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Differential gene expression signatures of auxin response factors and auxin/ indole 3-acetic acid genes in storage root as compared to non-tuber forming fibrous root of sweet potato (*Ipomoea batatas*)

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ABSTRACT

The phytohormone auxin is involved in the cell division, proliferation and initial thickening of storage root of sweet potato. This article reports the differential expression of functionally distinct auxin responsive candidate genes such as Auxin Response Factors (ARF) and Auxin/Indole 3-Acetic Acid (Aux/IAA) in the storage root of sweet potato [*Ipomoea batatas* (L.) Lam]. The differential expression of ESTs 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 *ARF1*, *ARF2, ARF10, ARF9* and *ARF16* are proposed to be involved in regulating genes controlling cell division pattern while *ARF7*, *ARF8* promote cell elongation/expansion and links brassinosteroid, ethylene and auxin and JA interaction, whereas *ARF4* is involved in asymmetric pattern establishment. Several *Aux/IAA* genes, viz. *OsIAA2*, *OsIAA7*, *OsIAA10*, *OsIAA21*, *OsIAA30* were up-regulated whereas, *OsIAA4*, *OsIAA10*, *OsIAA17*, *OsIAA21*, *OsIAA30*, *OsIAA31* were down-regulated in the storage root as compared to fibrous root of sweet potato. The down-regulation of *IAA4* may be significant in determining the storage root length of sweet potato.

Key words: Gene expression, Sweet potato, Storage root

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 fresh root, whereas the fibrous root had > 4 pmol auxin/g 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 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

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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 expression signatures of ESTs related to auxin response factors (ARFs) and auxin/ indole 3-acetic acid (Aux/IAA) gene in the storage root (tuber forming root) and non-storage root (fibrous root) in sweet potato.

MATERIALS AND METHODS

Sweet potato plants of variety Sree Arun were grown in earthen pots of 7 kg soil holding capacity and irrigated daily during December 2013. 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 at 30°C ± 2°C during day time and 23°C ± 1°C 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 10 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. 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 65°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. 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.

ARF protein may function either as an activator or repressor of auxin responsive genes (Chandler 2016, Li *et al*. 2016). The ARF transcription factors (TF) families have been identified and characterized in Arabidopsis and in a number of crop species such as maize, rice, tomato, banana, papaya, citrus, grapes, cucumber, brassioca and Chinese cabbage (Wu *et al*. 2011, Xing *et al*. 2011, Mun *et al*. 2012, Wang *et al*. 2012; Li *et al*. 2016). The numbers of ARFs vary between 11 (in papaya) and 51 (in soybean genome) (Li *et al*. 2016).

In the present study, one EST of *ARF2* which had 100% homology with cassava was highly up-regulated (3.62 fold) in the storage root of sweet potato as compared to fibrous root of sweet potato. Two ESTs of *ARF10* was moderately (1.67-2.69 fold) up-regulated which had 84.9-86.87% homology with cassava and 84.29-84.55% homology with potato. One EST of *ARF17* with 100% homology with potato was moderately 2.44 fold up-regulated in the storage root as compared to fibrous root of sweet potato. Two ESTs of *ARF18* with 78.99-80.57% homology with *Arabidopsis thaliana* were 1.92-2.69 fold upregulated in the storage root as compared to fibrous root of sweet potato. Two ESTs of *ARF 4* had 79.45 – 80.48% homology with cassava and 84.04-84.29% homology with potato were 1.58-1.78 fold upregulated in the storage root as compared to fibrous root of sweet potato. Two ESTs of ARF 8 had 83.12-84.77% homology with cassava and 83.16% homology with potato were 1.3-1.80 fold upregulated in the storage root as compared to fibrous root of sweet potato. The EST of *ARF9* had 93.33% homology with cassava and 86.44% homology

with potato was 1.52 fold upregulated in the storage root as compared to fibrous root of sweet potato. The EST of *ARF16* had 83.76% homology with cassava and 84.19% homology with potato and was 1.92 fold upregulated in the storage root as compared to fibrous root of sweet potato (Table 1). ESTs of several auxin response factors (*ARF*s), three of *ARF 7* (with 88.57% - 95.24% homology with *A. thaliana*), three of *ARF 9* (with 80.14% homology with *A. thaliana* and 80.81-100% homology with potato) and three of *ARF 11* (81.03-88.89% homology with cassava and 100% homology with potato) were highly down-regulated in the storage root as compared to fibrous root of sweet potato (Table 2). Several ESTs of *ARF*s, viz. four of *ARF1*, two of *ARF4*, three of *ARF8,* three of *ARF18*, two of *ARF16,* one of *ARF10* were down-regulated at lower level (-1.05 - -1.95 fold) in the storage root as compared to fibrous root of sweet potato (data not given).

