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Original Paper

Comparative analysis of common genes involved in early fruit development in tomato and grape

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Abstract Fleshy fruits are important worldwide crops that are rich sources of useful and functional compounds in the human diet. Although fruit ripening has been extensively studied, early fruit development has not been paid much attention despite its contribution to the sensorial and nutritional quality of the fruit. This study aimed at identifying candidate genes involved in early fleshy fruit development that can contribute to the control of final fruit size and composition by comparative analysis of tomato and grape genes. By mining public sequences and microarray database, we identified 23 transcription factors belonging to 14 classes (AP2-EREBP, ARF, bHLH, bZIP, C2C2-GATA, FHA, GeBP, GRAS, HB, LIM, MYB, PBF-2-like, SBP and WRKY) as candidate regulatory genes for early fruit development. The function of these candidate genes will be confirmed by several reverse genetic approaches using the miniature tomato cv. Micro-Tom.

Key words: Tomato, grape, early fruit development, transcription factor.

Fleshy fruits are important worldwide crops that are rich sources of useful and functional compounds in the human diet. These compounds (e.g. sugars, flavonoids, and volatile compounds) are mainly produced and/or accumulated at the ripening stage of fruit development (Giovannoni 2004). Extensive studies on fruit ripening have been done especially using tomato (*Solanum lycopersicum*) and have identified several key regulatory genes for the fruit ripening processes (Bemer et al. 2012; Karlova et al. 2011; Manning et al. 2006; Vrebalov et al. 2002, 2009). In contrast, early stages of fruit development have not been paid much attention despite their large contribution to the visual, sensorial and nutritional quality of the fruit. After fruit set, successive cell division and cell expansion events mostly determine final fruit size (Gillaspy et al. 1993). At the same time, sugars, amino acid and organic acids accumulate during the cell expansion phase (Baxter et al. 2005; Carrari et al. 2006; Mounet et al. 2009). Although a few regulatory genes for fruit size and shape have been characterized (Cong et al. 2002; Frary et al. 2000; Xiao et al. 2008), molecular mechanisms underlying the regulation of fruit growth and metabolism during early fruit development are not fully addressed.

To identify candidate genes regulating early fruit development, we focused on grape (*Vitis vinifera*) which bears berry type fleshy fruits like tomato. In both tomato and grape, young fruits which have a green color present a rapid size increase by cell division and expansion. The transition phase to ripening is called "veraison" in grape, and breaker stage in tomato. After that, ripening stage consists in color changes, sugars accumulation and fruit softening, in both tomato and grape in spite of a main difference considering that tomato is climacteric and grape is non-climacteric. While grape has some unique characteristics such as the accumulation of tartaric acid instead of ascorbate (DeBolt et al. 2006) and the absence of endoreduplication-associated cell growth (Chevalier et al. 2011), tomato and grape have similar fruit developmental processes. In addition, comparative analysis of full-length cDNA sequences of Micro-Tom tomato cultivar with other plants indicated that tomato had higher similarity to grape than to other fleshy fruits like apple and orange (Aoki et al. 2010). Accordingly, a digital expression profiling revealed that some regulatory genes are up-regulated both in tomato and grape during fruit ripening (Fei et al. 2004).

In this study, we searched for candidate genes involved in early stages of fruit development that can contribute to final size and taste of fleshy fruit. After identification of tomato and grape common genes, transcriptome data mining highlighted several transcription factors having known and unknown biological role were found as the candidate genes.

Materials and methods

Identification of common genes between tomato and grape

To identify common genes between tomato and grape, unigene data sets of the Tomato SGN Unigene (SGN build Tomato200607 #1) and the NCBI Vitis vinifera UniGene (Build #9) were retrieved from SGN and NCBI ftp site, respectively. Using the TBLASTX program (Altschul et al. 1990) with a cutoff *e*-value at 1e-10, the unigene sequences of tomato were compared with those of grape and vice versa. Reciprocal best hit pairs were determined as common gene pairs.

Transcriptome data mining

Publicly available microarray data of fruit development series in tomato and grape were obtained from TFGD (http://ted.bti.cornell.edu/cgi-bin/TFGD/miame/experiment.cgi?ID=E025; data set E025; Osorio et al. 2011) and PLEXdb (http://www.plexdb.org/modules/PD_browse/experiment_browser.php?plex_name=GrapePLEX; data set VV5; Deluc et al. 2007), respectively. For TOM1 cDNA spotted array data set, the print-tip LOWESS normalized data were used for further expression analysis. For grape microarray data set VV5, only the data of Cabernet Sauvignon berries from well-watered plants were used. The Affymetrix raw CEL files were processed for background correction, quantile normalization and a median polish with the robust multiarray averaging (RMA) method using RMAexpress program (Bolstad et al. 2003). Differentially expressed genes during fruit development were determined by one-way ANOVA with a false discovery rate (FDR) correction ($p<0.05$; Benjamini and Hochberg, 1995). Pearson's correlation *k*-means clustering of the differentially expressed probes corresponding to the common genes were performed using TM4: MeV 4.3 software (http://www.tm4.org; Saeed et al. 2003).

Result and discussion

Comparison of unigene sequences between tomato and grape

To identify common genes between tomato and grape, we compared 34,829 unigene data sets of tomato to 23,166 of grape. The TBLASTX reciprocal best hit method determined 8,229 unigenes as common gene pairs. This number should however be treated with caution and also take into account the redundancy derived from a same gene and the underestimate for paralogous gene families. Nevertheless, functional classification of common genes into Mapman BIN structure of tomato (Urbanczyk-Wochniak et al. 2006) showed higher proportion of common genes in the vital functions like those coding for co-factor and vitamin metabolism, C1-metabolism, mitochondrial electron transport/ ATP synthesis, biodegradation of xenobiotics and tetrapyrrole biosynthesis (Supplemental Figure 1). In contrast lower proportion of common genes was found in stress, glycolysis, photosynthesis, cell wall and not assigned categories.

Comparative transcription analysis of common genes

To identify common genes expressed in early stage of fruit development in tomato and grape, data-mining of publicly available microarray data of tomato and grape was performed. Among the 8,229 unigenes common to both tomato and grape, 2,503 unigenes (represented by 2,757 spotted probes) were present on tomato TOM1 array and 4,977 unigenes (represented by 6,203 spotted probes) were present on grape Genechip array. ANOVA analysis with a FDR cutoff of 5% identified 1,713 probes in TOM1 and 3,922 probes in grape Genechip corresponding to genes differentially expressed throughout fruit development in tomato and grape, respectively. Among these, 885 probes representing genes included in both the tomato TOM1 and the grape Genechip were used for subsequent analysis.

