Review

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Berry antioxidants: small fruits providing large benefits

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Abstract

Small berry fruits are consumed because of their attractive colour and special taste, and are considered one of the richest sources of natural antioxidants. Their consumption has been linked to the prevention of some chronic and degenerative diseases. The term 'berry fruits' encompasses the so-called 'soft fruits', primarily strawberry, currants, gooseberry, blackberry, raspberry, blueberry and cranberry. The objective of this review is to highlight the nutraceutical value of berries and to summarize the factors affecting berry fruit antioxidants. Particular attention is given to postharvest and processing operation factors that may affect fruit phytochemical content. The structure–antioxidant relationships for phenolic compounds – the main group of antioxidants in this fruit group – are presented and major areas for future research are identified.

Keywords: polyphenols; bioactive compounds; phytochemicals; *Rubus*; *Ribes*; *Vaccinium*; *Fragaria*

INTRODUCTION

Small berries represent a very diverse group, including a variety of red, blue or purple small-sized and highly perishable fruits. Also named as soft fruits, this group includes strawberry, currant (black, red or white), gooseberry, blackberry, raspberry (black or red), blueberry, cranberry and others of minor economic importance (i.e. boysenberry, bilberry, jostaberry, cloudberry, loganberry, lingoberry) (Table 1).

Berries are highly appreciated for their sharp colour, delicate texture and unique flavour. Despite having a number of common attributes, the group is quite diverse and comprises simple (e.g. blueberry, cranberry) and composite fruits derived from single or multiple fused fertilized ovaries (e.g. strawberry, mulberry, raspberry, blackberry).[1] Over-ripening, excessive softening and pathogen attack, mainly by the necrotroph *Botrytis cinerea*, are the leading causes of berry fruit postharvest losses.[2,3] Preventing deterioration and extending storage capacity have been the main challenges in the distribution of premium-quality berries.

Early on, epidemiological studies recognized the protective effect that the consumption of berry fruit may have against chronic diseases.[4–6] More recently, strong evidence supports the benefits of consuming strawberry, blueberry, cranberry, bilberry, raspberry, currants, blackberry and their hybrids in amelioration of an array of human ailments (e.g. disorders in neuronal communication, inflammatory responses). Berry fruits have been also shown to enhance cognitive functions (e.g. improved memory in older adults).[7–11]

For any given fruit, the diversity and concentration of antioxidants (AOXs) are highly dependent on the species and cultivar considered. Preharvest practices, environmental conditions, maturity at harvest, postharvest storage and processing operations are also important determinants of the phytochemical profiles.[12]

In this review, we briefly describe the main antioxidant groups present in selected berry fruits and summarize the main structure–activity relationships for phenolic compounds. The effect of the most relevant genetic, pre- and postharvest factors on the steady-state content of berry fruit antioxidants is also discussed. In addition, areas in which further research is needed are identified.

ANTIOXIDANT COMPOUNDS IN BERRY FRUITS

Ascorbic acid, carotenoids, vitamin E and phenolic compounds are the most widespread antioxidants in the plant kingdom.[13] Although all of them are represented in berry fruits, ascorbic acid and especially phenolics are the most abundant (Fig. 1). Phenolic compounds are the most prevalent AOX group and are analytically described in the next section. Ascorbic acid is particularly abundant in some berries such as blackcurrant and strawberry, whereas most other berries show moderate concentrations.[14–16]

Common carotenoids (xanthophylls and carotenes) found in other fruit species such as lutein and β-carotene, lycopene, α-carotene, β-cryptoxanthin, neoxanthin, *cis*-and *trans*-violaxanthin, 5,6-epoxylutein and zeaxanthin have also been identified in berry fruits.[15,17] However, their concentration in berry fruits is at a relatively low concentration.[17,18] Tocopherols and tocotrienols are

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Table 1. Nomenclature of small berry fruits

Common name	Scientific name
Fragaria genus (family: Roseaceae)	
Cultivated strawberry	*Fragaria* × *ananassa*
Chilean (coastal) strawberry	*Fragaria chiloensis*
Wild strawberry	*Fragaria virginiana*
Alpine strawberry	*Fragaria vesca*
Musk strawberry	*Fragaria moschata*
Ribes genus (family: Glossulariaceae)	
Black currant	*Ribes nigrum*
Red currant	*Ribes rubrum*
White currant	*Ribes glandulosum*
Gooseberry	*Ribes uva-crispa*
Rubus genus (family: Rosaceae)	
Blackberry	*Rubus fruticosus*
Black raspberry	*Rubus occidentalis*
Red raspberry	*Rubus idaeus*
Boysenberries	*Rubus ursinus* × *idaeus*
Cloudberries	*Rubus chamaemorus*
Loganberry	*Rubus loganobaccus*
Vaccinium genus	
Highbush blueberry	*Vaccinium corymbosum*
Lowbush blueberry	*Vaccinium angustifolium*
Rabbit eye blueberries	*Vaccinium virgatum*
Velvet leaf blueberry	*Vaccinium myrtilloides*
Bilberry	*Vaccinium myrtilus*
Cranberry	*Vaccinium macrocarpon*
Other berries	
Mulberry	*Morus alba, Morus nigra*
Bayberry	*Myrica rubra*

more prevalent in fat-rich fruit species such as avocado and are present at low levels in berries.[19]

PHENOLIC COMPOUNDS IN BERRY FRUITS

Phenolics represent a large group of secondary metabolites, consisting of one or more aromatic rings with variable degrees of hydroxylation, methoxylation and glycosylation, contributing to fruit colour, astringency and bitterness.[20] The main categories of phenolic compounds found in berry fruit are phenolic acids, flavonoids, tannins and stilbenes.[15,21]

Phenolic acids (PA) are one of the most well-studied chemical groups. They can be subdivided into cinnamic and benzoic acid derivatives. Cinnamic acids are usually esterified, whereas hydroxybenzoic acid derivatives are mainly glycosylated.[22] Free PA in fruits rarely exceed 5% of the total.[23] Ferulic, caffeic and *p*-coumaric acids and caffeoylquinic esters are the major hydroxycinnamates identified in berries; benzoic acid derivatives that have been primarily identified in berry fruits include gallic, salicylic, *p*-hydroxybenzoic and ellagic acids.[15,21]

Flavonoids (FL) represent the most diverse group of phenolics, with two aromatic (A and B) rings associated via C-C bonds by a 3 C oxygenated heterocycle. On the basis of the oxidation state of the central ring, FLs are further divided into anthocyanins, flavonols, flavanols, flavones, flavanones and isoflavonoids. Berries are particularly rich in anthocyanins, which are responsible for their typically vibrant colours.[24] The basic $C_6—C_3—C_6$ anthocyanidin structure modified by chemical combination with sugars and/or acyl groups, metals and other phenolic compounds yield a variety of colours, from scarlet to blue (Fig. 2). Anthocyanins are glycosides of anthocyanidins and are particularly abundant in berry fruits. Six different anthocyanidins are found in nature (pelargonidin, cyanidin, delphinidin, peonidin, petunidin and malvidin), differing in the position and number of hydroxyl groups as well on their degree of methylation.[25] Anthocyanin glycosylation increases their stability and solubility, but may result in a slight reduction in radical scavenging capacity. In berries, mono-, di- or triglycosides and the position C-3 are the most common forms, while glycosylation via C-5 and C-7 is less frequent. Glucose, galactose, rhamnose, arabinose, rutinose, sambubiose and sophorose are the main sugars associated with berry anthocyanidins. The sugar moieties may be further decorated with *p*-coumaric, caffeic, ferulic, malonic and acetic acid.[15,26,27] The anthocyanin profiles have been used for taxonomic purposes of berry fruits as well as to determine the authenticity of berry-derived food products.[24,28,29] Anthocyanin profiles have also been used for the authenticity of fruit jams, e.g. adulteration of blackberry jams with strawberries was identified by analysis of the pelargonidin:cyanidin 3-*O*-glucoside ratio.[30] Anthocyanin fingerprinting has been developed for use in authenticity studies of bilberry (*Vaccinium myrtillus* L.) populations and/or cultivars.[31] Anthocyanins were the major contributors to total antioxidant capacity of blueberries and blackcurrants (84% and 73%, respectively), while their contribution did not exceed 21% in raspberry and redcurrant.[32]