*ARF*s -1, -2, -7 and -8 have been postulated to act redundantly in auxin-mediated gene regulation implicated in differential cell growth in the hypocotyls and in the roots (Hardtke *et al*. 2004, Li *et al*. 2004, Okushima *et al*. 2005a) in the auxin-dependent manner. *ARF1*, *ARF2* and *ARF7* have been postulated to interact in some way to read auxin gradients (Ellis *et al*. (2005). In rice, *OsARF1* gene had been implicated in vegetative and reproductive development (Xing *et al.* 2011). *ARF1* which is also a transcriptional repressor, acts in a partially redundant manner with *ARF2*. *ARF1* and *ARF2* integrate ethylene and light signals and promote transitions between developmental phases in apical hook opening, seed, stem and cotyledon, and hypocotyl development (Li *et al*. 2004, Okushima *et al*. 2005b, Schruff *et al*. 2006). ARF2 was reported to be a target of ethylene signaling in etiolated seedlings (Li *et al*. 2004). ARF2 has also been proposed to control growth and cell division in stems (Schruff *et al*. 2005, Okushima *et al*. 2005b). In *A. thaliana*, ARF2 is the most analogous to ARF1 (Remington *et al*. 2004) and interact with each other (Ulmasov *et al*. 1997a, Boer *et al*. 2014). Both have some functions in common but they also have distinct activities (Ellis *et al*. 2005). *ARF2* has been proposed as a general repressor of cell division in many aerial organs of the plant. *ARF2* repressed cell division and organ growth in *A. thaliana* Schruff *et al*. (2006). Loss of *ARF2* function in *Arabidopsis* increased growth of aerial organs and seed size due to extra cell division (Ellis *et al*. 2005, Okushima *et al*. 2005b, Schruff *et al*. 2006) and inhibits expression of three members of the gene family involved in ethylene biosynthesis (Okushima et al. 2005b). In addition, it has been proposed that *ARF2* regulates differential cell elongation / cell expansion (Li *et al*. 2004, Shruff *et al*. 2006) and links brassinosteroid (BR) and auxin biosynthetic pathways (Vert *et al*. 2008). *ARF1*, *ARF2* function as repressors (Ulmasov *et al*. 1999a, Tiwari *et al*. 2003, Lim *et al*. 2010), whereas *ARF7*, *ARF8* function as activators of auxin-induced genes (Tiwari *et al*. 2003, Wang *et al*. 2005, Chapman and Estelle 2009). Different combinations of ARF heterodimers have been postulated to perform various selective functions in regulating targeted gene expression (Hardtke *et al*. 2004). The heterodimer of ARFs, namely, ARF1/ARF2, act redundantly in a distinct developmental manner in *A. thaliana* ((Hardtke *et al*. 2004, Okushima *et al*. 2005b).

In tomato (*Solanum lycopersicum* L.), *ARF7* (*SlARF7*) acts as a modulator of both auxin and gibberellin responses during fruit set and development and is proposed to be a part of the cross-talk between these two hormones (de Jong *et al*. 2009, 2011). The silencing of *SlARF7* in transgenic tomato plants resulted in seedless (parthenocarpic) fruits. In these plants, the levels of GAs were strongly reduced and the phase of auxin- regulated cell division was bypassed and fruit growth mainly depended on cell expansion. It was