Figure 1 shows transcription profiles along fruit development in tomato and grape resulting from *k*-means clustering for the 885 probes selected. The dot-lines on each panel represent the transition phase to ripening, breaker at 42 DPA in tomato and veraison (8 to 9 weeks after flowering) in grape. Based on this transition phase, 188 probes (21% of the total number of probes analysed) represent genes induced during early development in both tomato and grape (clusters C, L, P and S). Conversely, 146 probes represent genes induced during ripening in both fruits (clusters D, E and F). The other probes did not show the same transcription profile in tomato and grape. Indeed the probes grouped in clusters H, M and R represent genes induced during ripening in tomato but repressed during ripening in grape.

Mapman classification of the 182 genes (188 probes) expressed in early stages included e.g. 15 genes in the Photosynthesis category, 7 genes in Cell wall, 6 genes in Amino acid metabolism, 6 genes in Hormone metabolism, 5 genes in Stress, 20 genes in Protein synthesis, 8 genes in Protein degradation (see Supplemental Table S1 for exhaustive list). Comparison of apple and tomato gene expression data by Janssen et al. (2008) highlighted 41 genes expressed during early fruit development in both species. Only five of these genes were also found in the present study. They included 4 genes related to photosynthesis (SGN-U313179, SGN-U317999, SGN-U313194 and SGN-U312690) and one gene related to protein degradation (SGN-U313166). This may reflect actual variations in the control of early fruit development in the various fleshy fruit species, e.g. variations linked to fruit ontogeny (tomato and grape are berries while the fleshy tissues from apple arise from flower receptacle). However, possible

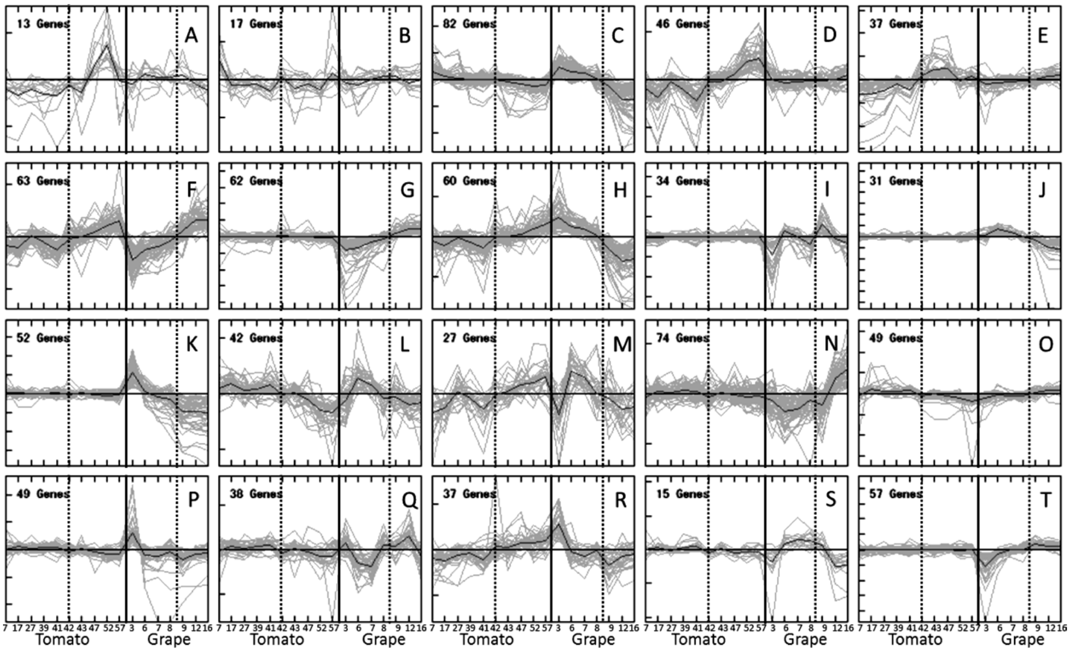

Figure 1. *k*-means clustering of tomato and grape common genes during fruit development. The dot-lines on each panel represent the breaker and veraison in tomato and grape, respectively. The scales on *x*-axis indicate the days post anthesis (DPA) and the weeks after flowering (WAF) in tomato and grape, respectively. The number indicated on the upper left corner indicates the number of probes in each cluster.

biases cannot be excluded, though the tomato TOM1 microarrays, cultivar and fruit stage of development were identical in the tomato/apple and tomato/grape experiments. Nevertheless, the 182 genes identified by current comparative transcript analysis of tomato and grape represent the major biological processes previously identified in early developing fruit (Gillaspy et al. 1993; Lemaire-Chamley et al. 2005; Mounet et al. 2009). Although several transcription factors (TFs) such as a Myb (SGN-U317694) and a bHLH (SGN-U320741) were included in the 182 early-expressed genes (Supplemental Table 1), no likely candidate regulatory gene controlling these biological processes was identified. The main reason was the lack of enough expression data, which resulted from the low number of probe sets corresponding to common genes that were spotted on the tomato TOM1 array (2,757 probes) compared to the grape Genechip array (6,203 probes).

Candidate transcription factors involved in early fruit development

To obtain further information on TFs expression during fruit development, we analyzed the data from Rohrmann et al. (2011) who accurately quantified the expression of approximately 1,000 tomato TFs using a high throughput quantitative real-time PCR platform and of Sweetman et al. (2012) who reported on the global transcriptome profiling of grape berry development by RNA-seq analysis. By mining the gene expression profiles obtained from the microarray analyses and from these references, we found 23 TFs which belong to 14 TF classes (AP2-EREBP, ARF, bHLH, bZIP, C2C2-GATA, FHA, GeBP, GRAS, HB, LIM, MYB, PBF-2-like, SBP and WRKY; Perez-Rodriguez et al. 2010), which were expressed during early stages of fruit development in both tomato and grape (Table 1). Some of them have already been functionally characterized in tomato or in *Arabidopsis*, thus validating this tomato/grape comparative data-mining approach for the identification of candidate gene for early fruit development. As an example, the auxin response factor *SlARF4* (SGN-U319581) has been shown to be involved in the control of chlorophyll accumulation in the young fruit, in pericarp cell division, in fruit firmness and cell wall composition (Guillon et al. 2008; Jones et al. 2002). Recently, the involvement of *SlARF4* in the control of sugar metabolism has also been reported (Sagar et al. 2013). Thus it is clear that *SlARF4* is one of the important regulatory genes involved in early fruit development in tomato.