Flavonols and 3-hydroxyflavones are also widespread in berries. They usually occur as *O*- and *C*-glycosides of quercetin, myricetin and kaempferol.[33–35] Isorhamnetin (a methoxy derivative of quercetin) and syringetin (a dimethoxy derivative of myricetin) have also been identified as flavonol aglycons in berries.[36] As for anthocyanins, a great diversity in sugar moieties has been observed, leading to a variety of derived compounds. A recent study described 50 different flavonols in 28 wild and cultivated berry species.[36] However, in general, quercetin and kaempferol are the major flavonols and occur as 3-glucosides and 3-glucuronides.[37,38] The contribution of flavonols to berry antioxidant capacity is lower than that of anthocyanins and does not exceed 14% of the total.[32] Berries also contain the flavanol monomers (+)-catechin and (−)-epicatechin. They may be found as monomers, oligomers and polymeric proanthocyanidins.[39]

Tannins are classified into hydrolysable and condensed (or non-hydrosable) forms. Hydrolysable tannins are multiple esters of gallic or ellagic acid with glucose and products of their oxidative reactions and are known as galloyl tannins and ellagitannins, respectively.[40,41] Hydrolysable tannins are found in strawberry, raspberry and blackberry but are less common in other berry fruits.[42,43] Together with anthocyanins, ellagitannins are the major antioxidant phytochemicals in raspberries.[44] The ellagitannins lambertianin C and sanguiin H-6 represent almost 60% of raspberry antioxidants. Condensed tannins are oligomers or polymers of two or more flavan-3-ols – usually catechin and epicatechin – and contain several subtypes that differ in stereochemistry and hydroxylation pattern of the constituent flavonoids.[40] A great variation in condensed tannin content is observed in berries. Chokeberries presented the highest concentration of condensed tannins among about 100 plant foods tested.[45] Tannins are also present in other berry species.[44–47]

Stilbenes are a subgroup of phenolic compounds with a particular carbon skeleton, viz. $C_6—C_2—C_6$.[48] Resveratrol is the best-known stilbene. Small quantities of resveratrol, pterostilbene

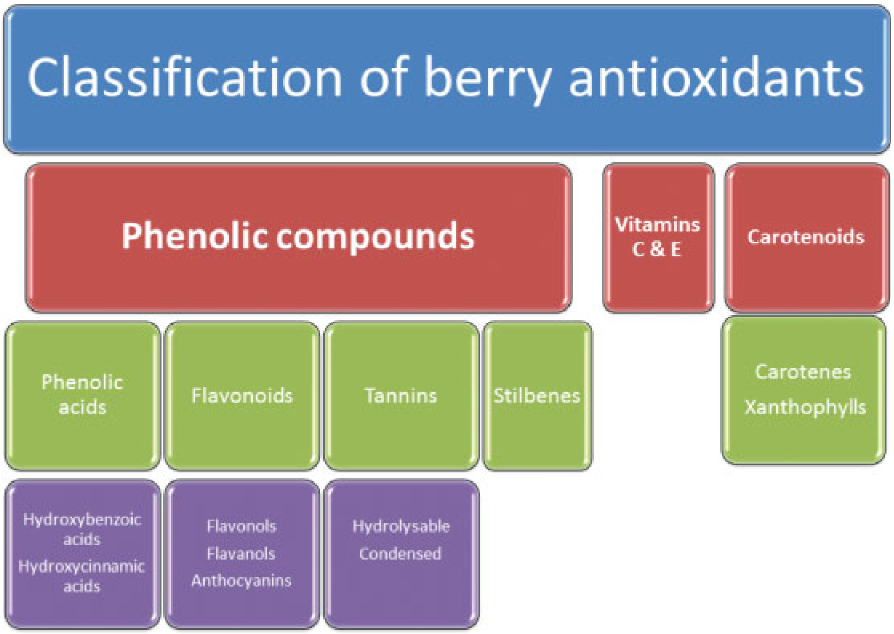
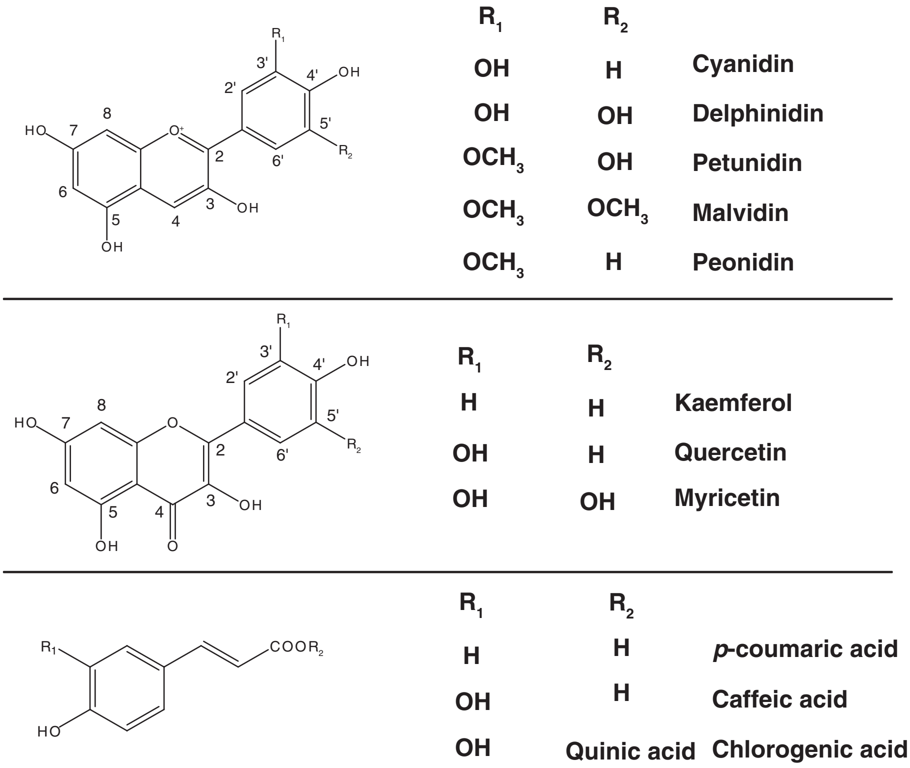


Figure 1. Main group of antioxidants found in berries.



