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Review

Improvement for agronomically important traits by gene engineering in sweetpotato

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Sweetpotato is the seventh most important food crop in the world. It is mainly used for human food, animal feed, and for manufacturing starch and alcohol. This crop, a highly heterozygous, generally self-incompatible, outcrossing polyploidy, poses numerous challenges for the conventional breeding. Its productivity and quality are often limited by abiotic and biotic stresses. Gene engineering has been shown to have the great potential for improving the resistance to these stresses as well as the nutritional quality of sweetpotato. To date, an *Agrobacterium tumefaciens*-mediated transformation system has been developed for a wide range of sweetpotato genotypes. Several genes associated with salinity and drought tolerance, diseases and pests resistance, and starch, carotenoids and anthocyanins biosynthesis have been isolated and characterized from sweetpotato. Gene engineering has been used to improve abiotic and biotic stresses resistance and quality of this crop. This review summarizes major research advances made so far in improving agronomically important traits by gene engineering in sweetpotato and suggests future prospects for research in this field.

Key Words: sweetpotato (*Ipomoea batatas* (L.) Lam.), abiotic stresses, diseases and pests, herbicide, quality, gene engineering.

Introduction

Sweetpotato, *Ipomoea batatas* (L.) Lam., was originally domesticated at least 8000–10000 years ago in tropical America (Woolfe 1992). Based on the numerical analysis of key morphological characters of sweetpotato and the wild *Ipomoea* species, Austin (1987) postulated that sweetpotato originated in the region between the Yucatán Peninsula of Mexico and the Orinoco River in Venezuela, within which the four major American taxa of the *batatas* group are distributed. Sweetpotato was introduced from the Americas into Europe by Columbus in 1492. From Europe, it was taken by the Portuguese explorers of the sixteenth century to Africa, India, Southeast Asia, and the East Indies. This crop was introduced to China in the late sixteenth century from Philippines to Fujian of China (O'Brien 1972). Other data suggest that sweetpotato was introduced to China from Vietnam, India, and Burma. From China, this crop was introduced to Japan about 400 years ago.

Sweetpotato is the seventh most important food crop in the world (FAO 2014). This crop is mainly used for human food (as such or in processed form), animal feed, and for manufacturing starch and its products. It is also an alternative source of bio-energy as a raw material for fuel production. In most developing countries, it is a smallholder crop tolerant of a wide range of edaphic and climatic conditions and grown with limited inputs. Sweetpotato provides more edible energy per hectare per day than wheat, rice, or cassava and is an essential food source with very high production per capita across the relatively humid areas of Africa. Asia is the largest sweetpotato-producing region, with approximately 80% of the world's production and more than 50% of the world's area. China accounts for approximately 68% of world production, with more than 42% of the global area (FAO 2014).

Sweetpotato is a member of the family Convolvulaceae, Genus *Ipomoea*, section *Batatas*. The number of chromosomes in the sweetpotato plant is 2n = 6x = 90. This crop, a highly heterozygous, generally self-incompatible, outcrossing polyploidy, poses numerous challenges for the conventional breeding (Cervantes-Flores *et al.* 2011, Dhir *et al.* 1998). Its productivity and quality are often limited by abiotic and biotic stresses (Zhai *et al.* 2016). Gene engineering has been shown to have the great potential for improving the resistance to abiotic and biotic stresses as well as the nutritional quality of sweetpotato.

In the past decades, great progress in sweetpotato gene

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Table 1. Details of recent transgenic studies on the improvement for agronomically important traits in sweetpotato