Among the 23 candidate TFs identified here (Table 1), five belong to the bHLH TFs class (SGN-U319163, SGN-U319813, SGN-U319853, SGN-U327501 and SGN-U320741) were found. The homologous genes of SGN-U319163 and SGN-U320741 in *Arabidopsis* are involved in brassinosteroid and auxin signaling (Rampey et al. 2006; Yin et al. 2005). Although the detailed role of brassinosteroid in fruit development is still unclear, BIM1 homolog (SGN-U319163) might be involved in early fruit growth. Indeed, brassinosteroids are produced during early stages of fruit development in both tomato and grape (Montoya et al. 2005; Symons et al. 2006). In addition, recent studies have demonstrated that bHLH

Table 1. List of candidate transcription factors involved in early fruit development.

T F family	SGN-ID	iT AG-ID	Vv Unigene	Ref=seq ID	*E*-value[1]	Homologue in Arabidopsis	Gene name in Arabidopsis	Expression in tomato[2]	Expression in grape[3]
AP 2-EREBP	SGN-U313853	Solyc07g064890	Vvi.7125	XM_002275856	2E-30	AT1G50640	ATERF3	A	A
AP 2-EREBP	SGN-U319303	Solyc02g077370	Vvi.5349	XR_077949	4E-37	AT3G23240	ATERF1	A	A
ARF	SGN-U319581	Solyc11g069190	Vvi.20194	XM_002284983	4E-74	AT5G60450	ARF4	S	S
bHLH	SGN-U319163	Solyc03g114720	Vvi.505	XM_002273238	4E-38	AT5G08130	BIM1	S	A
bHLH	SGN-U319813	Solyc07g018010	Vvi.7115	XM_002263963	3E-62	AT5G57150		A, S	S
bHLH	SGN-U319853	Solyc09g083360	Vvi.15310	XM_002284195	2E-44	AT5G43650	BHLH92	S	S
bHLH	SGN-U327501	Solyc12g100140	Vvi.14484	XM_002282963	5E-71	AT1G51140	FBH3	S	A
bHLH	SGN-U320741	Solyc10g006510	Vvi.1904	XM_002282691	2E-79	AT5G54680	BHLH105, ILR3	A	A
bZIP	SGN-U318351	Solyc08g006110	Vvi.6616	XM_002283023	4E-41	AT5G24800	ATBZIP9	S	A
C2C2-GATA	SGN-U321735	Solyc05g056120	Vvi.24337	XM_002273466	1E-51	AT3G54810	BME3, GATA8	S	S
FHA	SGN-U318938	Solyc01g009080	Vvi.1391	XM_002273213	2E-45	AT2G21530		S	A
FHA	SGN-U337751	Solyc06g083350	Vvi.12002	XM_003634962	1E-65	AT3G07220		A	A
GeBP	SGN-U323492	Solyc02g068010	Vvi.2544	XM_002265084	5E-91	AT5G14280		A	A, S
GRAS	SGN-U328504	Solyc02g085340	Vvi.3301	XM_002267104	1E-114	AT5G66770		S	A, S
HB	SGN-U313977	Solyc04g074700	Vvi.14123	XM_002285707	3E-38	AT2G22430	ATHB6	S	S
HB	SGN-U315023	Solyc05g007180	Vvi.199	XM_002276853	2E-80	AT1G69780	ATHB13	S	A, S
HB	SGN-U316935	Solyc02g085630	Vvi.23029	XM_002272971	2E-53	AT4G36740	ATHB40	S	S
LIM	SGN-U320808	Solyc04g077780	Vvi.20672	XM_002285319	1E-107	AT1G10200	WLIM1	S	S
MYB	SGN-U317694	Solyc10g055410	Vvi.3225	XM_002278186	7E-97	AT4G38620	ATMYB4	A, S	A
PBF-2-like	SGN-U320703	Solyc05g007100	Vvi.2264	XM_002277242	1E-101	AT1G14410	ATWHY1	A	A
SBP	SGN-U323360	Solyc03g114850	Vvi.19942	XM_002265167	2E-67	AT1G69170		S	S
SBP	SGN-U342074	Solyc10g078700	Vvi.16055	XM_002278476	5E-62	AT2G42200	ATSP L9	S	S
WRKY	SGN-U315227	Solyc08g008280	Vvi.8889	XM_002280995	2E-39	AT4G23810	ATWRKY53	S	A, S

[1] *E*-value for the t blast x comparison between tomato and grape unigene sequences. [2] Reference data to identify genes expressed in early fruit development in tomato. A; array data set E025, S: Supplemental data from Rohrmann et al. (2011). [3] Reference data to identify genes expressed in early fruit development in grape. A; array data set VV5, S: Supplemental data from Sweetman et al. (2012).

TFs play important roles in the control of cell elongation in *Arabidopsis* (Bai et al. 2012; Ikeda et al. 2012; Zhang et al. 2009). Furthermore, cross-species TF network analysis revealed that the other bHLH TF SGN-U319813 (Solyc07g018010) which was highly expressed in fruit tissue was correlated with photosynthetic tissue specific TFs (Rohrmann et al. 2012), suggesting that SGN-U319813 would be involved in the regulation of photosynthesis in the fruit. Taken together, these results suggest that the 5 bHLH TFs identified here are likely important candidate genes for the regulation of biological processes taking place in early developing fruit.

This study attempted to identify genes involved in the regulation of early fruit development by focusing on genes displaying similar patterns of expression in tomato and grape. Despite the lack of exhaustive gene expression data on early fruit development available in tomato and grape at the time of that study, we found using this approach one already known ARF gene with important biological role in fruit development and several other candidate genes. The role of these candidate genes in early fruit development will be confirmed by reverse genetic approaches including stable transformation, Tilling or VIGS in the miniature tomato cv. Micro-Tom.