R_1	R_2	
OH	H	Cyanidin
OH	OH	Delphinidin
OCH_3	OH	Petunidin
OCH_3	OCH_3	Malvidin
OCH_3	H	Peonidin

R_1	R_2	
H	H	Kaemferol
OH	H	Quercetin
OH	OH	Myricetin

R_1	R_2	
H	H	*p*-coumaric acid
OH	H	Caffeic acid
OH	Quinic acid	Chlorogenic acid

Figure 2. Characteristic structures of anthocyanins, flavonols and hydroxycinnamic acids.

and piceatannol have been found in blueberry, bilberry, cranberry and strawberry.[15,21,49,50]

RELATIONSHIP BETWEEN PHENOLICS STRUCTURE AND ANTIOXIDANT CAPACITY

Many studies have associated the structure of phenolic compounds with their antioxidant properties.[51,52] In general, increasing the degree of hydroxylation in aromatic rings has positive effects on the antioxidant activity of hydroxycinnamic acids,[53] e.g. caffeic acid (two hydroxyl groups) has higher antioxidant activity than *p*-coumaric acid (one hydroxyl group). As previously reported, hydroxylation in adjacent carbons (*o*-diphenyl structure) enhances antioxidant activity.[54] Jing and co-workers[55] also outlined that the presence of: (i) bulky and/or electron-donating substituents on the aromatic ring, (ii) electron-donating groups at the *meta* position and/or hydrophobic groups at the *meta*–*ortho* position, and (iii) hydrogen bond donor/electron-donating groups at the *ortho* position strengthen the antioxidant activity of phenolic acids.

Hydroxylation and/or methoxylation on the C ring affects the antioxidant activity of anthocyanins. Anthocyanidins with B ring *o*-diphenyl patterns, such as cyanidin and delphinidin, have higher antioxidant activity than malvidin, pelargonidin, petunidin and peonidin.[56] Increasing the number of hydroxyl groups in the B ring also enhances the antioxidant activity,[57] while methoxylation at C-3′ decreases it. Additional insertions of hydroxyl and methoxy groups at position C-5′ have no major effect on antioxidant activity.[54]

The effect of glycosylation of anthocyanidin antioxidant capacity is variable. Monoglycosides of cyanidin, delphinidin and malvidin show similar antioxidant activity with free aglycons. However, glycosylation at C-3 decreases the antioxidant activity of peonidin and pelargonidin. Anthocyanins containing arabinose have lower antioxidant activity than glycosylated derivatives. The substitution with rutinose also has a similar effect to that of arabinose. In addition, the 3,5-*O*-diglucosides of cyanidin and malvidin showed significantly lower activities than the corresponding monoglycosides.[54,56] In summary, anthocyanins possess similar or slightly lower antioxidant activity than the corresponding anthocyanidins.

In general, flavonols are considered more powerful antioxidants than anthocyanins. This fact could be attributed to a 2,3-double bond in conjunction with a 4-oxo function in the C ring, which allows electron localization in the B ring.[54,58] The outcome of hydroxylation, methoxylation and glycosylation on flavonol antioxidant activity is similar to that described for anthocyanidins. Fruit phenolics may interact with other phytochemicals and macrocomponents during mastication and digestion, resulting in antagonistic, additive and/or synergistic effects.[4] These interactions have been studied mainly *in vitro* and may be important in berries in which a large number of AOXs coexist. However, the relevance of these interactions in terms of their contribution to health protection is still obscure.

FACTORS AFFECTING ANTIOXIDANTS IN BERRIES

Genetic factors (species, cultivar)

It is well documented that great differences in the phytochemical profile occur among genotypes/cultivars of the same species, including soft fruits.[2] Among berry fruits, blackberries, blueberries and blackcurrants are the richest sources of antioxidants (source: USDA, 2013).[59] Strawberry and cranberry have lower oxygen radical absorbance capacity (ORAC) values but are still higher than that found in most other fruit species, including citrus, pome and most stone fruits. A high content of phenolics is also found in bilberry (wild blueberry; *Vaccinium myrtillus*) cultivars (up to 600 mg gallic acid equivalent (GAE) 100 g^{-1} fresh weight), compared to cultivated blueberries (*Vaccinium corymbosum*), with a content of GAE close to 310 mg 100 g^{-1} FW.[60] Therefore, wild species could be considered as a potential source of germplasm for breeding programmes oriented to nutritional improvement. Phenolic profiles determined by liquid chromatographic–mass spectrometric analysis revealed clear metabolic differences among strawberry genotypes.[61] A comparative study among *Fragaria chiloensis* (white strawberry), *F. vesca* and *F.* × *ananassa* cv. 'Chandler' indicated that the highest phenolic content was found in *F. vesca*, while the lowest content was recorded in white strawberry.[62] The same group showed that the total anthocyanin and total flavonoid content was lower for white strawberries. The wild progenitor species *F. virginiana* had significantly higher antioxidant capacity, phenolics and total anthocyanins than the fruit of three accessions tested from either the other wild progenitor species *F. chiloensis* or *F.* × *ananassa*.[63] Capocasa and co-workers also found significant differences in antioxidant activity of 20 strawberry genotypes and results differed slightly according to the used assay. In addition, this study reported that the effect of genotype on strawberry antioxidant activity is stronger than that of the cultivation conditions.[64]

Maturity stage and intra-fruit variation

The distribution of antioxidants shows variations within tissues of the same fruit, normally AOXs are more abundant at the surface. In strawberries, i.e., the achenes represent only 1% of the total mass but contribute to about 11% of total phenolics and 14% of total antioxidant activity.[37]

Fruit maturation is reported to influence the total phenolic and anthocyanin contents of blackberry, raspberry, and strawberry cultivars.[65] Total anthocyanins increase during ripening in all berries. The antioxidant capacity peaks in some species at early stages of development. However, from a practical perspective berries should be harvested fully ripe since flavour and taste are severely influenced by the maturity stage.

Field conditions

Several studies have suggested that environmental conditions, field management system and growing season have a great impact on the levels of antioxidants.[66–68] Deficit irrigation significantly increased the antioxidant capacity in ripe strawberry fruit.[69,70]

The effect of organic farming on AOXs is still inconclusive. Organically grown 'Selva' strawberries had significantly higher levels of anthocyanins and ascorbic acid than conventionally grown fruits.[71] Higher AOX in organically-grown strawberries has also been reported,[72] but in other studies no differences in antioxidants were found between these management systems.[73,74]

Postharvest management

Temperature management after harvest is a major factor affecting fruit postharvest performance as well as composition, including phytochemical profile. In general, high storage temperature results in losses of some antioxidants, rather ascorbic acid being the most labile. Significant fluctuations in antioxidant capacity of fruits during storage and even an increase after several days at room temperature have been reported.[75] This was mainly associated with the continued biosynthesis of anthocyanins. However, other quality attributes markedly deteriorated when berry fruits are stored over 0 °C. Even under these conditions the shelf life is still fairly short: 1–2 weeks for strawberries and blueberries, and 2–5 days for raspberries and blackberries.