Host cultivar	Transgene	Origin	Improved trait	Reference
Yulmi	*CuZnSOD*, *APX*	Sweetpotato	Drought tolerance	Li *et al.* 2006
Yulmi	*CuZnSOD*, *APX*	Sweetpotato	Tolerance to oxidative stress and chilling	Lim *et al.* 2007
Yulmi	*SCOF-1*	Soybean	Low temperature	Kim *et al.* 2011
Lizixiang	*AtLOS5*	*Arabidopsis*	Salt tolerance	Gao *et al.* 2011c
Xushu 18	*AtSOS*	*Arabidopsis*	Salt tolerance	Gao *et al.* 2012
Sushu 2	*SoBADH*	Spinach	Tolerance to salt, oxidative stress, and low temperature	Fan *et al.* 2012
Lizixiang	HDG_{11}	*Arabidopsis*	Drought tolerance	Ruan *et al.* 2012
Lizixiang	*IbNFU1*	Sweetpotato	Salt tolerance	Liu *et al.* 2014b
Kokei 14	*IbP5CR*	Sweetpotato	Salt tolerance	Liu *et al.* 2014a
Shangshu 19	*IbMas*	Sweetpotato	Salt tolerance	Liu *et al.* 2014c
Shangshu 19	*IbSIMT1*	Sweetpotato	Salt tolerance	Liu *et al.* 2015
Xushu 22	*AtNHX1*	*Arabidopsis*	Salt and cold tolerance	Fan *et al.* 2015
ND98	*IbNHX2*	Sweetpotato	Salt and drought tolerance	Wang *et al.* 2016a
Lizixiang	*IbMIPS1*	Sweetpotato	Resistance to salt, drought, and stem nematodes	Zhai *et al.* 2016
Kokei 14	*αHT*	Barley	Black rot resistance	Muramoto *et al.* 2012
Xushu 18	*OCI*	Rice	Stem nematode resistance	Gao *et al.* 2011a
Lizixiang	*OCI*	Rice	Stem nematode resistance	Gao *et al.* 2011b
Jonathan	*OCI*	Rice	SPFMV resistance	Cipriani *et al.* 2001
Chikei 682-11	SPFMV-CP	SPFMV	SPFMV resistance	Okada *et al.* 2001
Blesbok	CP	Sweetpotato viruses	Virus resistance	Sivparsad and Gubba 2014
Tainung 57	*IbNAC1*	Sweetpotato	Herbivore resistance	Chen *et al.* 2016
Tainung 57	*IbpreproHypSys*	Sweetpotato	Insect resistance	Li *et al.* 2016
Kokei 14	*Bar*	*Streptomyces hygroscopicus*	Herbicide resistance	Otani *et al.* 2003
Yulmi	*Bar*	*S. hygroscopicus*	Herbicide resistance	Choi *et al.* 2007
Yulmi	*Bar*	*S. hygroscopicus*	Herbicide resistance	Yi *et al.* 2007
Lizixiang	*Bar*	*S. hygroscopicus*	Herbicide resistance	Zang *et al.* 2009
Kokei 14	*GBSSI*	Sweetpotato	Starch composition	Kimura *et al.* 2001
Kokei 14	*GBSSI*	Sweetpotato	Starch composition	Otani *et al.* 2007
Kokei 14	*IbSBEII*	Sweetpotato	Amylose content	Shimada *et al.* 2006
Kokei 14	*SRF*1	Sweetpotato	Dry matter content	Tanaka *et al.* 2009
Xu 55-2	SBD2	Sweetpotato	Starch granule morphology	Zhang *et al.* 2013
Yulmi	*IbEXP1*	Sweetpotato	Storage root development	Noh *et al.* 2013
Lizixiang	*IbAATP*	Sweetpotato	Starch structure and composition	Wang *et al.* 2016c
Ayamurasaki	*Lc*	Maize	Lignification, yield and starch content	Wang *et al.* 2016b
Kokei 14	*NtFAD3*	Tobacco	Linolenic acid content	Wakita *et al.* 2001
Sinzami	*IbOr-Ins*	Sweetpotato	Carotenoid content	Park *et al.* 2015
Ayamurasaki	*IbDFR*	Sweetpotato	Anthocyanin content, antioxidant capacity	Wang *et al.* 2013a
Sinhwangmi	*IbMYB1*	Sweetpotato	Anthocyanin content, antioxidant activity	Park *et al.* 2015

engineering has been made. An *Agrobacterium tumefaciens*-mediated transformation system has been developed for a wide range of sweetpotato genotypes. Several genes associated with abiotic stresses tolerance, diseases and pests resistance, and starch, carotenoids and anthocyanins biosynthesis have been isolated and characterized from sweetpotato. Gene engineering has been used to improve abiotic and biotic stresses resistance and nutritional quality of this crop. This review summarizes major research advances made so far in improving the resistance to abiotic stresses, diseases, pests, and herbicides and nutritional quality of sweetpotato by gene engineering (**Table 1**). Future prospects of research in gene engineering of this crop are also suggested.

Transformation system

An efficient genetic transformation system is very important for the successful application of gene engineering to sweetpotato improvement. Lots of studies have been done to develop an efficient transformation system in sweetpotato. Particle bombardment and electroporation were attempted for this crop, only transient gene expression, transformed calli, or a few transgenic plants were obtained (Dhir *et al.* 1998, Lawton *et al.* 2000, Okada *et al.* 2001, Prakash and Varadarajan 1992). Using *A. rhizogenes*-mediated transformation, Otani *et al.* (1993) observed the formation of shoots from hairy roots induced on leaf explants of five sweetpotato cultivars among 14 tested. Leaves, petioles, stems, storage roots, and embryogenic calli of sweetpotato have been used for *A. tumefaciens*-mediated transformation and the stable transgenic plants have also been obtained, but most of studies gave only a low transformation efficiency (Cipriani *et al.* 1999, Gama *et al.* 1996, Liu 2011, Luo *et al.* 2006, Morán *et al.* 1998, Newell *et al.* 1995, Otani *et al.* 1998, 2001, 2003, Song *et al.* 2004).

A few transgenic plants were produced from embryogenic suspension cultures of sweetpotato cv. Lizixiang through the use of *A. tumefaciens* strains A208SE and LBA4404 (Jiang *et al.* 2004, Zhai and Liu 2003). Using *A. tumefaciens* strain EHA105 and embryogenic suspension cultures of cv. Lizixiang, Yu *et al.* (2007) succeeded in developing an efficient *A. tumefaciens*-mediated transformation system of sweetpotato. Cell aggregates from embryogenic suspension

cultures were co-cultivated with EHA105 harboring a binary vector pCAMBIA1301 with *gusA* and *hpt*II genes for three days. Addition of 30 mg/l acetosyringone to the co-cultivation medium resulted in the significant increase of transformation efficiency. Selection culture was conducted using 25 mg/l hygromycin. Approximately 500 transgenic plants were produced from cell aggregates of one gram fresh weight with this transformation system. Thus, the *A. tumefaciens* strain EHA105 and embryogenic suspension cultures are strongly recommended for sweetpotato transformation. The study of Zang *et al.* (2009) has showed that the *bar* gene can be used a selectable marker gene under 0.5 mg/l phosphinothricin (PPT), which can be combined with other agronomically important genes for the improvement of sweetpotato. This *A. tumefaciens*-mediated transformation system with embryogenic suspension cultures is suitable for a wide range of sweetpotato genotypes (Fan *et al.* 2012, 2015, Gao *et al.* 2011c, 2012, Liu 2011, Liu *et al.* 2014a, 2014c, Wang *et al.* 2016a).

