Journal of Root Crops, 2016, Vol. 42 No. 1, pp. 14-21
Indian Society for Root Crops
ISSN 0378-2409, ISSN 2454-9053 (online)

Differential Gene Expression Signatures of Small Auxin Up-Regulated RNA(SAUR) and Gretchen-Hagen 3 (GH3) Genes in Storage Root as Compared to Non-tuber Forming Fibrous Root of Sweet Potato (*Ipomoea batatas*)

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Received: 01 June 2016; Accepted: 28 June 2016

Abstract

The phytohormone auxin is involved in the cell division, proliferation and initial thickening of storage root of sweet potato. The present paper reports the expression of auxin responsive functionally distinct candidate genes such as Small Auxin Up-Regulated RNA (*SAUR*) and Gretchen-Hagen 3 (GH3) genes regulated by auxin in the storage root of sweet potato. The differential expression of these auxin regulated genes were analyzed in the storage root of sweet potato as compared to non-storage root using the Gene Expression Hybridization kit (Part Number 5190-0404; Agilent). During the initial storage root development of sweet potato *SAUR* genes viz., *OsSAUR9, OsSAUR28, OsSAUR29, OsSAUR57* were up-regulated whereas *OsSAUR17, OsSAUR30, OsSAUR31* were down-regulated. These genes are presumably involved in auxin synthesis and transport, regulation of cell elongation and cell expansion, root growth, vascular tissue and interaction with cytokinin. These *SAUR* genes may interact with CalCaM-binding protein that acts to transduce second messenger signals into a wide array of cellular signal transduction responses involving auxin and brassinosteroid. *OsGH3.1* a probable IAA amido synthase was moderately up-regulated and presumably involved in the regulation of auxin content, morphology and growth of storage root in sweet potato. Several *OsGH3.8*, *OsGH3.1*, *OsGH3.3 and OsGH3.11* which are probable IAA-amido synthetase were down-regulated. The down-regulation of *GH3.11* in the storage root relates to its interaction with jasmonic acid during storage root formation of sweet potato.

Key words: Sweet potato, storage root, gene expression

Introduction

Sweet potato [*Ipomoea batatas* (L.) Lam.] ranks among the top six most important food crops in the world (CIP 2010). It is widely grown for its succulent, starchy storage root and leaves with multiple uses viz., staple food, animal feed, industrial material or raw material for industrial purposes as a starch source in alcohol production (Ravi and Saravanan, 2012). More than 105 million tonnes of sweet potatoes are produced globally each year, 95% of which are grown in developing countries (CIP 2010). In India, 1088 x 10^3 tonnes of sweet potato has been produced in an area of 106 x 10^3ha. The major sweet potato growing states are Odisha (36%), West Bengal (22%) and Uttar Pradesh (21%) with a National average productivity of 10.3 t/ha (Indian Horticulture Data-base 2014). Sweet potato has one of the highest dry matter productivity rates among crops. Growth and / or the yield of the storage root have been shown to be affected by

environmental factors, including soil moisture and temperature, humidity, light, photoperiod, and carbon dioxide (Ravi and Saravanan, 2012; Ravi et al., 2014) and involve highly coordinated expression of many genes.

Sweet potato storage roots are capable of storing starch grains through localized lateral bulking in a specific sub-apical region of thick adventitious roots originating from the nodal region of underground portion of vine cuttings. The initial development of a storage root involves cessation of the longitudinal growth of the root and radial expansion for rapid thickening (growth / bulking). The secondary growth involves genesis of a circular primary vascular cambium as well as several anomalous circular cambia in the subapical region of thick roots. Interstitial cambial strips unassociated with vascular tissues also develop within the secondary parenchyma and contribute to storage roots growth. Active cell divisions in these cambia results in the formation of thin walled starch storing parenchyma cells, causing thickening of storage roots. Increase in cell number and cell size in sweet potato storage roots is under the control of endogenous growth regulators such as cytokinin and auxin [indole-3-acetic acid (IAA)] (Ravi and Saravanan, 2012).

