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Review

Functional components in sweetpotato and their genetic improvement

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In addition to the nutritionally important components such as starches, vitamins and minerals, storage roots and leaves of sweetpotato (*Ipomoea batatas*) contains several components with health-promoting functions. Of these, the functionalities of carotenoids, anthocyanins and caffeoylquinic acids have been well established by *in vitro* and *in vivo* experiments. Several sweetpotato cultivars containing high levels of these components have been developed in Japan; e.g., 'Ayamurasaki', which has high amounts of anthocyanin in its storage roots. To further improve the content and also to change the composition of these functional components, the identification of the genes involved in their biosynthesis and genetic modification of the biosynthetic pathway has been attempted. In this review, we summarize the present status of the research and breeding for these functional components, and we discuss the future prospects for improving sweetpotato functionality.

Key Words: sweetpotato, carotenoid, anthocyanin, caffeoylquinic acid, functionality.

Introduction

Sweetpotato (*Ipomoea batatas*) is one of the most important food crops in tropical and subtropical regions with approx. 100 million tons of annual global production. Although sweetpotato originated in the tropical Americas, about 75% of its production now comes from Asian countries (FAO 2015). Sweetpotato shows the highest energy yield per hectare among the major food crops produced in developing countries (Woolfe 1992), as well as relatively high tolerance to unfavorable weather and cultivation conditions. The storage roots of sweetpotato are an important nutrition source especially in developing countries, because they are rich in vitamins and minerals, and also contain a large amount of starch (for detailed nutritional value, see Woolfe 1992).

In addition to these nutritional components, it was revealed that sweetpotato has many functional components with various health-promoting functions (Yoshimoto 2010). In Japan, the identification of these functional components has attracted the interest of health-conscious consumers and has promoted the development of a number of sweetpotato food products. The functional components in sweetpotato storage roots include carotenoids, anthocyanins, caffeoylquinic acids (CQAs), dietary fiber (Tamiya *et al.* 1999, Yoshimoto *et al.* 2005), and resistant starch (Katayama *et al.* 2011). Of these, carotenoids, anthocyanins and CQAs have been most extensively studied. In addition to storage roots, sweetpotato leaves have been shown to contain functional components such as CQAs and carotenoids, and the leaves have been used as processing material for functional foods.

Improvements in the content of these functional components have been a target of breeding, and several cultivars rich in these functional components have already been developed and utilized (see below). Because sweetpotato is an allogamous autohexaploid with self- and cross-incompatibility, its genetic analysis has been difficult. Nevertheless, recent genetic studies have identified genes involved in the accumulation of carotenoids and anthocyanins, and researchers have attempted to use these genes to improve the efficiency of cultivar development.

In this review we first summarize the chemical characteristics, physiological functions, genetic variation, and the present status of the sweetpotato cultivar development for

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carotenoids, anthocyanins, and CQAs. We then summarize the recent progress achieved in genetic studies, and we discuss the future prospects of improving the functionality of sweetpotato.

Carotenoids

Sweetpotato varieties with orange and yellow flesh have been developed in Japan (Takahata 2014). For example, the following cultivars have been released: 'Sunny-Red' (Yamakawa *et al.* 1999a), 'J-Red' (Yamakawa *et al.* 1997), 'Hamakomachi' (Yoshinaga *et al.* 2006) and 'Ayakomachi' (Kai *et al.* 2004) with orange flesh, and 'Quick Sweet' (Katayama *et al.* 2003), 'Tamaotome' (Ishiguro *et al.* 2004b), 'Benimasari' (Ishiguro *et al.* 2004c), 'Beniharuka' (Kai *et al.* 2010), 'Himeayaka' (Ohara-Takada *et al.* 2011) and 'Aikomachi' (Ohara-Takada *et al.* 2016) with yellow flesh. Many commercial products such as chips, cakes, juices, distilled spirits and steamed dried cakes have been developed using orange and yellow cultivars (Komaki and Yamakawa 2006). The main pigment is β-carotene in the varieties with orange flesh (Kimura *et al.* 2007). Reports of the carotenoid composition of yellow-fleshed cultivars are scarce, although such cultivars are popular in Japan.

Maoka *et al.* (2007) analyzed the components of the yellow pigment in the cv. 'Benimasari' with deep yellow flesh. The analytical high-performance liquid chromatography (HPLC) separations of carotenoids in 'Benimasari' showed seven known carotenoids and four new carotenoids. They identified a novel series of carotenoids with a 5,6-dihydro-5,6-dihydroxy-β-end group, named ipomoeaxanthins A, B, C1 and C2 (**Fig. 1A**).