Abiotic stresses tolerance

Abiotic stresses such as salinity and drought are major environmental factors affecting crop productivity and quality worldwide (Munns and Tester 2008, Zhai *et al.* 2016). The development of crops with elevated levels of salinity and drought tolerance is therefore highly desirable. Though sweetpotato can grow under many different climatic conditions, its yield is often reduced by salinity and drought stresses. Especially, sweetpotato as source of bio-energy will mainly be grown on marginal land in the future, and improving its salinity and drought tolerance is therefore important for maintaining the productivity.

Osmotic stress often results in higher accumulation of proline and superoxide dismutase (SOD) and lower level of malonaldehyde (MDA), which are related to the extent of osmotic stresses tolerance (Liu *et al.* 2014a). Abscisic acid (ABA) accumulates extensively in plants under adverse conditions, which enhances plant resistance to environmental stresses (Ikegami *et al.* 2009, Xie and Yang 2003). Enhancement of the reactive oxygen species (ROS) scavenging system is expected to confer tolerance to various types of stresses in plants (Kikuchi *et al.* 2015, Liu *et al.* 2014a).

LOW OSMOTIC STRESS 5 (LOS5), which encodes a molybdenum cofactor sulfurase (MCSU), catalyzes the generation of the sulfurylated form of molybdenum cofactor, a cofactor required by aldehyde oxidase functioning in the last step of ABA biosynthesis in plants. LOS5/ABA3 is a key regulator in the tolerance of *Arabidopsis* to freezing, salinity, or drought stress (Xiong *et al.* 2001). Sweetpotato (cv. Lizixiang) plants overexpressing the *AtLOS5* gene exhibited enhanced salt tolerance (Gao *et al.* 2011a). Their salt tolerance was evaluated with Hoagland solution containing 86 mM NaCl in a greenhouse, and the copy number of integrated *AtLOS5* gene ranging from 1 to 3 was confirmed by Southern blot analysis. In *Arabidopsis*, ion homeostasis is mediated mainly by the salt overly sensitive (SOS), consisting of *SOS*1, *SOS*2 and *SOS*3, signal pathway (Yang *et al.* 2009). Gao *et al.* (2012) transferred *SOS*1+*SOS*2+*SOS*3 to sweetpotato (cv. Xushu 18) and obtained salt-tolerant transgenic sweetpotato plants. In these studies, transgenic plants had significantly higher levels of proline, SOD, and ABA and significantly lower MDA content than those in untransformed control plants.

Late embryogenesis-abundant (LEA) proteins belong to a large group of plant proteins that are synthesized abundantly and stored during seed maturation. These proteins play a protective role under osmotic stress conditions (Ingram and Bartels 1996). Late embryogenesis abundant 14 (*LEA14*) cDNA was isolated from an EST library prepared from dehydration-treated fibrous roots of sweetpotato. Transgenic calli overexpressing *IbLEA14* showed enhanced tolerance to drought and salt stress, suggesting that *IbLEA14* might positively regulate the response to various stresses by enhancing lignification (Park *et al.* 2011).

Iron-sulfur cluster scaffold protein (*IbNFU1*), pyrroline-5-carboxylate reductase (*IbP5CR*), maspardin (*IbMas*), salt-induced methyltransferase (*IbSIMT1*), and vacuolar Na^+/H^+ antiporters (*IbNHX2*) genes were isolated from a salt-tolerant sweetpotato line ND98, respectively (Liu *et al.* 2014b, 2014c, 2015, Wang *et al.* 2013b, 2016a). These five genes were introduced into sweetpotato cultivars Lizixiang, Kokei 14, Shangshu 19, Shangshu 19, and ND98, respectively, and the overexpressing plants exhibited significantly higher salt tolerance compared with the wild-type (Liu *et al.* 2014a, 2014b, 2014c, 2015, Wang *et al.* 2016a). The *IbNHX2*-overexpressing sweetpotato plants also showed the improved drought tolerance (Wang *et al.* 2016a). Proline content and SOD and photosynthesis activities were significantly increased, whereas MDA content was significantly decreased in the transgenic plants. H_2O_2 was also found to be significantly less accumulated in the transgenic plants. Their overexpression up-regulated the genes involved in stress responses, photosynthesis and ROS scavenging system. These findings suggest that these genes enhances salt and drought tolerance of the transgenic sweetpotato plants by regulating osmotic balance, protecting membrane integrity and photosynthesis and activating ROS scavenging system. These genes, especially *IbP5CR*, have the potential to be used for improving salinity and drought tolerance of sweetpotato and other plants. In addition, the *AtNHX1* gene was introduced into sweetpotato (cv. Xushu 22) to confer salt and cold stress tolerance (Fan *et al.* 2015).