In controlled and/or modified atmospheres (CA/MA), increasing CO_2 partial pressure decreased the concentrations of pelargonidin glycoside and ascorbic acid.[76] High CO_2 concentrations (10–30%) have been suggested to stimulate the oxidation of ascorbic acid or to inhibit mono- or dehydroascorbic acid reduction to ascorbic acid.[77] Anthocyanins, flavonoids and total antioxidant activity were higher in air-stored fruit than in berries held in MA conditions. High CO_2 storage generally decreases total phenolics, total anthocyanins and antioxidant capacity.[76,78]

Sulfur dioxide fumigation of eight fresh blueberry cultivars (*Vaccinium corymbosum*) followed by CA (3% O_2 + 6% or 12% CO_2) reduced decay and maintained high antioxidant capacity after prolonged storage.[2] Other postharvest treatments such as UV-C irradiation may increase anthocyanin content and prevent AOX losses.[79,80] Added edible coatings have been shown to prevent deterioration and AOX turnover in various fruits;[81–83] however, a number of practical limitations need to be resolved to increase its adoption at a commercial scale in the soft fruit industry. That is, berries do not lend themselves to additional postharvest handling since they tend to be picked straight into the punnet ready for retail.

Processing

Several studies have investigated the effect of pH, metal ions, exposure to light, temperature, oxygen and enzymatic activities on the main groups of fruit AOXs.[84] Processing operations may largely affect the extraction and stability of antioxidants in berry fruits. Ascorbic acid shows high sensitivity to thermal processing.[85] In general, freezing causes moderate variations in phenolic compounds; a study on four raspberry cultivars showed variable results, ranging from no change to an increase of 12% and decreases of 21% and 28%, during 12 months frozen storage.[85] No loss of anthocyanins was observed after pasteurization, decantation, filtration and concentration of blackcurrant juice.[86] On the other hand, thermal pasteurization and high-pressure processing caused significant change in strawberry fruit antioxidant capacity.[87] During drying, anthocyanins were more readily degraded than other phenolic compounds. Losses of anthocyanins in processed berries may be reduced by blanching, indicating that they are probably mediated by phenolic compound degrading enzymes.[73] Blackcurrant polyphenols were significantly retained when incorporated both before or after fermentation.[88] Microencapsulation by spray drying, spray chilling/cooling, coacervation, extrusion, fluidized coating, liposome entrapment and molecular inclusion, have been tested in different food matrices.[89]

Food preparation can also affect the levels of antioxidants. Depending on the cooking method used, losses of ascorbic acid during home cooking range from 15% to 55%.[85] Boiling for 10 min did not result in marked losses of AOX.[90] Strawberry processing to produce jams has been shown to decrease the total ellagic acid and flavonol content by ∼20%.[91,92] Microwave heating resulted in lower losses of AOX as compared to conventional heating.[93] Increased free ellagic acid was found in thermally treated raspberry pulp. This was likely due to the release of insoluble ellagitannins. After canning, total anthocyanins decreased by up to 44%, but phenolic contents and antioxidant activity increased by up to 50% and 53%, respectively.[73] Antioxidants present in foods are mostly found in the form of esters, glycosides or polymers, which cannot be absorbed through the intestinal wall such that the hydrolysis of aglycones may increase their bioavailability.[94,95] Finally, enzyme-assisted processing increases antimicrobial and antioxidant activity of bilberry.[96]

AREAS OF ONGOING AND CHALLENGES FOR FUTURE RESEARCH

Antioxidants in the laboratory

Most research studies in the field of phenolic metabolism use a chemical approach focusing exclusively on compounds extracted with organic acids of quite different extraction efficiencies.[97] In addition, under these conditions a large part of polyphenols are not extracted and thus ignored.[98] Recent studies have shown that these non-extractable polyphenols are a major part of total dietary polyphenols and that they may exhibit significant biological activity. The relevance of these commonly non-extracted antioxidants is almost unexplored.

Elucidating the identity, nature and abundance of the great number of existing metabolites present in diverse berry samples has been a challenge for analytical chemists. This has resulted in the development of a number of methodologies aimed at determining what is defined as ‘total antioxidant capacity’.[99,100] The different available procedures are recognized to have pros and cons regarding their specific target, informative value, accuracy, repeatability, simplicity, time consumption and cost. The development of standard analytical protocols for sample preparation and measurement of antioxidant capacity will reduce at least in part the variability observed in the literature. However, no single procedure will likely achieve the main goal of estimating the total potential health-promoting properties of any given sample in humans. *In vitro* tests will continue to be used, but the requirement for validation in cellular, animal model systems and humans will increase. High-performance liquid chromatography (HPLC) coupled with the DPPH (di(phenyl)-(2,4,6-trinitrophenyl)iminoazanium) assay has been used to determine the contribution of individual metabolites to the overall antioxidant capacity of fruits.[32,101,102] High-resolution screening techniques, combining an established separation technique like HPLC with post-column biochemical detection, can be used to identify active compounds.[103]

Accelerated development of metabolomics and high-throughput methods to perform studies with cellular lines in the last few years suggest that it may be realistic to envision strategies integrating multiple metabolite quantification and testing of physiological effects of food antioxidants in complex matrices.

Individual antioxidants studied in clinical trials do not appear to have consistent preventive effects that have been reported in whole fruits,[104] suggesting that the health benefits of fruits result from the interactions of bioactive compounds and other nutrients in whole foods.[105] The nature and relevance of these interactions are still obscure and active research is needed in this area.

Antioxidant metabolism *in planta*

The main goal in this area is the generation through breeding programmes of novel berry cultivars with improved nutritional properties. In certain cases, increasing AOX accumulation would be beneficial from both plant and human perspectives. A recent study demonstrated the successful combination of interspecies back-crosses and intra-species crosses in order to improve the nutraceutical content of strawberry fruit.[106] Increasing the level of AOX may result in improved responses to some biotic and abiotic stresses. Many compounds with antioxidant activity are actually pre-formed antifungal compounds.[107] From a breeder’s perspective, the availability of ‘highly nutritious berries’ with enhanced health-promoting properties would be a strong asset, encouraging both berry producers and consumers. The antioxidant potency in combination with phenolic content of fruits has been proposed as a standardized method for the evaluation of fruit germplasms.[108,109] Antioxidant-rich berries could be generated by taking advantage of the large, yet unexploited, natural variation in these species, as well as by genetic engineering.

However, the public's attitude toward genetically modified (GM) crops is, at least in Europe, still rather sceptical, and EU regulations are very restrictive.[108]

The general pathways leading to the biosynthesis of the main AOXs in plants are established, and in the last years some transcription factors that directly regulate multiple steps of these routes have been identified.[110] Some regulators such as myeloblastosis (MYB) transcription factors (TFs) are emerging as central players in the coordinated activation of sets of genes specific for the anthocyanin and tannin accumulation. It has been shown that MrMYB1b TF is a major regulator of anthocyanin accumulation in Chinese red bayberry.[111] A SQUAMOSA-class MADS box transcription factor, VmTDR4, has been associated with anthocyanin biosynthesis in bilberry.[112] However, the whole regulatory networks controlling the accumulation of the main AOX groups in non-model berry species are far from being understood.

The existence of metabolic channels in the biosynthetic pathway of some phenolic compounds increases the potential regulatory steps. These molecular associations could prevent the free diffusion of intermediate metabolites and thus control the flux directions. Progress on the molecular genetics and cellular biology of AOX homeostasis of berry fruits will be useful to identify appropriate candidates for genetic engineering as well as to assist breeding programmes aimed at improving berry fruit nutritional properties.