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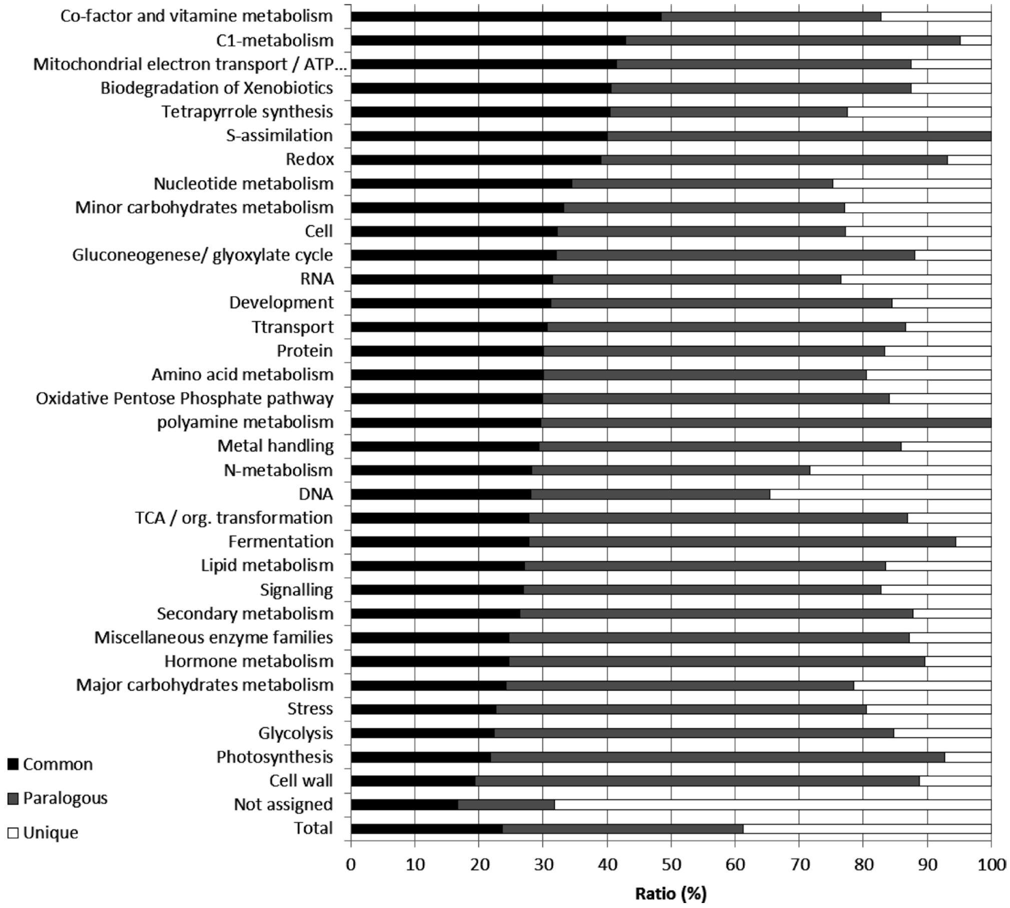

Figure S1 Ratio of common genes in Mapman BIN classifications.

Table S1 List of 182 common genes between Tomato and Grape expressed in early stages of fruit development.

SGN-U ID	TOM1 SGN-M ID	Vv-Unigene ID	Genechip ID	*E*-Value	BIN Code	Function	Cluster ID in Figure 1
SGN-U313205	1-1-5.4.11.1 1-1-1.2.7.11	Vvi.7811	1621351_s_at	1E-152	1.1.1.1	PS.lightreaction.photosystem II.LHC-II	C
SGN-U312449	1-1-4.3.14.15	Vvi.6644	1614593_at	1E-102	1.1.1.1	PS.lightreaction.photosystem II.LHC-II	C
SGN-U312871	1-1-2.2.9.3	Vvi.7580	1613428_at	7E-79	1.1.1.2	PS.lightreaction.photosystem II.PSII polypeptide subunits	C
SGN-U312572	1-1-7.2.4.14	Vvi.6846	1613494_s_at	1E-78	1.1.1.2	PS.lightreaction.photosystem II.PSII polypeptide subunits	C
SGN-U314260	1-1-7.4.10.14 1-1-8.2.1.15	Vvi.390	1611364_at	1E-93	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U312648	1-1-3.2.10.11	Vvi.6967	1618370_at	1E-81	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U312347	1-1-1.1.1.19	Vvi.7853	1611515_s_at	7E-59	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U313179	1-1-3.3.12.5	Vvi.2543	1622534_at	5E-55	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U313194	1-1-4.3.2.12 1-1-2.3.4.21	Vvi.6851	1621532_at	7E-48	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U313447	1-1-1.4.7.13	Vvi.78	1617771_at	1E-34	1.1.2.2	PS.lightreaction.photosystem I.PSI polypeptide subunits	C
SGN-U312858	1-1-5.1.9.2	Vvi.6860	1620919_at	2E-97	1.1.3	PS.lightreaction.cytochrome b6/f	L
SGN-U313693	1-1-1.4.17.15	Vvi.7057	1612645_at	2E-88	1.1.4	PS.lightreaction.ATP synthase	C
SGN-U317999	1-1-4.3.10.21	Vvi.7830	1606996_s_at	1E-40	1.1.40	PS.lightreaction.cyclic electron flow-chlororespiration	P
SGN-U312690	1-1-1.4.2.13 1-1-2.1.2.8	Vvi.7011	1620744_at	1E-53	1.1.5.1	PS.lightreaction.other electron carrier (ox/red).plastocyanin	C
SGN-U312461	1-1-1.1.1.12 1-1-1.2.12.13	Vvi.6670	1622715_s_at	1E-139	1.3.4	PS.calvin cyle.GAP	C
SGN-U312506	1-1-7.1.11.8	Vvi.10967	1612272_at	1E-101	2.1.1.3	major CHO metabolism.synthesis.sucrose.FBPase	C
SGN-U316178	1-1-1.2.2.9	Vvi.13654	1607272_at	1E-139	10.2	cell wall.cellulose synthesis	C
SGN-U315835	1-1-4.1.11.15	Vvi.9313	1607721_at	1E-175	10.1.10	cell wall.precursor synthesis.RHM	P
SGN-U314369	1-1-4.3.13.10	Vvi.7532	1607874_at	1E-117	10.1.5	cell wall.precursor synthesis.UXS	C
SGN-U319923	1-1-1.1.10.13	Vvi.2019	1607189_at	1E-164	10.2.1	cell wall.cellulose synthesis.cellulose synthase	P
SGN-U316912	1-1-6.2.13.5	Vvi.5254	1609520_at	8E-67	10.6.2	cell wall.degradation.mannan-xylose-arabinose-fucose	P
SGN-U318875	1-1-4.4.1.10	Vvi.10	1619468_at	0	10.8.1	cell wall.pectin*esterases.PME	S
SGN-U328806	1-1-3.4.18.12	Vvi.1413	1608799_at	1E-100	10.8.1	cell wall.pectin*esterases.PME	C
SGN-U316743	1-1-1.1.1.11	Vvi.1881	1607421_at	0	11.8.8	lipid metabolism. 'exotics' (steroids, squalene etc).squalene synthase	C
SGN-U313529	1-1-6.3.1.18	Vvi.6941	1607434_s_at	0	13.1.3.4.11	amino acid metabolism.synthesis.aspartate family.methionine.S-adenosylmethionine synthetase	P
SGN-U318552	1-1-3.3.6.5	Vvi.2090	1610780_at	1E-80	13.1.6.1.5	amino acid metabolism.synthesis.aromatic aa.chorismate.shikimate kinase	L
SGN-U318165	1-1-3.1.15.1	Vvi.7608	1607427_at	1E-150	13.1.6.5	amino acid metabolism.synthesis.aromatic aa.tryptophan	P
SGN-U317382	1-1-8.2.6.7	Vvi.3219	1622427_at	1E-161	13.1.6.5.5	amino acid metabolism.synthesis.aromatic aa.tryptophan.tryptophan synthase	P
SGN-U317571	1-1-4.2.8.4	Vvi.527	1622521_at	2E-77	13.1.7.6	amino acid metabolism.synthesis.histidine.histidinol-phosphate aminotransferase	P
SGN-U313818	1-1-2.3.9.18	Vvi.7572	1607663_at	6E-20	13.2.7	amino acid metabolism.degradation.histidine	C
SGN-U322128	1-1-6.3.5.1	Vvi.1230	1618177_at	1E-121	16.1.5	secondary metabolism.isoprenoids.terpenoids	C
SGN-U320341	1-1-6.2.12.12	Vvi.11662	1609568_at	1E-131	16.2.1.10	secondary metabolism.phenylpropanoids.lignin biosynthesis.CAD	P
SGN-U318705	1-1-4.3.18.21	Vvi.600	1622301_at	2E-79	17.2.3	hormone metabolism.auxin.induced-regulated-responsive-activated	P
SGN-U322082	1-1-1.3.6.8	Vvi.15060	1608284_at	5E-77	17.2.3	hormone metabolism.auxin.induced-regulated-responsive-activated	S