Myo-inositol-1-phosphate synthase (MIPS) is a key rate limiting enzyme in myo-inositol biosynthesis (Abreu and Aragáo 2007). The *MIPS* gene has been shown to improve the tolerance to abiotic stresses, including salt, dehydration and chilling in *Arabidopsis* (Joshi *et al.* 2013, Kaur *et al.* 2013), rice (Das-Chatterjee *et al.* 2006), tobacco (Tan *et al.* 2013), and *Brassica juncea* (Goswami *et al.* 2014). The *IbMIPS1* gene was isolated from sweetpotato cv. Nongda 603 (Zhai and Liu 2009) and its expression was induced by

NaCl, polyethylene glycol (PEG), and ABA (Zhai *et al.* 2016). Its overexpression up-regulated the various genes involved in inositol biosynthesis, phosphatidylinositol and ABA signalling pathways, stress responses, photosynthesis and ROS scavenging system under salt and drought stresses, which significantly enhanced salt and drought tolerance in transgenic sweetpotato under field conditions (Zhai *et al.* 2016).

Accumulation of glycine betaine (GB) in higher plants is known to enhance the tolerance of plants to various abiotic stresses such as drought, salinity and cold (Zhang *et al.* 2011). The gene encoding betaine aldehyde dehydrogenase (BADH) is involved in GB biosynthesis in plants, and its overexpression increases the accumulation of GB and subsequently enhances plant tolerance to abiotic stresses (Jia *et al.* 2002, Park *et al.* 2004, Quan *et al.* 2004, Yang *et al.* 2005, Zhang *et al.* 2011). A chloroplastic *BADH* gene from *Spinacia oleracea* (*SoBADH*) was introduced into sweetpotato (cv. Sushu 2) and the transgenic plants showed improved tolerance to various abiotic stresses, including salt, oxidative stress, and low temperature (Fan *et al.* 2012). The increased BADH activity and GB accumulation in the transgenic plants enhanced the protection against cell damage through the maintenance of cell membrane integrity, stronger photosynthetic activity, and activation of ROS scavenging (Fan *et al.* 2012).

Oxidative stress is one of the major factors causing injury to plants exposed to environmental stresses. Kwak *et al.* (1995) and Kim *et al.* (1999, 2003) cloned a strong oxidative stress inducible peroxidase gene (*SWPA2*) from cultured cells of sweetpotato and subsequently characterized its function in transgenic tobacco plants and transgenic sweetpotato cultured cells subjected to environmental stresses. Transgenic sweetpotato (cv. Yulmi) plants with the enhanced tolerance to methyl viologen-mediated oxidative stress, chilling, and drought were developed by expressing the genes of both CuZn superoxide dismutase (CuZnSOD) and ascorbate peroxidase (APX) under the control of an oxidative stress-inducible SWPA2 promoter (Li *et al.* 2006, Lim *et al.* 2007). Zinc finger proteins are associated with abiotic stress responses in plants. Transgenic sweetpotato (cv. Yulmi) plants expressing the soybean cold-inducible zinc finger protein (*SCOF-1*) gene under control of SWPA2 promoter showed enhanced tolerance to low-temperature stress (Kim *et al.* 2011).

Trehalose plays an important role in abiotic stress tolerance in plants and its biosynthesis is catalyzed by two key enzymes: trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP). Jiang *et al.* (2014) isolated a *TPS* gene, named *IbTPS*, from sweetpotato (cv. Lushu 3). The *IbTPS*-overexpressing tobacco (cv. Wisconsin 38) plants exhibited significantly higher salt tolerance compared with the wild type. Trehalose and proline content was found to be significantly more accumulated in transgenic tobacco plants and several stress-responsive genes were up-regulated. This study suggests that *IbTPS* may enhance salt tolerance of plants by increasing the amount of treahalose and proline, which regulates the expression of stress-responsive genes.

Yu *et al.* (2008) identified a novel drought tolerance gene, *HOMEODOMAIN GLABROUS 11* (*HDG11*), in *Arabidopsis*, which encodes a protein in the HD-START transcription factor family. *HDG11* plays important roles in tolerance to drought and salinity stress. Ruan *et al.* (2012) introduced the *HDG11* gene into sweetpotato (cv. Lizixiang) and found that the transgenic plants showed increased drought tolerance.

Carotenoids and anthocyanins are important antioxidants in plants and their accumulation often increases tolerance of plants to abiotic stresses. Down-regulation of the beta-carotene hydroxylase (CHY-beta) and lycopene ε-cyclase (LCY-ε) genes, *IbCHY-beta* and *IbLCY-ε*, enhanced salt tolerance of transgenic cultured cells or calli of sweetpotato due to the increased accumulation of carotenoids (Kim *et al.* 2012, 2013b). Transgenic calli with sweetpotato orange (*IbOr*) gene also exhibited increased antioxidant activity and tolerance to salt stress (Kim *et al.* 2013a). A sweetpotato geranylgeranyl pyrophosphate synthase (GGPS) gene, *IbGGPS*, enhanced osmotic stress tolerance in *Arabidopsis*, suggesting that this gene is involved in osmotic stress tolerance of sweetpotato (Chen *et al.* 2015). Down-regulation of dihydroflavonol-4-reductase (DFR) gene (*IbDFR*) in transgenic sweetpotato using an RNAi approach reduced antioxidant capacity due to the decreased anthocyanin accumulation compared to the wild type (Wang *et al.* 2013a). An orange-fleshed cultivar (Sinhwangmi) with high carotenoid levels was transformed with the *IbMYB1* gene and transgenic lines displayed much higher antioxidant activities (Park *et al.* 2015a).