Antioxidants during storage and processing

In the last few years, a number of studies have evaluated the influence of storage and processing on berry fruit AOXs. Continuing accumulation of AOXs in the postharvest environment led to the conclusion that postharvest treatments activating bioactive compounds biosynthesis could be envisaged as a nutritional-enhancing strategy.[113] While some treatments have induced AOX accumulation, achievements in the technological arena are still limited. Postharvest treatment conditions maximizing the activation of AOX biosynthetic pathways need to be determined.

The food-processing industry has made significant efforts to maximize the yield of extraction of AOX (e.g. ultrasound) as well as to increase their stability during processing (e.g. microencapsulation). Additional studies are still needed in this area, since large amounts of health-promoting antioxidants are annually lost during retail, storage and food formulation and preparation.

Although increasing antioxidant levels in fruit through breeding is an appealing alternative to support higher intake, large amounts of AOXs are annually discarded in food by-products. The cost benefit of recovering these will depend on the commodity considered, but the revalorization of AOX suggest that such interventions may become more convenient in the future.

Antioxidants in humans

A great deal of work is still required to establish the bioavailability, metabolism and bioactivity of the main berry AOXs. As previously indicated, the nutritional properties of different fruits have been frequently derived from results from *in vitro* studies, which may not be relevant *in vivo*, due to poor absorption and metabolism. In fact, there are cases where *in vitro* tests for antioxidant capacity showed poor correlation with *in vivo* radical scavenging capacity or physiological effects.[114] In the last few years, the protective role of dietary antioxidants against oxidative damage has been investigated in cell culture systems.[115] While this represents a great advance, it is still uncertain whether the effects in cell cultures, often observed with higher doses of single compounds than would be expected during normal intake, can be extrapolated to humans.

Studies using animal models have suggested that the intact forms of complex dietary polyphenols have limited bioavailability, with low circulating levels in plasma.[116] For instance, flavonoids require deglycosylation by mammalian hydrolases in the small intestine before absorption. The concentration of plasma metabolites after a normal dietary intake is commonly below nmol L^{-1} levels.[28] A major part of the polyphenols persist in the colon, where they can be altered by microbiota. Bacterial enzymes can perform multiple transformations, including dehydroxylations, demethylation and fragmentations. These compounds may be further metabolized upon absorption.[117] Consequently, bioavailability values reported in the literature should be re-evaluated taking into account both parental and derived metabolites, such as colonic ring-fission products.[28] Finally, colonic bioconversion has been shown to be markedly dependent on the microflora diversity and diet.[117] Understanding the fate of antioxidants in a real context will shed light on the indirect mechanisms by which dietary antioxidants may exert beneficial effects in humans. Overall, coordinated activities through an interdisciplinary approach that will encompass scientists from different disciplines (agricultural and food sciences, analytical chemistry, human nutrition) may shed additional light on better understanding the mechanisms behind the reported effects of berry-derived antioxidants on human health.

REFERENCES

1 Vicente AR and Sozzi GO, Ripening and postharvest storage of 'soft fruits'. *Fruit Veg Cereal Sci Biotechnol* **1**:95–103 (2007).
2 Cantín CM, Minas IS, Goulas V, Jiménez M, Manganaris GA, Michailides TJ *et al.*, Sulfur dioxide fumigation alone or in combination with CO_2-enriched atmosphere extends the market life of highbush blueberry fruit. *Postharvest Biol Technol* **67**:84–91 (2012).
3 Terry LA. Soft fruit, in *Crop Post-harvest: Science and Technology – Perishables*, ed. by Rees D, Farrell G and Orchard J. Wiley-Blackwell, Chichester, pp. 226–246 (2011).
4 Heinonen IM, Meyer AS and Frankel EN, Antioxidant activity of berry phenolics on human low-density lipoprotein and liposome oxidation. *J Agric Food Chem* **46**:4107–4112 (1998).
5 Meydani M, Nutrition interventions in aging and age-associated disease. *Ann New York Acad Sci* **928**:226–235 (2001).
6 Kong JM, Chia LS, Goh NK, Chia TF and Brouillard R, Analysis and biological activities of anthocyanins. *Phytochemistry* **64**:923–933. (2003).
7 Zafra-Stone S, Yasmin T, Bagchi M, Chatterjee A, Vinson JA and Bagchi D, Berry anthocyanins as novel antioxidants in human health and disease prevention. *Mol Nutr Food Res* **51**:675–683 (2007).
8 Lau FC, Bielinski DF and Joseph JA, Inhibitory effects of blueberry extract on the production of inflammatory mediators in lipopolysaccharide-activated BV2 microglia. *J Neurosci Res* **85**:1010–1017 (2007).
9 Krikorian R, Shidler MD, Nash TA, Kalt W, Vinqvist-Tymchuk MR, Shukitt-Hale B *et al.*, Blueberry supplementation improves memory in older adults. *J Agric Food Chem* **58**:3996–4000 (2010).
10 Giné Bordonaba JG and Terry LA, Ribes and Rubus, in *Health-Promoting Properties of Fruit and Vegetables*, ed. by Terry LA. CABI, Wallingford, UK, pp. 260–290 (2011).
11 Giné Bordonaba JG and Terry LA. Strawberry, in *Health-Promoting Properties of Fruit and Vegetables*, ed. by Terry LA. CABI, Wallingford, UK, pp. 291–320 (2011).
12 Jimenez-Garcia SN, Guevara-Gonzalez RG, Miranda-Lopez R, Feregrino-Perez AA, Torres-Pacheco I and Vazquez-Cruz MA, Functional properties and quality characteristics of bioactive compounds in berries: biochemistry, biotechnology, and genomics. *Food Res Int* http://dx.doi.org/10.1016/j.foodres.2012.11.004.
13 Larson RA, The antioxidants of higher plants. *Phytochemistry* **27**:969–972 (1998).

14 Hakala M, Lapvetelainen A, Huopalahti R, Kallio H and Tahvonen R, Effect of varieties and cultivation conditions on the composition of strawberries. *J Food Comp Anal* **16**:67–80 (2003).

15 Szajdek A and Borowska EJ, Bioactive compounds and health-promoting properties of berry fruits: a review. *Plant Foods Hum Nutr* **63**:147–156 (2008).

16 Giné Bordonaba J and Terry LA, Biochemical profiling and chemometric analysis of seventeen UK-grown black currant cultivars. *J Agric Food Chem* **56**:7422–7430 (2008).

17 Lashmanova KA, Kuzivanova OA and Dymova OV, Northern berries as a source of carotenoids. *Acta Biochim Pol* **59**:133–134 (2012).

18 Marinova D and Ribarova F, HPLC determination of carotenoids in Bulgarian berries. *J Food Comp Anal* **20**:370–374 (2007).

19 Piironen V, Syväoja EL, Varo P, Salminen K and Koivistoinen P, Tocopherols and tocotrienols in Finnish foods: vegetable, fruits, and berries. *J Agric Food Chem* **34**:742–746 (1986).

20 Crozier A, Yokota T, Jaganath IB, Marks S, Saltmarsh M, and Clifford MN, Secondary metabolites as dietary components in plant-based foods and beverages, in *Plant Secondary Metabolites: Occurrence, Structure and Role in the Human Diet*, ed. by Crozier A, Clifford MN and Ashihara H. Blackwell, Oxford, pp. 208–302 (2006).