Ishiguro *et al.* (2010) analyzed the total content and composition of carotenoids in yellow-fleshed cultivars and breeding lines as well as in orange-fleshed cultivars. The total carotenoid contents in eight sweetpotato cultivars or breeding lines with yellow flesh were evaluated by absorption spectrophotometry and compared with those of four cultivars with orange flesh. The carotenoid contents ranged from 1.3 mg/100 g to 3.9 mg/100 g dry weight in yellow-fleshed cultivars and from 13.5 mg/100 g to 39.9 mg/100 g dry weight in the orange-fleshed cultivars. Seventeen carotenoids were detected in yellow- and orange-fleshed sweetpotato by the HPLC analysis (**Fig. 2**). The main carotenoids were β-carotene 5,8;5′,8′-diepoxide (approx. 32%–51%) and β-cryptoxanthin 5′,8′-epoxide (approx. 11%–30%) in the yellow-fleshed cultivars/lines, whereas β-carotene (approx. 80%–92%) was dominant in orange-fleshed cultivars (**Figs. 1B**, **2**).

These results suggest that the content of each carotenoid differs according to the flesh color, i.e., yellow or orange, although the carotenoid component in the yellow and orange flesh was almost identical. In the carotenoid pathway, β-cryptoxanthin is synthesized by adding a hydroxyl group to a β-ring of β-carotene (Burns *et al.* 2003). The balance of the synthesis of β-carotene and metabolization to the β-carotene epoxide or β-cryptoxanthin epoxide could be a determinant of the flesh color of the sweetpotato storage root.

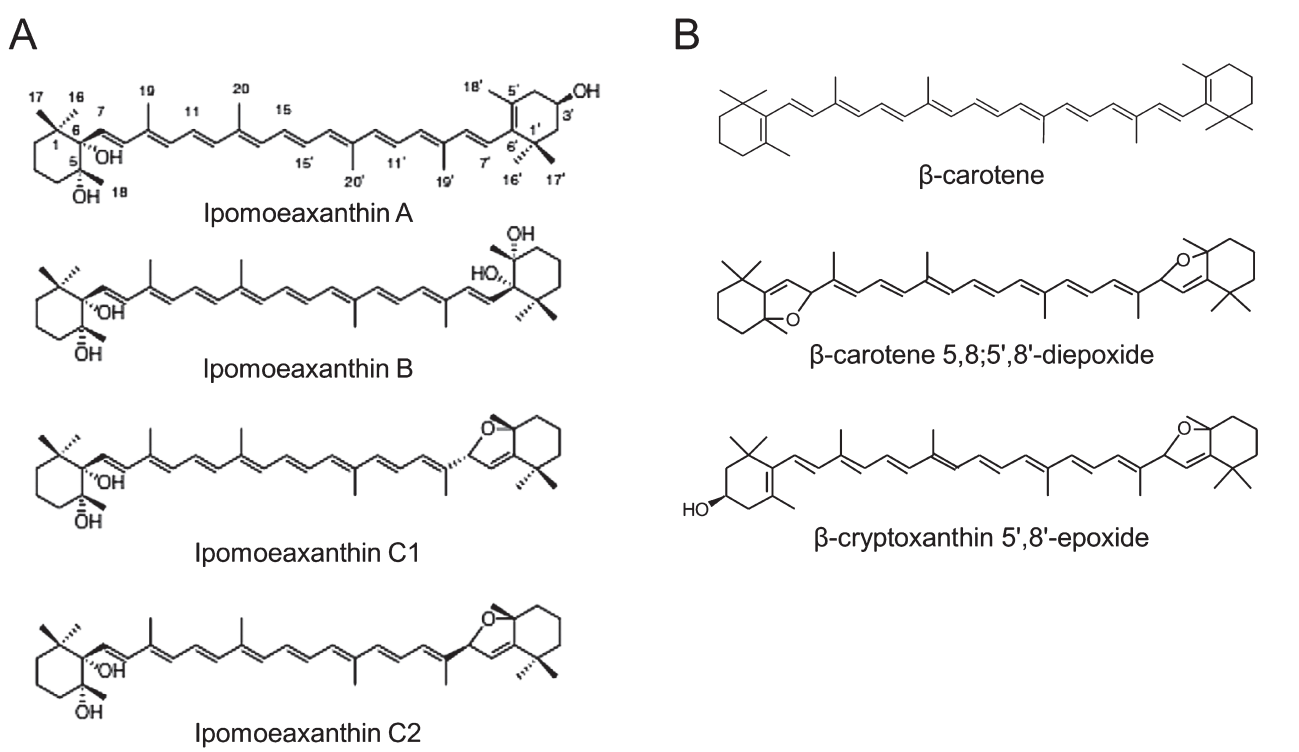


Fig. 1. Structures of the major carotenoids in sweetpotato storage roots. (A) Ipomoeaxanthin A, B, C1 and C2, in yellow-fleshed sweetpotatoes. (B) β-carotene, β-carotene 5,8;5′,8′-diepoxide and β-cryptoxanthin 5′,8′-epoxide.