Table 1 The up-regulated differential gene expression signature ESTs of auxin response factors (ARFs) 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 (%)
JP151712	3.62	Integral to membrane, GDU1 (95.65%)	ARF2 (100%)	sequence-specific DNA binding transcription factor activity/protein dimerization activity/AGAMOUS-like 96 (100%)
JP125549	2.69	ARF 18 (78.99%)	ARF10 (84.9%)	ARF 10 (84.55%)
JP154210	2.44	Protein binding/ kinase activity/ signal transduction/ defense response (100%)	F-box family protein (100%)	ARF17 (100%)
JP 122150	1.92	ARF 18 (80.57%)	ARF16 (83.76%)	ARF 16 (84.19%)
JP 110042	1.80	ARF (81.77%)	ARF8 (83.12%)	ARF 8 (83.16%0
JP 120353	1.78	ARF (92.86%)	ARF4 (80.48%)	ARF 4 (84.29%)
JP 125852	1.67	ARF 18 (96.0%)	ARF10 (86.87%)	ARF 10 (84.29%)
JP 109740	1.58	ARF (97.5%)	ARF4 (79.45%)	ARF 4 (84.04%)
JP 107848	1.52	ARF (84.68%)	ARF9 (93.33%)	ARF 9 (86.44%)
JP 119306	1.30	ARF (81.94%)	ARF8 (84.77%)	Ring H2 finger C1A (83.22%)

Table 2 The down-regulated differential gene expression signature ESTs of auxin response factors (ARFs) 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 137606	-1.05	ARF 18 (100%)	mRNA slicing factor thioredoxin like U5 SnRP (100%)	Major facilitator super family protein (100%)
JP104930	-1.19	ARF9 (80.14%)	ARF 1 (79.85%)	ARF 1 (83.63%)
JP142344	-1.28	Lignan biosynthetic process (100%)	Protein binding F-box and associated interaction domains-containing protein (100%)	ARF 4 (93.55%)
JP127309	-1.44	Potassium ion transmembrane transporter activity (100%)	Protein binding/protein kinase activity/ATP binding protein phosphorylation / transmembrane kinase 1(100%)	ARF 11 (100%)
JP106108	-1.46	ARF 7 (89.36%)	ARF11 (81.03%)	ARF18(83.45%)
JP112929	-1.48	transcription factor activity / response to auxin stimulus/abaxial cell fate specification/auxin metabolic process (100%)	ARF 4 (100%)	Regulation of transcription activity/ transcriptional factor B3 family protein/ auxin-responsive factor AUX/IAA-related (100%)
JP148346	-1.57	Transcription factor activity / response to ethylene stimulus (96%)	DNA binding, regulation of transcription activity Nucleotidyltransferase family protein (100%)	ARF8 (96%)
JP150699	-1.90	Molecular function membrane (100%)	ARF8 (95.65%)	tRNAse Z4 (100%)
JP124654	-2.50	Zinc ion binding vacuolar protein sorting-associated protein 18 (95.83%)	Zinc ion binding OBF-binding protein 3, regulation of transcription activity (100%)	DNA binding, regulation of transcription activity ARF9 (100%)
JP111129	-3.12	ARF 7 (88.57%0	ARF 11 (88.89%)	ARF9 (80.81%)
JP139428	-3.56	ARF 7 (95.24%)	Zinc ion binding FAR1-related sequence 3(100%)	ARF18 (95.45%)

Table 3 The up-regulated differential gene expression signature ESTs of Auxin responsive Auxin / IAA gene family members 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 123223	1.27	Os IAA10 (95.45%)	Pectin acetylesterase family protein (95.24%)	Ca dependent lipid binding GLB domain family protein (100%)
JP 116371	1.29	Os IAA21 (90.91%)	Phytochrome associated protein 2 (92.68%)	Phytochrome associated protein 2 (94.2%)
JP 114169	1.84	Os IAA 30 (90.77%)	IAA inducible (85.31%)	Phytochrome associated protein 2 (83.56%)
JP 132452	1.75	Os IAA2 (100%)	Co-chaperon GrpE family protein (100%)	AT hook motif nuclear localized protein 1 (95.65%)
JP 114393	1.72	Os IAA 30 (80.3%)	IAA inducible 14 (85.84%)	IAA inducible 14 (85.89%)
JP 157128	1.70	Os SAUR9 (100%)	-	Protein kinase superfamily protein (95.45%)
JP158588	1.61	Os IAA 21 (90.91%)	Phytochrome dissociated protein 2 (89.13%)	Homeoodomain like superfamily protein (100%0
JP 149489	1.39	Os IAA 21 (100%0	Tetratrico peptide repeat (TPR) like superfamily protein (100%)	
JP 107538	1.16	Os IAA 7 (85.92%)	Phytochrome associated protein 1 (87.76%)	Phytochrome associated protein 1 (79.52%)
JP 130279	1.06	Os IAA 30 (89.36%)	IAA 7 (93.62%)	IAA protein 16 (94.12%)