Indol-3-acetic acid (IAA) is involved in maintaining the meristematic state of the cambial zone cells and peak IAA level occurs in cambial zone of stems (Nieminen et al., 2008). Application of IAA induced larger tuber formation in potato by counteracting effects of endogenous GA (Ravi et al., 2009). Auxin content was high in the stage before tuber initiation and decreased during tuber formation in potato. Auxin and cytokinin are known to control the secondary growth of radish and carrot (*Dacus carota* L.) roots. Increase in cell division and expansion and storage root growth are associated with high IAA levels as well as low IAA oxidase activities. Auxin content increases with advancing storage root growth while the storage roots contain greater amount of auxins than the fibrous roots in sweet potato (Ravi et al. 2009). The thick storage root had > 8 pmol auxin g^{-1} fresh root, whereas the fibrous root had > 4 pmol auxin g^{-1} fresh root (Noh et al., 2010). Studies by Nakatani and Komeichi (1992) and Noh et al., (2010) revealed that endogenous IAA gradually increased during the early stage of storage root growth in sweet potato. Auxin and GA have been proposed as possible spatial regulators of cambial activity. IAA appears to be involved in the initial thickening (secondary growth) of storage root (Nakatani and Komeichi, 1992; Ravi et al., 2009). At the level of the whole plant, auxin, regulates a variety of physiological processes including apical dominance, root and shoot architecture, tropic responses, root meristem zonation, lateral root formation, vascular differentiation, embryo cell patterning, shoot elongation, leaf expansion, inflorescence, fruit set and development, formation of the early apical basal embryo axis and the organized shoot and root lateral primordium initiation. At the cellular level, auxin typified by indole-3-acetic acid (IAA) regulates cell division, extension and differentiation. In roots, the auxin response genes maximum serves as a positional cue for cell fate determination and distal organization and cell patterning in the root meristem (Mockaitis and Estelle 2008; Chapman and Estelle, 2009; Pierre-Jerome et al., 2013; Su *et al*., 2014; Li et al., 2016).

At the molecular level, auxin regulates expression of a variety of auxin responsive genes, which include the auxin response factors (ARFs), the Aux/IAA, Gretchen Hagen 3 (GH3), and Small Auxin-Up RNA (SAUR) gene families and the components of the Aux/IAA protein degradation pathway (Leyser, 2002; Hagen and Guilfoyle, 2002; Dharmasiri and Estelle, 2004; Guilfoyle and Hagen, 2007; Mockaitis and Estelle, 2008; Chapman and Estelle, 2009; Rademacher et al., 2011; Kemal Kazan, 2013; Bargmann and Estelle, 2014; Korasick et al. 2014; Li et al., 2016). Most of the genes in these three families are primary / early response genes activated rapidly by auxin. In recent years, different microarrays have been constructed using available expressed sequence tag (EST) data and transcriptome profiling studies have been conducted and gene expression analyzed for identifying potential candidate genes involved in the formation (initiation) and development (growth) of storage root in sweet potato (Schafleitner et al., 2010; Wang et al., 2010; Tao et al., 2012; Firon et al., 2013; Ravi et al., 2014). We conducted microarray experiment using transcripts extracted from the storage root (tuber) forming root and non-storage root forming (fibrous) root in sweet potato and analyzed the differentially expressed gene signatures. This paper reports the differential gene expression signatures related to auxin response genes such as Small Auxin-Up RNA (SAUR) and Gretchen Hagen 3 (GH3) genes in the storage root (tuber forming root) and non-storage root (fibrous root) in sweet potato.

Materials and Methods

Sweet potato (*Ipomoea batatas*) plants of variety Sree Arun were grown in earthen pots of 7 kg soil holding capacity