21 Paredes-Lopez O, Cervants-Ceja ML, Vigna-Perez M and Hernandez-Perez M, Berries: improving human health and healthy aging, and promoting quality life – a review. *Plant Foods Hum Nutr* **65**:299–308 (2010).

22 Mattila P, Hellstrom J and Törrönen R, Phenolic acids in berries, fruits, and beverages. *J Agric Food Chem* **54**:7193–7199 (2006).

23 Zadernowski R, Naczk M and Nesterowicz J, Phenolic acid profiles in some small berries. *J Agric Food Chem* **53**:2118–2124 (2005).

24 Del Rio D, Borges G and Crozier A, Berry flavonoids and phenolics: bioavailability and evidence of protective effects. *Br J Nutr* **104**:S67–S90 (2010).

25 Jaakola L, New insights into the regulation of anthocyanin biosynthesis in fruits. *Trends Plant Sci* **18**:477–483 (2013).

26 Clifford MN, Anthocyanins: nature, occurrence and dietary burden. *J Sci Food Agric* **80**:1063–1072 (2000).

27 Castañeda-Ovando A, Pacheco-Hernandez MDL, Paez-Hernandez ME, Rodriguez JA and Galan-Vidal CA, Chemical studies of anthocyanins: a review. *Food Chem* **113**:859–871 (2009).

28 Del Rio D, Costa LG, Lean ME and Crozier A, Polyphenols and health: what compounds are involved? *Nutr Metab Cardiovasc Dis* **20**:1–6 (2010).

29 Goulas V, Vicente AR and Manganaris GA, Structural diversity of anthocyanins in fruits, in *Anthocyanins: Structure, Biosynthesis and Health Benefits*, ed. by Motohashi N. Nova Science Publishers, Hauppage, NY, pp. 225–250 (2012).

30 Garcia-Viguera C, Zafrilla P and Tomas-Barberan FA, Determination of authenticity of fruit jams by HPLC analysis of anthocyanins. *J Sci Food Agric* **73**:207–213 (1997).

31 Primetta AK, Jaakola L, Ayaz FA, Inceer H and Riihinen KR, Anthocyanin fingerprinting for authenticity studies of bilberry (*Vaccinium myrtillus* L.). *Food Control* **30**:662–667 (2013).

32 Borges G, Degeneve A, Mullen W and Crozier A, Identification of flavonoid and phenolic antioxidants in blackcurrants, blueberries, raspberries, red currants and cranberries. *J Agric Food Chem* **58**:3901–3909 (2010).

33 Häkkinen SH and Auriola S, High-performance liquid chromatography with electrospray ionization mass spectrometry and diode array ultraviolet detection in the identification of flavonol aglycones and glycosides in berries. *J Chromatogr A* **829**:91–100 (1998).

34 Häkkinen S, Heinonen M, Kärenlampi S, Mykkänen H, Ruuskanen J and Törrönen R, Screening of selected flavonoids and phenolic acids in 19 berries. *Food Res Int* **32**:345–353 (1999).

35 Häkkinen SH, Karenlampi SO, Heinonen M, Mykkanen HM and Torronen AR, Content of the flavonols quercetin, myricetin, and kaempferol in 25 edible berries. *J Agric Food Chem* **47**:2274–2279 (1999).

36 Mikulic-Petkovsek M, Slatnar A, Stampar F and Veberic R, HPLC-MS^n identification and quantification of flavonol glycosides in 28 wild and cultivated berry species. *Food Chem* **135**:2138–2146 (2012).

37 Aaby KG, Skrede G and Wrolstad RE, Phenolic composition and antioxidant activities in flesh and achenes of strawberries (*Fragaria ananassa*). *J Agric Food Chem* **53**:4032–4040 (2005).

38 Aaby KG, Mazur S, Nes A and Skredea G, Phenolic compounds in strawberry (*Fragaria* × *ananassa* Duch.) fruits: composition in 27 cultivars and changes during ripening. *Food Chem* **132**:86–97 (2012).

39 Del Bubba M, Checchini L, Chiuminatto U, Doumett S, Fibbi D and Giordani E, Liquid chromatographic/electrospray ionization tandem mass spectrometric study of polyphenolic composition of four cultivars of *Fragaria vesca* L. berries and their comparative evaluation. *J Mass Spectrom* **47**:1207–1220 (2012).

40 Barbehenn RV and Constabel CP, Tannins in plant–herbivore interactions. *Phytochemistry* **72**:1551–1565 (2011).

41 Arapitsas P, Hydrolyzable tannins analysis in food. *Food Chem* **135**:1708–1717 (2012).

42 Hassimotto NMA and Lajolo FM, Antioxidant status in rats long-term intake of anthocyanins and elagitannins from blackberries. *J Sci Food Agric* **91**:523–531 (2011).

43 Josuttis M, Verall S, Stewart D, Kruger E and McDougall GJ, Genetic and environmental effects on tannin composition in strawberry (*Fragaria* × *ananassa*) cultivars grown in different European locations. *J Agric Food Chem* **61**:790–800 (2013).

44 Rao AV and Snyder DM, Raspberries and human health: a review. *J Agric Food Chem* **58**:3871–3883 (2010).

45 Hellstrom JK, Torronen AR and Mattila PH, Proanthocyanidins in common food products of plant origin. *J Agric Food Chem* **57**:7899–7906 (2009).

46 Nybakken L, Selas V and Ohlson V, Increased growth and phenolic compounds in bilberry (*Vaccinium myrtillus* L.) following forest clear-cutting. *Scand J Forest Res* **28**:319–330 (2013).

47 Krueger CG, Reed JD, Feliciano RP and Howell AB, Quantifying and characterizing proanthocyanidins in cranberries in relation to urinary tract health. *Anal Bioanal Chem* **405**:4385–4395 (2013).

48 Bravo L, Polyphenols: chemistry, dietary sources, metabolism, and nutritional significance. *Nutr Rev* **56**:317–333 (1998).

49 Rimando MA, Kalt W, Magee BJ, Deway J and Ballington RJ, Resveratrol, pterostilbene and piceatannol in *Vaccinium* berries. *J Agric Food Chem* **52**:4713–4719 (2004).

50 Ehala S, Vaher M and Kaljurand M, Characterization of phenolic profiles of Nothern European berries by capillary electrophoresis and determination of their antioxidant activity. *J Agric Food Chem* **53**:6484–6490 (2005).

51 Rice-Evans CA, Miller NJ and Paganga G, Structure–antioxidant activity relationships of flavonoids and phenolic acids. *Free Radic Biol Med* **20**:933–956 (1996).

52 Zheng CD, Li G, Li HQ, Xu XJ, Gao JM and Zhang AL, DPPH-scavenging activities and structure–activity relationships of phenolic compounds. *Nat Prod Commun* **5**:1759–1765 (2010).

53 Fan GJ, Jin XL, Qian YP, Wang Q, Yang RT, Dai F *et al.*, Hydroxycinnamic acids as DNA-cleaving agents in the presence of Cu^{II} ions: mechanism, structure–activity relationship, and biological implications. *Chem Eur J* **15**:12889–12899 (2009).

54 Zheng W and Wang SY, Oxygen radical absorbing capacity of phenolics in blueberries, cranberries, chokeberries, and lingonberries. *J Agric Food Chem* **51**:502–509 (2003).