postulated that the reduction of *SlARF7* transcript levels in transgenic plants may release the repression of the auxin and GA signalling pathways that are imposed by *SlARF7* resulting in the partial activation of these pathways and thus in parthenocarpic fruit growth. In cucumber *CsARF2*, and *CsARF7* were mainly expressed in the vegetative organs (root, stem and leaf) implicating that these genes are involved in vegetative growth of cucumber (Wu *et al*. 2014). *ARF7* operates in differential growth responses of hypocotyls such as phototropism, gravitropism and apical hook maintenance (Wang *et al*. 2005). *ARF7* also play a critical role in ethylene responses in *A. thaliana* roots, indicating that these ARFs may serve as a cross talk point between auxin and GA.

In *Arabidopsis*, *ARF7* gene has been implicated in the formation of the apicobasal axis of the embryo, the organized outgrowth of lateral organs, cell patterning in the root meristem and vascular differentiation (Hardtke *et al*. 2004). *ARF7* relay auxin signals that are required for proper patterning at early stages of organ development. *ARF7* has a regulatory function in lateral root initiation. *ARF7*/*ARF19* pair have been postulated to act redundantly in controlling leaf expansion and lateral root growth (Okushima *et al*. 2005a, Wilmoth *et al*. 2005). *ARF7* acts as transcriptional activator of 47% of auxin-regulated genes (Okushima *et al*. 2005a) and play a positive role in regulation of lateral root development via the auxin-mediated transcription of genes involved in boundary establishment or communication links between the meristems and initiating lateral organs in an auxin-dependent local activation of pericycle cells at the xylem poles ((Shuai *et al*. 2002, Hu *et al*. 2003, Casimiro *et al*. 2003, Okushima *et al*. 2007, Wilmoth *et al*. 2005, Van Ha *et al*. 2013). The auxin response factor 6 (*ARF6*) has been reported to be involved in tuberization in potato (Faivre-Rampant *et al*. 2004). The expression of *ARF6* decreased by 10-fold upon transition from a longitudinal (transverse cell division) to a lateral (longitudinal cell division) stolon expansion.

Different combinations of ARF heterodimers have been postulated to perform various selective functions in regulating targeted gene expression (Hardtke *et al*. 2004), whereas related pairs of ARFs, namely, *ARF1*/*ARF2*, *ARF6*/*ARF8* and *ARF7*/*ARF19* act redundantly in a distinct developmental manner in *A. thaliana* ((Hardtke *et al*. 2004,

Table 4 The down-regulated differential gene expression signature ESTs of Auxin responsive Auxin / IAA gene family members 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 (%)
JP119557	-1.33	OsIAA31 (86.81%)	AUX/IAA transcriptional regulator family protein (85.32%)	AUX/IAA transcriptional regulator family protein (84.88%)
JP114665	-1.33	OsIAA17 (88.46%)	AUX/IAA transcriptional regulator family protein (84.42%)	Auxin-induced protein 13 (86.54%)
JP156388	-1.37	OsIAA4 (91.43%)	IAA 29 (92%)	IAA inducible 29 (90.48%
JP114719	-1.64	OsIAA31 (88.54%)	AUX/IAA transcriptional regulator family protein (84.19%)	AUX/IAA transcriptional regulator family protein (82.3%)
JP152604	-1.69	OsIAA4 (100%)	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein (100%)	Ankyrin repeat family protein (100%)
JP157818	-1.69	OsIAA30 (100%)	P-loop containing nucleoside triphosphate hydrolases superfamily protein (100%)	WD-40 repeat family protein (100%
JP110754	-1.82	OsIAA21	Chromatin remodeling factor CHD3 (PICKLE) (82.72%)	IAA 13 (85.71%)
JP114665	-1.82	OsIAA17	AUX/IAA transcriptional regulator family protein (94.44%)	IAA induced protein 13 (91.51%)
JP114014	-2.30	OsIAA10- (82.88%)	Auxin induced protein 13 (83.77%)	Auxin induced protein 13 (89.47%)
JP143466	-2.48	OsIAA10 (100%)	ethylene-forming enzyme (100%)	Ribosomal protein L1p/L10e family (100%)
JP126691	-2.67	OsIAA30 (91.18%)	Protein of unknown function (DUF3411) (95.83%)	Eukaryotic translation initiation factor 2B (eIF-2B) family protein (100%)
JP121702	-2.82	OsIAA30 (85.19%)	IAA inducible 14 (84.46%)	indole-3-acetic acid inducible 14 (85.55%)
JP126691	-2.27	OsIAA30 (100%)	Protein of unknown function (DUF3411) (95.83%)	Eukaryotic translation initiation factor 2B (eIF-2B) family protein (100%)
JP156642	-6.21	OsIAA30		

