1-134 mg/100g DW	(Chen et al. 2007)		
I-3-*O*-rutinoside	15–38 mg/100 g FW	(Ma et al. 2016)	0.7–1.8 mg/g DW	(Ma et al. 2019)
	11-292 mg/100g DW	(Chen et al. 2007)	0–49.6 mg/100 g DW	(Pop et al. 2013)
I-3-*O*-glucoside-7-*O*-rhamnoside	8.5–22 mg/100 g FW	(Ma et al. 2016)	2.0 mg/g DW	(Ma et al. 2019)
	15-44.7 mg/100 g FW	(Yang et al. 2009)	69.1–111 mg/100 g DW	(Pop et al. 2013)
I-3-*O*-sophoroside-7-*O*-rhamnoside	5-176 mg/100 g DW	(Chen et al. 2007)	25-44.6 mg/100 g DW	(Pop et al. 2013)
K-7-*O*-rhamnoside	4-48 mg/100 g DW	(Chen et al. 2007)		
Acylated FGs	157–260 mg/100 g DW	(Chen et al., 2013)	24–115 mg/100 g DW	(Chen et al. 2013)
Total FGs	23–407 mg/100 g FW	(Ma et al. 2016)	14 mg/g DW	(Ma et al. 2019)
	~300 mg/100 g FW	(Teleszko et al. 2015)	1118 mg/100 g DW	(Pop et al. 2013)
	27-130 mg/100 g FW	(Yang et al. 2009)		
Proanthocyanidins (mg/100g DW)				
Dimers	1.0–8.9	(Yang et al. 2017; Yang et al. 2016; Kallio et al. 2014)		
Trimers	1.3–9.5			
tetramers	0.8–7.1			
PA oligomers	3.7–25.5			
Total PAs	167–1941			
Ellagitannins (mg/g DW)				
Stachyurin			7.8–8.5	(Ma et al. 2019)
Casuarinin			11.5-13.0	(Ma et al. 2019)
mean			76	(Moilanen et al. 2015; Suvanto et al. 2018).
Total ETs			29.2–109.1	(Ma et al. 2019; Suvanto et al. 2018)
Phenolic acids (mg/kg DW)				

Gallic acid	7.9–15.9	(Bittová et al. 2014)	19.1–79.1	(Bittová et al. 2014)
	0.2–7	(Zadernowski et al. 2005)	28.4–102.4	(Sytařová et al. 2020)
	1–2.6 mg/ml juice	(Rösch et al. 2003)		
Salicylic acid	21–47.5	(Zadernowski et al. 2005)		
p-coumaric acid	1.4–22.3	(Zadernowski et al. 2005)	8.4–13.4	(Bittová et al. 2014)
Total phenolic acids	3570–4439	(Zadernowski et al. 2005)	804-4988	(Arimboor et al. 2008)
Total Phenolics				
	260-490 mg/100 g FW	(Olas 2016)	98 mg/g DW	(Ma et al. 2019)
Sugars and orgainic acids				
β-EG	0.1–2.0 g/100 mL juice	(Ma et al. 2017; Yang 2009)		
Methyl inosotol	0.1–1.4 g/100 mL juice	(Yang 2009)		
L-quebrachitol	0.2–1.1 g/100 mL juice	(Kortesniemi et al. 2014; Zheng et al. 2012)		
Ascorbic acid	56–3909 mg/100 g FW	(Korekar et al. 2014)		
	360-1676 mg/100 g FW	(Tiitinen et al. 2006b)	2139.6 mg/kg DW	(Korekar et al. 2014)
	52- 130 mg/100 g FW	(Teleszko et al. 2015)		
	0.98–3.65 g/kg DW	(Sytařová et al. 2020)	22.81–46.32 g/kg DW	Sytařová et al. 2020)
Lipids				
triacylglycerols	15–85 g/kg FW	(Kallio, Yang, Peippo, Tahvonen, et al. 2002)		
glycerophospholipids	1.8–2.5 g/kg FW	(Kallio, Yang, Peippo, Tahvonen, et al. 2002)		
Total tocopherols and tocotrienols	6–14 mg/100 g FW	(Kallio, Yang, Peippo, Tahvonen, et al. 2002; Yang 2001)		
α-tocopherol	6.98–29.91 g/kg DW	Sytařová et al. 2020)	71.54–153.99 g/kgDW	Sytařová et al. 2020)
	4.3–11.6 mg/100 g DW	(Kallio, Yang, Peippo, Tahvonen, et al. 2002)		
	1–120 mg/100 g FW	(Yang 2001)		
Total carotenoids	53–97 mg/100 g DW	(Pop et al. 2014)	3.5–4.2 mg/100 g DW	(Pop et al. 2014)
	6–24 mg/100 g FW	(Teleszko et al. 2015)		
β-carotene	0.2–17 mg/100 g FW	(Yang 2001)		
Lycopene	8 mg/100 g FW	(Malinowska and Olas 2016)		
Total sterols	34–52mg/100g FW	(Yang et al. 2001)		
Phytosterols	13–20 g/kg FW	(Bal et al. 2011)		
	6–13 mg/100 mL lipid fraction	(Teleszko et al. 2015)		