Table S1 Continued.

SGN-U ID	TOM1 SGN-M ID	Vv-Unigene ID	Genechip ID	*E*-Value	BIN Code	Function	Cluster ID in Figure 1
SGN-U320790	1-1-6.4.15.15	Vvi.1843	1620345_at	1E-122	17.3.1.2.4	hormone metabolism.brassinosteroid.synthesis-degradation.sterols.FACKEL	C
SGN-U319303	1-1-3.2.9.2	Vvi.5349	1619311_at	4E-37	17.5.2	hormone metabolism.ethylene.signal transduction	C
SGN-U313853	1-1-1.1.6.13	Vvi.7125	1621760_at	2E-30	17.5.2	hormone metabolism.ethylene.signal transduction	L
SGN-U315636	1-1-5.1.12.17	Vvi.2210	1608502_at	1E-113	17.7.1.5	hormone metabolism.jasmonate.synthesis-degradation.12-Oxo-PDA-reductase	C
SGN-U317367	1-1-8.4.17.8	Vvi.990	1609646_at	1E-119	18.5	Co-factor and vitamine metabolism.folate & vitamine K	P
SGN-U314404	1-1-1.3.13.6	Vvi.9104	1607878_at	1E-129	19.2	tetrapyrrole synthesis.glu-tRNA reductase	C
SGN-U317044	1-1-1.4.3.2	Vvi.7232	1618324_s_at	1E-26	20	stress	L
SGN-U318907	1-1-1.4.2.1	Vvi.17661	1617379_at	1E-145	20.2.3	stress.abiotic.drought/salt	P
SGN-U317374	1-1-8.1.11.17	Vvi.221	1608308_at	3E-64	20.2.3	stress.abiotic.drought/salt	P
SGN-U342119	1-1-1.4.2.1	Vvi.16842	1606501_s_at	3E-24	20.2.3	stress.abiotic.drought/salt	P
SGN-U313046	1-1-6.3.8.3	Vvi.458	1611765_at	4E-41	20.2.4	stress.abiotic.touch/wounding	L
SGN-U323179	1-1-4.2.8.9	Vvi.2593	1614001_s_at	1E-125	21.1	redox.thioredoxin	L
SGN-U314114	1-1-3.2.6.4	Vvi.13445	1608569_s_at	1E-110	21.1	redox.thioredoxin	S
SGN-U314625	1-1-1.3.13.5	Vvi.13128	1609648_at	1E-113	21.99	redox.misc	S
SGN-U314886	1-1-2.1.6.3	Vvi.2088	1619220_at	1E-139	22.1.6	polyamine metabolism.synthesis.spermidine synthase	P
SGN-U323335	1-1-4.1.1.11	Vvi.16316	1609458_at	1E-134	23.1.2.31	nucleotide metabolism.synthesis.purine.GMP synthetase	P
SGN-U320103	1-1-4.1.10.6	Vvi.1663	1609873_at	1E-145	24.2	Biodegradation of Xenobiotics.lactoylglutathione lyase	C
SGN-U312851	1-1-5.2.4.19	Vvi.8061	1615352_s_at	1E-134	25.1	C1-metabolism.glycine hydroxymethyltransferase	P
SGN-U316355	1-1-3.2.3.6	Vvi.8502	1607912_at	8E-95	25.8	C1-metabolism.tetrahydrofolate synthase	P
SGN-U313331	1-1-7.2.12.16	Vvi.15272	1607942_at	1E-120	26.12	misc.peroxidases	P
SGN-U317732	1-1-5.3.8.12	Vvi.7921	1609305_at	6E-53	26.13	misc.acid and other phosphatases	P
SGN-U313495	1-1-1.1.7.1	Vvi.759	1608514_at	1E-74	26.19	misc.plastocyanin-like	C
SGN-U312888	1-1-3.3.15.20	Vvi.2948	1610036_at	2E-44	26.24	misc.GCN5-related N-acetyltransferase	P
SGN-U313359	1-1-2.4.5.6	Vvi.15597	1614514_at	2E-95	26.4	misc.beta 1,3 glucan hydrolases	P
SGN-U324088	1-1-6.4.2.9	Vvi.15252	1609732_at	1E-70	26.7	misc.oxidases -copper, flavone etc.	P
SGN-U316861	1-1-2.3.14.4	Vvi.12312	1607958_at	1E-110	27.1	RNA.processing	L
SGN-U320479	1-1-4.3.1.18	Vvi.8951	1621679_at	2E-42	27.1	RNA.processing	C
SGN-U321303	1-1-2.3.6.4	Vvi.8983	1607530_at	2E-12	27.1.19	RNA.processing.ribonucleases	L
SGN-U320205	1-1-3.4.9.15	Vvi.384	1613234_at	1E-47	27.2	RNA.transcription	C
SGN-U318718	1-1-6.4.4.16	Vvi.8018	1621694_at	2E-45	27.3	RNA.regulation of transcription	S
SGN-U317204	1-1-2.3.1.21	Vvi.7791	1613430_a_at	1E-40	27.3	RNA.regulation of transcription	C
SGN-U317694	1-1-4.1.10.13 1-1-1.2.10.3	Vvi.3225	1620713_s_at	7E-97	27.3.25	RNA.regulation of transcription.MYB domain transcription factor family	C
SGN-U317708	1-1-3.1.15.2	Vvi.3873	1608316_at	1E-122	27.3.44	RNA.regulation of transcription.Chromatin Remodeling Factors	L
SGN-U337751	1-1-7.4.10.5	Vvi.12002	1616165_at	1E-65	27.3.48	RNA.regulation of transcription.FHA transcription factor	P
SGN-U323492	1-1-3.4.6.4	Vvi.2544	1621794_at	5E-91	27.3.49	RNA.regulation of transcription.GeBP like	C
SGN-U320741	1-1-5.4.6.6	Vvi.1904	1610421_at	2E-79	27.3.6	RNA.regulation of transcription.bHLH,Basic Helix-Loop-Helix family	C
SGN-U320703	1-1-3.3.11.6	Vvi.2264	1611369_at	1E-101	27.3.67	RNA.regulation of transcription.putative transcription regulator	C
SGN-U341901	1-1-5.3.16.18	Vvi.15682	1611621_at	5E-29	27.3.67	RNA.regulation of transcription.putative transcription regulator	L
SGN-U319781	1-1-3.1.8.9	Vvi.7164	1610822_at	3E-70	27.4	RNA.RNA binding	L
SGN-U324375	1-1-2.2.3.3	Vvi.3865	1616203_at	2E-34	27.4	RNA.RNA binding	L