Okushima *et al*. 2005a). *ARF7*/ NONPHOTOTROPIC (*NPH4*) interact strongly and selectively themselves and with other ARF pairs like *ARF5*/*MP* to form homo as well as heterodimers respectively and are implicated in both axis formation in the embryo and auxin-dependent cell expansion (Hardtke *et al*. 2004). *ARF7*/*NPH4* mediates auxin-dependent differential cell expansion mainly in the mature hypocotyl and involved in gravitropism (Harper *et al*. 2000). Furthermore, *ARF7*/*NPH4* positively regulate PLETHORA (PLT) genes, which encode AP2-type putative transcription factors and determine the root stem cell niche (Aida *et al*. 2004).

The Arabidopsis *ARF10*, *ARF16*, and *ARF17* share high amino acid sequence similarities and form a subgroup in the ARF family (Guilfoyle and Hagen 2001, Remington *et al*. 2004, Okushima *et al*. 2005a). Transcripts of all three genes were detected in roots, stems, leaves. The three closely related ARF genes are also post-transcriptionally regulated by miR160 (Mallory *et al*. 2005, Wang *et al*. 2005). The level of *ARF16* transcripts increased by approximately threefold after treating the *Arabidopsis* seedlings with 50 mM IAA for 5 h, whereas other phytohormones did not affect *ARF16* expression. *ARF16* expression has been reported in the basal region of embryos, root caps, vascular tissue of roots, and leaves. *ARF10* and *ARF16* function redundantly restricting cell division and promoting columella cell differentiation and generate a spatial pattern for root cap development and lateral root production in *Arabidopsis* (Wang *et al*. 2005, Quint and Gray 2006). The PLT1 and PLT2 factors which induce ectopic root meristem cells and provide positional information of the stem cell niche, and auxin directs their spatial expression via ARF5 and ARF7 (Aida *et al*. 2004).

ARF8 functions in the hypocotyl elongation and in auxin homeostasis (Tian *et al*. 2004, Okushima *et al*. 2005a). *ARF4* facilitate lateral organ asymmetry/asymmetric pattern establishment (Pekker *et al*. 2005). The *ARF4* protein is expressed in the abaxial domain of all lateral organ primordial and required for specification of abaxial cell types, although it's expression is found in the apical meristem and the adaxial domain of lateral organs as well (Pekker *et al*. 2005). *ARF8* have been proposed to regulate anther dehiscence by inducing JA production (or decreasing JA conjugation or breakdown), and jasmonic acid and auxin homeostasis (Tian *et al*. 2004, Punitha *et al*. 2005). *ARF8* is expressed constitutively in shoot and root apical regions and was proposed to integrate auxin and light signals to control plant development (Tian *et al*. 2004). *ARF10* and *ARF16* have been proposed to control the expression of *ABI3* during seed germination via interaction with ABA signaling pathway (Liu *et al*. 2013). Down regulation of *ARF7* and *ARF9* have been implicated in regulating cell division and cell expansion in developing tomato fruit and in other plant tissues with high cell division activity, such as the axillary meristems and root meristems (de Jong *et al*. 2015).

Based on the functions *ARF1*, *ARF2*, *ARF4*, *ARF7*, *ARF8, ARF10,* and *ARF16* reported in other crops, we suggest that *ARF1*, *ARF2, ARF 9, ARF10* and *ARF16* are involved in regulating genes controlling cell division pattern while *ARF7* and *ARF8* promote cell elongation/ expansion and links brassinosteroid, ethylene and auxin and JA interaction whereas *ARF4* is involved in asymmetric pattern establishment during storage root formation in sweet potato. Furthermore, it is suggested that the downregulated ARF genes, viz. *ARF8*, *ARF9*, *ARF10*, *ARF16* and *ARF18* are presumably the isoforms of the same genes upregulated in storage root of sweet potato.