Metallothioneins (MTs) are cysteine-rich, low molecular weight, metal-binding proteins that are widely distributed in living organisms. Plants produce metal-chelating proteins such as MTs to overcome the toxic effects of heavy metals. Kim *et al.* (2014) cloned three MT genes, *IbMT1*, *IbMT2*, and *IbMT3*, from sweetpotato leaves. The expression level of *IbMT1* and *IbMT3* was strongly elevated in response to Cd and Fe. Furthermore, *IbMT1* responded strongly to methyl viologen (MV; paraquat) and NaCl, whereas *IbMT3* was induced by low temperature and PEG. These results indicate that these genes might be involved in responses of sweetpotato to heavy metals, MV, and abiotic stresses.

Diseases and pests resistance

Numerous diseases and pests/insects have been reported on sweetpotato from different regions of the world and their species are rather different in different regions. Sweetpotato diseases generally fall into three types: bacterial, fungal, and virus. Major bacterial and fungal diseases include sclerotial blight (*Sclerotium rolfsii* Sacc.), black rot (*Ceratocystis fimbriata* Ell. & Halst.), scurf (*Monilochaetes infuscans* Ell. & Halst. ex Harter), foot rot (*Plenodomus destruens* Harter),

and stem and leaf scab (*Sphaceloma batatas* Saw). To date, more than 20 viruses have been found to infect sweetpotato, among which sweetpotato feathery mottle virus (SPFMV) and sweetpotato chlorotic stunt virus (SPCSV) are the most common sweetpotato viruses worldwide. The mixed infection of SPFMV and SPCSV significantly decreases sweetpotato yield, and even no yield in the field if seriously infected. Aphids, whiteflies, and leafhoppers can transmit many of the viruses known to infect sweetpotato. The major pests and insects that cause considerable damage to sweetpotato are root-knot nematodes (*Meloidogyne incognita* var. *acrita* Chitwood), stem nematodes (*Ditylenchus destructor* Thorne), and weevil (*Cylas formicarius* Fab.). Other insects such as wireworms, rootworms, and flea beetles also cause damage to this crop. Sweetpotato storage roots are also injured by a complex of Coleopterous soil insects, which can cause significant economic losses (Liu *et al.* 2014d). In sweetpotato, several studies have been focused on the improvement for diseases and pests resistance by gene engineering.

Black rot of sweetpotato caused by pathogenic fungus *Ceratocystis fimbriata* severely deteriorates both plant growth and post-harvest storage of this crop. Plant thionin peptide exhibited anti-fungal activity against *C. fimbriata*. A gene for barley α-hordothionin (*αHT*), which was placed downstream of a strong constitutive promoter of E12Ω or the promoter of a sweetpotato gene for β-amylase of storage roots, was introduced into sweetpotato (cv. Kokei 14). Leaves of *E12Ω:αHT* plants exhibited reduced yellowing upon infection by *C. fimbriata* and storage roots of both *E12Ω:αHT* and *β-Amy:αHT* plants showed reduced lesion areas around the site inoculated with *C. fimbriata* spores (Muramoto *et al.* 2012).

Oryzacystatin-I (OCI) protein is one member of proteinase inhibitors, which can inhibit the proteinase activity in insects' intestinal canal and prevent the assimilation of proteins (Murdock *et al.* 1988). It plays a role in inhibiting cysteine proteinase and may play an important role in biodefense in rice seed (Abe *et al.* 1987). A rice *OCI* gene was used to transform sweetpotato (cvs. Xushu 18 and Lizixiang, susceptible to stem nematodes) and the transgenic plants exhibited the enhanced resistance to stem nematodes compared to the untransformed control plants by the field evaluation and the inoculation test with stem nematodes, and stem nematode-resistant plants were selected from the transgenic plants (Gao *et al.* 2011b, 2011c).

The role of *MIPS* gene in resistance to biotic stresses has not been reported though it has been shown to improve tolerance to abiotic stresses in plants. Zhai *et al.* (2016) found that the expression of *IbMIPS1* was strongly induced by stem nematodes, and its overexpression up-regulated the resistance-responsive genes, including callose synthase (CAS), peroxidase (POD), hydroxyproline-rich glycoprotein (HRGP), lipid transfer protein (LTP), leucine-rich repeat protein (LRP), proteinase inhibitor (PI), cysteine PI (CPI), and anti-microbial protein (AMP) genes, and altered the resistance-associated components (callose, lignin, H_2O_2 etc.), which resulted in significant improvement of stem nematode resistance of the transgenic sweetpotato plants. This study indicates that the *IbMIPS1* gene has the potential to be used to improve the resistance to stem nematodes as well as the tolerance to abiotic stresses in sweetpotato and other plants.

Okada *et al.* (2001) transferred the SPFMV coat protein (CP) gene to sweetpotato (cv. Chikei 682-11) and the transgenic lines showed a high resistance not only to primary but also to secondary infection by SPFMV-S, indicating that the transgenic lines with the CP gene of SPFMV-S can be used for coat protein-mediated resistance to the virus. The *OCI* gene from rice was introduced to sweetpotato (cv. Jonathan, susceptible to SPFMV) and improved the resistance to SPFMV in the transgenic lines (Cipriani *et al.* 2001).

Sivparsad and Gubba (2014) developed transgenic sweetpotato (cv. Blesbok) plants with broad virus resistance. Coat protein gene segments of SPFMV, SPCSV, sweetpotato virus G (SPVG), and sweetpotato mild mottle virus (SPMMV) were used to induce gene silencing in transgenic sweetpotato. The transgenic plants were challenged by graft inoculation with SPFMV, SPCSV, SPVG, and SPMMV-infected *I. setosa* Ker and all of them displayed delayed and milder symptoms of chlorosis and mottling of lower leaves compared with the untransformed control plants, although virus presence was detected in them.