Table S1 Continued.

SGN-U ID	TOM1 SGN-M ID	Vv-Unigene ID	Genechip ID	*E*-Value	BIN Code	Function	Cluster ID in Figure 1
SGN-U312333	1-1-3.1.7.5	Vvi.2501	1620684_at	2E-76	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	C
SGN-U315726	1-1-3.3.9.2	Vvi.1470	1612544_at	5E-74	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	C
SGN-U316164	1-1-1.2.12.8	Vvi.6913	1606900_at	1E-58	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	L
SGN-U315932	1-1-1.3.1.17	Vvi.5097	1615609_at	2E-58	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	C
SGN-U319691	1-1-7.2.10.14	Vvi.7829	1607422_s_at	6E-50	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	C
SGN-U318954	1-1-4.4.10.18	Vvi.9023	1613729_at	2E-14	29.2.1.1	protein.synthesis.mito/plastid ribosomal protein.plastid	C
SGN-U312442	1-1-3.1.8.4	Vvi.11629	1616883_at	1E-124	29.2.2	protein.synthesis.misc ribososomal protein	S
SGN-U316615	1-1-1.2.2.6	Vvi.5313	1613210_at	1E-115	29.2.2	protein.synthesis.misc ribososomal protein	P
SGN-U312555	1-1-5.2.9.8	Vvi.14925	1612458_at	1E-114	29.2.2	protein.synthesis.misc ribososomal protein	L
SGN-U312446	1-1-8.3.12.8	Vvi.4518	1610095_s_at	1E-104	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U313352	1-1-4.4.6.2	Vvi.16015	1608333_at	1E-104	29.2.2	protein.synthesis.misc ribososomal protein	L
SGN-U312563	1-1-7.3.9.7	Vvi.13111	1609733_at	4E-80	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U313518	1-1-1.1.9.5	Vvi.767	1610560_at	5E-75	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U312328	1-1-5.3.1.15	Vvi.6746	1607953_at	4E-68	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U314170	1-1-4.2.14.4	Vvi.8015	1611713_s_at	7E-66	29.2.2	protein.synthesis.misc ribososomal protein	L
SGN-U313606	1-1-5.4.11.2	Vvi.7262	1621022_at	5E-63	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U319196	1-1-1.2.2.12	Vvi.14910	1607915_at	5E-62	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U319407	1-1-2.4.18.9	Vvi.2426	1606942_at	4E-61	29.2.2	protein.synthesis.misc ribososomal protein	L
SGN-U312341	1-1-2.4.1.12	Vvi.3166	1618074_s_at	2E-55	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U315788	1-1-6.2.9.1	Vvi.6836	1616096_s_at	5E-51	29.2.2	protein.synthesis.misc ribososomal protein	C
SGN-U315448	1-1-5.4.10.18	Vvi.9124	1614237_a_at	6E-96	29.3	protein.targeting	S
SGN-U322007	1-1-4.4.18.9	Vvi.12652	1606564_at	3E-75	29.3.3	protein.targeting.chloroplast	L
SGN-U316623	1-1-1.4.15.7	Vvi.6708	1614009_at	0	29.4	protein.postranslational modification	S
SGN-U317032	1-1-8.3.10.5	Vvi.21085	1610674_at	0	29.4	protein.postranslational modification	P
SGN-U315426	1-1-5.4.12.13	Vvi.13700	1609974_at	1E-164	29.4	protein.postranslational modification	P
SGN-U316387	1-1-2.1.18.1	Vvi.9651	1608710_at	1E-133	29.4	protein.postranslational modification	L
SGN-U317839	1-1-6.4.6.4	Vvi.1590	1613085_at	1E-94	29.4	protein.postranslational modification	P
SGN-U314656	1-1-5.4.16.2	Vvi.1173	1609665_a_at	9E-84	29.4	protein.postranslational modification	P
SGN-U329503	1-1-2.1.2.13	Vvi.14471	1607240_at	5E-52	29.5.1	protein.degradation.subtilases	P
SGN-U315769	1-1-3.4.20.7	Vvi.8319	1607743_at	1E-125	29.5.11.20	protein.degradation.ubiquitin.proteasom	L
SGN-U315200	1-1-5.3.9.14	Vvi.3197	1621177_at	1E-113	29.5.11.20	protein.degradation.ubiquitin.proteasom	P
SGN-U318139	1-1-6.3.6.18	Vvi.761	1615115_at	1E-111	29.5.11.3	protein.degradation.ubiquitin.E2	C
SGN-U317273	1-1-2.1.12.6	Vvi.1494	1615999_at	1E-55	29.5.11.4.2	protein.degradation.ubiquitin.E3.RING	L
SGN-U313166	1-1-6.1.9.20	Vvi.14013	1618440_s_at	2E-49	29.5.11.4.2	protein.degradation.ubiquitin.E3.RING	C
SGN-U318569	1-1-1.3.4.14	Vvi.299	1609190_at	9E-47	29.5.11.4.2	protein.degradation.ubiquitin.E3.RING	L
SGN-U318322	1-1-3.3.18.20	Vvi.12451	1620875_at	1E-169	29.5.11.4.6	protein.degradation.ubiquitin.E3.DCX	P
SGN-U315722	1-1-2.4.12.21	Vvi.6106	1609502_at	9E-80	29.6	protein.folding	L
SGN-U326067	1-1-4.1.2.7	Vvi.4952	1614567_at	1E-105	30.2.2	signalling.receptor kinases.leucine rich repeat II	C
SGN-U322321	1-1-1.3.18.3	Vvi.2011	1608808_at	3E-69	30.2.22	signalling.receptor kinases.proline extensin like	L
SGN-U320527	1-1-7.4.2.8	Vvi.5959	1607921_at	1E-66	30.2.99	signalling.receptor kinases.misc	P
SGN-U315167	1-1-1.2.12.3	Vvi.10646	1614588_s_at	1E-130	30.3	signalling.calcium	L