We found ESTs having 80.30% to 100% homology with *OsIAA* in *A. thaliana* (*OsIAA2*, *OsIAA7*, *OsIAA10*, *OsIAA21*, *OsIAA30*) were found to be 1.27 – 1.72 fold up-regulated in the storage root of sweet potato whereas, *OsIAA4*, *OsIAA17*, *OsIAA21*, *OsIAA31* were down-regulated at lower level (-1.33 - -1.82 fold), whereas *OsIAA10*, *OsIAA30*, were moderately (-2.48 and -2.82 fold respectively) down-regulated in the storage root as compared to fibrous root of sweet potato (Table 3). One EST of *OsIAA30* having homology with *A. thaliana* was -6.21 fold down-regulated in the storage root as compared to fibrous root of sweet potato. In the published literature, no ARF was found to be pairing with these Aux/IAA factors and therefore, the significance of up and down regulated Aux/IAA genes in the storage root of sweet potato is not clear. Since *ARF1* has been reported to heterodimerize with *IAA17* (Ouellet *et al*. 2001), it is suggested that the down regulation of *IAA17* may regulate the *ARF1* function in the storage root of sweet potato. In transgenic rice plants, overexpression of *OsIAA4* significantly reduced root length but increased number of crown roots than wild type plants whereas shoots showed dwarfism, increased tiller angle, insensitivity to the inhibitory effect of auxin on root elongation and impaired gravity response (Song and Xu 2013). Therefore, the downregulation of *IAA4* may be significant in determining the storage root length of sweet potato. Furthermore, it is suggested that the downregulated Aux/IAA genes, viz. *OsIAA21*, *OsIAA10*, *OsIAA30* are presumably the isoforms of the same genes upregulated in storage root of sweet potato (Table 4).

The Aux/IAA genes are present as a multigene family in nearly all plants examined, including soybean, pea, mungbean, tobacco, tomato, *Arabidopsis*, *Populus*, wheat, maize and loblolly pine (Singla *et al*. 2006; Wang *et al*. 2010; Wu *et al*. 2012, Ludwig *et al*. 2013). There are 29 Aux/IAA family genes (CsIAA01-CsIAA29) identified and characterized in cucumber (Gan *et al*. 2013) and *Arabidopsis* (Reed 2001, Liscum and Reed, 2002, Dharmasiri and Estelle 2004) and 31 in the rice genome (Jain *et al*. 2006, Wang *et al*. 2007, Song *et al*. 2009). The Aux/IAA family genes have not been found in bacterial, animal or fungal genomes and are therefore probably unique to plants.

The auxin-inducible AUX/IAAs genes encode the short-lived transcription factors AUX/IAAs that act as repressors of the ARFs (Kim *et al*. 1997, Reed 2001, Tiwari *et al*. 2001, Gray *et al*. 2001, Teale *et al*. 2006). Auxin-responsive gene expression may be attenuated by Aux/IAA and ARF pairing and this interaction display

specifity (Weijers *et al*. 2005, Korasick *et al*. 2014). Under low auxin concentrations or below a threshold level, Aux/IAA proteins repress ARF transcription factors via direct interaction or dimerization/multimerization resulting in the repression of primary/early auxin response genes preventing gene transcription (Guilfoyle and Hagen 2001, Hardtke *et al*. 2004, Tiwari *et al*. 2004, Song *et al*. 2009, Poutrain *et al*. 2011, Van Ha *et al*. 2013, Korasik *et al*. 2014). When auxin concentrations are high, auxin bind to the F-box protein TIR1 or the related AFBs and accelerates the proteasome-mediated proteolysis of Aux/IAAs by promoting their interaction with the SCFTIR1/AFBs ubiquitin-ligase complex (Wu *et al*. 2014). This proteolysis relieves ARF transcription factor repression to form ARF/ARF homo- or heterodimers that then bind to the cis auxin response elements (AuxREs, TGTCTC) found in the promoter region of primary/early auxin-responsive genes through its DNA binding domain (DBD) and activate or derepress auxin-regulated downstream gene transcription (Wu *et al*. 2014).

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