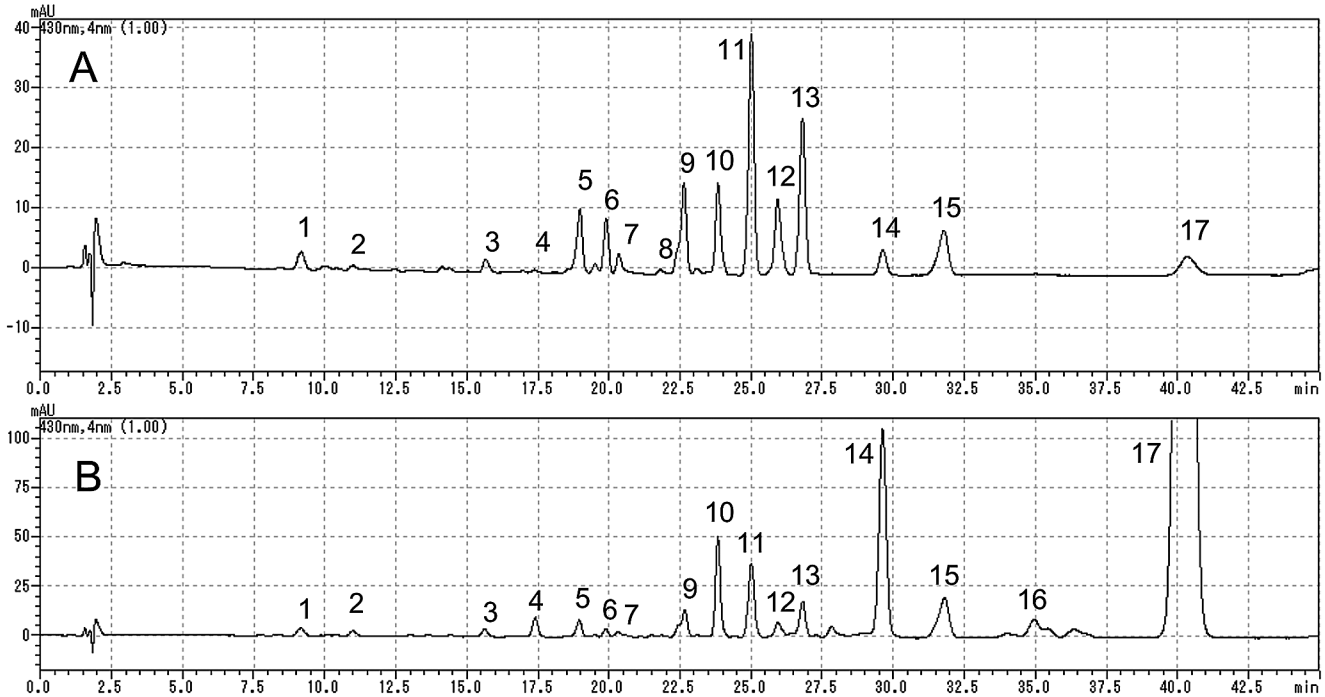


Fig. 2. HPLC chromatograms of carotenoids from (A) the yellow-fleshed cultivar 'Tamaotome' and (B) the orange-fleshed cultivar 'Sunny-Red'. Peak identifications 1: unknown, 2: unknown, 3: ipomoeaxanthin A, 4: unknown, 5: unknown, 6: ipomoeaxanthin C1, 7: ipomoeaxanthin C2, 8: β-cryptoxanthin 5,8;5′,8′-diepoxide, 9: β-cryptoxanthin 5′,8′-epoxide, 10: unknown, 11: β-carotene 5,8;5′,8′-diepoxide (cis-isomer), 12, 13: β-carotene 5,8;5′,8′-diepoxide (giastereomer), 14: unknown, 15: β-carotene 5,8-epoxide, 16: unknown, 17: β-carotene.

In other words, a higher expression of β-carotene results in orange flesh, and a higher accumulation of β-carotene epoxide and β-cryptoxanthin epoxide leads to yellow flesh in sweetpotato storage roots.

These carotenoids showed anti-oxidative activities (Ishiguro *et al.* 2010, Oki *et al.* 2006). Carotenoids as antioxidants have also been reported to have preventive effects for some diseases in vitro and in animal models (Paiva and Russel 1999). Epidemiological studies have demonstrated that dietary carotenoids result in lower risks for lifestyle-related diseases (Sugiura 2015). One objective of sweetpotato breeders is to develop a variety with deep-orange or yellow flesh. Deep orange or yellow is an attractive color in processed foods, and their carotenoids may contribute to the prevention of some diseases.

Anthocyanins

Sweetpotato storage roots with purple flesh contain anthocyanins, whereas those with other flesh colors such as white, yellow or orange contain little or no anthocyanins. Anthocyanins belong to a class of flavonoids synthesized via the phenylpropanoid pathway, and they are responsible for colors ranging from pale pink to purple and deep blue. They are present in a wide range of plant tissues, principally flowers and fruits, but also storage organs, such as storage roots and tubers.