Sporamin is a storage protein with trypsin inhibitory activity in sweetpotato, which accounts for 85% of the soluble proteins of storage roots. Its expression in plants enhanced resistance to herbivore (*Spodoptera litura*) (Chen *et al.* 2006, 2014, Yeh *et al.* 1997). Chen *et al.* (2016) identified a 53-bp DNA region, sporamin wound-response *cis*-element (SWRE), in the sporamin promoter and determined its responsibility for the wounding response. The *IbNAC1* gene that was specifically bound to the 50-TACAATATC-30 sequence in SWRE was isolated from a cDNA library from wounded leaves of sweetpotato. The *IbNAC1*-overexpressing sweetpotato plants had greatly increased sporamin expression, increased trypsin inhibitory activity, and elevated resistance against herbivore. It is further demonstrated that IbNAC1 is a core transcription factor which reprograms the transcriptional response to wounding via the jasmonic acid (JA)-mediated pathway in sweetpotato.

Hydroxyproline-rich glycopeptides (HypSys) are small signaling peptides. HypSys peptides were isolated from sweetpotato and the mRNA sequence of *IbpreproHypSys* was identified (Chen *et al.* 2008). Li *et al.* (2016) created transgenic sweetpotatoes overexpressing and silencing (RNA interference) *IbpreproHypSys* and concluded that wounding induced the expression of *IbpreproHypSys*, whose protein product was processed into IbHypSys. IbHypSys stimulated *IbpreproHypSys* and ipomoelin (*IPO*) expression and enhanced lignin biosynthesis, which protected plants from insects.

Herbicides resistance

Herbicide application can efficiently reduce losses of crop yield and quality caused by weed infestation. The introduction of genes coding for herbicide-detoxifying enzymes is one important genetic engineering strategy adopted for the production of herbicide-tolerant plants. The *bar* gene encoding phosphinothricin acetyltransferase (PAT) was isolated from the bialaphos biosynthetic pathway of *Streptomyces hygroscopicus* (Murakami *et al.* 1986). This gene is widely used for producing herbicide-resistant plants in many crop species. Transgenic crop plants expressing herbicide tolerance have been commercialized due to economically superior weed control. Weed control in the sweetpotato field after planting of cuttings is critical for high productivity. The application of *bar* should enable the development of herbicide-resistant sweetpotato plants.

Otani *et al.* (2003) transferred the *bar* gene to sweetpotato cv. Kokei 14 and obtained transgenic plants. Leaves of freshly sprouting shoots from harvested storage roots of the transgenic plants exhibited bialaphos resistance. The *bar* gene was also used to transform sweetpotato cv. Yulmi and the obtained transgenic plants remained green and healthy after spraying with Basta (Choi *et al.* 2007, Yi *et al.* 2007). Shin *et al.* (2011) evaluated herbicide resistance of transgenic sweetpotato plants (cv.Yulmi) and found that they were 20- to 82-fold more resistant to glufosinate than the wild-type. The representative transgenic line 7171 also showed resistance to methionine sulfoximine, but was not resistant to oxyfluorfen and paraquat.

Zang *et al.* (2009) successfully developed transgenic plants exhibiting functional expression of the *bar* gene. The copy number of integrated *bar* gene ranged from one to three. The transgenic plants flourished after spraying with 1000 mg/l PPT of Basta (normal field dosage) directly to the leaves, and they still survived at 2000 mg/l PPT of Basta. This study also provides a simple and efficient transformation system for sweetpotato using the *bar* gene as a selectable marker gene.

Transgenic plants with an enhanced expression of multiple P450 isoforms have the potential to improve herbicide resistance or reduce herbicide residues (Inui *et al.* 2000). Anwar *et al.* (2011) obtained transgenic sweetpotato plants expressing mammalian cytochrome P450. An *in vivo* herbicide tolerance assay using chlortoluron was conducted to determine the resistance of transgenic plants to herbicides. After sprayed with 17.6 μmol of chlortoluron, transgenic plants exhibited the tolerance to chlortoluron, whereas the control plants were susceptible to chlortoluron.

Quality improvement

Sweetpotato is an important starch crop. The potential of this crop as a food and carbohydrate source is widely recognized (Jarret *et al.* 1992). Orange-fleshed sweetpotato cultivars are an excellent source of β-carotene (a vitamin A precursor) and vitamin C, as well as fiber, iron, potassium, and protein (Low *et al.* 2007, Woolfe 1992). Purple sweetpotatoes are rich in anthocyanins, which are a group of very efficient bioactive compounds (Park *et al.* 2015b). The quality improvement for sweetpotato has been focused on breeding different types of cultivars with high content and altered composition of starch, carotenoids, or anthocyanins for their various uses.

Granule-bound starch synthase I (GBSSI) is one of the key enzymes which catalyze the formation of amylose, a linear α(1,4)D-glucan polymer, from ADP-glucose. The full-length sense cDNA of sweetpotato *GBSSI* was introduced into the cultivar Kokei 14. It was found that one of the 26 transgenic plants showed the absence of amylose in the storage roots, suggesting that starch composition in sweetpotato storage roots can be altered by gene engineering (Kimura *et al.* 2001). Amylose-free transgenic sweetpotato plants were also produced by inhibiting sweetpotato *GBSSI* gene expression through RNA interference, suggesting that RNA interference is an effective method for inhibiting gene expression in the starch metabolic pathway of sweetpotato (Otani *et al.* 2007).