Table S1 Continued.

SGN-U ID	TOM1 SGN-M ID	Vv-Unigene ID	Genechip ID	*E*-Value	BIN Code	Function	Cluster ID in Figure 1
SGN-U321819	1-1-7.3.19.21	Vvi.10144	1614933_at	1E-124	30.3	signalling.calcium	C
SGN-U317074	1-1-5.2.8.6	Vvi.1962	1613846_at	2E-47	30.3	signalling.calcium	P
SGN-U319627	1-1-3.3.15.15	Vvi.17480	1618348_at	1E-127	30.5	signalling.G-proteins	L
SGN-U312495	1-1-3.1.10.12	Vvi.1523	1619471_at	1E-107	30.5	signalling.G-proteins	P
SGN-U318915	1-1-3.4.15.15	Vvi.16449	1613393_at	1E-152	31.1	cell.organisation	P
SGN-U317855	1-1-1.3.13.1	Vvi.6835	1614602_at	1E-143	31.1	cell.organisation	C
SGN-U322456	1-1-6.2.10.6	Vvi.14119	1615815_at	8E-88	31.1	cell.organisation	C
SGN-U314431	1-1-4.2.8.12	Vvi.3380	1620312_at	2E-83	31.2	cell.division	L
SGN-U315160	1-1-1.3.14.15	Vvi.7692	1611204_s_at	1E-105	31.3.1	cell.cycle.peptidylprolyl isomerase	C
SGN-U316860	1-1-4.4.6.17	Vvi.9314	1612302_at	1E-112	31.4	cell. vesicle transport	L
SGN-U319371	1-1-6.3.11.19	Vvi.8931	1619882_at	1E-91	31.4	cell. vesicle transport	C
SGN-U319814	1-1-4.3.5.3	Vvi.12410	1616388_at	1E-136	33.99	development.unspecified	P
SGN-U325187	1-1-5.1.10.2	Vvi.15884	1621131_at	1E-116	33.99	development.unspecified	L
SGN-U317293	1-1-2.3.9.15	Vvi.5619	1608789_at	3E-79	33.99	development.unspecified	P
SGN-U318134	1-1-2.1.13.1	Vvi.2044	1620816_at	2E-25	33.99	development.unspecified	S
SGN-U313650	1-1-5.1.11.11	Vvi.13498	1607144_at	1E-144	34.1	transport.p-and v-ATPases	P
SGN-U321039	1-1-3.1.11.1	Vvi.5374	1618917_at	1E-163	34.13	transport.peptides and oligopeptides	C
SGN-U313561	1-1-8.2.11.16	Vvi.5743	1610982_at	1E-163	34.19.1	transport.Major Intrinsic Proteins.PIP	C
SGN-U315027	1-1-8.3.6.17	Vvi.13947	1622610_at	1E-109	34.2	transport.porins	P
SGN-U312399	1-1-5.4.5.3	Vvi.9605	1619989_s_at	1E-148	34.9	transport.metabolite transporters at the mitochondrial membrane	C
SGN-U324043	1-1-5.3.11.19	Vvi.5515	1616563_s_at	1E-148	35.2	not assigned.unknown	L
SGN-U316540	1-1-1.3.19.4	Vvi.4844	1615102_at	1E-142	35.2	not assigned.unknown	L
SGN-U326598	1-1-3.4.18.13	Vvi.10064	1614015_at	1E-142	35.2	not assigned.unknown	P
SGN-U319855	1-1-3.4.20.11	Vvi.1437	1619954_at	1E-139	35.2	not assigned.unknown	C
SGN-U322022	1-1-1.3.2.5	Vvi.8353	1620462_at	1E-131	35.2	not assigned.unknown	C
SGN-U315298	1-1-6.4.8.10	Vvi.7071	1619759_at	1E-125	35.2	not assigned.unknown	L
SGN-U318700	1-1-4.1.2.12	Vvi.1832	1618397_at	1E-123	35.2	not assigned.unknown	C
SGN-U318372	1-1-5.1.3.20	Vvi.3278	1618757_at	1E-121	35.2	not assigned.unknown	L
SGN-U318901	1-1-1.3.6.2	Vvi.6547	1608749_at	1E-117	35.2	not assigned.unknown	L
SGN-U320494	1-1-3.4.12.17	Vvi.6730	1614177_at	1E-107	35.2	not assigned.unknown	P
SGN-U318497	1-1-4.1.13.8	Vvi.3487	1614591_at	1E-106	35.2	not assigned.unknown	C
SGN-U321733	1-1-6.4.8.2	Vvi.3402	1622329_at	1E-104	35.2	not assigned.unknown	S
SGN-U312549	1-1-4.1.2.3	Vvi.8883	1617770_at	1E-100	35.2	not assigned.unknown	C
SGN-U318827	1-1-4.1.14.21	Vvi.1348	1613826_at	2E-98	35.2	not assigned.unknown	P
SGN-U317324	1-1-1.4.4.16	Vvi.3384	1616141_at	3E-98	35.2	not assigned.unknown	P
SGN-U320573	1-1-5.4.6.2	Vvi.5202	1614411_at	4E-94	35.2	not assigned.unknown	S
SGN-U316792	1-1-8.2.10.2	Vvi.766	1608878_s_at	3E-89	35.2	not assigned.unknown	L
SGN-U318179	1-1-1.2.6.2	Vvi.2779	1613696_at	1E-85	35.2	not assigned.unknown	C
SGN-U318603	1-1-3.1.11.13	Vvi.14845	1619300_at	7E-78	35.2	not assigned.unknown	P
SGN-U315173	1-1-6.3.6.16	Vvi.1382	1611744_s_at	2E-77	35.2	not assigned.unknown	S
SGN-U320984	1-1-5.2.10.4	Vvi.1671	1610990_at	3E-75	35.2	not assigned.unknown	C