The cultivar 'Ayamurasaki' is a sweetpotato with purple flesh that is used for processing. It was developed at the Kyushu Okinawa Agricultural Research Center, NARO in 1995 (Yoshinaga 1995). This cultivar has a high level of anthocyanin and excellent agronomic characteristics such as high productivity. 'Ayamurasaki' was obtained by cross-breeding the line 'Kyushu No.109' containing anthocyanins with the white-flesh cultivar 'Satsumahikari' which lacks β-amylase activity. 'Kyushu No.109' originates from the indigenous purple-fleshed cultivars 'Yamagawamurasaki' and 'Chiranmurasaki'. **Fig. 3** is the pedigree diagram of 'Ayamurasaki' and two other purple-fleshed sweetpotato cultivars with high anthocyanin content used for processing purposes in Japan.

Purple-fleshed sweetpotato cultivated in Japan contains more than eight species of anthocyanins with different chemical structures, and the anthocyanin composition and content vary according to cultivars. As illustrated in **Fig. 4**, the chemical structures of major eight anthocyanins are mono- or di-acylated forms of cyanidin and peonidin (Goda *et al.* 1997, Terahara *et al.* 1999). Among these anthocyanins, two anthocyanins (YGM-2 and YGM-5b) are mono-acylated by caffeic acid, and the others are di-acylated by caffeic acid alone (YGM-1b and YGM-4b), caffeic acid and *p*-hydroxybenzoic acid (YGM-1a and YGM-5a), or caffeic acid and ferulic acid (YGM-3 and YGM-6).

In 'Ayamurasaki', 'Murasakimasari' and 'Akemurasaki', peonidin-type anthocyanins (YGM-4b, 5a, 5b, and 6) are dominant, whereas cyanidin-type anthocyanins (YGM-1a,

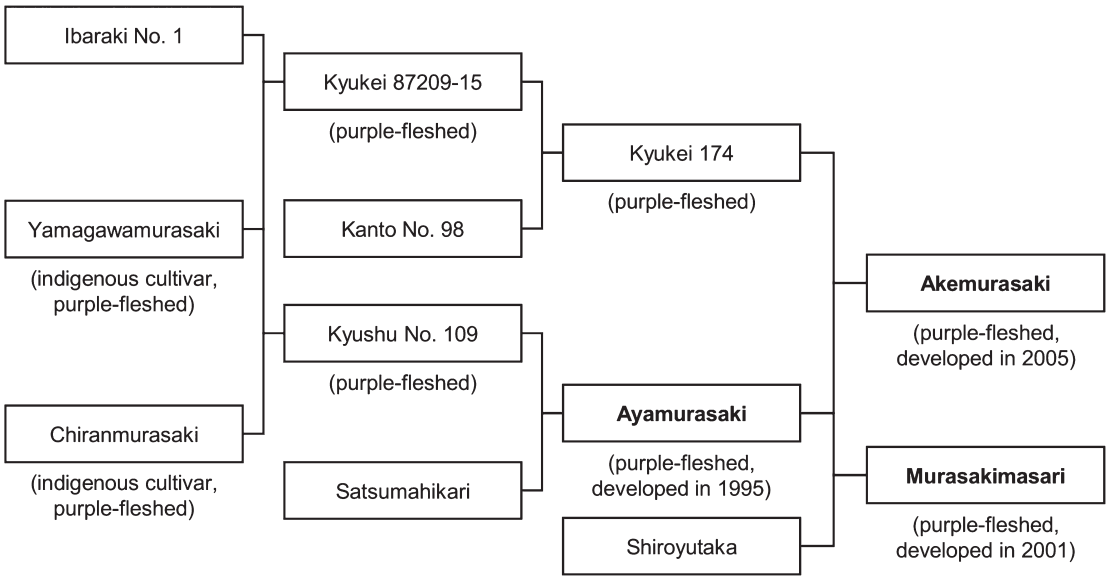
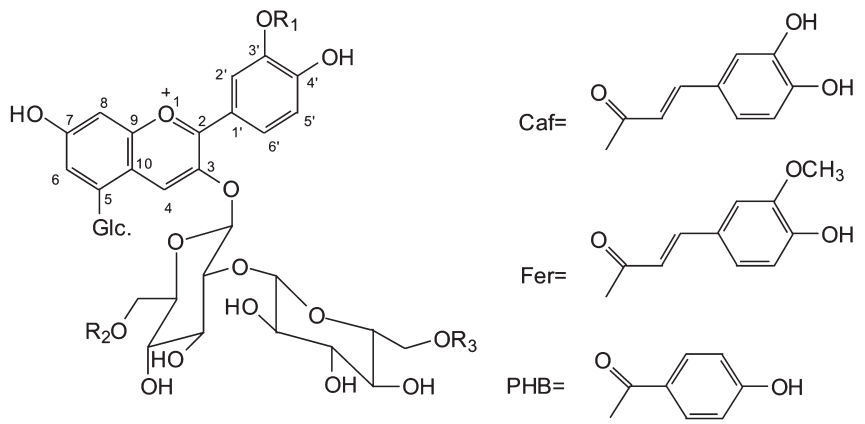


Fig. 3. Pedigree diagram of 'Ayamurasaki' and other purple-fleshed sweetpotato cultivars for processing purposes released by the breeding program in Kyushu Okinawa Agricultural Research Center, NARO.