55 Jing P, Zhao SJ, Jian WJ, Qian BJ, Dong Y and Pang J, Quantitative studies on structure–DPPH scavenging activity relationships of food phenolic acids. *Molecules* **17**:12910–12924 (2012).

56 Kähkönen MP and Heinonen M, Antioxidant activity of anthocyanins and their aglycons. *J Agric Food Chem* **51**:628–633 (2003).

57 Cao G, Sofic E and Prior RL, Antioxidant and prooxidant behavior of flavonoids: structure–activity relationships. *Free Radic Biol Med* **22**:749–760 (1997).

58 Melidou M, Riganakos K and Galaris D, Protection against DNA damage offered by flavonoids in cells exposed to hydrogen peroxide: the role of iron chelation. *Free Radic Biol Med* **39**:1591–1600 (2005).

59 US Department of Agriculture, Agricultural Research Service. 2013. USDA Database for the Flavonoid Content of Selected Foods, *Release* **3.1** (2013).

60 Giovanelli G and Buratti S, Comparison of polyphenolic composition and antioxidant activity of wild Italian blueberries and some cultivated varieties. *Food Chem* **112**:903–908 (2009).

61 Muñoz C, Sánchez-Sevilla JF, Botella MA, Hoffmann T, Schwab W and Valpuesta V, Polyphenol composition in the ripe fruits of *Fragaria* species and transcriptional analyses of key genes in the pathway. *J Agric Food Chem* **59**:12598–12604 (2011).

62 Cheel J, Theoduloz C, Rodríguez JA, Caligari PDS and Schmeda-Hirschmann G, Free radical scavenging activity and phenolic content in achenes and thalamus from *Fragaria chiloensis* ssp.

chiloensis, *F. vesca* and *F.* × *ananassa* cv. Chandler. *Food Chem* **102**:36–44 (2007).

63 Wang SY and Lewers KS, Antioxidant capacity and flavonoid content in wild strawberries. *J Am Soc Hortic Sci* **132**:629–637 (2007).

64 Capocasa F, Scalzo J, Mezzetti B and Battino M, Combining quality and antioxidant attributes in the strawberry: the role of genotype. *Food Chem* **111**:872–878 (2008).

65 Wang SY and Lin HS, Antioxidant activity in fruits and leaves of blackberry, raspberry, and strawberry varies with cultivar and developmental stage. *J Agric Food Chem* **48**:140–146 (2000).

66 Howard L, Clark J and Brownmiller C, Antioxidant capacity and phenolic content in blueberries as affected by genotype and growing season. *J Sci Food Agric* **83**:1238–1247 (2003).

67 Crespo P, Giné Bordonaba J, Terry LA and Carlen C, Characterisation of major taste and health-related compounds of four strawberry genotypes grown at different Swiss production sites. *Food Chem* **122**:16–24 (2010).

68 Krüger E, Dietrich H, Schöpplein E, Rasima E and Kürbel P, Cultivar, storage conditions and ripening effects on physical and chemical qualities of red raspberry fruit. *Postharvest Biol Technol* **60**:31–37 (2011).

69 Giné Bordonaba J and Terry LA, Manipulating the taste-related composition of strawberry fruits (*Fragaria* × *ananassa*) from different cultivars using deficit irrigation. *Food Chem* **122**:1020–1026 (2010).

70 Terry LA, Chope GA and Giné Bordonaba J, Effect of water deficit irrigation and inoculation with *Botrytis cinerea* on strawberry (*Fragaria* × *ananassa*) fruit quality. *J Agric Food Chem* **55**:10812–10819 (2007).

71 Crecente-Campo J, Nunes-Damaceno M, Romero-Rodríguez MA and Vázquez-Odériz ML, Color, anthocyanin pigment, ascorbic acid and total phenolic compound determination in organic versus conventional strawberries (*Fragaria* × *ananassa* Duch, cv Selva). *J Food Comp Anal* **28**:23–30 (2012).

72 Fernandes VC, Domingues VF, De Freitas V, Delerue-Matos C and Mateus N, Strawberries from integrated pest management and organic farming: phenolic composition and antioxidant properties. *Food Chem* **134**:1926–1931(2012).

73 Sablani SS, Andrews PK, Davies NM, Walters T, Saez H, Syamaladevi RM and Mohekar PR, Effect of thermal treatments on phytochemicals in conventionally and organically grown berries. *J Sci Food Agric* **90**:769–778 (2010).

74 You Q, Wang B, Chen F, Huang Z, Wang X and Luo PG, Comparison of anthocyanins and phenolics in organically and conventionally grown blueberries in selected cultivars. *Food Chem* **125**:201–208 (2011).

75 Kevers C, Falkowski M, Tabart J, Defraigne J-O, Dommes J and Pincemail J, Evolution of antioxidant capacity during storage of selected fruits and vegetables. *J Agric Food Chem* **55**:8596–8603 (2007).

76 Gil MI, Holcroft DM and Kader AA, Changes in strawberry anthocyanins and other polyphenols in response to carbon dioxide treatments. *J Agric Food Chem* **45**:1662–1667 (1997).

77 Agar IT, Streif J and Bangerth F, Effect of high CO_2 and controlled atmosphere (CA) on the ascorbic and dehydroascorbic acid content of some berry fruits. *Postharvest Biol Technol* **11**:47–55 (1997).

78 Terry LA, Crisosto CH and Forney CF, Small fruit and berries, in *Modified and Controlled Atmospheres for the Storage, Transportation, and Packaging or Horticultural Commodities*, ed. by Yahia EM. CRC Press, Boca Raton, FL, pp. 363–395 (2009).

79 Pan J, Vicente AR, Martínez GA, Chaves AR and Civello PM, Combined use of UV-C irradiation and heat treatment to improve postharvest life of strawberry fruit. *J Sci Food Agric* **84**:1831–1834 (2004).

80 Vicente AR, Repice B, Martínez GA, Chaves AR, Civello PM and Sozzi GO, Maintenance of fresh boysenberry fruit quality with UV-C light and heat treatments combined with low storage temperature. *J Hortic Sci Biotechnol* **79**:246–251 (2004).

81 Han C, Zhao Y, Leonard SW and Traber MG, Edible coatings to improve storability and enhance nutritional value of fresh and frozen strawberries (*Fragaria* × *ananassa*) and raspberries (*Rubus ideaus*). *Postharvest Biol Technol* **33**:67–78 (2004).

82 Duan J, Wu R, Strik BC and Zhao Y, Effect of edible coatings on the quality of fresh blueberries (Duke and Elliott) under commercial storage conditions. *Postharvest Biol Technol* **59**:71–79 (2011).

83 Wang SY and Gao H, Effect of chitosan-based edible coating on antioxidants, antioxidant enzyme system, and postharvest fruit quality of strawberries (*Fragaria* × *ananassa* Duch.). *LWT – Food Sci Technol* **52**:71–79 (2013).

84 Bakowska A, Kucharska AZ and Oszmiański J, The effects of heating, UV irradiation, and storage on stability of the anthocyanin-polyphenol copigment complex. *Food Chem* **81**:349–355 (2003).

85 Rickman B, Barrett DM and Bruhn CM, Nutritional comparison of fresh, frozen and canned fruits and vegetables. Part 1. Vitamins C and B and phenolic compounds. *J Sci Food Agric* **87**:930–944 (2007).