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[1] I, isorhamnetin; Q, quercetin; K, kaempherol; FGs, flavonol glycosides; PAs, proanthocyanins; ETs, ellagitannins; *β*-EG, Ethyl *β*-D-glucopyranoside

[2] FW = fresh weight, DW = dry weight

Table 2. Human taste recognition thresholds for astringency, bitterness and sourness of main bioactive components in sea buckthorn.

	Taste threshold (mg/L)					
Component	**Astringency**	**Bitterness**	**Sourness**	**Sensory test**	**Medium**	**References**
Flavonols						
Q-3-*O*-rutinoside	0.61			Triangle test	Water	(Scharbert, Holzmann, and Hofmann 2004)
I-3-*O*-glucoside	1.1	nd		Triangle test	Water	(Hufnagel and Hofmann 2008)
Q-3-O-glucoside	4.6			Triangle test	Water	Hufnagel and Hofmann 2008)
Q-3-*O*-rhamnoside	8.9	8.9		Pairs	Water	(Delcour et al. 1984)
I		0.04		ns	Water	(Roland et al. 2013)
Q	10	10		Pairs	5% ethanol	(Roland et al. 2013)
K	20	20		Pairs	5% ethanol	(Roland et al. 2013)
Flavanols						
(+)-Catechin	119	290		Half-tongue test	Water	(Hufnagel and Hofmann 2008)
(-)-Epicatechin	270	270		Half-tongue test	Water	(Hufnagel and Hofmann 2008)
Theaflavins	9			Half-tongue test	Water	(Scharbert, Holzmann, and Hofmann 2004)
Procyanidin B1	139	231		Half-tongue test	Water	(Hufnagel and Hofmann 2008)
Procyanidin B2	110	280		Half-tongue test	Water	(Hufnagel and Hofmann 2008)
Procyanidin B3	116	289		Half-tongue test	Water	Hufnagel and Hofmann 2008)
Procyanidin C1	260	347		Half-tongue test	Water	(Hufnagel and Hofmann 2008)
Trimers and tetramers	4.1	4.1		Triangle test	Water	(Delcour et al. 1984)
Oligomers	0.2			Half-tongue test	Water	(Rossi and Singleton 1966)
Condensed tannins	0.035	0.12		Pairs	Water	(Rossi and Singleton 1966)
Ellagitannins						
Castalagin	1.03	1578		Half-tongue test	Water	(Glabasnia and Hofmann 2006)
Vescalagin	1.03	1578		Half-tongue test	Water	(Glabasnia and Hofmann 2006)
Phenolic acids						
Gallic acid	45	nd		Triangle test	Water	(Hufnagel and Hofmann 2008)