Abbreviation	R_1	R_2	R_3	Formula	Molecular weight
YGM-2	H	Caf	H	Cy-Caf•Sop-Glc	935
YGM-1b	H	Caf	Caf	Cy-diCaf•Sop-Glc	1097
YGM-1a	H	Caf	PHB	Cy-Caf•PHB•Sop-Glc	1055
YGM-5b	Me	Caf	H	Pn-Caf•Sop-Glc	949
YGM-3	H	Caf	Fer	Cy-Caf•Fer•Sop-Glc	1111
YGM-4b	Me	Caf	Caf	Pn-diCaf•Sop-Glc	1111
YGM-5a	Me	Caf	PHB	Pn-Caf•PHB•Sop-Glc	1069
YGM-6	Me	Caf	Fer	Pn-Caf•Fer•Sop-Glc	1125

Fig. 4. Chemical structure of major anthocyanins in storage roots of purple-fleshed sweetpotato cultivars in Japan. Me, methyl; Cy, cyanidin; Pn, peonidin; Caf, (*E*)-caffeic acid; Sop, sophoroside; PHB, *p*-hydroxybenzoic acid; Fer, (*E*)-ferulic acid; Glc, glucopyranoside.

1b, 2, and 3) are dominant in 'Bise' and 'Miyano No.36' (Oki *et al.* 2002). Takahata *et al.* (2011) clearly demonstrated that cyanidin-type anthocyanins are closely related to the radical-scavenging activity against 1,1-diphenyl-2-picrylhydrazyl (DPPH) of sweetpotato storage roots with purple flesh.

It was reported that the paste made from purple-fleshed sweetpotato rich in peonidin- and cyanidin-type anthocyanins is reddish-purple and bluish-purple, respectively (Yoshinaga *et al.* 1999). The color stability of extracts from purple-fleshed sweetpotato storage roots is superior to those from apple (*Malus pumila* Mill.), perilla (*Perilla frutescens* L. var. *crispa*), red cabbage (*Brassica oleracea* L. var. *capitata*), and strawberry (*Fragaria×ananassa* Duch.) against heating and ultraviolet light irradiation, due to the high degree of acylation of anthocyanins in purple-fleshed sweetpotato (Tsukui *et al.* 1999). Due to these unique characteristics, purple-fleshed sweetpotato storage roots have been used as an excellent source to produce a natural colorant for food. Purple-fleshed sweetpotatoes have become the principal sources of anthocyanin-type food colorant along with grape skins and red radish roots in the Japanese market of natural food colorants derived from plants containing anthocyanin (Aoki 2004).

Purple-fleshed sweetpotatoes have also recently become available for table use in markets nationwide in Japan, but in the Okinawa region (southwest Japan), purple-fleshed sweetpotato, also called as 'beni-imo', has been familiar and eaten since the 17th century. NARO has developed two purple-fleshed sweetpotato cultivars, 'Purple Sweet Lord' (Tamiya *et al.* 2003) and 'Kyushu No.137' (Yoshinaga *et al.* 2006) in addition to those used for processing. 'Purple Sweet Lord' was released in 2002 for table use nationwide, and 'Kyushu No. 137' was released in 2004 for hoshi-imo (dried sweetpotato) as a traditional processed sweetpotato made by steaming and drying. The Okinawa Prefectural Agricultural Research Center also developed two purple-fleshed sweetpotato cultivars: 'Okiyumemurasaki' in 2003 (Yamada *et al.* 2012) and 'Churakoibeni' in 2009, of which the areas under cultivation in Okinawa Prefecture have increased gradually in place of 'Bise' and 'Miyano No.36'.

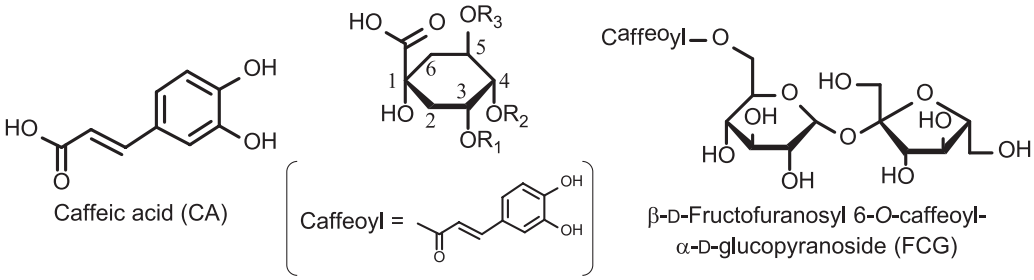
In the past decade, anthocyanin-rich foods and preparations have attracted attention because of their health benefits in terms of the potential ability to counteract some lifestyle-related diseases (He and Giusti 2010, Tsuda 2012, Yousuf *et al.* 2016). In Japan, many studies have been conducted to investigate the physiological functions of the purple-fleshed sweetpotato cultivar 'Ayamurasaki'. *In vitro* studies were performed using the extract and/or the purified anthocyanin from the storage roots of 'Ayamurasaki'. These materials exhibited multiple physiological functions such as radical-scavenging activity (Furuta *et al.* 1998, Kano *et al.* 2005, Oki *et al.* 2002), oxygen radical absorbance capacity (Oki *et al.* 2009), angiotensin I converting enzyme inhibitory activity (Yamakawa *et al.* 1999b), α-glucosidase inhibitory activity (Matsui *et al.* 2001a, 2001b), and antimutagenic activity (Yoshimoto *et al.* 1999, 2001). It was also reported that in animal models, purple-fleshed sweetpotato or beverages derived from it containing anthocyanins showed physiological functions such as an antihyperglycemic effect through α-glucosidase inhibition (Matsui *et al.* 2002) and an anti-atherosclerotic effect (Miyazaki *et al.* 2008), and beneficial effects on hypertension and hepatitis have been observed in both animal models (Kobayashi *et al.* 2005, Suda *et al.* 1997) and clinical trials (Suda *et al.* 1998, 2007).