86 Woodward GM, McCarthy D, Pham-Thanh D and Kay CD, Anthocyanins remain stable during commercial blackcurrant juice processing. *J Food Sci* **76**:S408–S414 (2011).

87 Terefe NS, Kleintschenk T, Gamange T, Fanning KJ, Netzel G, Versteeg C *et al.*, Comparative effects of thermal and high pressure processing on phenolic phytochemicals in different strawberry cultivars. *Innov Food Sci Emerg Technol* **19**:57–65 (2013).

88 Waterhouse DS, Zhou J and Wadhwa SS, Drinking yoghurts with berry polyphenols added before and after fermentation. *Food Cont* **32**:450–460 (2013).

89 Gouin S, Microencapsulation: Industrial appraisal of existing technologies and trends. *Trends Food Sci Technol* **15**:330–347 (2004).

90 Arancibia Avila P, Namiesnik J, Toledo F, Werner E, Martinez-Ayala AL, Rocha-Guzmán NE *et al.*, The influence of different time durations of thermal processing on berries quality. *Food Control* **26**:587–593 (2013).

91 Häkkinen SH, Karenlampi SO, Mykkanen HM, Heinonen IM and Torronen AR. Ellagic acid content in berries: influence of domestic processing and storage. *Eur Food Res Technol* **212**:75–80 (2000).

92 Häkkinen SH, Kärenlampi SO, Mykkänen HM and Törrönen AR, Influence of domestic processing and storage on flavonol contents in berries. *J Agric Food Chem* **48**:2960–2965 (2000).

93 Yousefi G, Yousefi S and Emam-Djomeh Z, A comparative study on different concentration methods of extracts obtained from two raspberries (*Rubus idaeus* L.) cultivars: evaluation of anthocyanins and phenolics contents and antioxidant activity. *Int J Food Sci Technol* **48**:1179–1186 (2013).

94 Hollman PC and Katan MB, Absorption, metabolism and health effects of dietary flavonoids in man. *Biomed Pharmacother* **51**:305–310 (1997).

95 Manach C, Morand C, Texier O, Favier M-L, Agullo G, Demigne C *et al.*, Quercetin metabolites in plasma of rats fed diets containing rutin or quercetin. *J Nutr* **125**:1911–1922 (1995).

96 Puuponen-Pimia R, Nohynek L, Alakomi HL and Oksman-Caldentey KM, Bioactive berry compounds-novel tools against human pathogens. *Appl Microbiol Biotechnol* **67**:8–18 (2005).

97 Giné Bordonaba J and Terry LA, A new acetonitrile-free mobile phase for HPLC-DAD determination of individual anthocyanins in blackcurrant and strawberry fruits: a comparison and validation study. *Food Chem* **129**:1265–1273 (2011).

98 Saura-Calixto F, Concept and health-related properties of nonextractable polyphenols: the missing dietary polyphenols. *J Agric Food Chem.* **60**:195–200 (2012).

99 Huang D, Ou B and Prior RL, The chemistry behind antioxidant capacity assays. *J Agric Food Chem* **53**:1841–1856 (2005).

100 Giné Bordonaba J and Terry LA, Electrochemical behaviour of polyphenol rich fruit juices using disposable screen-printed carbon electrodes: towards a rapid sensor for antioxidant capacity and individual antioxidants. *Talanta* **90**:38–45 (2012).

101 Bandonienė D, Murkovic M, On-line HPLC-DPPH screening method for evaluation of radical scavenging phenols extracted from apples (*Malus domestica* L.). *J Agric Food Chem* **50**:2482–2487 (2002).

102 Nuengchamnong N and Ingkaninan K, On-line HPLC-MS-DPPH assay for the analysis of phenolic antioxidant compounds in fruit wine: *Antidesma thwaitesianum* Muell. *Food Chem* **118**:147–152 (2010).

103 Niederländer HAM, van Beek TA, Bartasiute A and Koleva II, Antioxidant activity assays on-line with liquid chromatography. *J Chromatogr A* **1210**:121–134 (2008).

104 Liu RH, Potential synergy of phytochemicals in cancer prevention: mechanism of action. *J Nutr* **134**:3479S–3485S (2004).

105 Liu RH, Health-promoting components of fruits and vegetables in the diet. *Adv Nutr* **4**:384S–392S (2013).

106 Diamanti J, Capocasa F, Balducci F, Battino M, Hancock J and Mezzetti B, Increasing strawberry fruit sensorial and nutritional quality using wild and cultivated germplasm. *PLOS ONE* **7**:e46470 (2012).

107 Terry LA, Joyce DC, Adikaram NKB and Khambay BPS, Preformed antifungal compounds in strawberry fruit and flower tissue. *Postharvest Biol Technol* **31**:201–212 (2004).

108 Battino M, Beekwilder J, Denoyes-Rothan B, Laimer M, McDougall GJ and Mezzetti B, Bioactivities of berries relevant to human health. *Nutr Rev* **67**:145–150 (2009).

109 Diamanti J, Capocasa F, Denoyes B, Petit A, Chartier P, Faedi W *et al.*, Standardized method for evaluation of strawberry (*Fragaria* × *ananassa* Duch.) germplasm collections as a genetic resource for fruit nutritional compounds. *J Food Comp Anal* **28**:170–178 (2012).

110 Allan AC, Hellens RP and Laing WA. MYB transcription factors that colour our fruit. *Trends Plant Sci* **13**:99–102 (2008).

111 Niu SS, Xu CJ, Zhang WS, Zhang B, Li X, Lin-Wang K *et al.*, Coordinated regulation of anthocyanin biosynthesis in Chinese bayberry (*Myrica rubra*) fruit by a R2R3 MYB transcription factor. *Planta* **231**:887–899 (2010).

112 Jaakola L, Poole M, Jones MO, Kämäräinen-Karppinen T, Koskimäki JJ, Hohtola A *et al.*, SQUAMOSA MADS box gene involved in the regulation of anthocyanin accumulation in bilberry fruits. *Plant Physiol* **153**:1619–1629 (2010).

113 Terry LA and Joyce DC, Elicitors of induced resistance in postharvest horticultural crops: a brief review. *Postharvest Biol Technol* **32**:1–13 (2004).

114 Konic-Ristic A, Šavikin K, Zdunic G, Tankovic T, Juranic Z, Menkovic N *et al.*, Biological activity and chemical composition of different berry juices. *Food Chem* **125**:1412–1417 (2011).

115 Barbuti A, Briasoulis E and Galaris D, Protective effects of olive oil components against hydrogen peroxide-induced DNA damage: the potential role of iron chelation, in *Olives and Olive Oil in Health and Disease Prevention*, ed. by Preedy VR and Watson RR. Elsevier, Amsterdam, pp. 1103–1109 (2010).

116 Willis LM, Shukitt-Hale B and Joseph JA, Recent advances in berry supplementation and age-related cognitive decline. *Curr Opin Clin Nutr Met Care* **12**:91–94 (2009).

117 van Duynhoven J, Vaughan EE, Jacobs DM, Kemperman RA, Van Velzen EJJ, Gross G, Roger LC *et al.*, Metabolic fate of polyphenols in the human superorganism. *Proc Natl Acad Sci USA* **108**:4531–4538 (2011).