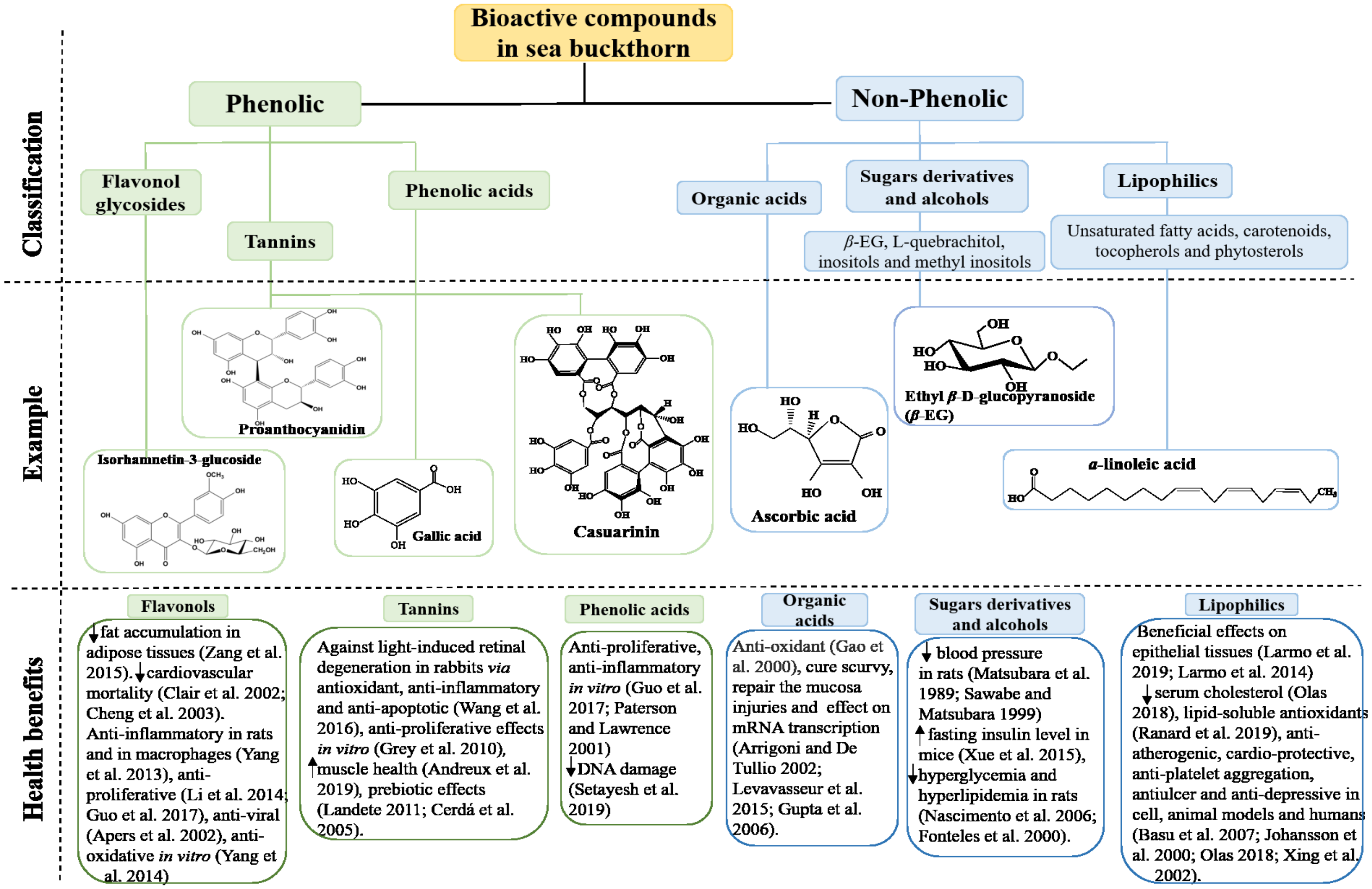
Caffeic acid	13	nd		Triangle test	Water	(Hufnagel and Hofmann 2008)
Ellagic acid	1.99			Triangle test	Water	(Hofmann et al. 2006)
Chlorogenic acid		10	10	Triangle test	5% ethanol	(Maga and Lorenz 1973)
Sugar derivative						
β-EG		1100		Duo-tri test	Water	(Ma et al. 2017a)
Non-phenolic organic acids						
Malic acid			494	Triangle test	Water	(Rotzoll et al. 2006; Scharbert and Hofmann 2005)
Citric acid			499	Triangle test	Water	(Rotzoll et al. 2006; Scharbert and Hofmann 2005)
Quinic acid		10		ns	Water	(Frank et al. 2006)

I, isorhamnetin; Q, quercetin; K, kaempherol; *β*-EG, Ethyl *β*-D-glucopyranoside.

ns, not specified, meaning that methodology for evaluation of recognition sensory threshold is not specified in reference.

nd, not detected for bitter thresholds.