Caffeoylquinic acids

CQAs and their basic structure, caffeic acid (CA), are a class of naturally occurring polyphenols that exist in a wide range of plants. These compounds have been shown in *in vitro* and *in vivo* experiments to have many beneficial properties, e.g., antivirus (Mahmood *et al*. 1993), anti-oxidative (Chuda *et al*. 1996), antihyperglycemic (Matsui *et al*. 2004) and antihypertensive (Mishima *et al*. 2005) effects, plus the inhibition of neurotoxicity of amyloid β-protein involved in Alzheimer's disease (Miyamae *et al*. 2012). Storage roots and greens of sweetpotato also contain polyphenols such as CQAs and CA. **Fig. 5** lists the polyphenols mentioned in this section and identified in the plant materials obtained or grown in Japan. Please note that the numbering system recommended by the International Union of Pure and Applied Chemistry (IUPAC 1976) is used and that chlorogenic acid therefore means 5-*O*-caffeoylquinic acid (5-CQA).

Hayase and Kato (1984) reported the isolation of six polyphenols, the identification of five of them as CA, 5-CQA and three isochlorogenic acids (dicaffeoylquinic acids), and the tentative identification of the rest as 4-*O*-caffeoylquinic (4-CQA). They also reported the contents of 5-CQA and three isochlorogenic acids in the roots of 'Kintoki' and 'Kokei No.14'. Shimozono *et a*l. (1996) isolated and identified 5-CQA, 3,4-di-*O*-caffeoylquinic (3,4-diCQA), 3,5-di-*O*-caffeoylquinic (3,5-diCQA) and 4,5-di-*O*-caffeoylquinic (4,5-diCQA) acid from the roots of 'Beniotome'. Takenaka *et al*. (2006) determined eight polyphenols in the roots of 'Beniazuma': CA, six CQAs, namely 3-*O*-caffeoylquinic acid (3-CQA), 4-CQA, 5-CQA, 3,4-diCQA, 3,5-diCQA and 4,5-diCQA, and β-D-fructofuranosyl 6-*O*-caffeoyl-α-D-glucopyranoside (FCG). They revealed that the major components were 5-CQA and 3,5-diCQA in fresh roots but FCG in long-stored roots.

In the roots of four cultivars, 'Benimasari', 'Koganesengan', 'J-Red' and 'Murasakimasari', Ishiguro *et al*. (2007) identified six polyphenols: CA, 5-CQA, 3,4-diCQA, 3,5-diCQA, 4,5-diCQA and FCG. They reported that the main components in all four of the cultivars tested were 5-CQA and 3,5-diCQA before and after storage (5°C and 15°C), and that the contents of these two compounds increased extensively during storage for 'Benimasari', 'Koganesengan' and 'J-Red' whereas the contents remained within relatively constant levels for 'Murasakaimasari'. Ishiguro *et al*. (2007) also revealed that in all cultivars tested, FCG increased during storage but did not exceed the



Compound name	Abbreviation	Structure		
		R_1	R_2	R_3
3-*O*-Caffeoylquinic acid	3-CQA	Caffeoyl	H	H
4-*O*-Caffeoylquinic acid	4-CQA	H	Caffeoyl	H
5-*O*-Caffeoylquinic acid (chlorogenic acid)	5-CQA	H	H	Caffeoyl
3,4-Di-*O*-caffeoylquinic acid	3,4-diCQA	Caffeoyl	Caffeoyl	H
3,5-Di-*O*-caffeoylquinic acid	3,5-diCQA	Caffeoyl	H	Caffeoyl
4,5-Di-*O*-caffeoylquinic acid	4,5-diCQA	H	Caffeoyl	Caffeoyl
3,4,5-Tri-*O*-caffeoylquinic acid	3,4,5-triCQA	Caffeoyl	Caffeoyl	Caffeoyl

Fig. 5. Structures of the sweetpotato root and leaf polyphenols mentioned in this section and found in the plant materials obtained or grown in Japan. The IUPAC numbering system (IUPAC 1976) is used for these compounds.

levels of 5-CQA or 3,5-diCQA. The latter result is not consistent with that obtained using 'Beniazuma' (Takenaka *et al*. 2006). Thus, the characteristics of polyphenols in sweetpotato roots such as changes during storage are dependent on the cultivar. Systematic investigations using more cultivars including purple-fleshed and orange-fleshed cultivars will provide more information on the compounds.