Santa-Maria *et al.* (2011) found that the transgenic sweetpotato plants expressing a hyperthermophilic α-amylase showed the ability to self-process starch. No significant enzyme activity could be detected below 40°C, but starch in the transgenic sweetpotato storage roots was readily hydrolyzed at 80°C.

The starch-branching enzyme (SBE), 1,4-α-D-glucan-6-α-[1,4-α-glucan]-transferase, is a key enzyme in starch biosynthesis. The *IbSBEI* gene was isolated from sweetpotato and was found to be strongly expressed in storage roots, indicating that *IbSBEI* may work in concert with the AGPase large subunit during the primary phase of starch granule formation (Hamada *et al.* 2006). Shimada *et al.* (2006) found that the amylose content of sweetpotato starch was increased by RNA interference of the *IbSBEII* gene.

A plastidic ATP/ADP transporter (AATP) is responsible for importing ATP from the cytosol into plastids. In dicotyledonous plants, increasing the ATP supply is a potential way to facilitate anabolic synthesis in heterotrophic plastids. A gene encoding the AATP protein, named *IbAATP*, was isolated from sweetpotato. Its overexpression in sweetpotato significantly increased the starch and amylose content, led to enlarged starch granules, and altered fine structure of amylopectin, which contained an increased proportion of chains with a degree of polymerization (DP) of 10–23 and a reduced number of chains with a DP of 5–9 and 24–40 (Wang *et al.* 2016c). Starch from the transgenic plants also exhibited different pasting properties. In addition, the transgenic sweetpotato (cv. Xu 55-2) plants modified with an engineered tandem repeat of a family 20 starch binding domain (SBD2) exhibited the altered granule morphology without altering the primary structure of the constituent starch molecules (Zhang *et al.* 2013).

Sucrose non-fermenting-1-related protein kinase-1

(SnRK1) plays an important role in plant carbohydrate metabolism and starch biosynthesis. A *SnRK1* gene, named *IbSnRK1*, was isolated from sweetpotato and its overexpression significantly increased the accumulation of sucrose, glucose, fructose, and starch in transgenic tobacco, suggesting that this gene may be applied for increasing soluble sugar and starch levels of sweetpotato (Jiang *et al.* 2013).

Dof proteins are a plant specific family of zinc finger transcriptional factors, containing a highly conserved DNA-binding motif called the Dof domain. Tanaka *et al.* (2009) isolated the sweetpotato *SRF1* gene and the *SRF1*-overexpressing sweetpotato plants showed significantly higher storage root dry matter content compared to the original cultivar Kokei 14. The starch content per fresh weight of the storage roots was also higher than that of the wild-type plants, while the glucose and fructose content drastically decreased. These results suggest that *SRF1* modulates the carbohydrate metabolism in the storage roots of sweetpotato and has the potential to be used in improving starch content of this crop.

Wang *et al.* (2016b) found that ectopic expression of the maize anthocyanin regulator Lc in sweetpotato increased lignification in adventitious roots and in developing storage roots, which was accompanied by significant yield reduction as well as repression of starch accumulation in the developing storage roots. Thus, it is thought that a cause-and-effect relationship between increased lignification and reduced storage root yield exists and lignification competes with starch accumulation for the distribution of photoassimilates in developing storage roots. In addition, Wakita *et al.* (2001) found the transgenic sweetpotato plants expressing a tobacco microsomal ω-3 fatty acid desaturase gene (*NtFAD3*) driven by the El2Ω promoter showed the increased linolenic acid content. Noh *et al.* (2013) found that an expansin gene (*IbEXP1*) played a negative role in the formation of sweetpotato storage roots by suppressing the proliferation of metaxylem and cambium cells to inhibit the initial thickening growth of storage roots. These findings are beneficial to improving the quality and yield of sweetpotato by gene engineering.

beta-Carotene hydroxylase (CHY-beta) is a key regulatory enzyme in the beta-beta-branch of carotenoid biosynthesis. Down-regulation of the *CHY-beta* gene increased beta-carotene and total carotenoids in transgenic cultured cells of sweetpotato (Kim *et al.* 2012). Lycopene ε-cyclase (LCY-ε) is involved in the first step of the α-branch synthesis pathway of carotenoids from lycopene. Down-regulation of *LCY-ε* increased carotenoid synthesis via the β-branch-specific pathway in the transgenic calli of sweetpotato (Kim *et al.* 2013b). Yu *et al.* (2013) cloned the *IbLCYe* gene from sweetpotato cv. Nongdafu 14 with high carotenoid content. Transgenic tobacco (cv. Wisconsin 38) expressing *IbLCYe* accumulated significantly more beta-carotene, showing that *IbLCYe* has an important function for the accumulation of carotenoids of sweetpotato. The formation of geranyl pyrophosphate and geranylgeranyl pyrophosphate (GGPP) is a key step in biosynthetic pathway of carotenoids and many other terpenes. This step is catalyzed by geranylgeranyl pyrophosphate synthase (GGPS) (Hirschberg 2001). A cDNA namely *IbGGPS* was cloned from the storage roots of sweetpotato and its overexpression in *Arabidopsis* increased the content of total carotenoids (Chen *et al.* 2015). The *IbOr* gene is involved in the accumulation of carotenoids. Sweetpotato plants overexpressing *IbOr*-Ins in an anthocyanin-rich purple-fleshed cultivar Sinzami exhibited increased carotenoid levels (up to 7-fold) in their storage roots (Park *et al.* 2015b).