Table S1 Continued.

SGN-U ID	TOM1 SGN-M ID	Vv-Unigene ID	Genechip ID	*E*-Value	BIN Code	Function	Cluster ID in Figure 1
SGN-U315202	1-1-4.3.13.14	Vvi.10385	1614066_at	5E-68	35.2	not assigned.unknown	C
SGN-U320503	1-1-4.1.10.10	Vvi.1288	1607514_at	1E-64	35.2	not assigned.unknown	C
SGN-U322849	1-1-1.4.13.7	Vvi.852	1618672_at	2E-61	35.2	not assigned.unknown	P
SGN-U313336	1-1-2.1.2.14	Vvi.2329	1610680_at	2E-56	35.2	not assigned.unknown	L
SGN-U319703	1-1-2.1.18.13	Vvi.5535	1617174_at	3E-49	35.2	not assigned.unknown	S
SGN-U317084	1-1-2.3.4.6	Vvi.13544	1608305_at	1E-45	35.2	not assigned.unknown	C
SGN-U319657	1-1-3.1.11.17	Vvi.6865	1618857_at	2E-45	35.2	not assigned.unknown	P
SGN-U322575	1-1-3.4.20.8	Vvi.11364	1619208_at	3E-43	35.2	not assigned.unknown	L
SGN-U331773	1-1-2.2.6.19	Vvi.6348	1615343_at	3E-41	35.2	not assigned.unknown	P
SGN-U325637	1-1-6.2.10.6	Vvi.9047	1620087_at	3E-35	35.2	not assigned.unknown	L
SGN-U320092	1-1-3.2.7.16	Vvi.12802	1616072_at	2E-34	35.2	not assigned.unknown	L
SGN-U323704	1-1-5.4.2.17	Vvi.5778	1607888_a_at	4E-33	35.2	not assigned.unknown	C
SGN-U322389	1-1-7.3.11.19	Vvi.7655	1608837_at	2E-32	35.2	not assigned.unknown	S
SGN-U316821	1-1-6.2.2.1	Vvi.14953	1616066_at	6E-32	35.2	not assigned.unknown	C
SGN-U320925	1-1-4.4.10.19	Vvi.7953	1612461_at	4E-29	35.2	not assigned.unknown	C
SGN-U321015	1-1-1.1.6.9	Vvi.1213	1610268_s_at	2E-28	35.2	not assigned.unknown	C
SGN-U322267	1-1-7.4.10.18	Vvi.556	1614894_at	2E-27	35.2	not assigned.unknown	C
SGN-U322532	1-1-6.2.10.1	Vvi.10748	1616707_at	1E-22	35.2	not assigned.unknown	C
SGN-U319689	1-1-5.2.2.3	Vvi.1770	1618138_at	5E-22	35.2	not assigned.unknown	L
SGN-U326076	1-1-4.3.20.11	Vvi.1401	1610681_at	5E-21	35.2	not assigned.unknown	L
SGN-U346454	1-1-3.1.17.3	Vvi.8563	1620148_at	2E-19	35.2	not assigned.unknown	C
SGN-U321359	1-1-5.1.15.8	Vvi.2190	1618523_at	1E-18	35.2	not assigned.unknown	S
SGN-U329447	1-1-8.4.2.7	Vvi.10381	1612490_at	4E-18	35.2	not assigned.unknown	C
SGN-U324910	1-1-6.4.5.1	Vvi.23723	1612008_at	6E-16	35.2	not assigned.unknown	P
SGN-U313284	1-1-2.2.12.13	Vvi.3230	1607364_at	3E-12	35.2	not assigned.unknown	L
SGN-U320981	1-1-4.4.19.1	Vvi.6842	1619345_s_at	5E-12	35.2	not assigned.unknown	C

CAD, cinnamyl alcohol dehydrogenase; FBPase, fructose 1,6-bisphosphatase; FHA, forkhead-associated; GAP, GTPase activating proteins; GeBP, GL1 enhancer binding protein; GMP, guanine monphosphate; LHC, light-harvesting complex; misc, miscellaneous; MYB, myeloblastosis; PDA, phytodienoic acid; PIP, plasma membrane intrinsic protein; PME, pectin methylesterase; PS, photosynthesis; PSI, photosystem I; PSII, photosystem II; RHM,UDP-L-rhamnose synthase; UXS, UDP-D-xylose sythases.