In Japan, polyphenols in sweetpotato leaves have been thoroughly investigated, especially at the Kyushu Okinawa Agricultural Research Center, NARO. Islam *et al*. (2002) identified six polyphenols in sweetpotato leaves: CA, 5-CQA, 3,4-diCQA, 3,5-diCQA, 4,5-diCQA and 3,4,5-tri-*O*-caffeoylquinic acid (3,4,5-triCQA). This was the first report of polyphenolic compositions in sweetpotato leaves and of 3,4,5-triCQA found in them, and to date there has been no report of the detection of 3,4,5-triCQA in sweetpotato roots. Islam *et al*. (2002) also identified these six compounds in the leaves of 20 sweetpotato genotypes, and they reported that 3,5-diCQA was the most abundant in all the genotypes (953–3,504 mg/100 g of freeze-dried leaves). Okuno *et al*. (2010) determined the six compounds in the leaves of 529 sweetpotato cultivars and reported that the contents of the compounds as mg/g of freeze-dried leaves were as follows: 0.08–3.09 for CA, 0.17–16.01 for 5-CQA, 0.50–34.08 for 3,4-diCQA, 1.86–56.52 for 3,5-diCQA, 0.69–20.73 for 4,5-diCQA, 0.25–13.81 for 3,4,5-triCQA and 8.49–111.83 mg/g for all of the compounds together. Thus, 3,5-diCQA was the most abundant, and this result was consistent with that reported by Islam *et al*. (2002).

The order of the antimutagenicity of CQAs is as follows: 3,4,5-triCQA > 3,4-diCQA = 3,5-diCQA = 4,5-diCQA > 5-CQA (Yoshimoto *et al*. 2002). The sweetpotato cultivar 'Suioh' was developed for the use of its tops (leaves and petioles) as an edible vegetable, and its leaves were shown to have a higher content of total polyphenols and higher activity for DPPH radical scavenging compared to other leafy vegetables (Ishiguro *et al*. 2004a). The reason why 'Suioh' was selected was mainly the better taste of its leaves and petioles compared to other cultivars, rather than its the polyphenol contents. In fact, the leaves of many cultivars have higher polyphenol content than those of 'Suioh' (Okuno *et al*. 2010).

Although many investigations of sweetpotato cultivars have been conducted to determine the polyphenol contents in their leaves as noted here, the genetic background (such as the father/mother in crosses) has not been discussed by researchers in this field of study, particularly in light of the regulation of the accumulation of these compounds. Digging into the relationship between the contents of polyphenols and the genetic properties of the examined materials may result in new findings that can be used for the development of new cultivars with higher contents of useful compounds.

Researchers in several countries other than Japan have also investigated polyphenols in sweetpotato greens. Truong *et al*. (2007) identified five polyphenols (CA, 5-CQA, 4,5-diCQA, 3,5-diCQA and 3,4-diCQA) in the leaves (and roots) of three commercial cultivars in the United States and revealed that 3,5-diCQA and 4,5-diCQA were predominant in the leaves. The three commercial cultivars are orange-

fleshed and their roots are consumed. Zheng and Clifford (2008) reported that feruloylquinic acids and caffeoylferuloylquinic acids were detected in the stem of sweetpotatoes from China. The number of species of polyphenols is thus increasing, and the methods for separating them will become more and more important in future. Sun *et al.* (2014) measured the total polyphenol content and antioxidant activity and assessed the nutritional compositions of the leaves of 40 sweetpotato cultivars in China. They obtained an enormous amount of data but did not determine the contents of individual polyphenols. To determine the usefulness of sweetpotato leaves, it will be necessary to identify the contents of individual polyphenols.

Progress in genetic studies

To elucidate the mechanism of carotenoid accumulation in storage roots, McGregor and LaBonte (2006) compared the gene expression between the orange-fleshed sweetpotato 'Jewel' and its mutant 'White Jewel' using a cDNA microarray. The results suggested that the mutant has differences in gene expression related to the development of the chromoplast, which is a form of plastid and functions as a storage organelle of carotenoids. A quantitative trait locus (QTL) analysis using F_1 progenies between orange- and white-fleshed cultivars (Cervantes-Flores *et al.* 2011) and association analyses using germplasm (Mwamburi and LaBonte 2010, Zhang *et al.* 2016) have been performed, and several QTLs associated with β-carotene content were detected. The DNA markers associated with these QTLs may be useful in efforts to improve the carotenoid content in storage roots.