and irrigated daily during December 2012. Nitrogen (0.6 g urea), phosphorous (0.3 g P_2O_5) and potassium (0.6 g K_2O) fertilizers were added one week after planting. Plants were grown under open sunlight conditions with ≈12 hours sun light per day under ≈1700 μ mol m^2 h^{-1} at 30ºC ± 2ºC during day time and 23ºC ± 1ºC during night time. Total RNA was extracted from the storage root and fibrous root (non-storage root) of sweet potato by the method described by Chomczynski and Sacchi (1987). Total intact high quality RNA were extracted from fibrous roots and 2.0 mm thick storage roots harvested from 30 days old sweet potato plants. The samples were labeled using Agilent Quick Amp Kit (Part number: 5190-0442). 500 ng of total RNA was reverse transcribed using oligodT primer tagged to T7 promoter sequence. cDNA thus obtained was converted to double stranded cDNA in the same reaction. Further the cDNA was converted to cRNA in the *in-vitro* transcription step using T7 RNA polymerase enzyme and Cy3 dye was added into the reaction mix. During cRNA synthesis Cy3 dye was incorporated into the newly synthesized strands. cRNA obtained was cleaned up using Qiagen RNeasy columns (Qiagen, Cat No: 74106). Concentration and amount of dye incorporated was determined using Nano Drop 2000, UV-Vis Spectrophotometer, Thermo Scientific, USA. The 60-mer oligomicroarray designed by Agilent using EST sequences available in NCBI (Agilent control grid IS-62976-8-V2-60K x 8-Gx-EQC-201000210; length of probe - 60 bp; probe orientation – sense; total number of features – 62976; total Agilent control features – 1319 with 5763 blank features filled by replicating the specific probes and 100 additional genes for technical quality check) was used for the study. 600 ng of labeled cRNA were hybridized on the array using the Gene Expression Hybridization kit (Part Number 5190-0404; Agilent) in Sure hybridization Chambers (Agilent) at 65º C for 16 hours. Hybridized slides were washed using Agilent Gene Expression wash buffers (Part No: 5188-5242). Slides were then scanned on a G2505C scanner (Agilent Technologies). The expression data were transformed into the log^2 ratio and features < 1.0 fold log values were filtered. The differentially expressed signatures data were deposited in NCBI site http://www.ncbi.nlm.nih.gov/geo/info/linking.html.

Results and Discussion

In the present study, in the case of storage root of sweet potato, out of 55794 ESTs tested, 489 ESTs related to auxin were differentially expressed (267 upregulated and 222 downregulated) compared to fibrous (non-storage) root. However, out of 267 upregulated ESTs 102 were weakly expressed and were filtered whereas 61 weakly expressed ESTs were filtered from 222 downregulated ESTs. In the remaining 165 distinctly upregulated ESTs, 14 were highly upregulated as indicated by high fold change values ranging between 3.05 and 4.21 whereas in the case of 161 distinctly downregulated ESTs, 9 were highly downregulated as indicated by fold change values ranging between – 3.12 and – 6.21.

We found ESTs having 100% homology with small auxin up-regulated genes (*OsSAUR*) in *A. thaliana* (*OsSAUR9, OsSAUR28, OsSAUR29, OsSAUR57*) were 1.19 – 1.48 fold up-regulated in the storage root as compared to fibrous root of sweet potato (Table 1). Many ESTs of *OsSAUR17, OsSAUR30, OsSAUR31* (with 84.0-100% homology with *A. thaliana*) were down-regulated at lower level (-1.07 - -1.1 fold) whereas *OsSAUR11* and *OsSAUR14* (with 100% homology) were moderately (-2.21 - -2.34 fold) down-regulated in the storage root as compared to fibrous root of sweet potato (Table 2).

Small auxin-up RNAs (*SAUR*s) are products of early auxin-responsive *SAUR* genes (Franco *et al*. 1990) and they act as negative regulators of auxin synthesis and transport in rice (Surya Kant et al., 2009; Ren and Gray, 2015). *SAUR* genes are transcriptionally induced by exogenous auxins within a few minutes after hormone application (Gil et al., 1994). The *SAUR* genes have been identiûed in different plants such as soybean (*Glycine max*) (McClure and Guilfoyle, 1987; McClure et al., 1989), tobacco (*Nicotiana tabacum*) (Roux et al. 1998), maize (*Zea mays*) (Knauss et al. 2003) and Solanaceae (Wu et al., 2012). Members of this class have also been isolated from mung bean, pea, Arabidopsis, tobacco and maize. Arabidopsis genome comprises 78 *SAUR* genes (Hagen and Guilfoyle, 2002). In rice, around 58 *SAUR* genes have been identified (Jain et al., 2006a). In the root, four genes were down-regulated (*SAUR 31*, *-36*, *-59*, and *-72*) and two were up-regulated (*SAUR 34* and *-45*) in response to auxin (Paponov et al., 2008).