Anthocyanidin synthase (ANS), a 2-oxoglutarate (2OG) iron-dependent oxygenase, catalyzes the penultimate step in the biosynthesis of anthocyanin, which is responsible for the formation of the colored anthocyanidins from the colorless leucoanthocyanidins (Welford *et al.* 2005). A full-length cDNA, designated *IbANS*, was isolated from purple-fleshed sweetpotato cv. Yamakawamurasaki, and its expression was highest in storage roots and most abundant during the formation of storage roots, suggesting that this gene is associated with anthocyanin biosynthesis in sweetpotato (Zhou *et al.* 2010). The *IbANS* gene was also cloned from purple-fleshed sweetpotato cv. Yuzi 263 (Liu *et al.* 2010). MADS-box proteins of known function are transcription factors, which play a range of fascinating biological roles. A MADS-box gene, *IbMADS10*, was cloned from sweetpotato (cv. Beniazuma) and was shown to be involved in the accumulation of anthocyanin (Lalusin *et al.* 2006). These genes have the potential to be used to increase the content of anthocyanin in sweetpotato.

MYB transcriptional factors have been identified in various plant species as regulators of flavonoid biosynthesis in flowers, seeds, and fruits. Mano *et al.* (2007) isolated the MYB genes *IbMYB1* and *IbMYB2* from purple-fleshed sweetpotato cv. Ayamurasaki and suggested that *IbMYB1* controls anthocyanin biosynthesis specifically in the flesh of sweetpotato storage roots. An orange-fleshed cultivar Sinhwangmi with high carotenoid levels was transformed with the *IbMYB1* gene and the transgenic lines displayed much higher level of anthocyanin (Park *et al.* 2015a).

Dihydroflavonol-4-reductase (DFR) is a key enzyme in the catalysis of the stereospecific reduction of dihydroflavonols to leucoanthocyanidins in anthocyanin biosynthesis. Down-regulation of *IbDFR* in transgenic sweetpotato using an RNAi approach dramatically reduced anthocyanin accumulation in young leaves, stems, and storage roots (Wang *et al.* 2013a).

Guo *et al.* (2015) isolated a full-length cDNA of chalcone isomerase (*IbCHI*) from sweetpotato cv. Yamakawamurasaki and think that *IbCHI* is a key enzyme in the anthocyanin biosynthetic pathway of sweetpotato, which is responsible for the activation of anthocyanin biosynthesis in the early stage of storage root development.

In addition, genetic linkage maps of sweetpotato have been developed based on randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism

(AFLP), sequence-related amplified polymorphism (SRAP), and simple sequence repeat (SSR) markers (Cervantes-Flores *et al.* 2008, Kriegner *et al.* 2003, Li *et al.* 2010b, Ukoskit and Thompson 1997, Zhao *et al.* 2013). Several major quantitative trait loci (QTLs) for storage root yield, starch content, and carotene content of sweetpotato have been also identified (Cervantes-Flores *et al.* 2011, Li *et al.* 2010a, 2014, Yu *et al.* 2014, Zhao *et al.* 2013). These studies represent an important step forward in cloning genes for the storage root yield and nutritional quality of sweetpotato and improving the yield and quality of this crop by gene engineering.

Conclusions and future prospects

A. tumefaciens-mediated transformation has been established using embryogenic suspension cultures of sweetpotato. Several important genes associated with abiotic and biotic stresses resistance and quality traits have been isolated and characterized from sweetpotato. Sweetpotato plants with the improved resistance to salt, drought, oxidative stress, low temperature, diseases, pests, and herbicides and increased content of starch, carotenoids, and anthocyanins have been produced by gene engineering, although engineering genetically modified (GM) sweetpotatoes have not been applied in the production of this crop to date. Gene engineering has shown its great potential for improving the resistance to abiotic and biotic stresses and the nutritional quality of sweetpotato.

Sweetpotato is a highly heterozygous, generally self-incompatible, outcrossing, and vegetatively propagated autohexaploid. Although there are many available genes from other plant species, exploring new genes from sweetpotato and its wild relatives is necessary for the sweetpotato breeding program and incorporating abiotic and biotic stresses resistance and high quality. Genomic approaches have been used for discovering the important genes involved in plant secondary metabolism pathways. The sweetpotato genome is still unavailable. A further goal for the near future should be to obtain the complete sequence of the sweetpotato genome. Transcriptome sequencing is an efficient way for discovering and characterizing novel enzymes and transcription factors from sweetpotato, which provides an important transcriptional data source for studying storage root formation, flower development, abiotic and biotic resistance, and starch, carotenoids, and anthocyanins biosynthesis and characterizing the important responsible genes of this crop (Firon *et al.* 2013, Li *et al.* 2015, Schafleitner *et al.* 2010, Tao *et al.* 2012, 2013, Wang *et al.* 2010, Xie *et al.* 2012). QTL analysis has become an efficient method to identify responsible genes by generating transformants of the corresponding DNA region. Fine mapping of major QTLs for storage root yield and nutritional quality is vitally important for their further isolation and utilization. Introduction of agronomically important genes to commercial sweetpotato cultivars will be conducted in a large scale for these genes to be utilized for the improvement of sweetpotato. Conventional breeding methods and molecular techniques should be used together to develop sweetpotato cultivars with the improved resistance to abiotic and biotic stresses and increased nutritional quality.

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