Transgenic studies showed that the suppression of β-carotene hydroxylase (CHY-β), which catalyzes the hydroxylation steps of both β-carotene into β-cryptoxanthin and β-cryptoxanthin into zeaxanthin, greatly increased the β-carotene and total carotenoid content in transgenic cultured cells of sweetpotato (Kim *et al.* 2012). Similarly, the suppression of lycopene β-cyclase (LCY-β), which catalyzes the cyclization steps of lycopene to produce β-carotene, increased the total carotenoid content (Kim *et al.* 2014). These results suggested that the CHY-β and LCY-β are key enzymes of carotenoid biosynthesis in sweetpotato and, thus, good targets for molecular breeding.

However, the above-cited studies did not identify a specific regulatory gene that controls carotenoid accumulation. In cauliflower, it is reported that a gain-of-function mutation in *Or* gene induced carotenoid accumulation in various tissues (Lu *et al.* 2006). The *Or* gene encodes a plastid-associated protein containing a DnaJ Cys-rich domain, and this gene is likely to function in the development of the chromoplast. Transgenic sweetpotato plants overexpressing an *Or* homologue of sweepotato, *IbOr*, showed increased carotenoid contents compared to non-transformed control plants (Park *et al.* 2015a).

In many plants, a tissue-specific accumulation of anthocyanin is controlled by transcription factors belonging to MYB-family. By conducting a gene expression analysis using purple-fleshed cultivars and transformation experiments using sweetpotato leaves and calli, Mano *et al.* (2007) demonstrated that one of the MYB-type transcription factors in sweetpotato, IbMYB1, is responsible for anthocyanin accumulation in storage roots. Overexpression of the *IbMYB1* gene successfully induced anthocyanin accumulation in the storage roots of an orange-fleshed sweetpotato cultivar, resulting in higher radical scavenging activity (Park *et al.* 2015b). Tanaka *et al.* (2012) compared the structure of the *IbMYB1* genes between cultivars with high-anthocyanin content and cultivars without anthocyanins, and they found that distinct *IbMYB1* copies, named *IbMYB1-2a* and *IbMYB1-2b*, are shared only in the high-anthocyanin cultivars and their common ancestor 'Yamagawamurasaki'. The polymerase chain reaction (PCR) fragment amplified from *IbMYB1-2a* and *IbMYB1-2b* cosegregated with the pigmentation of storage roots in the F_1 progenies of high-anthocyanin cultivars, and this PCR fragment thus seems to be useful as a selection marker for high-anthocyanin lines (Tanaka *et al.* 2012).

As for the CQAs, their biosynthetic pathway has not been well elucidated, although the early steps of the biosynthetic pathway of CQAs are in common with those of anthocyanins. Park *et al.* (2015b) reported that the transgenic plants overexpressing *IbMYB1* showed an elevated total polyphenol level. In these plants, the gene expression of phenylalanine ammonia lyase (PAL), cinnamate 4-hydroxylase (C4H), and 4-hydroxycinnamoyl-CoA ligase (4CL), all of which are involved in the early steps of both anthocyanin and CQA biosynthesis, was upregulated. Tanaka *et al.* (2012) also observed a suppressed expression of these genes in a white-fleshed mutant of 'Ayamurasaki'. Because variations in the CQA content in the storage roots of non-purple-fleshed cultivars have also been observed (Padda and Picha 2008), one can speculate that a specific regulation mechanism of CQA content exists, in addition to a co-regulation of the anthocyanin content. To date, however, the mechanism of such CQA-specific regulation has not been reported.

Conclusion

As described above, several cultivars containing anthocyanin and carotenoid in their storage roots have been developed in Japan. A cultivar for top use, rich in polyphenols ('Suioh') has also been developed. The breeding of cultivars with functional components is still underway with the goals of increasing the content of functional components and improving their agricultural traits, processing suitability, and disease and pest resistance. The incorporation of newly developed genetic tools into traditional breeding schemes will contribute to these breeding programs. However, the genetic studies cited above have not yet fully clarified the molecular mechanisms underlying the metabolic regulation of the functional components of sweetpotato. The biosynthesis

and regulation mechanisms of CQAs (which exist as mono-, di- and tri-substituted quinic acids) remain mostly unknown, though there have been several important studies on their biosynthesis (e.g., Kojima and Uritani 1973). Quantitative variations in anthocyanin and carotenoid content are likely to be controlled by multiple genes. Further phytochemical, biochemical and genetic studies are required. Whole-genome sequencing of sweetpotato and *Ipomoea trifida*, the closest wild relative of sweetpotato, is ongoing (Isobe *et al.* 2017), and draft sequence data of these genomes have recently been published (Hirakawa *et al.* 2015, Yang *et al.* 2016). Gene sequences and DNA markers obtained from these genome studies will be useful tools for understanding the genetic mechanism regulating the content of functional components.

It has been clarified that the content of functional components changes depending on environmental factors (Hammet 1974, Islam *et al.* 2003, Kobayashi *et al.* 1998). The storage conditions used for storage roots and processing methods also affect the final amounts of functional components (Grace *et al.* 2014, Ishiguro *et al.* 2007, Oki *et al.* 2010). The effects of these factors on the content of functional components should be further clarified in order to promote the use of the sweetpotato cultivars developed in the future.

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