The *SAUR* genes encode short-lived proteins (McClure and Guilfoyle 1989) and accumulate in the cells that are implicated in the regulation of cell elongation and cell expansion (Gee et al., 1991; Knauss et al., 2003; Jain and Khurana, 2009; Ren and Gray, 2015). *AtSAUR32* gene

Table 1. The up-regulated differential gene expression signature ESTs of *SAUR* genes in the storage root compared with fibrous root of sweet potato

Gene ID	Fold change	Function in *Arabidopsis thaliana* and homology (%)	Function in *Manihot esculenta* (cassava) and homology (%)	Function in *Solanum tuberosum* (potato) and homology (%)
JP 107732	1.38	*Os SAUR57* auxin responsive *SAUR* gene family membrane (100%)	Galactosyl transferase family (96.97%)	-
JP 119477	1.2	*Os SAUR 9* auxin responsive *SAUR* gene family membrane (100%)	GRAS family transcription factor (100%)	Basic-helix loop –helix (bHLH) DNA binding super family protein (95.45%)
JP 126226	1.19	*Os SAUR 29* (100%)	Hydroxy proline rich glycoprotein family protein (100%)	Tetratricopeptide repeat TPR like superfamily protein (100%)
JP 120379	1.48	*Os SAUR28* auxin responsive SAUR gene family member (100%)	Histone deacetylase 8 (92.68%)	Histone deacetylase 8 (82.73%)
JP 149489	1.39	*Os IAA 21* Auxin responsive Auxin / IAA gene family member (100%)	Tetratrico peptide repeat (TPR) like superfamily protein (100%)	-
JP 157128	1.7	*OsSAUR9* auxin responsive SAUR gene family membrane (1m00%)	-	Protein kinase superfamily protein (95.45%)

Table 2. The down-regulated differential gene expression signature ESTs of *SAUR* genes in the storage root compared with fibrous root of sweet potato

Gene ID	Fold change	Function in *Arabidopsis thaliana* and homology (%)	Function in *Manihot esculenta* (cassava) and homology (%)	Function in *Solanum tuberosum* (potato) and homology (%)
JP 107382	-1.07	*OsSAUR31* Auxin-responsive *SAUR* gene family member (100%)	Mitogen activated protein kinase (MAPK-15) (100%0	Homeodomain like super family protein (100%)
JP 147400	-1.09	*OsSAUR31* Auxin-responsive *SAUR* gene family member (85.06%)	IAA inducible 9 (85.00%)	Phytochrome associated protein 2 (79.94%)
JP 133637	-1.09	*OsSAUR17* Auxin-responsive *SAUR* gene family member (84.00%)	IAA inducible protein 19 (85.62%)	Phytochrome associated protein 2 (84.54%)
JP 132084	-1.12	*OsSAUR17* Auxin-responsive *SAUR* gene family member (100%)	mannose-1-phosphate guanylyltransferase (GDP)s;GDP-galactose:mannose-1-phosphate guanylyltransferases;GDP-galactose: glucose-1-phosphate guanylyltransferases; GDP-galactose:myoinositol-1-phosphate guanylyltransferases;glucose-1-phosphate guanylyltransferase (100%)	^{2}-amylase 5 (95.65%)
JP 154326	-1.11	*OsSAUR11* Auxin-responsive *SAUR* gene family member (100%)	-	Mitogen activated protein kinase kinase kinase 5 (95.45%)
JP140507	-2.21	*OsSAUR11* - Auxin-responsive *SAUR* gene family member, expressed (100%)	Major facilitator superfamily protein (95.83%)	Ergosterol biosynthesis ERG4/ ERG24 family (100%)
JP136568	-2.34	*OsSAUR14* - Auxin-responsive *SAUR* gene family member (100%)	ILI1 binding bHLH 1 (85.71%)	RNA helicase 1 (100%)