Figure 1.



Flavonols: ↓fat accumulation in adipose tissues (Zang et al. 2015).↓cardiovascular mortality (Clair et al. 2002; Cheng et al. 2003). Anti-inflammatory in rats and in macrophages (Yang et al. 2013), anti-proliferative (Li et al. 2014; Guo et al. 2017), anti-viral (Apers et al. 2002), anti-oxidative *in vitro* (Yang et al. 2014)

Tannins: Against light-induced retinal degeneration in rabbits *via* antioxidant, anti-inflammatory and anti-apoptotic (Wang et al. 2016), anti-proliferative effects *in vitro* (Grey et al. 2010), ↑muscle health (Andreux et al. 2019), prebiotic effects (Landete 2011; Cerdá et al. 2005).

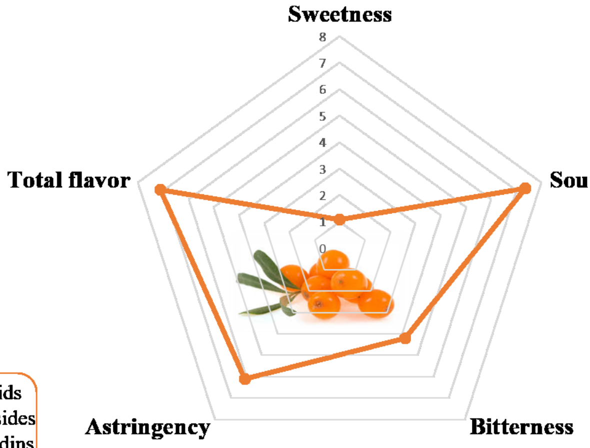
Phenolic acids: Anti-proliferative, anti-inflammatory *in vitro* (Guo et al. 2017; Paterson and Lawrence 2001) ↓DNA damage (Setayesh et al. 2019)

Organic acids: Anti-oxidant (Gao et al. 2000), cure scurvy, repair the mucosa injuries and effect on mRNA transcription (Arrigoni and De Tullio 2002; Levavasseur et al. 2015; Gupta et al. 2006).

Sugars derivatives and alcohols: ↓ blood pressure in rats (Matsubara et al. 1989; Sawabe and Matsubara 1999) ↑fasting insulin level in mice (Xue et al. 2015), ↓hyperglycemia and hyperlipidemia in rats (Nascimento et al. 2006; Fonteles et al. 2000).

Lipophilics: Beneficial effects on epithelial tissues (Larmo et al. 2019; Larmo et al. 2014) ↓serum cholesterol (Olas 2018), lipid-soluble antioxidants (Ranard et al. 2019), anti-atherogenic, cardio-protective, anti-platelet aggregation, antiulcer and anti-depressive in cell, animal models and humans (Basu et al. 2007; Johansson et al. 2000; Olas 2018; Xing et al. 2002).

Figure 2.



Glucose, fructose
Sugars/phenolics
Sugars/acids

Malic and quinic acids
Total acids

Flavonol aglycones
Acids/phenolics
Ethyl *β*-D-glucopyranoside (*β*-EG), *β*-EG/sugars, *β*-EG/acids
Castalagin and vescalagin (Leaves)

Malic and quinic acids
Isorhamnetin glycosides
Total proanthocyanidins
Phenolics/sugars

Malic and quinic acids
Glucose
Total acids and sugars
Isorhamnetin-3-*O*-sophoroside-7-*O*-rhamnoside
Dimer-2