has been shown to be involved in apical hook development in Arabidopsis (Park et al., 2007). In rice, *OsAUR39* acts as a repressor of auxin synthesis and transport. In rice, *SAUR39* gene regulates polar auxin transport, shoot and root growth, shoot morphology, vascular tissue (Surya Kant et al., 2009) and was expressed at higher levels in older leaves. The *SAUR39* gene responds to salinity stress (Walia et al., 2005), cytokinin (Hirose et al., 2007), anoxia (Lasanthi-Kudahettige et al., 2007) and auxin (Surya Kant et al., 2009). Some of the short-lived *SAUR* nuclear proteins mediate auxin signaling by binding with Ca+-binding/calmodulin proteins in maize and Arabidopsis (Reddy et al., 2002; Knauss et al., 2003). A *SAUR* gene from *Zea mays* (ZmSAURi) encodes a CalCaM-binding protein suggesting that CalCaM might regulate the function of this early responsive gene at the post-translational level (Yang and Poovaiah, 2000). Two *Z. mays* *SAUR* proteins have been shown to bind with calmodulin (CaM) (protein that acts to transduce second messenger signals into a wide array of cellular signal transduction responses (auxin, brassinosteroid, light, and stress) and is represented by a multigene family in higher plants) *in vitro* (Yang and Poovaiah, 2000; Knauss et al., 2003).

Based on the functions of *SAUR* genes reported in other crops, we suggest that the upregulated *SAUR* genes viz., *OsSAUR9, OsSAUR28, OsSAUR29, OsSAUR57* and downregulated *SAUR* genes viz., *OsSAUR17, OsSAUR30, OsSAUR31* are presumably involved in auxin synthesis and transport, regulation of cell elongation and cell expansion, root growth, vascular tissue and interaction with cytokinin. Furthermore, these *SAUR* genes may interact with CalCaM-binding protein that acts to transduce second messenger signals into a wide array of cellular signal transduction responses involving auxin and brassinosteroid as reported in *Z. mays*.

In the present study, *OsGH3.1* was moderately up-regulated (2.18 fold) and had 86.4% and 80.46% homology with cassava and potato GH3 gene respectively whereas this EST had 81.25% - 100% homology with IAA amido synthase in *A. thaliana* (Table 3). Based on the functions of *GH3* genes reported in other crops, we suggest that *OsGH3.1* is presumably involved in the regulation of auxin content, morphology and growth of storage root in sweet potato.

In the present study, several *OsGH3.8 / OsGH3.1 / OsGH3.11* which are probable IAA-amido synthetase ESTs having 80.66% -100% homology with *A. thaliana* were moderately down-regulated (-2.04 - -2.99 fold) whereas *OsGH3.3,* probable IAA-amido synthetase (with 86.36% homology with *A. thaliana*) was down-regulated at lower level (-1.75 fold) (Table 3). The downregulated *OsGH3.1* and *OsGH3.8* are presuamably the isoforms of the same genes. The downregulation of *GH3.11* in the storage root relates to it's interaction with jasmonic acid during storage root formation of sweet potato.

Gretchen Hagen3 (GH3) gene family, first identified in *Glycine max* (soybean), are early auxin responsive linkers among the auxin, jasmonic acid (JA) and salicylic acid (SA) signal transduction pathways (Yuan et al., 2013). These genes maintain hormonal homeostasis by conjugating excess indole-3-acetic acid (IAA), salicylic acid (SA), and jasmonic acids (JAs) to amino acids during hormone and stress-related signaling pathways. The conversion of active IAA to an inactive form via conjugation of IAA with amino acids (such as Asp, Ala, and Phe), is catalyzed by IAA-amido synthetases encoded by IAA catabolism-related genes belonging to the GH3 family (Staswick *et al*. 2005).

The *GH3* proteins are conserved in monocots and dicots, and there are 13 members in rice (Staswick et al., 2005; Jain et al., 2006b). The *GH3* proteins in Arabidopsis were proposed to modulate multiple developmental processes including photomorphogenesis, light and auxin signaling (Tanaka et al., 2002; Takase et al., 2004), and auxin homeostasis (Staswick et al., 2005). The expression of *MdGH3*s is regulated by phytohormones which regulate the auxin pool, effectively modulating auxin responses (Yuan et al., 2013). *MdGH3*s might participate in the crosstalk between SA- and JA-dependent defense pathways (Yuan et al., 2013). *GH3.11* (*JAR1*) can conjucate jasmonic acid (JA) to amino acids. *GH3.11* mRNA increased approximately by one fold by JA treatment. *ARF8* was postulated to control the free IAA level in a negative feedback fashion by regulating *GH3* gene expression (Tian et al., 2004). *OsGH3.3* was expressed at relatively higher levels during seed development stages (Yuan et al., 2013). *OsGH3.1*, (and also *OsGH3.8*) showed relatively high expression in all stages of panicle and seed development, with some quantitative differences. In rice, *OsGH3.1* (and also *OsGH3.8*) regulated auxin content, plant growth, development and morphology (Yuan et al., 2013). In *Vitis vinifera* (grapevine), *GH3.1* encodes an IAA-amido

Table 3. The up and down regulated differential gene expression signature ESTs of GH3 genes in the storage root compared with fibrous root of sweet potato

Gene ID	Fold change	Function in *Arabidopsis thaliana* and homology (%)	Function in *Manihot esculenta* (cassava) and homology (%)	Function in *Solanum tuberosum* (potato) and homology (%)
JP 143148	2.18	*OsGH3.1* putative IAA amido synthetase (81.25%)	Auxin responsive *GH3* family protein (86.4%)	Auxin responsive *GH3* family protein (80.46%)
JP 140717	2.37	*OsGH3.1* putative IAA amido synthetase (81.25%)	’-galactosidase 3 (96.15%0	SPT2 chromatin protein (100%)
JP 118351	1.12	*OsGH3.1* putative, IAA amido synthetase (100%0	Glutamyl / glutaminyl t RNA synthetase class Ic (80.7%)	Glutamyl / glutaminyl t RNA synthetase class Ic (83.61%)
JP 147832	-1.02	*OsGH3.1* putative IAA amido synthetase (95.45%)	-	-
JP147832	-1.44	*OsGH3.1* - Probable indole-3-acetic acid-amido synthetase (95.45%)	-	-
JP124173	-1.75	*OsGH3.3* - Probable indole-3-acetic acid-amido synthetase (86.36%)	Auxin-responsive *GH3* family protein (79.74%)	SMAD/FHA domain-containing protein (100%)
JP134270	-2.04	*OsGH3.1* - Probable indole-3-acetic acid-amido synthetase (80.59%)	Auxin-responsive *GH3* family protein (83.33%)	Auxin-responsive *GH3* family protein (83.08%)
JP129036	-2.08	*OsGH3.1* - Probable indole-3-acetic acid-amido synthetase, expressed (80.66%)	Auxin-responsive *GH3* family protein (83.12%)	Auxin-responsive *GH3* family protein (84.18%)
JP118597	-2.36	*OsGH3.8* - Probable indole-3-acetic acid-amido synthetase (82.93%)	Auxin-responsive *GH3* family protein (80.44%)	Auxin-responsive *GH3* family protein (85.38%)
JP129469	-2.37	*OsGH3.11* - Probable indole-3-acetic acid-amido synthetase (100%)	-	RAD-like 6 (81.5%)
JP137672	-2.99	*OsGH3.8* - Probable indole-3-acetic acid-amido synthetase (88%)	Auxin-responsive *GH3* family protein (81.75%)	Auxin-responsive *GH3* family protein (82.69%)

*The down-regulated genes are indicated by fold changes with – sign.

synthetase involved in the maintenance of low IAA concentrations, which enables fruit ripening.

Conclusion

During the initial storage root development of sweet potato SAUR genes viz., *OsSAUR9, OsSAUR28, OsSAUR29, OsSAUR57* were upregulated whereas *OsSAUR17, OsSAUR30, OsSAUR31* were downregulated in the storage root of sweet potato. These genes are presumably involved in auxin synthesis and transport, regulation of cell elongation and cell expansion, root growth, vascular tissue and interaction with cytokinin. Furthermore, these SAUR genes may interact with CalCaM-binding protein that acts to transduce second messenger signals into a wide array of cellular signal transduction responses involving auxin and brassinosteroid as reported in *Z. mays*. *OsGH3.1* a probable IAA amido synthase was moderately up-regulated and presumably involved in the regulation of auxin content, morphology and growth of storage root in sweet potato. *OsGH3.8*, *OsGH3.1*, *OsGH3.3 and OsGH3.11* which are probable IAA-amido synthetase were down-regulated. The downregulated *OsGH3.1* and *OsGH3.8* are presuamably the isoforms of the same genes. The downregulation of *GH3.11* in the storage root relates to it’s interaction with jasmonic acid during storage root formation of sweet potato.

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